



ORIGINE ET EVOLUTION DES CHONDRICHTHYENS

Perspectives évo-dévo et dynamiques macro-évolutives

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© **Richard Flament**

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Composition du jury :

Martin-Hugues Saint-Laurent, président du jury, Université du Québec à Rimouski

Richard Cloutier, directeur de recherche, Université du Québec à Rimouski

Michael Lee, co-directeur de recherche, Flinders University

John Long, examinateur externe, Flinders University

Jorge Mondéjar-Fernández, examinateur externe, Fulda University

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RÉSUMÉ

L'origine des requins, et plus largement celle des poissons cartilagineux (chondrichthyens), dans le cadre de la radiation évolutive des vertébrés à mâchoires (gnathostomes), demeure encore mal comprise et constitue l'un des principaux points d'incertitude de l'évolution des vertébrés. Le mode et le tempo de leur évolution, c'est-à-dire la manière dont ils ont évolué et la vitesse à laquelle ces changements se sont produits, ont jusqu'à présent été peu étudiés. En effet, les travaux consacrés à l'origine des chondrichthyens se sont majoritairement focalisés sur l'évolution de leur diversité taxonomique au cours du temps et sur l'identification d'épisodes d'explosion de diversité. Cette relative rareté d'études s'explique par plusieurs facteurs majeurs : (i) l'incomplétude du registre fossile, particulièrement marquée chez les poissons cartilagineux en raison de leur faible potentiel de fossilisation ; (ii) le manque de caractères clairement homologues servant de base aux comparaisons phylogénétiques ; (iii) l'existence de jeux de données incomplets, excluant des taxons clés tels que les chondrichthyens putatifs ; et (iv) le recours fréquent à une seule méthode de reconstruction phylogénétique. En conséquence, de nombreuses hypothèses demeurent ouvertes concernant l'origine des requins, notamment l'identification du premier représentant des chondrichthyens, les relations phylogénétiques internes au groupe, la calibration temporelle des nœuds évolutifs (en particulier celui du groupe couronne), ainsi que les taux d'évolution, les taux de diversification et la variation temporelle de la disparité morphologique. Afin de tester ces différentes hypothèses, cette thèse propose d'établir une nouvelle base comparative pour l'étude des chondrichthyens, d'examiner leurs affinités potentielles avec les gnathostomes et les agnathes, de proposer une calibration plus précise des principaux nœuds évolutifs de leur lignée et, enfin, d'analyser leurs taux d'évolution, de diversification et de disparité morphologique dans un cadre bayésien. Le cadre méthodologique de cette thèse repose sur plusieurs axes majeurs. Le premier consiste en la reconstruction de la plus vaste matrice de caractères morphologiques et de taxons fossiles de chondrichthyens jamais compilée. Cette matrice a été conçue pour être aussi exhaustive et objective que possible. De nouveaux caractères ont été définis à partir de données développementales, offrant une base d'homologie plus robuste. Par ailleurs, la matrice a été standardisée afin de garantir un langage descriptif homogène et de limiter les biais liés à la terminologie. Le premier chapitre de la thèse détaille ainsi la démarche employée pour définir des caractères morphologiques fondés sur le développement, et donc plus étroitement liés à des relations d'homologie. Le deuxième axe majeur concerne l'approche méthodologique en phylogénie. En l'absence de consensus quant à la méthode la plus appropriée pour reconstruire les relations de parenté entre espèces fossiles, l'ensemble des principales méthodes de reconstruction a été mobilisé afin d'obtenir le signal phylogénétique le plus robuste possible. Le maximum de parcimonie, ainsi que des approches bayésiennes calibrées et non calibrées, ont été utilisés pour inférer les relations de parenté

des chondrichthyens de la période Siluro-dévonienne. Enfin, un troisième volet méthodologique repose sur l'exploration de différentes approches bayésiennes permettant d'inférer l'évolution temporelle des taux d'évolution, de diversification et de disparité morphologique. L'objectif est de caractériser précisément la dynamique évolutive ayant façonné l'histoire précoce des chondrichthyens. En définitive, les résultats de cette thèse ont permis de décrire de nouveaux caractères morphologiques fondés sur le développement des aiguillons de nageoires, intégrés à la plus grande matrice phylogénétique jamais construite pour ce groupe. Les analyses phylogénétiques issues de cette matrice convergent vers une affinité étroite entre les thélodontes, un groupe de poissons fossiles traditionnellement considérés comme dépourvus de mâchoires, et les chondrichthyens. Enfin, les résultats révèlent une phase d'évolution rapide au début de la lignée des chondrichthyens, suivie d'un épisode marqué de disparification morphologique.

Mots clés : évolution, chondrichthyens, phylogénie, vertébrés basaux, statistiques bayésiennes, évo-dévo

ABSTRACT

The origin of sharks, and more broadly that of cartilaginous fishes (chondrichthyans), within the context of the evolutionary radiation of jawed vertebrates (gnathostomes), remains poorly understood and constitutes one of the major unresolved questions in vertebrate evolution. The mode and tempo of their evolution—that is, how they evolved and the rate at which evolutionary changes occurred—have so far received limited attention. Indeed, most studies addressing the origin of chondrichthyans have focused primarily on taxonomic diversity through time and on identifying episodes of diversity expansion. This paucity of studies can be attributed to several major factors: (i) the incompleteness of the fossil record, which is particularly pronounced in cartilaginous fishes due to their low fossilization potential; (ii) the lack of clearly homologous characters suitable for phylogenetic comparison; (iii) the use of non-exhaustive datasets that omit key taxa, such as putative chondrichthyans; and (iv) a frequent reliance on a single phylogenetic reconstruction method. Consequently, multiple hypotheses remain unresolved regarding the origin of sharks, including the identity of the earliest chondrichthyan representative, the internal phylogenetic relationships of chondrichthyans, the temporal calibration of evolutionary nodes (notably the crown-group node), and the rates of evolution, the rates of diversification, and the variation of morphological disparity. To test these hypotheses, this thesis establishes a new comparative framework for the study of chondrichthyans, investigates their potential affinities with both gnathostomes and agnathans, proposes a revised calibration of key evolutionary nodes within the chondrichthyan lineage, and ultimately examines their rates of evolution, diversification, and morphological disparity within a Bayesian framework. The methodological framework of this thesis is structured around several major components. The first involves the reconstruction of the largest morphological character matrix of fossil chondrichthyan taxa compiled to date. This matrix was designed to be as exhaustive and objective as possible. New characters were defined based on developmental data, providing a more robust basis for homology. In addition, the matrix was standardized to ensure a unified descriptive language, thereby minimizing biases associated with terminology. The first chapter of the thesis details the methodological approach used to define new morphological characters grounded in developmental biology and, consequently, closer to true homologies. The second major component concerns the phylogenetic methodology employed. In the absence of a consensus regarding the most appropriate method for reconstructing phylogenetic relationships among fossil taxa, all major reconstruction approaches were applied in order to recover the most robust possible phylogenetic signal. Maximum Parsimony, as well as calibrated and uncalibrated Bayesian approaches, were used to infer the relationships of early chondrichthyans. Finally, a third methodological component involved the exploration of a range of Bayesian methods to infer the temporal dynamics of evolutionary rates, diversification, and morphological disparity. The overarching goal was to

precisely characterize the evolutionary processes that shaped the history of chondrichthyans. In summary, the results of this thesis allowed the description of new morphological characters based on the developmental patterns of fin spines, which were incorporated into the largest phylogenetic matrix ever assembled for this group. Phylogenetic analyses derived from this matrix consistently support a close affinity between thelodonts—a group of fossil fishes traditionally regarded as jawless—and chondrichthyans. Ultimately, the chondrichthyan lineage is shown to have undergone a rapid phase of early evolution, followed by a pronounced episode of morphological disparification.

Keywords: evolution, chondrichthyan, phylogeny, early vertebrate, Bayesian statistics, evo-devo

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LISTE DES ABRÉVIATIONS, DES SIGLES ET DES ACRONYMES

BAMM	Bayesian Analysis for Macroevolutionary Mixtures
BDSKY	Birth Death Skyline Serial
BM	Brownian Motion
CI	Consistency Index
EB	Early Burst
EQ	Entity Quality
ESS	Effective Sampling Size
FBD	Fossilized Birth-Death model
MCC	Maximum Clade Credibility
MCMC	Markov Chain Monte Carlo
ML	Maximum Likelihood
MOTH	Man On The Hill
MP	Maximum Parsimony
MRCA	Most Recent Common Ancestor
MSCC	Maximum Sum Clade Credibility
NYSM	New-York State Museum
OU	Ornstein Uhlenbeck

PCM Phylogenetic Comparative Method

PE Punctuated Equilibrium

INTRODUCTION GÉNÉRALE

1. Biologie évolutive : une brève synthèse

1.1 L'évolution en tant que théorie

L'évolution en biologie est un concept complexe dont la définition a évolué au fil du temps (Chodasewicz, 2014). Le développement de la théorie de l'évolution a été marqué par trois grandes étapes historiques (Figure 1). Tout d'abord, le darwinisme mettait l'accent sur la sélection naturelle tout en intégrant encore des aspects de l'hérédité dite « lamarcienne ». Il a été suivi par le néodarwinisme, qui plaçait la sélection naturelle au centre du changement évolutif, puis par la Synthèse moderne (ou théorie synthétique de l'évolution), qui intègre la génétique, la génétique des populations, la systématique ainsi que les théories de la spéciation et de la macroévolution (Huxley, 2010). Brian K. Hall a défini de manière concise l'évolution comme une « descendance avec modification » (Hall, 2012), soulignant que les processus évolutifs impliquent intrinsèquement des changements au fil des générations.

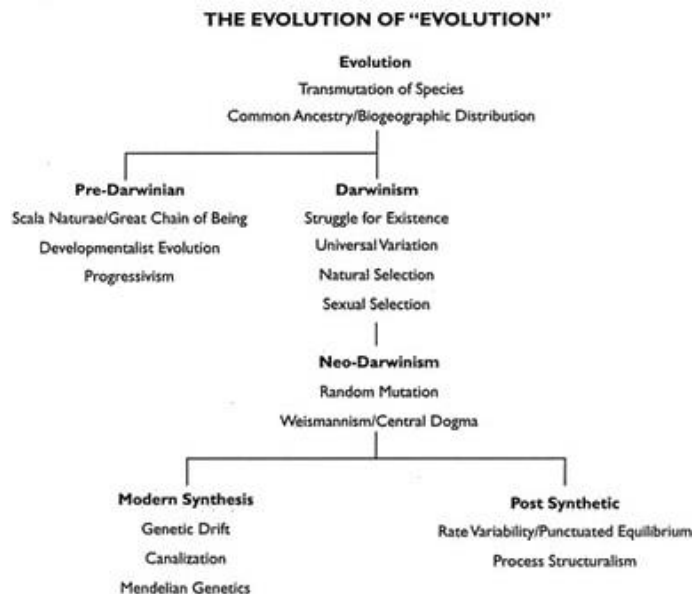


Figure 1 : schématisation des différentes étapes de l'évolution de l'« évolution », d'après Hall (2012)

Cependant, la définition de l'évolution englobe un large éventail de concepts formalisés au sein de la théorie synthétique de l'évolution (Kutschera & Niklas, 2004). La Synthèse moderne est issue des travaux de plusieurs auteurs entre 1937 et 1950 et a été principalement formulée à travers six ouvrages fondamentaux, rédigés par Theodosius Dobzhansky (Dobzhansky, 1937), Ernest Mayr (Mayr, 1942), Julian Huxley (Huxley, 1942), George G. Simpson (Simpson, 1944), Bernhard Rensch (Rensch, 1947) et Ledyard Stebbins (Stebbins, 1950). Cette synthèse, également appelée Synthèse moderne, a été largement acceptée en biologie évolutive et progressivement affinée au cours des décennies suivantes, notamment grâce aux contributions de Hamilton (Hamilton, 1964), Williams (Williams, 2018), Wilson (Wilson, 1978) et Lewis (Lewis, 1994).

Plus récemment, certains auteurs ont proposé une Synthèse évolutive étendue (Pigliucci & Müller, 2010 ; Pigliucci, 2007 ; Dickins, 2021), visant à intégrer des domaines émergents de la recherche en biologie. En particulier, la biologie évolutive du développement (évo-dévo) cherche à expliquer comment les changements du développement embryonnaire au sein des générations sont liés aux changements évolutifs entre les générations (Hall, 2012). D'autres mécanismes souvent discutés incluent l'hérédité épigénétique et la plasticité phénotypique (Huneman & Walsh, 2017).

Malgré les débats en cours concernant la capacité de la Synthèse moderne à intégrer pleinement les avancées de l'évo-dévo et des domaines connexes, ses principes fondamentaux restent largement soutenus et ont été clairement résumés par plusieurs auteurs au début des années 2000 (Reif *et al.*, 2000 ; Kutschera & Niklas, 2004). Ces principes de base incluent : (i) la population comme unité de l'évolution plutôt que l'individu ou le type ; (ii) la recombinaison génétique comme source fondamentale de variation génétique et phénotypique chez les plantes et les animaux ; (iii) la sélection naturelle comme principale force façonnant l'évolution phénotypique en réponse aux environnements changeants ; (iv) les mécanismes d'isolement pré- et post-accouplement (par exemple, la spéciation allopatrique) ; et (v) des transitions évolutives graduelles, la macroévolution étant comprise comme le résultat cumulatif de processus micro-évolutifs (Figure 2).

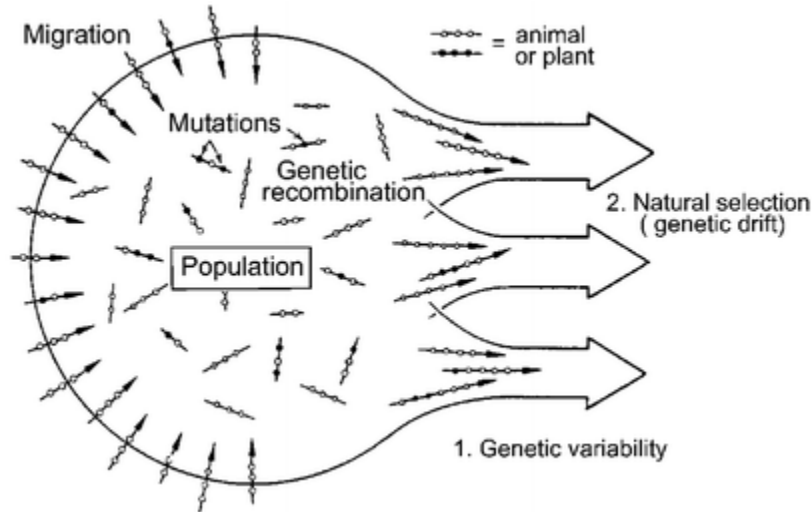


Figure 2 : Interactions des processus basiques dans l'évolution phénotypique dans une population variable d'organisme (d'après Kutschera & Niklas 2004)

1.2 Patron et processus d'évolution

Dans le contexte de la Synthèse moderne, plusieurs cadres conceptuels ont émergé afin d'offrir de nouvelles perspectives sur les forces qui participent aux changements évolutifs à différentes échelles biologiques. Au cours des années 1960 et 1970, les termes « pattern » et « process » sont progressivement apparus dans la littérature, devenant centraux dans le développement de la cladistique. Une contribution majeure d'Eldredge et Cracraft (1980) visait à intégrer la systématique, comprise comme les motifs observés dans le monde organique, à la théorie de l'évolution, qui traite des processus responsables de la génération de ces motifs. La paléontologie joue un rôle crucial en fournissant des preuves empiriques de cette distinction conceptuelle. De manière générale, les patron (« patterns ») peuvent être considérés comme les résultats des processus évolutifs (De Ricqlès, 2014). Ils sont explicitement définis comme l'identification et la description de la structure relationnelle entre les taxons, telle que la structure ramifiée de l'arbre du vivant (De Ricqlès, 2014). Les processus (« processes »), en revanche, représentent l'ensemble des mécanismes biologiques qui opèrent et sont contraints à travers les échelles spatiales et temporelles par leurs

interactions avec l'environnement (De Ricqlès, 2014). La distinction entre patron et processus reflète l'organisation fonctionnelle et hiérarchique des systèmes biologiques, englobant les molécules, les codons, les cellules, les tissus, les organes, les individus, les populations et les espèces (Eldredge & Cracraft, 1980). Plus largement, ce cadre vise à élucider comment des modifications génotypiques à petite échelle se traduisent en changements phénotypiques au cours du temps évolutif, et comment les processus micro-évolutifs contribuent en fin de compte aux motifs macro-évolutifs observables dans le registre fossile (Raff, 2000).

1.3 Macroévolution

Le succès évolutif des clades actuels peut s'expliquer par des histoires évolutives ponctuées par un ou plusieurs événements macro-évolutifs, tels que les radiations évolutives (Schluter, 2000 ; Krassilov, 2004 ; Levinton, 2001 ; Lieberman, 2012). Ces événements se caractérisent généralement par une augmentation des taux de diversification et de disparité morphologique, et/ou par une accélération des taux d'évolution morphologique (Simões *et al.*, 2016). De telles dynamiques permettent aux espèces de coloniser de nouvelles niches écologiques ou des niches spécialisées, améliorant ainsi l'efficacité de leurs fonctions physiologiques et écologiques (Ripa, 2018 ; Wright, 1982).

Les études macro-évolutives se concentrent traditionnellement sur des changements évolutifs à grande échelle affectant des groupes taxonomiques supérieurs, mais elles fournissent également des éclairages essentiels sur la récupération du vivant après des événements d'extinction de masse (Ausich & Deline, 2012), sur l'influence des facteurs écologiques sur la dynamique des clades (Schweizer *et al.*, 2011) et sur l'évolution des interactions entre espèces au cours du temps (Harmon *et al.*, 2019). Malgré des avancées considérables, les mécanismes sous-jacents aux changements macro-évolutifs restent en partie non résolus et continuent de faire l'objet de débats actifs (Jablonski, 2007 ; Erwin, 2011). La Macroévolution est étudiée à différentes échelles taxonomiques et temporelles, souvent en

relation avec son pendant conceptuel, la Microévolution (Reznick & Ricklefs, 2009 ; Erwin, 2001). Notamment, la définition précise de la Macroévolution ne fait toujours pas l'objet d'un consensus strict, malgré de nombreuses tentatives récentes de formalisation du concept (Hautmann, 2019 ; Jablonski, 2017 ; Dresow, 2019).

Le terme macroévolution a connu une évolution conceptuelle importante depuis sa première introduction par le généticien et biologiste du développement russe Iurii Filipchenko (Filipchenko, 1927). Pour Filipchenko, la Macroévolution désignait des changements évolutifs se produisant au-dessus du niveau de l'espèce, c'est-à-dire au moins au niveau du genre dans la taxonomie linnéenne, une définition qui persiste encore aujourd'hui sous une forme modifiée (Hautmann, 2020). Pour caractériser la Macroévolution, Filipchenko distinguait l'hérédité mendélienne opérant au sein des espèces et une hérédité cytoplasmique non mendélienne, qu'il considérait responsable de l'émergence des taxons au-dessus du niveau spécifique (Erwin, 2000). En revanche, la Microévolution était décrite comme gouvernée par la sélection naturelle agissant sur des variations héréditaires explicables par la génétique classique (Alexandrov, 1994). Filipchenko soutenait ainsi que les caractères distinguant les catégories systématiques supérieures nécessitent des mécanismes évolutifs différents de ceux impliqués dans l'origine des unités taxonomiques inférieures, telles que les espèces (Filipchenko, 1927).

En distinguant formellement Microévolution et Macroévolution, il rejetait l'hypothèse selon laquelle la Macroévolution pourrait être expliquée comme le résultat cumulatif des processus micro-évolutifs. Selon cette perspective, les changements majeurs dans l'organisation des plans corporels et de l'architecture fonctionnelle ne résultaient pas de l'accumulation progressive de variations darwiniennes à petite échelle (Hautmann, 2020). Cette interprétation de la Macroévolution a été reprise par la suite par le généticien Richard Goldschmidt, qui considérait que la mutation et la sélection naturelle suffisent à expliquer les changements évolutifs au sein des espèces, mais soutenait que l'origine des espèces et des taxons supérieurs impliquait des processus fondamentalement différents, incluant des réorganisations génomiques à grande échelle (Goldschmidt, 1940).

En 1937, Theodosius Dobzhansky, élève de Filipchenko, introduisit le terme Macroévolution auprès du public anglophone. Dobzhansky rejeta explicitement les interprétations de Goldschmidt (1940) et de Filipchenko, soutenant qu'il n'existe pas de discontinuité fondamentale entre Microévolution et Macroévolution. Compte tenu de l'état des connaissances à la fin des années 1930, il affirma que les mêmes mécanismes évolutifs opèrent à la fois aux échelles micro- et macro-évolutives (Dobzhansky, 1937). Une avancée majeure ultérieure dans la conceptualisation de la Macroévolution provient de George Gaylord Simpson, notamment à travers son ouvrage influent *Tempo and Mode in Evolution* (Simpson, 1944), qui est resté l'une des références les plus importantes sur le sujet jusqu'à la fin des années 1960 (Erwin, 2000). Simpson considérait que la macroévolution opère principalement aux niveaux des espèces et des genres, tout en réservant le terme « mégaévolution » aux changements évolutifs se produisant au-dessus du niveau du genre (Simpson, 1944).

Dans ce cadre, il déclarait notamment que « la Macroévolution implique l'apparition et la divergence de groupes discontinus, et il reste à débattre si elle diffère en nature ou seulement en degré de la microévolution. Si les deux se révélaient fondamentalement différentes, les innombrables études de microévolution deviendraient relativement peu importantes et auraient une valeur limitée dans l'étude de l'évolution dans son ensemble » (Simpson, 1944, p. 97). Simpson introduisit également le concept d'évolution quantique, qu'il définissait comme un passage rapide d'une zone adaptative à une autre, médié par la dérive génétique et différent, tant par sa vitesse que par sa nature, de la spéciation et de l'évolution phylétique. Il révisa toutefois ultérieurement cette position, suggérant que l'évolution quantique devait plutôt être interprétée comme une forme particulièrement rapide d'évolution phylétique (Simpson, 1953). Le concept d'évolution quantique est considéré comme un précurseur de la théorie des équilibres ponctués, formalisée plus tard par Eldredge et Gould (1972).

L'équilibre ponctué (PE) est une théorie qui traite de l'origine et de la dynamique temporelle des espèces (Eldredge & Gould, 1972) et vise à expliquer le rôle macro-évolutif des espèces et de la spéciation tel qu'il s'exprime à l'échelle des temps géologiques (Gould, 2002). À

l'origine, le PE est apparu comme une tentative de traduire l'hypothèse des isolats périphériques de Mayr (1963) en prédictions testables dans le registre fossile. Il s'oppose ainsi à la vision gradualiste classique de l'évolution, selon laquelle les changements évolutifs se produisent de manière lente et continue au cours du temps (Figure 3).

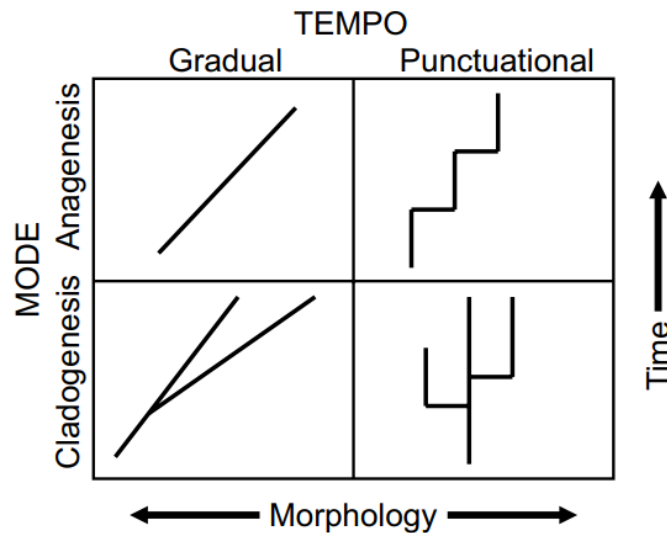


Figure 3 : Modes et rythmes évolutifs. Le quadrant supérieur gauche correspond au gradualisme phylétique classique ; le quadrant inférieur droit correspond à l'équilibre ponctué. Toutes les combinaisons sont observées dans le registre fossile. D'après Jablonski (2007).

La théorie des équilibres ponctués repose sur trois concepts fondamentaux : la stase, la ponctuation et la fréquence relative dominante (Eldredge & Gould, 1972). La stase renvoie à l'observation selon laquelle une espèce présente souvent peu ou pas de changement morphologique entre sa première apparition dans le registre fossile et sa dernière occurrence avant son extinction, une durée pouvant s'étendre sur plusieurs millions d'années. La ponctuation désigne des intervalles relativement brefs de changement morphologique rapide, généralement associés à des événements de spéciation, produisant des différences statistiquement significatives entre les échantillons anciens et récents au sein d'un même intervalle géologique. Le concept de fréquence relative dominante est plus difficile à définir,

mais il constitue une affirmation centrale de la théorie : celle-ci ne se contente pas d'énoncer l'existence de phases de stase et de changements rapides, elle soutient que ce schéma prédomine dans le registre fossile (Gould, 2002). Ainsi, l'équilibre ponctué avance une hypothèse concernant le patron macro-évolutif dominant à l'échelle des temps géologiques, plutôt que l'occurrence occasionnelle de phases d'évolution rapide.

L'équilibre ponctué postule en outre que la spéciation introduit souvent une discontinuité fondamentale entre l'évolution phylétique au sein des lignées et les changements évolutifs à grande échelle (Erwin, 2000). Cette insistance sur la discontinuité entre spéciation et tendances macro-évolutives est également partagée par Stanley (1975) dans ses tentatives d'expliquer les changements évolutifs au-dessus du niveau spécifique — une perspective qui a été largement acceptée dans la communauté scientifique au cours de la décennie suivante. De même, Eldredge et Cracraft (1980), ainsi que Stebbins et Ayala (1981), ont défini la macroévolution comme un changement évolutif se produisant au-dessus du niveau de l'espèce. Cependant, les définitions de la macroévolution fondées sur des critères taxonomiques ont fait l'objet de débats soutenus.

Levinton (2001), par exemple, a soutenu que la Macroévolution devrait plutôt être définie comme l'ensemble des processus responsables des transitions d'états de caractères qui permettent de diagnostiquer les différences évolutives entre les grands rangs taxonomiques. Sur cette base, il a critiqué des définitions telles que celles proposées par Eldredge et Cracraft (1980), en soulignant qu'elles supposent implicitement que les grandes transitions évolutives ne peuvent être correctement analysées qu'à travers la spéciation et la sélection au niveau de l'espèce ou au-dessus, limitant ainsi la prise en compte d'hypothèses alternatives. Levinton (2001) s'est ainsi opposé à une séparation conceptuelle stricte entre microévolution et macroévolution, une position partagée par plusieurs biologistes de l'évolution. La question de savoir si les patrons macro-évolutifs sont entièrement réductibles aux processus micro-évolutifs demeure l'un des débats les plus persistants en biologie évolutive, reflétant plus largement des interrogations sur la structure hiérarchique des processus évolutifs.

Le débat autour de la Macroévolution est actif depuis près d'un siècle et reste marqué par de nombreuses questions non résolues, notamment en ce qui concerne la théorie des équilibres ponctués. Dans une analyse critique, Pennell *et al.* (2014) ont soutenu que cette théorie a principalement servi de catalyseur au développement de nouveaux concepts et ont suggéré que le domaine devrait désormais « aller de l'avant plutôt que de regarder en arrière ». Dans cette perspective, ils ont adopté une définition de la Macroévolution comme l'étude des processus et des patrons de l'évolution se produisant au niveau de l'espèce ou au-dessus, une définition également retenue par Krassilov (2004). Cette position n'est toutefois pas unanime. Lieberman et Eldredge (2014), par exemple, ont proposé une définition alternative de la Macroévolution comme « les patrons et processus relatifs à la naissance, à la disparition et à la persistance des espèces », en intégrant explicitement les avancées récentes en modélisation évolutive. Selon Lieberman et Eldredge (2014), cette définition constitue une formulation contemporaine fidèle de la théorie des équilibres ponctués.

Face à la coexistence de multiples définitions, Hautmann (2020) a examiné le paysage conceptuel de la macroévolution et a identifié trois définitions principales dans sa synthèse *What is macroevolution?*. La première, qu'il considère comme la plus neutre, définit la Macroévolution comme une évolution opérant à grande échelle temporelle. Toutefois, cette définition ne fournit pas de critères clairs pour distinguer les processus micro-évolutifs des processus macro-évolutifs, limitant ainsi son utilité conceptuelle. La deuxième définit la Macroévolution comme l'évolution de taxons de rang supra-spécifique, conformément à la taxonomie linnéenne. Cette interprétation présente l'avantage de correspondre étroitement à la conception initiale de la Macroévolution telle qu'envisagée par les auteurs de la Synthèse évolutive. La troisième définit la Macroévolution comme une évolution résultant du tri des variations intraspécifiques, une approche qui s'écarte des critères taxonomiques traditionnels mais permet une distinction conceptuelle claire entre Microévolution, où les organismes constituent les unités de sélection, et macroévolution, où les espèces deviennent les unités de sélection.

Étant donné que chacune de ces définitions présente des limites conceptuelles, la première définition proposée par Hautmann (2020) est souvent privilégiée en raison de son usage plus large et plus répandu aujourd'hui. Néanmoins, parvenir à un consensus strict sur la définition de la Macroévolution demeure difficile, ce qui reflète la complexité persistante de ce concept et son rôle central dans la théorie de l'évolution.

1.4 Diversité des macro-évolutions

Parmi les événements macro-évolutifs, les radiations évolutives occupent une place centrale en raison de la complexité et de la diversité des processus qu'elles englobent, conduisant souvent à l'émergence de taxons de rang élevé. Les radiations évolutives sont définies comme la prolifération rapide de taxons au sein d'un clade (Simões *et al.*, 2016). Elles se caractérisent généralement par des taux élevés d'évolution morphologique et des épisodes de diversification rapide, exprimés par un taux accru de spéciation, et ont fréquemment été associées à l'origine de grands groupes taxonomiques ayant dominé les biotes terrestres (Alfaro *et al.*, 2009). Historiquement, les radiations évolutives étaient traitées de manière relativement indifférenciée et étaient presque exclusivement décrites comme des « radiations adaptatives » durant une grande partie du XXe siècle (par exemple, Osborn, 1902 ; Walls, 1944 ; Simpson, 1953 ; Fisher, 1967 ; Schluter, 2000). Toutefois, des développements théoriques plus récents ont conduit à un cadre conceptuel plus nuancé pour comprendre les radiations évolutives. En particulier, le modèle conceptuel émergent proposé par Simões *et al.* (2016) reconnaît quatre types distincts de radiations évolutives, chacun associé à différentes combinaisons de facteurs biotiques et abiotiques (Figure 4), susceptibles de déclencher des augmentations rapides de la diversité taxonomique et de la disparité morphologique (Lieberman, 2012 ; Schluter, 2000 ; Neige *et al.*, 2013 ; Vrba, 1992). Cette classification affinée permet de limiter l'usage excessif du terme « radiation adaptative » et souligne que tous les épisodes de cladogenèse rapide accompagnés de diversification écologique et morphologique ne sont pas nécessairement de nature adaptative (Simões *et al.*, 2016).

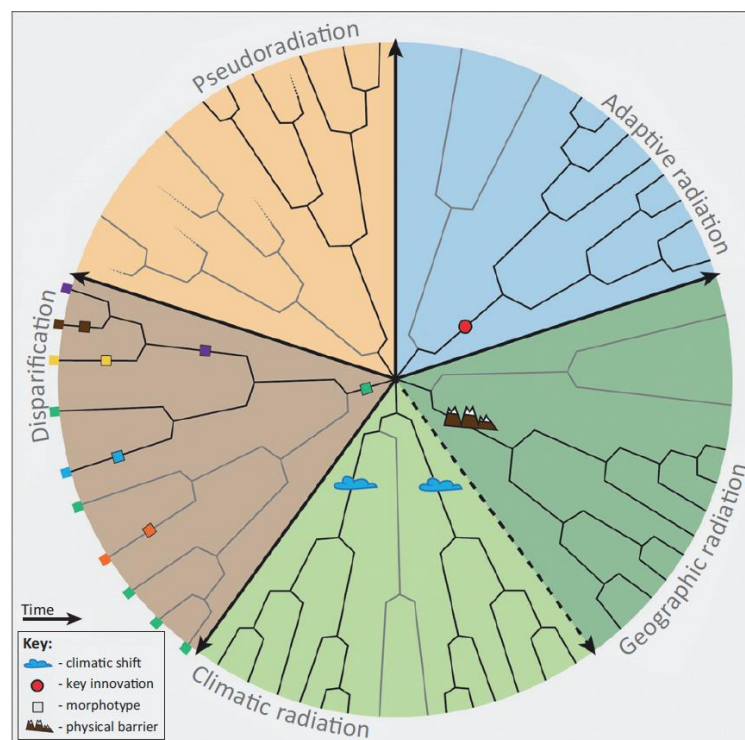


Figure 4 : Les différents types de radiations, d'après Simões et al., 2016.

Décrits dans cette nouvelle synthèse, deux types de radiations évolutives sont supposés être déclenchés par des facteurs biotiques. Le premier, le plus popularisé en raison de son usage massif jusqu'au début des années 2000, est la radiation adaptative. Une radiation adaptative correspond à l'évolution d'une disparité écologique et phénotypique au sein d'une lignée en multiplication rapide (Schluter, 2000 ; Seehausen, 2004 ; Gillespie, 2001 ; Givnish, 1997). Elle a été considérée comme l'un des motifs évolutifs les plus importants à l'échelle des temps géologiques (Alfaro *et al.*, 2009 ; Simpson, 1953) et est fréquemment associée aux phases de récupération après des crises d'extinction (Erwin, 2001 ; Jablonski, 2005 ; Brayard *et al.*, 2009). Elle est déclenchée par une « innovation clé », c'est-à-dire une nouvelle adaptation critique (c'est-à-dire le processus par lequel une espèce devient adaptée à son environnement) (Soulebeau *et al.*, 2015 ; Bond & Opell, 1998). De plus, la radiation

adaptative implique généralement une spéciation sympatrique associée à des divergences écomorphologiques (Schluter, 2000 ; Harmon *et al.*, 2010). La diversification rapide des pinsons de Darwin aux îles Galápagos est considérée comme un exemple classique de radiation adaptative déclenchée par la modification du bec comme clé d'innovation (Grant, 1999 ; Sato *et al.*, 2001).

Le second type de radiation évolutive guidé par des facteurs biotiques est la radiation exaptative. Ce concept a été introduit par Gould et Vrba (1982) afin de proposer une nouvelle perspective sur le potentiel évolutif et la nature des adaptations. L'exaptation désigne un caractère qui n'a pas initialement évolué sous l'effet de la sélection naturelle pour sa fonction actuelle, mais qui a néanmoins été disponible pour une cooptation fonctionnelle dans des lignées descendantes. En d'autres termes, une caractéristique qui n'avait initialement aucune valeur adaptative pour un rôle donné peut ultérieurement augmenter la valeur adaptative, définie ici comme la capacité d'un organisme à se reproduire et à transmettre son génotype aux générations suivantes. Un exemple classique de radiation exaptative est la terrestrialisation des tétrapodes souches et des premiers tétrapodes au Dévonien, où des modifications des membres, initialement évoluées pour la locomotion aquatique, ont été cooptées pour la locomotion terrestre (Triques & Christoffersen, 2015).

Les radiations géographiques et climatiques représentent deux autres types de radiations évolutives principalement déclenchées par des facteurs abiotiques (Herrera-Alsina *et al.*, 2018 ; Condamine *et al.*, 2018). Ces radiations impliquent une augmentation de la diversification au sein d'un clade résultant d'opportunités accrues de spéciation allopatrique, soit par isolement géographique (radiation géographique), soit par changements environnementaux et climatiques (radiation climatique) (Simões *et al.*, 2016). Un exemple bien documenté de radiation climatique est fourni par Near *et al.* (2012), qui ont montré que le refroidissement global a joué un rôle clé dans la diversification des poissons notothenioïdes grâce à l'évolution de glycoprotéines antigel. La radiation géographique a également été impliquée dans la diversification précoce des dinosaures, qui semble avoir été fortement influencée par l'isolement géographique (O'Donovan *et al.*, 2018).

Deux phénomènes évolutifs supplémentaires, la disparification et la pseudoradiation, sont étroitement liés aux radiations évolutives, mais en sont conceptuellement distincts (Simões *et al.*, 2016). La disparification désigne l'évolution de la disparité morphologique ou phénotypique au sein d'un clade sans augmentation correspondante du taux de diversification (Ackerly, 2009 ; Rundell & Price, 2009). Elle peut précéder ou suivre une radiation adaptative. Un exemple est fourni par Davis *et al.* (2016), qui ont mis en évidence une divergence morphologique dentaire accrue associée à l'évolution de l'herbivorie chez les Terapontidae, sans augmentation marquée de la richesse spécifique. La pseudoradiation, quant à elle, décrit une augmentation de la diversité d'un clade principalement due à une diminution des taux d'extinction plutôt qu'à une augmentation des taux de spéciation (Simões *et al.*, 2016). Ce type d'événement évolutif reste peu documenté et est rarement invoqué dans les études évolutives.

Paradoxalement, les grandes extinctions de masse peuvent également agir comme de puissants moteurs de diversification évolutive. Les extinctions de masse se caractérisent par des déclin rapides et globaux de la richesse spécifique, affectant plusieurs niveaux taxonomiques et entraînant souvent la disparition de grands clades terrestres et marins (Sepkoski, 1986 ; Hallam & Wignall, 1997 ; Bambach, 2006 ; Benton, 1995). Ces crises sont déclenchées par une grande variété de facteurs, incluant des changements climatiques, des impacts extraterrestres (par exemple, des astéroïdes ou des météorites), un volcanisme à grande échelle ou des combinaisons de ces facteurs (Bond & Grasby, 2017). Leur durée peut varier de moins d'un million d'années, comme lors de la crise de l'Ordovicien supérieur (Sheehan, 2001), à plusieurs millions d'années, comme cela a été proposé pour l'extinction Crétacé–Paléogène (Keller *et al.*, 2009). Les cinq grandes extinctions de masse auraient éliminé plus de 70 % de la richesse spécifique mondiale, atteignant jusqu'à 96 % lors de la crise Permien–Trias (Benton, 1995).

Ces événements façonnent profondément les trajectoires évolutives en imposant de fortes pressions de sélection et en restructurant les écosystèmes (Currie, 2019 ; Hull, 2015). La disparition de taxons sur de longues périodes crée des niches écologiques vacantes qui

favorisent l'innovation évolutive, et les extinctions de masse sont donc fréquemment suivies de radiations évolutives (Reznick & Ricklefs, 2009). L'importance macro-évolutive des extinctions de masse se manifeste également par des changements dans la sélectivité de l'extinction, où les trajectoires évolutives sont davantage influencées par les taxons survivants que par ceux qui disparaissent (Jablonski, 2005).

À la suite d'un événement d'extinction, les dynamiques évolutives entrent dans une phase de récupération, généralement plus longue que l'intervalle d'extinction lui-même, permettant aux lignées survivantes de se diversifier et d'occuper les niches écologiques vacantes (Erwin, 1998). Des phases de récupération plus longues augmentent le potentiel de tri des espèces, ce qui peut biaiser l'interprétation des trajectoires évolutives post-extinction (Jablonski, 2005). Malgré leur importance, les dynamiques régissant ces phases de récupération restent encore mal comprises (Chen & Benton, 2012). Les trajectoires de récupération varient considérablement selon les clades : certains se rétablissent en un à deux millions d'années (Brayard *et al.*, 2009 ; Stanley, 2010 ; Song *et al.*, 2011), tandis que d'autres nécessitent plusieurs dizaines de millions d'années (Erwin, 2007 ; Hallam, 1991). Ces différences reflètent l'interaction entre des facteurs intrinsèques, tels que la dynamique des écosystèmes, et des facteurs extrinsèques, incluant les conditions environnementales et climatiques, qui varient au cours du temps (Chen & Benton, 2012). Par conséquent, certains grands clades ont traversé plusieurs extinctions de masse et transitions macro-évolutives au cours de leur histoire tout en conservant des rôles dominants dans les écosystèmes actuels.

2. Chondrichthyens

2.1 Les poissons cartilagineux et leur diversité

Parmi les groupes d'organismes vivants ayant connu un grand succès évolutif, les chondrichthyens occupent une position de premier plan. Au cours de leur histoire évolutive, les chondrichthyens ont développé une large gamme d'adaptations écologiques qui restent visibles aujourd'hui. Ils occupent des écosystèmes variés, incluant les environnements

lacustres et estuariens, les systèmes d'eau douce ainsi que l'ensemble des milieux marins à l'échelle mondiale (Lucifora *et al.*, 2015 ; Carrier *et al.*, 2022 ; Hamilton *et al.*, 2022). Les chondrichthyens ont majoritairement évolué en tant que prédateurs de sommet, occupant des niveaux trophiques élevés dans la plupart des écosystèmes (Belleggia *et al.*, 2019). On les retrouve dans des habitats pélagiques, benthiques et profonds, bien qu'ils soient notablement absents des environnements abyssaux (Camhi *et al.*, 2009 ; Musick & Cotton, 2015 ; Kyne & Simpfendorfer, 2010 ; Priede *et al.*, 2006). La large amplitude écologique des chondrichthyens reflète un ensemble d'adaptations spécifiques, exprimées par des spécialisations métaboliques, des innovations morphologiques, des stratégies comportementales ou une combinaison de ces éléments (Parsons, 1990 ; Miyake & McEachran, 1991 ; Musick & Cotton, 2015 ; Klimley *et al.*, 2023). Ces adaptations ont permis aux chondrichthyens d'exploiter une grande variété de niches écologiques, conduisant à une diversité taxonomique remarquable. La classe des Chondrichthyes comprend actuellement deux sous-classes (Figure 5), 18 ordres et 55 familles (Heinicke *et al.*, 2009). Selon des synthèses récentes, le groupe compte 1 292 espèces actuelles valides (Pollerspöck & Straube, 2021).

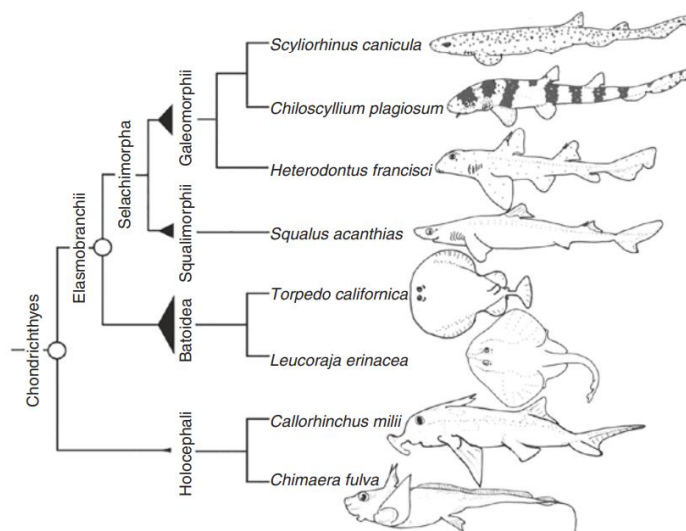


Figure 5 : Phylogénie simplifiée des grands groupes actuels de chondrichthyens. D'après Boisvert *et al.*, 2019.

Les deux sous-classes sont les Holocephali et les Elasmobranchii. Les Holocephali incluent les chimères et formes apparentées, tandis que les Elasmobranchii comprennent les requins, les raies, les poissons-scies et les poissons-guitares. Les Holocephali sont nettement moins diversifiés, avec environ 54 espèces, contre 1 238 espèces d'Elasmobranchii. Malgré cette disparité, tous les chondrichthyens partagent une synapomorphie squelettique distinctive : un cartilage calcifié prismatique (ou tessellé) (Maisey *et al.*, 2021). Le cartilage prismatique est un tissu périchondral biominéralisé unique formant le squelette des chondrichthyens et représentant l'un des trois types de calcification observés dans ce groupe. Les autres incluent la calcification aréolaire, largement restreinte aux centres vertébraux (Dean & Summers, 2006), et le cartilage calcifié globulaire, par exemple dans les aiguillons de nageoires (Janvier & Arsenault, 2002). Le cartilage prismatique est constitué de minuscules tesselles polygonales d'hydroxyapatite, organisées selon divers agencements architecturaux, incluant des monocouches simples ou multiples ainsi que des organisations complexes de type claveau (Maisey *et al.*, 2021). Outre leur squelette cartilagineux, les chondrichthyens présentent plusieurs autres caractères morphologiques clés, notamment des écailles placoides (Cooper *et al.*, 2023). Ces minuscules structures dermiques, semblables à des dents, recouvrent la surface du corps et sont constituées d'une cavité pulpaire entourée de dentine et recouverte d'un émailloïde hyperminéralisé (Raschi & Tabit, 1992 ; Manzanares *et al.*, 2014). Cette organisation tissulaire correspond à l'odontode, une unité structurale fondamentale du squelette dermique des vertébrés (Reif, 1982). Les chondrichthyens présentent également une fécondation interne, réalisée grâce à des ptérygopodes pelviens mâles dérivés de nageoires pelviennes modifiées (O'Shaughnessy *et al.*, 2015). Bien que des structures similaires aient été décrites chez des « placodermes » fossiles, les chondrichthyens sont les seuls vertébrés actuels à conserver ce caractère reproductif (Long *et al.*, 2015). Certains chondrichthyens actuels conservent également des traits morphologiques fréquemment observés dans le registre fossile paléozoïque, tels que des aiguillons de nageoires situées sur le bord antérieur des nageoires, présentes chez certains élasmobranches (par exemple, *Centroscyllium fabricii*) et holocéphales (par exemple, les chimères) (Jerve *et al.*, 2014).

2.2 L'origine des chondrichthyens

Les premiers chondrichthyens seraient apparus durant l'Ordovicien, d'après le registre fossile des mongolépides, un groupe de chondrichthyens précoces supposés (Andreev *et al.*, 2016). Les mongolépides sont attribués aux chondrichthyens sur la base de l'ultrastructure de leurs écailles, qui présente une organisation de type odontode appelée odontocomplexe (Karatajūtė-Talimaa, 1995). À ce jour, seules des écailles isolées sont connues pour ce groupe. D'autres restes attribués aux premiers chondrichthyens, tels que des dents, des écailles et des aiguillons de nageoires, apparaissent progressivement au cours du Silurien et du Dévonien. Les enregistrements fossiles du Silurien sont dominés par des chondrichthyens souches, tandis que le Dévonien marque l'émergence des chondrichthyens du groupe couronne, définis par la présence de cartilage prismatique (Janvier & Pradel, 2015). Le plus ancien élément dermique, autre que les écailles et les aiguillons, attribué avec certitude aux chondrichthyens correspond à des dents, notamment celles de *Leonodus carlsi* du Lochkovien (Dévonien inférieur) (Botella *et al.*, 2009). Bien que des dents potentiellement attribuables aux chondrichthyens aient été signalées dans des dépôts siluriens plus anciens (Burrow *et al.*, 2013), *Leonodus carlsi* est généralement considéré comme la preuve la plus fiable des dents de chondrichthyens du groupe-couronne (Long & Young, 1995 ; Martínez-Pérez *et al.*, 2018).

Les aiguillons de nageoires posent un problème taxonomique plus complexe, car des structures similaires sont également présentes chez les « acanthodiens » fossiles, ce qui rend difficile l'attribution d'aiguillons isolés aux chondrichthyens du groupe-couronne sur la seule base de leur morphologie. Les plus anciennes aiguillons de nageoires du registre fossile remonteraient probablement au début du Silurien, comme le suggèrent les sinacanthidés de Chine (Liu *et al.*, 2024). Toutefois, les aiguillons de nageoires attribuables sans ambiguïté aux chondrichthyens du groupe-couronne sont principalement connues au Dévonien moyen et supérieur (Potvin-Leduc *et al.*, 2015 ; Frey *et al.*, 2020). Le plus ancien chondrichthyen articulé connu à ce jour est *Doliodus latispinosus*, un chondrichthyen souche datant de

l'Emsien (Dévonien inférieur) (Miller *et al.*, 2015). Ce taxon présente plusieurs caractères proches de ceux du groupe-couronne, mais ne possède pas de cartilage prismatique, ce qui indique sa position en dehors de celui-ci (Miller *et al.*, 2003 ; Burrow *et al.*, 2017). *Doliodus latispinosus* représente ainsi l'un des plus proches parents connus des chondrichthyens du groupe-couronne. Bien que le registre fossile des chondrichthyens soit souvent considéré comme excellent en raison de l'abondance de dents, d'écailles et d'éléments dermiques isolés, il reste relativement pauvre en matériel articulé, ce qui reflète le faible potentiel de préservation des squelettes cartilagineux (Maisey, 1986 ; Schnetz *et al.*, 2024). Par conséquent, les chondrichthyens du groupe-couronne articulés ou partiellement articulés sont rares, en particulier avant le Dévonien supérieur. Des exemples notables pour cette période incluent *Cladodoides wildungensis*, *Ferromirum oukherbouchki* et *Tamiodontis vetustus* (Maisey, 2005 ; Frey *et al.*, 2019 ; Williams, 1998). Alors que le Dévonien ne fournit qu'un nombre limité de spécimens articulés, la période suivante, le Carbonifère, se caractérise par un registre fossile nettement plus riche (Boisvert *et al.*, 2019), offrant des informations essentielles sur la diversification précoce et la trajectoire évolutive de la lignée des chondrichthyens.

2.3 Histoire évolutive des chondrichthyens

L'histoire évolutive des chondrichthyens débute à l'Ordovicien, mais un tournant majeur se produit au début du Carbonifère (Schnetz *et al.*, 2024). À la fin du Dévonien, les écosystèmes globaux ont été profondément affectés par l'extinction de masse Frasnien–Famennien, la deuxième grande crise d'extinction du Phanérozoïque (McGhee, 1996). Cet événement a entraîné la disparition de plusieurs groupes majeurs de vertébrés, notamment les « placodermes », qui avaient dominé les écosystèmes marins durant une grande partie du Dévonien (Friedman & Sallan, 2012). En revanche, d'autres lignées ont exploité les opportunités écologiques créées par cette crise et se sont rapidement diversifiées au cours du Carbonifère, parmi lesquelles les chondrichthyens se distinguent comme l'un des groupes les

plus prospères (Schnetzer *et al.*, 2024) (Figure 6).

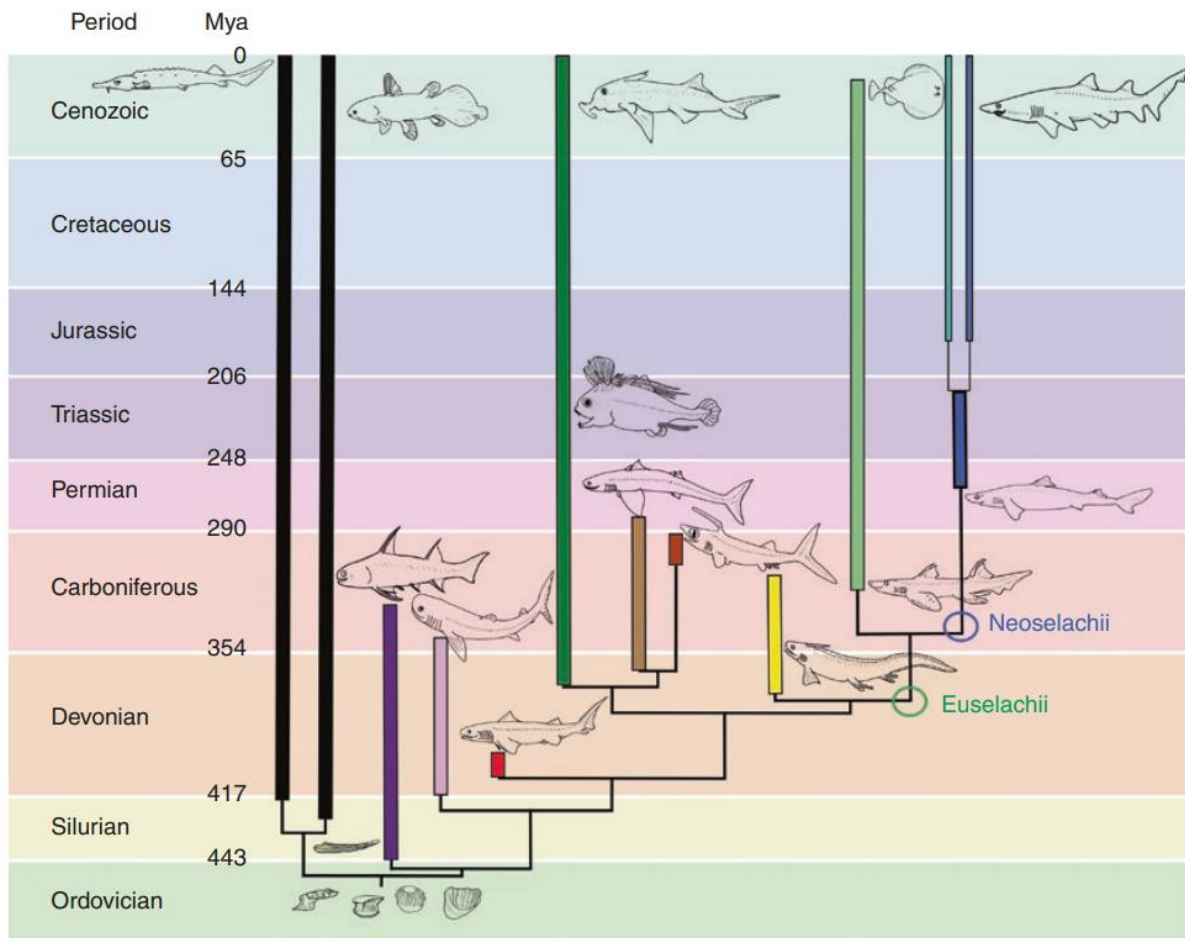


Figure 6 : Phylogénie des chondrichthyens montrant le moment approximatif de leur première apparition dans le registre fossile. Les écailles et les aiguillons des chondrichthyens et des « acanthodiens » sont connues dès l'Ordovicien et le Silurien, et sont illustrées par des écailles et des nageoires à la base de la phylogénie, modifiée d'après Boisvert *et al.* (2019).

Au cours de cette période, les chondrichthyens ont connu une augmentation rapide de leur diversité taxonomique accompagnée d'innovations morphologiques marquées, entraînant une expansion sans précédent de leur diversité morphologique (Grogan & Lund, 2004 ; Stahl,

1999). Les chondrichthyens du Carbonifère présentent une remarquable diversité de nouveaux caractères anatomiques, incluant des structures crâniennes et dorsales hautement spécialisées. Un exemple frappant est le développement du « brush-complex », observé chez *Akmonistion zangerli* (Coates & Sequeira, 2001) ainsi qu'une structure étroitement apparentée chez *Falcatus falcatus* (Lund, 1985), tous deux appartenant aux Stethacanthidae (Figure 7).

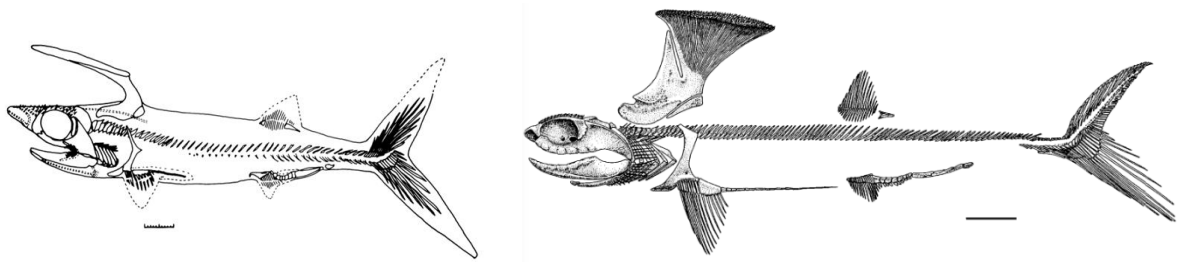


Figure 7 : Reconstruction de *Falcatus falcatus* à gauche d'après Lund (1985), et *Akmonistion zangerli* à droite d'après Coates & Sequeira (2001).

Ces morphologies inhabituelles illustrent l'ampleur de la diversité des plans d'organisation corporelle au sein des premières lignées de chondrichthyens. Cette diversification rapide durant le Carbonifère a également conduit à la divergence précoce des principales lignées de chondrichthyens, notamment la séparation entre les holocéphales et plusieurs groupes souches tels que les inioptérygiens (Grogan & Lund, 2009). Alors que la lignée sœur des holocéphales, les symmoriidés, incluant les stethacanthidés, s'est éteinte à la fin du Carbonifère ou au début du Permien, les holocéphales ont persisté et survécu à toutes les extinctions de masse ultérieures (Brownstein *et al.*, 2024). Malgré cette longue histoire évolutive, les holocephales ont connu un déclin important de leur richesse spécifique et sont aujourd'hui représentés par 54 espèces des grands fonds (Cotton & Grubbs, 2015).

En revanche, la lignée menant aux requins et raies modernes présente une trajectoire évolutive plus soutenue et diversifiée. Une divergence majeure s'est produite vers la fin du Dévonien, donnant naissance aux Xénacanthiformes et aux Euselachii. Les Xénacanthiformes s'étendent du Dévonien au Trias supérieur et occupaient une grande variété d'environnements, incluant des milieux marins peu profonds, marginaux et d'eau douce (Hampe, 2003 ; Turner & Burrow, 2011). Ce groupe est principalement connu à partir de restes isolés, en particulier des aiguillons céphaliques et dorsales, bien que quelques spécimens articulés soient également préservés (Beck *et al.*, 2016). Les Xénacanthiformes se caractérisent généralement par des corps fusiformes et des dents diplodontes distinctives, portant typiquement deux grandes cuspides latérales encadrant une cuspide médiane plus petite (Ginter, 2004).

Suite à l'extinction des Xénacanthiformes, la seule lignée survivante de ce clade fut celle des Euselachii, qui s'est ensuite diversifiée en Hybodontiformes et Néoselachii (élasmodontes modernes) (Figure 6). Les Hybodontiformes représentent le groupe frère éteint de tous les requins et raies actuels. Leur registre fossile est dominé par des dents isolées et montre une diversification relativement limitée (Rigal & Cuny, 2016 ; Böttcher, 2024), bien que plusieurs squelettes articulés aient été découverts dans des dépôts du Pennsylvanien, du Permien et du Trias en Amérique du Nord, en Asie, en Afrique et en Europe (Maisey, 1989 ; Wang *et al.*, 2009 ; Maisey, 1990 ; Mutter *et al.*, 2007 ; Klug *et al.*, 2009 ; Rieppel, 1982). Les Hybodontiformes ont persisté jusqu'au Cénozoïque (Cumbaa *et al.*, 2010), indiquant une lignée durable mais finalement éteinte.

L'histoire évolutive des Néoselachii est plus difficile à reconstituer, en raison d'un registre fossile marqué par des lignées fantômes et des occurrences précoces rares (Boisvert *et al.*, 2019). Bien que des restes incontestables de néosélaciens soient connus dès le Trias (Cuny, 1998), la plupart des représentants des deux clades modernes, Selachii et Batoidea, apparaissent abondamment dans les dépôts jurassiques (Maisey, 2012). La diversité des néosélaciens augmente fortement au Jurassique moyen et s'accroît de manière spectaculaire vers la fin du Mésozoïque, donnant finalement naissance aux taxons actuels

d'élasmobranches (Underwood, 2006). Cette lignée couvre ainsi une histoire évolutive s'étendant sur près de 250 millions d'années (Cappetta, 2012).

Au cours de leur histoire évolutive, les chondrichthyens ont subi des transformations anatomiques et fonctionnelles profondes, en partie sous l'effet de changements environnementaux majeurs dans les écosystèmes marins (Pimiento *et al.*, 2017). Ces transformations ont affecté de nombreux traits fonctionnels liés à l'utilisation des habitats, aux stratégies alimentaires et aux systèmes sensoriels (Boisvert *et al.*, 2019). Notamment, les mécanismes de suspension des mâchoires présentent une diversité exceptionnelle chez les chondrichthyens, reflétant différents modes de capture et d'alimentation des proies (Wilga, 2002).

La dentition constitue un autre axe majeur de diversification, allant de dents pavimenteuses adaptées à l'écrasement chez les batoïdés (Underwood *et al.*, 2015), à des plaques dentaires robustes chez les chiméroïdes (Patterson, 1992), en passant par des dents coupantes et dentelées chez de nombreux requins (Moyer & Bemis, 2017), jusqu'à des dentitions réduites adaptées à la filtration chez le requin pèlerin (Sims, 2000). La présence de verticilles dentaires chez les premiers chondrichthyens souligne également la plasticité évolutive des patrons dentaires au sein du groupe (Maisey *et al.*, 2014).

En plus des adaptations alimentaires, les chondrichthyens ont développé des systèmes sensoriels hautement spécialisés, contribuant à leur succès à long terme en tant que prédateurs. L'une des innovations les plus remarquables est l'électroréception, assurée par les ampoules de Lorenzini chez les élasmobranches et par des structures homologues chez les holocéphales, permettant la détection des champs électriques produits par les proies (Lisney, 2010). Cette capacité est complétée par un système olfactif très développé, capable de détecter des signaux chimiques émis par les proies, les prédateurs et les congénères (Hart & Collin, 2015).

Ainsi, l'ensemble de ces adaptations morphologiques, fonctionnelles et sensorielles souligne le succès évolutif remarquable des chondrichthyens, qui constituent des composantes majeures des écosystèmes aquatiques depuis plus de 400 millions d'années.

3. Les problématiques liées à l'origine des chondrichthyens

3.1 Les interrelations des gnathostomes

Les relations phylogénétiques entre les premiers gnathostomes (c'est-à-dire les vertébrés à mâchoires) restent loin d'être entièrement résolues (Forey & Janvier, 1993 ; Zhu *et al.*, 2021 ; Brownstein, 2023). Depuis la fin du XIX^e siècle, de nombreuses hypothèses ont été proposées pour expliquer l'origine et les relations entre les vertébrés à mâchoires (Gegenbaur, 1878 ; Balfour, 1881 ; de Beer, 1937 ; Reif, 1982). Dans le cadre phylogénétique moderne, les gnathostomes comprennent deux lignées monophylétiques actuelles, les Chondrichthyes et les Osteichthyes, ainsi que deux assemblages éteints et paraphylétiques, à savoir les « placodermes » et les « acanthodiens » (Brazeau & Friedman, 2015). Les deux lignées vivantes sont bien soutenues par des données moléculaires et morphologiques (Hallström & Janke, 2009), tandis que la position phylogénétique des « placodermes » et des « acanthodiens » demeure controversée (Qiao *et al.*, 2016 ; King *et al.*, 2017).

Plusieurs controverses majeures persistent, notamment concernant le statut phylogénétique des « placodermes » (Johanson & Smith, 2005 ; Young, 2010 ; Long *et al.*, 2014), la transition entre les « acanthodiens » et les chondrichthyens (Carrier *et al.*, 2004 ; Grogan *et al.*, 2004 ; Brazeau, 2015 ; Chevrinais *et al.*, 2017 ; Coates *et al.*, 2017 ; Boisvert *et al.*, 2019), ainsi que la morphologie du dernier ancêtre commun des gnathostomes (Zhu *et al.*, 2013 ; Davis *et al.*, 2012). La nature phylogénétique des « placodermes » est débattue depuis la fin du XX^e siècle (Burrow & Turner, 1999 ; Goujet & Young, 2004). Ils ont longtemps été considérés comme un assemblage paraphylétique de gnathostomes basaux (Friedman, 2007 ; Brazeau, 2009), bien que certaines analyses bayésiennes récentes les aient retrouvés comme monophylétiques (King *et al.*, 2017). Malgré ces résultats, la majorité des études récentes continue de soutenir

la paraphylie des « placodermes » (Zhu *et al.*, 2021 ; Brazeau *et al.*, 2023). Indépendamment de leurs relations internes, les « placodermes » sont largement considérés comme représentant le grade le plus basal des gnathostomes (King *et al.*, 2017).

En revanche, depuis Miller *et al.* (2003), les « acanthodiens » sont universellement considérés comme un assemblage paraphylétique de chondrichthyens souches qui, avec les chondrichthyens du groupe-couronne, constituent le groupe total des chondrichthyens (Brazeau & de Winter, 2015 ; Chevrinais *et al.*, 2017). Leur paraphylie s'explique par une mosaïque de caractères morphologiques partagés, combinant des traits autrement associés à la fois aux chondrichthyens et aux ostéichthyens (Brazeau & Friedman, 2015). À ce jour, aucune synapomorphie ne définit sans ambiguïté les « acanthodiens » comme un clade.

Historiquement, les « acanthodiens » ont souvent été interprétés comme des ostéichthyens souches, principalement sur la base de l'ultrastructure de leurs écailles et de la présence de dents dans certains groupes tels que les ischnacanthiformes (Maisey, 1986 ; Rücklin *et al.*, 2021). Cependant, de nombreux taxons d'« acanthodiens » présentent des caractères clairement proches de ceux des chondrichthyens, incluant des aiguillons de nageoires, certains aspects de l'anatomie neurocrânienne et des mécanismes de suspension des mâchoires (Brazeau, 2009 ; Davis *et al.*, 2012).

Malgré ces avancées, le registre fossile des acanthodiens reste limité, et seuls quelques spécimens conservent des éléments squelettiques ou neurocrâniens articulés (Brazeau, 2009). Cette rareté complique l'interprétation de leur position évolutive et obscurcit la nature de la transition vers les chondrichthyens du groupe-couronne. Plusieurs taxons d'« acanthodien » se situent près du nœud des chondrichthyens du groupe-couronne, notamment les taxons dits « Man On The Hill » (MOTH), incluant *Obtusacanthus corroconis*, *Paucicanthus vaneltzi*, *Kathemacanthus rosulentus* et *Brochoadmones milesi* (Chevrinais *et al.*, 2017).

Certains taxons se rapprochent encore davantage du groupe-couronne, ne s'en distinguant principalement que par l'absence de cartilage prismatique (tessellé). Un exemple notable est *Doliodus latispinosus*, qui présente des dents et des écailles proches de celles des

chondrichthyens du groupe-couronne, ainsi que plusieurs autres caractères morphologiques typiques des premiers chondrichthyens du groupe-couronne (Miller *et al.*, 2003 ; Burrow *et al.*, 2017).

La plupart des autres « acanthodiens » sont édentés (Rücklin *et al.*, 2021) et possèdent des écailles polyodontodes organisées selon un mode de croissance en « oignon », très différent des écailles placoïdes et des écailles polyodontodes à développement aréolaire des premiers chondrichthyens (Qu *et al.*, 2013 ; Potvin-Leduc *et al.*, 2015).

Dans l'ensemble, le registre fossile limité participe à l'instabilité phylogénétique des premiers gnathostomes et continuent de brouiller notre compréhension des relations évolutives entre les « placodermes », les « acanthodiens » et les chondrichthyens, ainsi que de l'anatomie du dernier ancêtre commun des vertébrés à mâchoires (Davis *et al.*, 2012).

3.2 Le registre fossile : une ligne du temps confuse

L'un des principaux défis dans la reconstitution de l'origine et de l'histoire évolutive des taxons fossiles réside dans l'incomplétude du registre fossile, largement due aux processus taphonomiques (Behrensmeyer, 2021). Les chondrichthyens sont particulièrement affectés par cette limitation en raison du faible potentiel de fossilisation de leur squelette cartilagineux (Schnetzer *et al.*, 2024). Par conséquent, notre compréhension de l'anatomie squelettique des premiers chondrichthyens demeure fragmentaire, ce qui obscurcit la chronologie et la séquence des innovations évolutives majeures telles que l'origine des mâchoires, des aiguillons de nageoires pectorales appariées, et des organes internes comme l'estomac chez les chondrichthyens du groupe souche et du groupe couronne. Par exemple, les mâchoires de chondrichthyens sont principalement connues à partir de dépôts du Dévonien (Brazeau, 2009), malgré la présence de restes de chondrichthyens putatifs remontant à l'Ordovicien. La grande majorité du registre fossile des chondrichthyens est constituée d'éléments dermiques isolés, incluant dents, écailles et aiguillons de nageoires (e.g. Andreev *et al.*, 2022 ; Cui *et al.*, 2021 ; Duffin & Ivanov, 2008), tandis que les spécimens

articulés ou partiellement articulés sont extrêmement rares (Miller *et al.*, 2003 ; Hanke *et al.*, 2013).

Les plus anciens restes attribués aux chondrichthyens sont des écailles assignées aux mongolépides, notamment *Solinalepis levis*, datant du Darriwilien (~465 Ma ; Andreev *et al.*, 2016). Si les mongolépides sont effectivement des chondrichthyens, cela placerait la lignée souche des chondrichthyens à au moins 465 millions d'années. Cependant, en raison de l'incertitude persistante concernant leur position phylogénétique, la plupart des phylogénies récentes calibrées dans le temps excluent les mongolépides ou les traitent avec prudence (Andreev *et al.*, 2016 ; Coates *et al.*, 2018), renforçant ainsi l'incertitude quant au moment réel de l'origine des chondrichthyens. Malgré ces limites, des études récentes estiment le nœud des chondrichthyens du groupe couronne à environ 389 Ma (Coates *et al.*, 2018 ; Schnetz *et al.*, 2024), bien que des origines plus anciennes, proches de 400 Ma, aient également été proposées (Janvier & Pradel, 2015). Cela implique un intervalle temporel d'environ 65 à 76 millions d'années entre les plus anciens restes de chondrichthyens putatifs et la divergence inférée du nœud couronne. Durant cet intervalle, les fossiles de chondrichthyens sont extrêmement rares comparativement au registre fossile riche documenté dans les périodes géologiques ultérieures.

Les fossiles les plus significatifs comblant partiellement cet intervalle sont les sinacanthidés du Silurien de Chine, qui représentent les plus anciennes aiguillons de nageoires attribuées aux chondrichthyens souches et datent du Telychien (~435 Ma ; Andreev *et al.*, 2020). Ces aiguillons de nageoires sont contemporaines d'assemblages supplémentaires d'écailles de mongolépides (Andreev *et al.*, 2016). De nombreuses autres aiguillons de nageoires ont été découvertes dans des dépôts du Silurien supérieur (Jerve *et al.*, 2017 ; Andreev *et al.*, 2022), cependant les premières dents de chondrichthyens indiscutables et les premiers spécimens articulés n'apparaissent que plus tard, respectivement au Lochkovien et à l'Emsien (Botella *et al.*, 2009 ; Miller *et al.*, 2003). Ces fossiles dévoniens montrent que les chondrichthyens à mâchoires étaient déjà bien établis dans les écosystèmes lacustres dès le Dévonien inférieur,

ce qui est cohérent avec les hypothèses proposant une évolution quasi simultanée des mâchoires et des dentitions marginales (Johanson & Smith, 2005).

Néanmoins, un intervalle d'environ 30 millions d'années subsiste entre les plus anciennes écailles de chondrichthyens putatifs et les premières aiguillons de nageoires, compliquant davantage la reconstitution de l'évolution précoce des chondrichthyens. Il est important de noter que le nœud couronne des gnathostomes est généralement calibré à des âges postérieurs au Darriwilien sur la base d'analyses phylogénétiques complètes (King *et al.*, 2017), soulevant ainsi des questions supplémentaires quant à la position des restes chondrichthyens du Darriwilien. À ce jour, aucune étude n'a entièrement résolu cette discordance dans le contexte de l'origine des chondrichthyens. Par conséquent, une incertitude substantielle persiste concernant la chronologie, le rythme et la séquence anatomique de l'évolution précoce des chondrichthyens, reflétant des problématiques plus larges encore non résolues dans l'histoire évolutive initiale des gnathostomes dans leur ensemble.

3.3 Thélodontes et leurs affinités non-conventionnelle

La lignée souche des gnathostomes (c.-à-d. en dehors du groupe total des gnathostomes) est composée exclusivement de vertébrés sans mâchoires aujourd'hui éteints (Giles *et al.*, 2013 ; Donoghue & Keating, 2014). Bien que les vertébrés actuels sans mâchoires, soit, les myxines et les lamproies, souvent évoqués dans ce contexte, ils n'appartiennent pas à la lignée souche des gnathostomes et forment plutôt deux clades cyclostomes monophylétiques distincts (Near, 2009). Les gnathostomes de la lignée souche fossile sont principalement représentés par les conodontes, les anaspides, les pituriaspides, les hétérostracés, les galéaspides, les ostéostracés et les thélodontes, qui sont tous des groupes entièrement éteints (Donoghue & Keating, 2014).

Les conodontes ont longtemps été considérés comme l'un des groupes fossiles les plus énigmatiques et ont historiquement été assignés à un large éventail d'embranchements (Ginot & Goudemand, 2020). Ils sont principalement connus à partir d'éléments denticulaires isolés

s'étendant du Cambrien au Trias inférieur (Ginot & Goudemand, 2020). Cependant, des découvertes de préservation de tissus mous ont révélé que les conodontes étaient des chordés basaux de forme anguilliforme présentant des affinités avec les vertébrés (Donoghue *et al.*, 2000). Des formes plus dérivées au sein de la lignée souche incluent les hétérostracés, qui présentent un plan d'organisation corporelle plus reconnaissable comme « poisson » (Soehn & Wilson, 1990). Les hétérostracés sont souvent considérés comme le premier clade à exhiber plusieurs innovations majeures associées plus tard aux gnathostomes, telles que des nageoires pectorales appariées, un tube digestif différencié, un neurocrâne minéralisé, ainsi que des tissus osseux acellulaires et cellulaires (Donoghue & Keating, 2014). Ils constituent un assemblage paraphylétique diversifié s'étendant du Silurien au Dévonien supérieur (Blieck & Janvier, 1999 ; Sansom *et al.*, 2015) et se caractérisent par un bouclier céphalique dermique distinctif composé de plaques disposées dorsoventralement (Keating *et al.*, 2015). Historiquement, les hétérostracés ont reçu une attention limitée, ce qui a freiné les interprétations globales de l'évolution précoce des vertébrés (Randle & Sansom, 2017). Les hypothèses phylogénétiques actuelles les considèrent généralement comme moins dérivés que les galéaspides, les ostéostracés et les thélodontes (Randle & Sansom, 2017).

En revanche, les galéaspides ont fait l'objet d'études approfondies sur les plans anatomique, histologique et fonctionnel, notamment concernant leur architecture crânienne et leur anatomie interne (Nian-Zhong *et al.*, 2005 ; Min & Janvier, 1998 ; Gai *et al.*, 2019). Des travaux récents ont fourni des éclairages essentiels sur l'origine des appendices appariés et l'évolution locomotrice chez les gnathostomes de la lignée souche (Gai *et al.*, 2022, 2023). Les galéaspides représentent un assemblage paraphylétique de vertébrés sans mâchoires possédant un bouclier céphalique et un système bien développé de canaux de ligne sensorielle (Chen *et al.*, 2024). Ils sont principalement connus en Chine et au Vietnam et s'étendent du Silurien au Dévonien (Sansom, 2009). Les galéaspides ont été considérés comme le groupe frère des ostéostracés, un autre clade de vertébrés sans mâchoires caractérisé par un large bouclier céphalique et un registre fossile dominé par le Dévonien (Sansom, 2008). Les ostéostracés présentent une grande disparité morphologique dans l'architecture de leur bouclier céphalique (Ferrón *et al.*, 2020) et s'étendent du Llandovery au Dévonien supérieur

(Sansom, 2009). Ensemble, galéaspides et ostéostracés sont systématiquement retrouvés comme les plus proches parents de la lignée souche des gnathostomes du groupe couronne dans de nombreuses analyses phylogénétiques (Giles *et al.*, 2015 ; Qiao *et al.*, 2016 ; Sansom, 2009).

Néanmoins, les thélodontes ont été à plusieurs reprises proposés comme un candidat alternatif pour représenter les plus proches parents des gnathostomes (Janvier, 1996). Ce groupe présente une mosaïque remarquable de caractères plésiomorphes et dérivés qui complique leur position phylogénétique (Sansom *et al.*, 1996 ; Donoghue & Rücklin, 2016). Les thélodontes s'étendent de l'Ordovicien supérieur au Dévonien supérieur (Turner, 1992) et sont généralement reconstruits comme de petits poissons cartilagineux dépourvus de bouclier céphalique (Wilson & Märss, 2009). Leur corps est recouvert d'écailles de type denticule qui ressemblent étroitement aux écailles placoïdes des chondrichthyens (Žigaitė *et al.*, 2013). Chez des taxons plus dérivés, tels que *Loganellia scotica*, des structures analogues à des dents ont été identifiées (Rücklin *et al.*, 2011), et des preuves de la présence d'un organe de type estomac, auparavant considéré comme une synapomorphie des gnathostomes, ont également été rapportées (Janvier, 1996). Les thélodontes se distinguent en outre par leur grande diversité écologique, occupant des environnements pélagiques, marins peu profonds et benthiques, contrairement aux modes de vie principalement benthiques inférés pour la plupart des autres agnathes (Ferrón & Botella, 2017 ; Ferrón *et al.*, 2018). Cette polyvalence écologique suggère que certains thélodontes occupaient des rôles de prédateurs intermédiaires dans les écosystèmes marins paléozoïques (Ferrón & Botella, 2017). Malgré ces caractéristiques remarquables, les thélodontes restent mal intégrés dans les cadres phylogénétiques globaux. Ils ont fréquemment été exclus des analyses à grande échelle (Forey & Janvier, 1993 ; King *et al.*, 2017 ; Qiao *et al.*, 2016) ou placés plus éloignés des gnathostomes que les galéaspides ou les ostéostracés (Janvier, 2008 ; Randle *et al.*, 2025), malgré le partage de plusieurs caractères avec les gnathostomes du groupe couronne. Bien qu'un nombre limité d'études ait exploré les relations internes des thélodontes (Wilson & Märss, 2004, 2009), aucune analyse phylogénétique n'a encore pleinement intégré leur

morphologie distinctive aux côtés des autres « agnathes » et des gnathostomes dans un cadre unifié. Cela contribue probablement à l'instabilité de leur position dans les différentes études.

Dans l'ensemble, les signaux contradictoires issus du registre fossile des « agnathes » et des premiers gnathostomes obscurcissent la trajectoire évolutive menant aux gnathostomes du groupe couronne, y compris les chondrichthyens. Les relations mal résolues entre les vertébrés sans mâchoires, combinées aux lacunes du registre fossile et à un échantillonnage phylogénétique inégal, compliquent la reconstitution de l'ancêtre commun des gnathostomes et de l'évolution précoce des chondrichthyens. La résolution de ces incertitudes nécessitera des approches phylogénétiques intégratives combinant des données morphologiques discrètes et continues, un meilleur échantillonnage fossile et des protocoles standardisés de codage des caractères, afin de réduire la subjectivité dans l'interprétation de l'évolution précoce des vertébrés.

4. Les relations phylogénétiques et les dynamiques macro-évolutives : une approche méthodologique

L'exploration des relations entre fossiles repose sur un cadre méthodologique progressif. Tout d'abord, une matrice combinant taxons et caractères est nécessaire. Les caractères peuvent être exprimés de différentes manières. Dans le cas des études fossiles, les caractères morphologiques constituent la base de comparaison entre les taxons. Ensuite, des hypothèses phylogénétiques sont produites, intégrant plusieurs paramètres et représentant les relations entre taxons en fonction de leurs similarités morphologiques. Enfin, des post-analyses permettent d'explorer les patrons macroévolutifs à travers les taux d'évolution et de diversification, ainsi que la disparité morphologique.

4.1 Standardisation, compilation de caractères et supermatrice

Les méthodes utilisées pour reconstruire des supermatrices morphologiques n'ont pas encore atteint de consensus méthodologique. La construction de tels ensembles de données implique généralement plusieurs étapes successives : (1) la description de la morphologie et de l'anatomie des taxons d'intérêt ; (2) l'identification et la définition des unités descriptives ; (3) le codage de ces unités dans une matrice ou supermatrice ; et (4) la traduction de cette matrice dans un cadre analytique capable d'inférer des relations phylogénétiques. À chacune de ces étapes, l'absence de standardisation méthodologique peut conduire à des interprétations divergentes de l'homologie et, en fin de compte, à des hypothèses phylogénétiques contradictoires.

L'un des problèmes les plus persistants réside dans l'absence d'une terminologie morphologique standardisée. Les différences de qualité descriptive, d'organisation et de style entraînent fréquemment des descriptions divergentes de traits équivalents (Vogt, 2008). Lorsqu'elles sont combinées à des pratiques de codage hétérogènes, ces incohérences peuvent influencer de manière significative la topologie des arbres, les interprétations de l'homologie et les séries de transformation inférées (Pleijel, 1995 ; Hawkins *et al.*, 1997 ; Strong & Lipscomb, 1999 ; Forey & Kitching, 2000). De plus, une standardisation insuffisante dans la construction des métadonnées — définies comme la documentation détaillée du design expérimental, de la provenance et de la préparation du matériel, des méthodes descriptives, des cadres conceptuels et des paramètres analytiques — entrave à la fois la comparabilité et la reproductibilité des données (Vogt, 2008, 2010, 2013 ; Brazeau, 2011). Ces problèmes liés à la standardisation et à l'objectivité en phylogénie morphologique ont été soulignés à de nombreuses reprises dans la littérature (Maddison, 1993 ; Pleijel, 1995 ; Wilkinson, 1995 ; Hawkins *et al.*, 1997 ; Strong & Lipscomb, 1999 ; Sereno, 2007 ; Vogt, 2008 ; Brazeau, 2011 ; Simões *et al.*, 2017).

Dans ce contexte, la morphologie évolutive englobe plusieurs domaines de recherche interconnectés : la morphologie descriptive, qui documente la forme des organismes ; la morphologie fonctionnelle, qui étudie la biomécanique et la performance ; la morphologie comparative, où les homologies sont identifiées et les séquences de transformation inférées

par analyse phylogénétique ; et la morphologie causale, qui cherche à expliquer à la fois les processus adaptatifs et les contraintes sur l'évolvabilité (Richter & Wirkner, 2014). Un défi ancien en morphologie descriptive concerne la terminologie utilisée pour désigner les objets anatomiques décrits. Le terme caractère est fréquemment employé, mais il possède plusieurs significations (Wagner, 2001) et, en phylogénie, désigne principalement une unité évolutive plutôt qu'une entité descriptive. Son utilisation au niveau descriptif est donc problématique. De même, le terme structure est ambigu car il peut désigner à la fois une entité anatomique et une organisation compositionnelle (Dullemeijer, 1974 ; Young, 1993). Le terme « feature » est souvent trop vague pour être analytiquement utile (Bock & von Wahlert, 1965). D'autres termes, tels que des éléments morphologiques (Dullemeijer, 1974 ; Young, 1993) ou traits morphologiques (Vogt, 2008), sont relativement neutres mais manquent de définitions précises.

Pour résoudre cette ambiguïté terminologique, Richter et Wirkner (2014) ont proposé le terme morphème, emprunté à la linguistique, où il désigne la plus petite unité lexicale porteuse de sens. Appliqué à la morphologie, un morphème représente la plus petite unité significative de description anatomique, indépendante de toute interprétation évolutive. Par exemple, le cœur des vertébrés peut être considéré comme un morphème, tout comme ses composantes, l'oreillette et le ventricule, et même des subdivisions plus fines selon l'échelle de description. Les morphèmes sont donc intrinsèquement dépendants de l'échelle et fonctionnent comme des unités descriptives, et non comme des unités évolutives.

En revanche, les unités évolutives, traditionnellement appelées caractères, sont des entités conceptuelles dotées d'une signification évolutive explicite. Une unité évolutive peut correspondre directement à un seul morphème, mais elle peut aussi englober plusieurs morphèmes (par exemple en formant une unité fonctionnelle ou biologique) ou seulement une partie d'un morphème si elle est définie à une échelle analytique plus fine. Compte tenu de l'ambiguïté sémantique du terme caractère, Richter et Wirkner (2014) ont proposé de le remplacer par unité évolutive en morphologie évolutive. Dans cette logique, les états de

caractère doivent être compris comme des unités évolutives homologues putatives, représentant des expressions mutuellement exclusives d'une condition évolutive.

Malgré cette clarification conceptuelle, la traduction des morphèmes en unités évolutives demeure un défi majeur. Certaines stratégies de codage échouent à capturer le signal biologique recherché et peuvent introduire des artefacts dans les analyses phylogénétiques, en fonction de multiples facteurs interagissant (Brazeau, 2011). Les descriptions subjectives, un vocabulaire imprécis et une délimitation incohérente des unités compromettent davantage la comparabilité et la communicabilité des données (Mabee *et al.*, 2007 ; Vogt, 2010 ; Deans *et al.*, 2012).

Des progrès significatifs ont été réalisés au niveau descriptif grâce à l'adoption d'ontologies anatomiques. Les ontologies combinent des vocabulaires contrôlés avec des relations formellement définies, telles que la subsomption (« est un ») et les relations partie-tout (« partie de »), fournissant ainsi un cadre sémantique robuste pour la description morphologique (Smith, 2005 ; Trelease, 2006 ; Ramirez *et al.*, 2007 ; Mungall, 2010). Des outils tels que Phenex facilitent l'annotation des morphèmes basée sur les ontologies et réduisent la subjectivité dans les pratiques descriptives (Balhoff *et al.*, 2010). Par conséquent, les problèmes linguistiques mis en évidence par Vogt *et al.* (2010), à savoir l'absence d'une terminologie standardisée indépendante des taxons, le manque de méthodes descriptives formalisées et l'absence de justification pour la délimitation des unités morphologiques, ont en grande partie été résolus au niveau de la morphologie descriptive.

Cependant, les ontologies à elles seules ne résolvent pas les difficultés liées au codage des morphèmes en unités évolutives. La construction et l'attribution des scores aux unités évolutives demeurent parmi les étapes les plus influentes de l'analyse cladistique, comme l'ont souligné de nombreux auteurs (Maddison, 1993 ; Pleijel, 1995 ; Wilkinson, 1995 ; Hawkins *et al.*, 1997 ; Strong & Lipscomb, 1999 ; Sereno, 2007 ; Brazeau, 2011 ; Simões *et al.*, 2017). Parmi ces contributions, Sereno (2007) a fortement plaidé en faveur d'une terminologie explicite et standardisée ainsi que d'une schématisation des unités évolutives. Il a mis en évidence des ambiguïtés conceptuelles persistantes concernant l'homologie, les

caractères et les états de caractères, et a proposé une nouvelle nomenclature dans laquelle caractères et états de caractères étaient conjointement désignés comme des énoncés de caractère. Toutefois, cette terminologie introduit une ambiguïté supplémentaire.

Sereno (2007) a défini un caractère phylogénétique comme « une caractéristique héréditaire d'un organisme exprimée comme une variable indépendante », une définition largement adoptée dans la littérature (Freudenstein, 2005). Reformulée de manière moins ambiguë, une unité évolutive peut être définie comme une condition héréditaire observable exprimée comme une variable indépendante. De plus, les unités évolutives homologues putatives sont généralement comprises comme des conditions mutuellement exclusives (Freudenstein, 2005), de sorte qu'une condition donnée ne peut logiquement pas être à la fois présente et absente simultanément. Ce principe fournit une base conceptuelle nécessaire à des pratiques de codage rigoureuses.

Sereno (2007) a également distingué deux types fondamentalement différents d'unités évolutives : les unités néomorphiques, qui impliquent la présence ou l'absence d'une structure définie uniquement par des localisateurs, et les unités transformationnelles, qui décrivent des variations le long d'un gradient morphologique continu ou discret. Mélanger ces deux types au sein d'une même unité évolutive peut obscurcir le signal biologique et entraîner une perte d'information, en particulier en ce qui concerne les distinctions présence-absence. D'autres catégories d'unités évolutives problématiques, identifiées par Sereno (2007) à la suite de Poe et Wiens (2000), illustrent également comment des pratiques de codage imprécises peuvent biaiser les inférences phylogénétiques (Figure 8).

Category	No.	Criteria
Comparative	1	High variation
	2	High homoplasy
	3	Substantial missing data
	4	Unknown polarity
	5	Continuous variation
	6	Doubtful topology
	7	Doubtful connection
	8	Absence of special features
	9	Absence of intermediate forms
Logical	10	Character correlation
	11	Mixed character statements
Operational	12	Ambiguous or imprecise descriptions
	13	Incomplete quantitative-relative character statements

Figure 8 : Résumé des erreurs communes dans la description des unités évolutives (d'après Sereno 2007)

Ces fondements conceptuels sont indéniablement précieux, mais l'une des contributions majeures de Sereno (2007) réside dans sa proposition d'un cadre syntaxique explicite pour définir les unités évolutives, visant à standardiser leur construction et leur expression. Dans ce cadre, une unité évolutive est formalisée comme un énoncé structuré composé de plusieurs éléments.

Tout d'abord, elle inclut un ou plusieurs localisateurs (L_n), qui précisent le contexte anatomique de l'unité et correspondent généralement aux morphèmes d'intérêt. Les localisateurs sont organisés de manière hiérarchique, avec un localisateur principal (L_1) identifiant l'entité anatomique principale, et des localisateurs secondaires ou d'ordre supérieur (L_2 , L_3 , etc.) qui en précisent le contexte spatial, structurel ou relationnel.

Ensuite, une unité évolutive peut inclure une variable (V), représentant l'aspect du localisateur qui varie entre les taxons. Lorsque cette variable est présente, elle peut être précisée par un qualificatif (q), qui contraint ou décrit la nature de la variation (par exemple la forme, la taille, l'orientation ou le degré). L'ensemble formé par les localisateurs, la

variable et les qualificatifs permet de définir le champ et la signification de l'unité évolutive de manière explicite et reproductible.

Dans ce système syntaxique, les unités évolutives homologues putatives, traditionnellement appelées états de caractères, sont notées V_n et correspondent aux expressions mutuellement exclusives de la variable dans le contexte anatomique défini. Ces états représentent des conditions alternatives d'une même unité évolutive et sont traités comme logiquement exclusifs, garantissant la cohérence avec les principes de l'homologie et de l'inférence cladistique.

Sereno (2007) illustre cette syntaxe à l'aide d'exemples concrets, montrant comment des observations morphologiques complexes peuvent être décomposées en unités évolutives standardisées, dotées de localisateurs, de variables et d'états clairement définis. Un exemple de cette démarche est présenté dans la Figure 9.

Character type	Example	Symbolic notation
Neomorphic	Maxilla, anterior process: absent (0); present (1)	$L_2, L_1; v_0; v_1$
Transformational	Maxilla, anterior process, length relative to the posterior process: shorter (0); longer (1)	$L_2, L_1, Vq; v_0; v_1$
	Maxilla, anterior process, length: shorter (0), or longer (1), than the posterior process	$L_2, L_1, V; v_0, v_1, q$

Figure 9 : Exemple de syntaxe pour les unités évolutives d'après Sereno (2007)

Ce type de raisonnement et d'annotation représente l'une des premières tentatives de standardisation de la construction des unités évolutives en phylogénétique morphologique. Au-delà de la proposition de Sereno, plusieurs auteurs se sont attachés à développer des cadres syntaxiques plus formels afin de définir les unités évolutives et leurs conditions homologues putatives. Parmi ceux-ci, Gkoutos *et al.* (2004) ont proposé une approche influente visant à standardiser la représentation des unités morphologiques. Leurs travaux ont posé les bases conceptuelles et techniques de ce qui sera ensuite connu sous le nom de formalisme Entité–Qualité (EQ) (Sprague *et al.*, 2006 ; Mungall *et al.*, 2007).

Dans le cadre du formalisme EQ, une unité évolutive est décomposée en deux composantes complémentaires. L'*Entité* correspond à la structure anatomique ou morphologique d'intérêt, généralement dérivée d'un morphème décrit à l'aide d'une ontologie anatomique dédiée. La *Qualité* représente l'attribut variable ou l'état exprimé par cette entité et correspond à l'unité évolutive homologue putative, elle-même définie à l'aide d'une ontologie de phénotype ou de qualité.

Dans ce cadre, la variation morphologique est exprimée comme une association logique entre une entité et une qualité, permettant de décrire les unités évolutives et leurs différentes conditions de manière structurée, explicite et lisible par machine (Figure 10). En dissociant l'identité anatomique de la variation phénotypique, la syntaxe EQ propose une approche formalisée et fondée sur les ontologies pour la construction des caractères morphologiques. Ce cadre améliore la transparence, la reproductibilité et l'interopérabilité des jeux de données morphologiques, et fournit une base robuste pour intégrer la morphologie descriptive aux analyses phylogénétiques, en particulier dans les contextes où la variation anatomique complexe et l'évaluation de l'homologie constituent des enjeux centraux.

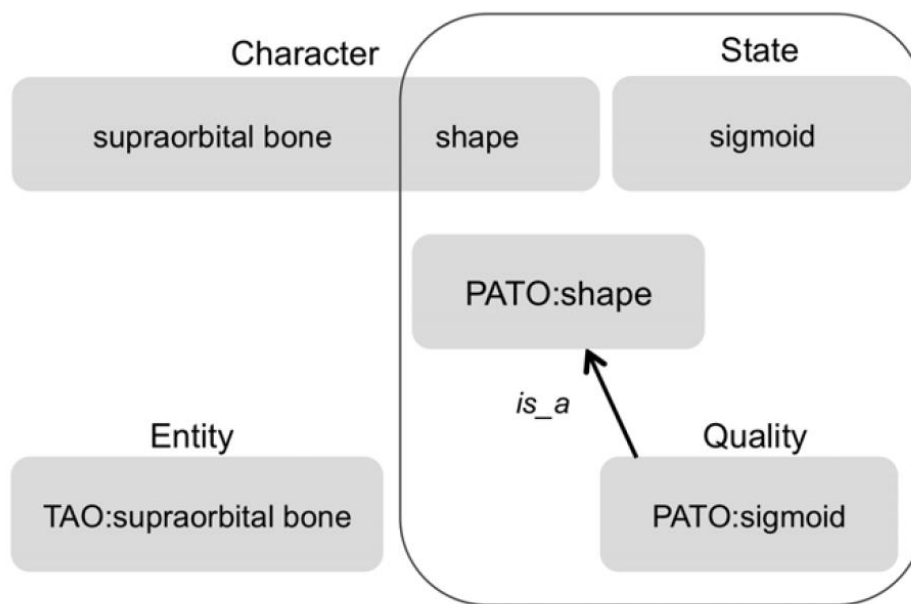


Figure 10 : Schéma du format Entité-Qualité, avec les ontologies associées (TAO, PATO)

Le formalisme EQ fournit une syntaxe à la fois rigoureuse et flexible pour la représentation des données morphologiques. Cette approche formalisée guide la construction des unités évolutives à l'aide de logiciels dédiés tels que Phenex (Balhoff *et al.*, 2010), réduisant ainsi de manière significative l'intervention subjective humaine. En conséquence, elle contribue à accroître l'objectivité dans la reconstruction des unités évolutives à partir de données morphologiques.

L'une des principales différences entre le format EQ et la syntaxe proposée par Sereno (2007) réside dans le fait que le EQ est explicitement contraint et structuré par des ontologies directement implémentées dans des environnements logiciels. Néanmoins, le format EQ n'est pas exempt de limites. L'un des inconvénients notables apparaît lorsqu'un morphème d'intérêt est absent de l'ontologie pertinente. Dans ce cas, sa description ne peut pas être formellement contrainte, ce qui peut réintroduire une part de subjectivité dans la construction d'une ou plusieurs unités évolutives.

Malgré cette limitation, la syntaxe EQ représente actuellement l'un des cadres les plus robustes et objectifs disponibles pour la reconstruction des unités évolutives à partir de données morphologiques. Sereno (2007) et Gkoutos *et al.* (2004) peuvent ainsi être considérés comme des pionniers dans l'effort de formalisation de la construction des unités évolutives. Ensemble, leurs contributions constituent une base conceptuelle solide pour poursuivre la recherche d'objectivité dans la reconstruction des supermatrices morphologiques.

Plusieurs auteurs ultérieurs s'appuyant sur Sereno (2007) se sont également intéressés à cette problématique, notamment Brazeau (2011). Celui-ci rejoint Sereno sur plusieurs points essentiels, en particulier sur l'idée que les unités évolutives ne doivent pas combiner simultanément des conditions néomorphiques et transformationnelles. Bien que Brazeau ne propose pas de syntaxe formelle pour la construction des unités évolutives et de leurs états homologues putatifs, il identifie trois conséquences méthodologiques majeures et

généralement indésirables associées à la construction des supermatrices : (1) l'incapacité à capturer des informations importantes de regroupement, (2) une pondération involontaire des unités évolutives, et (3) l'imposition non intentionnelle ou injustifiée de congruence entre unités évolutives.

Parmi ses observations les plus pertinentes figure la recommandation selon laquelle l'absence d'un morphème ne devrait être codée qu'une seule fois au sein d'une supermatrice. Le fait de coder à plusieurs reprises une même absence dans différentes unités évolutives traduit une mauvaise prise en compte de la symétrie des changements évolutifs et introduit une redondance dans les données. Toutefois, la discussion de Brazeau se concentre principalement sur le traitement des unités évolutives dans le cadre d'analyses fondées sur la parcimonie. Étant donné que ces approches ont été largement affinées au cours de la dernière décennie et sont de plus en plus supplantées par des méthodes bayésiennes et de maximum de vraisemblance, l'applicabilité directe de certaines de ses recommandations demeure limitée dans le contexte actuel.

Plus récemment, Simões *et al.* (2017) ont réexaminé la question de l'objectivité en phylogénétique morphologique et mis en évidence un ensemble de problèmes récurrents liés au codage des unités évolutives dans les supermatrices (Figure 11 ; voir Simões *et al.*, 2017 pour les détails).

Type	Name	Description
I		
A		
1	Non-additive binary coding	Each state becomes a different character creating redundancy
2	Absence coding	Extra weight for the “absent” condition creating redundancy
3	Compound statement coding	Multiple non-dependent properties as distinct states under the same character (exception: gain/loss of the structure)
4	Compound characters	Multiple non-dependent properties implicit in character description
5	Compound character-state coding	Alternative distinct non-dependent properties under the same state
6	Multiple character-state variables coding	Two or more non-dependent properties together under the same state
7	Unjustified composite locator coding	Multiple anatomical elements with no evidence to be treated as having evolutionary integration under the same character
B	Character splitting	Single transformation series broken into two or more
C	State accretion	One state includes the other states
D	Conjunction	Two or more structures occur in the same individuals and are treated as homologous (exception: serial homologues)
II		
A	Data treated as continuous with arbitrary state delimitations	Data treated as continuous, coded either quantitatively or qualitatively, in which states are delimited arbitrarily or not representing the frequency range for each terminal unit (e.g. segment coding)
B	Continuous data unjustifiably treated as discrete	Continuous data treated as discrete but with no disjoint distribution of its character-states
III	Biogeographical characters	
IV	Behavioural characters	
V	Character statements with no, little or vague explanations	Character descriptions or character-states that are ambiguous and likely to result in distinct scoring of taxa depending on the author
VI	Problems with the interpretation of the morphology during character construction	Misinterpretation of the identity of the structure (locator) being coded
VII	Taphonomy-biased characters	Characters that are easily altered during transportation or diagenesis of organic remains during the fossilization process; or may have different states when comparing a fresh specimen to a dry or fossil specimen.

Figure 11 : Problèmes récurrents dans le codage des unités évolutives d’après Simões et al. (2017)

Bien que leur évaluation soit en partie pertinente et constitue un avertissement utile contre certains écueils récurrents—en particulier la redondance et les effets de pondération involontaires—cette étude ne propose pas de solutions explicites ni de cadre formalisé permettant de limiter ces problèmes. À l’instar de Sereno (2007) et de Brazeau (2011), Simões *et al.* (2017) reconnaissent finalement qu’aucune méthode universelle n’existe actuellement pour coder les unités évolutives à partir des morphèmes.

Dans l’ensemble, la recherche d’objectivité dans la reconstruction des phylogénies à partir de données morphologiques a reçu une attention étonnamment limitée au cours de la dernière décennie, malgré son importance fondamentale. Des efforts supplémentaires sont clairement nécessaires pour mieux standardiser le processus de codage des unités évolutives à partir des morphèmes. À l’heure actuelle, les approches fondées sur les ontologies, appuyées par des

outils logiciels dédiés, constituent la solution la plus objective et méthodologiquement solide disponible. Ces approches permettent (1) de réduire la subjectivité des descriptions, (2) d'assurer une meilleure communicabilité et comparabilité des données morphologiques, et (3) de faciliter un codage des unités évolutives transparent et reproductible.

Malgré les progrès significatifs réalisés dans l'amélioration de l'objectivité de la construction des supermatrices morphologiques, il est regrettable que relativement peu d'études aient abordé cette problématique en profondeur, et que nombre de contributions se limitent à une critique des pratiques existantes sans proposer de cadres opérationnels concrets. Par ailleurs, la transcription des unités évolutives dans les algorithmes d'inférence phylogénétique demeure insuffisamment standardisée, ce qui constitue un défi supplémentaire et encore non résolu en phylogénétique morphologique.

4.2 Phylogénies et méthodes de reconstruction

Depuis le début des années 2000, des avancées majeures ont considérablement amélioré notre compréhension du registre fossile, notamment grâce à un échantillonnage accru et à des approches analytiques plus performantes (Alroy, 2016 ; Peters & McClennen, 2016), à des méthodes géochronologiques de plus en plus précises (Miall, 2022), à une meilleure résolution des relations phylogénétiques (e.g., Adoutte *et al.*, 2000 ; Halanych, 2004 ; Dunn *et al.*, 2014), ainsi qu'au développement de modèles d'évolution des traits et de diversification (e.g., Blomberg *et al.*, 2003 ; Harmon *et al.*, 2010 ; Nee, 2006). Parmi ces avancées, la création de bases de données à grande échelle et soigneusement curées, telles que Fossilworks (Alroy, 2016) et Paleobiology Database (PBDB ; Peters & McClennen, 2016), constitue une étape majeure. Ces plateformes visent à standardiser les données fossiles, en particulier les informations stratigraphiques, réduisant ainsi les biais et améliorant la reproductibilité des analyses ultérieures.

Parallèlement à l'augmentation de la disponibilité des données fossiles, les méthodes de datation sont devenues plus précises (Erwin, 2006), entraînant des révisions substantielles de

scénarios évolutifs établis de longue date. Par exemple, la durée de l’extinction de la limite Permien–Trias a été réévaluée, passant de plusieurs millions d’années à moins d’un million d’années (Shen *et al.*, 2011). Cette période a également vu le développement et l’amélioration continue de la charte chronostratigraphique internationale, qui fournit des limites temporelles actualisées pour les unités chronostratigraphiques (Cohen *et al.*, 2013). Ensemble, ces avancées permettent d’analyser avec une plus grande précision les histoires évolutives de taxons spécifiques, notamment à travers des approches phylogénétiques.

Les arbres phylogénétiques constituent l’un des outils les plus fondamentaux pour classer les organismes et étudier les patrons évolutifs, y compris les événements macro-évolutifs et l’origine des taxons de rang supérieur (Baum & Smith, 2012). Le développement rapide de méthodes et de logiciels sophistiqués de reconstruction phylogénétique (e.g., Ronquist & Huelsenbeck, 2003 ; Drummond & Rambaut, 2007 ; Stamatakis, 2006) a conduit à des hypothèses phylogénétiques de plus en plus robustes dans de nombreux clades, y compris les gnathostomes.

Historiquement, les études sur les premiers gnathostomes reposaient largement sur la morphologie fossile et produisaient des phylogénies basées sur une seule source de données (e.g., Cope, 1885 ; Robertson, 1953 ; Moy-Thomas & Miles, 1971 ; Maisey, 1986). Les premières reconstructions phylogénétiques étaient principalement fondées sur la ressemblance morphologique ou la complexité structurelle (Gaudry, 1866 ; Haeckel, 1866), bien avant l’intégration des données moléculaires. Les bases théoriques de la phylogénétique moléculaire ont été établies dans les années 1960 (Sibley, 1962 ; Zuckerkandl & Pauling, 1965 ; Margoliash & Smith, 1965), les premières phylogénies moléculaires apparaissant dans les années 1970 (De Ley, 1974 ; Read, 1975). Ces approches reposaient initialement sur des estimations quantitatives de divergence moléculaire à partir de protéines, de peptides ou de fragments d’ADN (Fitch & Margoliash, 1967).

Aujourd’hui, les phylogénies moléculaires utilisent généralement des données de séquences issues de marqueurs tels que les gènes ribosomiques 18S ou 28S et constituent l’approche dominante pour reconstruire les relations entre taxons actuels (e.g., Perelman *et al.*, 2011 ;

Rousset *et al.*, 2007). Toutefois, ces données sont par nature indisponibles pour les phylogénies reposant exclusivement sur des fossiles. L'inférence phylogénétique à partir de données morphologiques, en particulier pour les taxons fossiles, repose donc sur des caractères dérivés de l'anatomie et de la morphologie, qui peuvent être continus (e.g., longueur ou hauteur), méristiques (e.g., nombre d'éléments anatomiques) ou discrets (e.g., présence/absence d'une structure).

Au fil du temps, plusieurs méthodes analytiques ont été développées pour inférer les relations à partir de ces données. Le maximum de parcimonie (Maximum Parsimony, MP) a dominé la phylogénétique morphologique pendant la majeure partie du XXe siècle (e.g., Baba *et al.*, 1981 ; Swofford & Berlocher, 1987 ; Coates, 1994 ; Forey, 1995). Fondée sur les principes de la systématique phylogénétique établis par Hennig (1950, 1966) et formalisés par Fitch (1971), le MP cherche l'arbre (ou les arbres) minimisant le nombre total de changements d'état nécessaires pour expliquer les données observées. Les arbres également parcimonieux sont généralement résumés à l'aide de méthodes de consensus (Levasseur & Lapointe, 2006). Malgré son ancienneté, le MP reste largement utilisé dans les analyses morphologiques de taxons fossiles (e.g., Qiao *et al.*, 2016 ; Schrago *et al.*, 2018).

Cependant, depuis le début du XXIe siècle, la MP est de plus en plus complétée—voire partiellement remplacée, par des approches fondées sur des modèles, notamment le maximum de vraisemblance (Maximum Likelihood, ML) et l'inférence bayésienne. Bien que le ML ait été proposé dès les années 1960 (Edwards & Cavalli-Sforza, 1964), son application pratique en phylogénétique est apparue plus tard en raison de contraintes computationnelles (Felsenstein, 1981). Le ML traite l'inférence phylogénétique comme un problème probabiliste, en identifiant l'arbre qui maximise la probabilité d'observer les données compte tenu d'un modèle évolutif donné (Jin *et al.*, 2006).

L'inférence phylogénétique bayésienne, introduite à la fin des années 1990 (Rannala & Yang, 1996 ; Mau *et al.*, 1999), étend ce cadre en combinant fonctions de vraisemblance et probabilités a priori afin d'estimer des distributions a posteriori d'arbres, généralement à l'aide d'algorithmes de type Markov Chain Monte Carlo (MCMC) (Huelsenbeck *et al.*, 2001

; Dellaportas *et al.*, 2002). La probabilité a posteriori d'un arbre peut ainsi être interprétée comme sa probabilité d'être correcte, compte tenu des données et des hypothèses du modèle.

Ensemble, les approches ML et bayésiennes dominent aujourd'hui l'inférence phylogénétique dans la plupart des disciplines biologiques (Parry *et al.*, 2016 ; Drummond & Stadler, 2016 ; Silvestro *et al.*, 2019), bien que leur adoption reste relativement limitée pour les poissons paléozoïques (e.g., Qiao *et al.*, 2016 ; Giles *et al.*, 2017 ; Cloutier *et al.*, 2020). Ces méthodes présentent plusieurs avantages par rapport au MP, notamment une meilleure précision topologique, une meilleure capacité à traiter de grands jeux de données et la possibilité d'intégrer différentes sources d'information (Lewis, 2001 ; O'Reilly *et al.*, 2018).

En particulier, elles permettent d'intégrer directement les données d'occurrence fossile dans l'inférence phylogénétique (Lee & Palci, 2015), ce qui n'est pas possible dans les cadres classiques de parcimonie. Plusieurs études ont montré que les approches fondées sur des modèles surpassent la parcimonie à poids égaux pour l'analyse de données morphologiques fossiles (Brown *et al.*, 2017 ; Puttick *et al.*, 2017 ; Schrago *et al.*, 2018), bien que d'autres travaux rapportent des différences limitées selon les conditions (Rindal & Brower, 2011). La complexité computationnelle demeure toutefois une limite importante de ces approches (Durmuş *et al.*, 2018), et aucun consensus n'existe quant à une méthode universellement supérieure (Goloboff *et al.*, 2018 ; O'Reilly *et al.*, 2016).

Malgré ces débats, les méthodes fondées sur des modèles ont ouvert de nouvelles perspectives pour la reconstruction de phylogénies calibrées dans le temps, en intégrant explicitement les occurrences fossiles comme données plutôt que comme simples contraintes de calibration (Lee & Yates, 2018). Traditionnellement, les fossiles étaient utilisés principalement comme taxons terminaux ou pour contraindre les âges minimaux de divergence (Brochu, 1997), ou encore pour calibrer les horloges moléculaires (Smith & Littlewood, 1994). Les modèles d'horloge moléculaire, popularisés dans les années 1960 (Zuckerkandl & Pauling, 1962, 1965), restent largement utilisés, mais posent des problèmes liés à l'estimation de l'âge des nœuds (Puttick *et al.*, 2016 ; Lee & Yates, 2018).

Des développements récents, tels que le *tip-dating* bayésien et le modèle *fossilized birth-death* (FBD), offrent des cadres plus intégratifs en modélisant simultanément la spéciation, l'extinction et l'échantillonnage fossile (Heath *et al.*, 2014 ; Wright, 2017). Ces approches permettent d'analyser directement des données fossiles datées dans des modèles probabilistes et fournissent des informations plus précises sur les dynamiques de diversification, la disparification et les lignées fantômes (Pérez & Pol, 2012 ; King *et al.*, 2017).

En conclusion, le débat concernant la méthode optimale pour reconstruire les phylogénies à partir de données fossiles reste ouvert. La parcimonie maximale et les approches fondées sur des modèles présentent chacune des avantages et des limites, et leur utilisation combinée fournit souvent des résultats complémentaires. Néanmoins, pour la reconstruction de phylogénies calibrées dans le temps, les méthodes fondées sur des modèles sont aujourd'hui indispensables.

4.3 Méthodes comparatives en phylogénie et dynamique de taux

Le développement de la reconstruction des arbres phylogénétiques s'est accompagné de l'émergence d'un large éventail de méthodes comparatives phylogénétiques (PCM ; O'Meara, 2012). Les PCM regroupent un ensemble d'approches statistiques conçues pour analyser les arbres phylogénétiques et, dans de nombreux cas, les données de traits associées entre espèces (Pennell & Harmon, 2013). Les premières PCM ont été développées principalement pour tenir compte de l'ascendance commune lors du test de corrélations entre traits, corrigeant ainsi la non-indépendance phylogénétique (Felsenstein, 1985 ; Grafen, 1989). Depuis, ces méthodes se sont considérablement développées et sont aujourd'hui couramment utilisées pour étudier un large éventail de phénomènes évolutifs.

Parmi les applications les plus importantes des PCM figurent les études portant sur les dynamiques de diversification au sein des clades en évolution, notamment la détection de variations des taux de spéciation et d'extinction (Alfaro *et al.*, 2009 ; Stadler, 2011 ; Morlon *et al.*, 2011 ; Etienne & Haegeman, 2012 ; Condamine *et al.*, 2013). Les taux de spéciation

et d'extinction constituent des paramètres fondamentaux en macro-évolution, car ils déterminent les patrons de diversification et permettent de mieux comprendre les mécanismes à l'origine des radiations évolutives (Ricklefs, 2007 ; Simões *et al.*, 2016). De nombreuses méthodes ont été développées pour explorer ces dynamiques, souvent dans un cadre bayésien permettant d'identifier les lignées présentant des changements significatifs de taux au cours du temps (Moore & Donoghue, 2009 ; Silvestro *et al.*, 2011).

L'une des approches les plus utilisées est *Bayesian Analysis for Macroevolutionary Mixtures* (BAMM ; Rabosky *et al.*, 2014), qui modélise l'hétérogénéité des taux de diversification à travers les arbres phylogénétiques à l'aide d'algorithmes de type Markov Chain Monte Carlo à saut réversible. BAMM est conçu pour détecter et quantifier les changements de taux, la dépendance à la diversité ainsi que les innovations clés au sein des clades (Rabosky, 2014). Initialement développé pour des arbres ultramétriques issus de phylogénies moléculaires, BAMM a ensuite été étendu aux arbres non ultramétriques incluant des fossiles (BAMM-fossil), permettant d'inférer des dynamiques de diversification à partir de phylogénies exclusivement fossiles (Mitchell *et al.*, 2019 ; Černý *et al.*, 2022). En plus de la diversification, BAMM a également été utilisé pour étudier l'évolution de traits continus, comme la taille corporelle chez les vertébrés (Cooney & Thomas, 2021). En revanche, il n'est pas adapté à l'analyse des caractères morphologiques discrets.

Au-delà de la diversification, de nombreuses PCM visent à reconstruire le tempo et le mode de l'évolution des traits morphologiques et écologiques (O'Meara *et al.*, 2006 ; Thomas *et al.*, 2006 ; Eastman *et al.*, 2011 ; Revell *et al.*, 2012 ; Beaulieu *et al.*, 2012). Tester des hypothèses d'évolution des traits sur une phylogénie nécessite la formulation explicite de modèles évolutifs (Revell, 2010). Ces modèles fournissent un cadre pour inférer les processus ayant généré les distributions observées des traits (Hansen & Martins, 1996 ; Mooers *et al.*, 1999). Dans ce contexte, la phylogénie est considérée comme une source d'information biologique plutôt que comme un simple facteur de nuisance (Freckleton *et al.*, 2011).

Le choix du modèle dépend de la nature des traits étudiés, notamment s'ils sont continus ou discrets. Parmi les modèles les plus utilisés pour les traits continus figurent le mouvement

brownien (BM), le modèle d'Ornstein–Uhlenbeck (OU) et le modèle d'« early burst » (EB). Le modèle de mouvement brownien constitue le premier modèle formel d'évolution des traits continus en phylogénie. Introduit par Cavalli-Sforza et Edwards (1963), il repose sur un processus aléatoire équivalent à une marche aléatoire, dans lequel les valeurs des traits varient de manière stochastique au cours du temps. Ce modèle est défini par deux paramètres principaux : la valeur ancestrale du trait et le taux d'évolution, qui détermine la variance des changements. Sous ce modèle, la variance des traits augmente linéairement avec le temps. Bien qu'il suppose un taux constant, des extensions permettent d'explorer des variations de taux entre lignées.

Le modèle d'Ornstein–Uhlenbeck constitue une alternative intégrant la sélection stabilisante autour d'un optimum adaptatif. Il combine une composante aléatoire avec une force déterministe ramenant les traits vers une valeur optimale. Contrairement au BM, il impose des limites à la variance des traits et est particulièrement adapté à l'étude des contraintes adaptatives.

Enfin, le modèle « early burst » (EB), introduit par Harmon *et al.* (2010), s'inspire directement de la théorie des radiations adaptatives. Il décrit une évolution rapide des traits au début de l'histoire d'un clade, suivie d'un ralentissement progressif à mesure que les niches écologiques se saturent. Ce modèle permet ainsi de tester des hypothèses liées aux radiations adaptatives et aux phases initiales d'évolution rapide.

5. L'histoire évolutive des chondrichthyens : nouvelles avancées

Cette thèse vise à étudier l'origine des chondrichthyens en proposant un nouveau cadre méthodologique destiné à limiter les biais associés à la reconstruction des caractères, à l'inférence des arbres phylogénétiques et à l'interprétation post-analytique des dynamiques évolutives. L'hypothèse centrale de ce travail est qu'une augmentation de l'objectivité dans la description des caractères et le développement de méthodes plus précises de comparaison entre taxons sont essentiels pour résoudre l'évolution précoce des chondrichthyens.

Dans cette optique, l'étude adopte une approche multi-méthodologique, intégrant plusieurs cadres analytiques afin d'explorer des signaux phylogénétiques convergents et robustes. Les comparaisons entre taxons fossiles reposent idéalement sur des caractères homologues, qui devraient constituer la base principale de l'inférence phylogénétique lorsque cela est possible. À l'inverse, les caractères homoplasiques reflètent souvent des convergences fonctionnelles plutôt qu'un héritage génétique partagé issu d'un ancêtre commun récent, et peuvent ainsi conduire à des interprétations évolutives erronées.

L'identification de nouveaux caractères morphologiques reflétant véritablement l'homologie demeure un défi, en particulier dans le registre fossile. Les caractères développementaux représentent, dans ce contexte, des candidats prometteurs, car ils sont plus susceptibles de capturer des aspects liés à l'expression génique et aux voies de développement. En conséquence, cette étude met l'accent sur l'identification et l'analyse de caractères développementaux dans les éléments les plus fréquemment conservés chez les chondrichthyens précoces, à savoir les dents, les écailles et les aiguillons de nageoires. Les patrons de développement ont été étudiés à travers l'analyse de séries ontogénétiques, de caractéristiques histologiques et de la morphologie externe.

Le cadre méthodologique est présenté en détail dans le premier chapitre de cette thèse. En particulier, les caractéristiques histologiques et ornementales ont été utilisées pour reconstruire le patron de développement de l'aiguillon de nageoire de *Wellerodus priscus*, un chondrichthyen du Givétien. Ces analyses enrichissent considérablement la base de données de caractères morphologiques et fournissent de nouveaux caractères informés par le développement, pertinents pour les comparaisons entre gnathostomes précoces. Bien que ce cadre soit détaillé pour les aiguillons de nageoires, les mêmes principes méthodologiques ont été appliqués aux dents et aux écailles, générant des caractères supplémentaires intégrés dans la supermatrice finale.

En résumé, l'analyse des écailles se concentre sur l'ultrastructure des odontodes (organisation, chevauchement, séries de croissance), tandis que l'analyse des dents met l'accent sur l'organisation de la couronne (nombre et proportions des cuspides). Ces

nouveaux caractères ont été combinés avec des caractères morphologiques publiés antérieurement afin de produire un jeu de données complet. La supermatrice obtenue, qui constitue le jeu de données principal de cette thèse, intègre 18 matrices publiées ainsi que les nouveaux caractères définis. Elle comprend majoritairement des caractères interprétés comme homologues.

Afin d'assurer clarté, cohérence et reproductibilité, l'ensemble du jeu de données a été standardisé selon le cadre méthodologique présenté dans l'introduction. Ce processus a impliqué la suppression des caractères redondants et homoplasiques, l'utilisation d'ontologies pour améliorer l'interprétabilité universelle des descriptions, ainsi que la reformulation des caractères selon une syntaxe standardisée basée sur des localisateurs et des qualificatifs de variables. En incluant tous les taxons connus jusqu'en 2022, de l'Ordovicien au Dévonien, appartenant au groupe total des chondrichthyens, ainsi que des "agnathes" et gnathostomes représentatifs, cette supermatrice constitue le jeu de données morphologiques le plus complet à ce jour, avec 320 taxons et 977 caractères.

Étant donné l'absence de consensus sur les meilleures méthodes de reconstruction phylogénétique, une approche multi-méthodologique a été adoptée. Des cadres d'analyse en parcimonie maximale et en inférence bayésienne ont été utilisés pour produire plusieurs arbres phylogénétiques, permettant d'évaluer la convergence des topologies. Des analyses calibrées et non calibrées dans le temps ont été réalisées, et la robustesse des résultats a été testée via différentes configurations de groupes externes et par partitionnement de la supermatrice selon la complétude des données. Ces analyses révèlent un signal phylogénétique cohérent, indiquant des affinités robustes entre les thélodontes et le groupe total des chondrichthyens. L'étude propose également des calibrations affinées pour les principaux nœuds des gnathostomes et des « agnathes », fournissant les estimations de divergence les plus probables à ce jour. Les résultats confirment toutefois certaines incertitudes persistantes, notamment concernant la monophylie des « placodermes » et les relations internes ainsi que l'origine des chondrichthyens.

Afin d'inscrire l'origine des chondrichthyens dans un cadre macro-évolutif plus large, les résultats phylogénétiques ont été complétés par des analyses de diversification, de taux évolutifs et de disparité morphologique. Les dynamiques de diversification ont été étudiées à l'aide de BAMM, permettant de détecter des changements majeurs de taux. Ces analyses mettent en évidence une augmentation marquée du taux de diversification le long de la lignée des chondrichthyens basaux. Les analyses des taux évolutifs indiquent également des vitesses exceptionnellement élevées d'évolution morphologique dans cette même lignée, suggérant une forte corrélation entre diversification et évolution phénotypique.

Enfin, les analyses de disparité morphologique montrent que les chondrichthyens ont connu un événement majeur de disparification à la fin du Dévonien, postérieur aux pics de diversification et de taux évolutifs, apportant un éclairage crucial sur la nature de leur radiation évolutive. Dans son ensemble, cette thèse constitue une avancée significative dans la compréhension de l'évolution des chondrichthyens et des relations entre gnathostomes précoces. En réévaluant la phylogénie des gnathostomes et en apportant de nouveaux arguments en faveur des affinités entre thélodontes et chondrichthyens, ce travail contribue à résoudre des débats anciens sur l'origine des vertébrés à mâchoires. Le cadre méthodologique adopté est volontairement exploratoire et intégratif, mobilisant un large éventail d'outils analytiques afin de renforcer et de valider les résultats. Cette thèse documente en détail les processus, analyses et interprétations qui sous-tendent ces conclusions.

CHAPITRE 1

ONTOGENIE DES AIGUILLONS DE NAGEOIRES CHEZ LE REQUIN *WELLERODUS PRISCUS* DU DEVONIEN : PERSPECTIVES PALEO-EVO- DEVO DU DEVELOPPEMENT DU SQUELETTE DERMIQUE CHEZ LES CHONDRICHTHYENS BASAUX

1.1 RESUME EN FRANÇAIS DU PREMIER ARTICLE

Contexte

Les poissons cartilagineux (chondrichthyens) du Dévonien (419 à 359 millions d'années, Ma) sont principalement connus à partir d'éléments dermiques isolés fossilisés, tels que les dents, les écailles et les aiguillons de nageoires. Bien que des études antérieures aient décrit la morphologie et l'histologie de ces structures, leurs modalités de développement demeurent encore mal comprises. Or, les patrons de développement peuvent fournir des informations phylogénétiques précieuses et offrir de nouvelles perspectives pour les comparaisons évolutives. Dans cette étude, nous proposons d'explorer les patrons de développement des aiguillons de nageoires en intégrant des analyses de l'ornementation, de la morphologie et de l'histologie.

Résultats

Nous présentons la première description des patrons de développement des aiguillons de nageoires du requin du Dévonien moyen *Wellerodus priscus*, provenant du Lagerstätte de Cairo Quarry, dans l'État de New York (États-Unis). Sur la base des motifs d'ornementation et des caractéristiques paléohistologiques (coupes minces et micro-tomographie aux rayons X), nous identifions deux axes de croissance distincts dans les aiguillons pectorales et dorsales de *W. priscus* : un axe longitudinal (dans le sens de la longueur) et un axe transversal (dans le sens de la largeur), chacun étant associé à des zones spécifiques de production

tissulaire. Les patrons de développement des aiguillons observés chez *Wellerodus* sont comparés à ceux d'autres chondrichthyens paléozoïques et de leurs plus proches apparentés, les « acanthodiens » (requins aiguillonux éteints).

Conclusions

La comparaison taxonomique entre chondrichthyens et « acanthodiens » montre que les caractères structuraux identifiés permettent des inférences robustes concernant les modalités de développement. Plus largement, notre cadre d'analyse apporte une nouvelle ligne de preuve pour comprendre l'évolution du développement des aiguillons de nageoires, en montrant que, chez les chondrichthyens primitifs, la croissance des aiguillons de nageoires s'effectue selon deux axes distincts. Cette approche améliore notre compréhension des similarités développementales entre les chondrichthyens anciens et les chondrichthyens plus dérivés du Carbonifère, du Permien, voire les formes actuelles, et met en évidence le potentiel des patrons de développement des aiguillons de nageoires comme outil en recherche évolutive et phylogénétique. Les critères histo-morphologiques utilisés pour décrire ces patrons de développement fournissent ainsi des caractères pertinents pour les analyses phylogénétiques.

Cet article intitulé “*Fin spine ontogeny in the devonian shark Wellerodus priscus: paleo-evo-devo insights into early chondrichthyan dermal skeleton development*” a été soumis dans la revue “*Paleo-Evo-Devo: A Dialogue Between the Past and Present*” en janvier 2026. En tant que premier auteur, j’ai étudié le matériel, réalisé les analyses, interprété les résultats, réalisé les figures ainsi qu’écrit le manuscrit et réalisé les modifications post-corrections. Les autres auteurs, Daniel Potvin Leduc, Nathaniel Bertand Maltais et Richard Cloutier ont respectivement réalisé les premières descriptions, réalisés les coupes histologiques et supervisé le projet. Le projet a été présenté lors d’une présentation orale durant le « *International Symposium on Early and Lower Vertebrate* » à Valencia en juin 2022.

1.2 FIN SPINE ONTOGENY IN THE DEVONIAN SHARK *WELLERODUS PRISCUS*: PALEO-EVO-DEVO INSIGHTS INTO EARLY CHONDRICHTHYAN DERMAL SKELETON DEVELOPMENT

Abstract

Background Cartilaginous fishes (chondrichthyans) from the Devonian period (419 to 359 million years, Ma) are primarily known from fossilized isolated dermal elements such as teeth, scales, and fin spines. Although previous studies have described the morphology and the histology of these elements, their developmental patterns remain poorly understood. In this study, we propose to explore developmental patterns of fin spines by integrating analyses of ornamentation, morphology, and histology.

Results We present the first description of the developmental patterns for the fin spines of the Middle Devonian shark *Wellerodus priscus*, from the Cairo Quarry Lagerstätte in New York State, USA. Based on the ornamentation pattern and paleohistological (thin sections and micro-computed tomography) characteristics, we identify two distinct growth axes in the pectoral and dorsal fin spines of *W. priscus*: a longitudinal (length wise) axis and a transverse (width wise) axis, each associated with specific zones of tissue production. Spine developmental patterns observed in *Wellerodus* are compared among Paleozoic chondrichthyans and their closest relatives, the “acanthodians” (extinct spiny sharks).

Conclusions Our framework offers a new line of evidence for understanding the evolution of fin spine modular development by showing that fin spines in early chondrichthyans grow following two axes. It enhances our comprehension of developmental similarities between early chondrichthyans and more derived Carboniferous, Permian, and even extant chondrichthyans. The identified structural features enable well-supported inferences about developmental modularity. The histo-morphological criteria used to describe this developmental pattern provide characters potentially suitable for phylogenetic analyses.

Introduction

Our understanding of the morphology of Silurian and Early Devonian chondrichthyans has improved significantly in recent years (Long *et al.*, 2015; Coates *et al.*, 2018; Andreev *et al.*, 2020). However, knowledge of their developmental and growth patterns remains limited primarily owing to the fragmentary nature of their fossil record. Most early chondrichthyan fossils consist of isolated elements such as teeth, scales, and fin spines, while their largely cartilaginous skeletons are rarely preserved owing to the more delicate nature of the cartilage (Schnetzer *et al.*, 2024). Articulated specimens are exceptionally rare and typically incomplete, such as *Doliodus latispinosus* (Miller *et al.*, 2003) from the Lower Devonian (Emsian; ca. 409 Ma).

Despite these limitations, isolated dermal structures provide valuable developmental information (Cloutier, 2010; Cui *et al.*, 2021). Features such as the morphology (size and shape), ornamentation, and histology of fin spines—specifically tissue types and their organization—offer insights into growth patterns, even in the absence of an ontogenetic series (Jerve *et al.*, 2017; Maisey, 1979; Beck *et al.*, 2016).

Fin spines of several early chondrichthyans exhibit exceptional preservation, including Silurian sinacanthids from China (Liu *et al.*, 2024), the Emsian *Doliodus latispinosus* from New Brunswick, Canada (Miller *et al.*, 2003; Burrow *et al.*, 2017), and the Givetian *Antarctilamna prisca* from Antarctica (Young, 1982). Yet, none of these species have been studied in the context of fin spine development, a topic that has been explored primarily in “acanthodians” (Botella *et al.*, 2012; Jerve *et al.*, 2017) and modern taxa such as chimaerids (Jerve *et al.*, 2014) and heterodontiform sharks (Tovar-Avila *et al.*, 2008).

Understanding the developmental and growth patterns of fin spines is used for aging extinct and extant sharks (Beck *et al.*, 2016; Goldman *et al.*, 2012; Soler-Gijon 2004; Irvine *et al.*, 2006; Hedeholm *et al.*, 2021) or in reconstruction of paleoenvironments (Luccisano *et al.*, 2023). In addition, it could provide a foundation for phylogenetic comparisons, which is

crucial in clarifying interrelationships between chondrichthyans and their closest relatives, the “acanthodians”, with whom they share the presence of fin spine (Chevrinais *et al.*, 2017; Brazeau, 2009; Miller *et al.*, 2003).

The developmental patterns of fin spines in early chondrichthyans and most “acanthodians” remain poorly characterized, in contrast to our better understanding of spine growth in Carboniferous (Soler-Gijon, 1999) and Permian sharks (Beck *et al.*, 2016). To fill this gap for Devonian taxa, we conducted an integrated morphological and histological analysis of fin spine development, similar to prior studies on xenacanth sharks but with expanded analyses on the ornamentation pattern. Herein, this approach is applied to *Wellerodus priscus*, an early Givetian shark from Cairo, New York State, USA, known from articulated specimens and isolated dermal elements including scales, teeth, and fin spines (Potvin-Leduc *et al.*, 2015).

Material and methods

The material of *Wellerodus priscus* comes from the Middle Devonian (Givetian) deposit of the Cairo quarry Lagerstätte (Plattekill Formation) in New York State, USA (Potvin-Leduc *et al.*, 2015). The material was prepared mechanically in the Laboratory of Paleontology and Evolutionary Biology at the University du Québec à Rimouski (UQAR), eastern Canada. All specimens are curated in the New York State Museum (NYSM), Albany, New York State, USA.

A Leica MZ 16-A was used to document the external morphology. Fin spine ornamentation was analyzed using a JEOL JSM-6460LV SEM, especially on the apex of the spine to obtain more details of the denticles. One complete pectoral spine was used to prepare ten paleohistological sections from the distal to the proximal part based on the methodology used by Chevrinais *et al.*, 2017. The tomography analyses were carried out with a SKYSCAN 1173 X-Ray Microtomography (Exposure time 5000 ms, voltage 130 kv, Source current 61

μ A, Brass filter 0.25 mm, 0.2 degree rotation step) at UQAR on two pectoral and one dorsal fin spines. The resulting images were assembled in NRecon and visualized with Drishti-2.6.5.

Results

Fin spines, scale patches and teeth were found associated with disarticulated specimens present on multiple mudstone blocs (NYSM 19053 and 19052) extracted from the same stratigraphic layer of the Plattekill Formation (Potvin-Leduc *et al.*, 2015). This association of various dermal components correspond to a single species, *Wellerodus priscus*. Teeth and scales were unambiguously identified as *W. priscus* based on the striated bicuspid teeth and the polyodontode appositional ctenacanth-like scale ultrastructure described by Potvin-Leduc *et al.*, 2015.

Pectoral fin spine morphology

The pectoral fin spine of specimen NYSM 19057 reaches a maximum length of 73 mm and a maximum basal width of 16 mm, tapering distally toward the apex. The insertion zone is 2 mm long, representing less than 3% of the total spine length. The outer surface of the insertion zone bears parallel longitudinal striations (see annex 1). An open, concave pulp cavity is present on the proximal portion of the trailing (posterior) edge, extending for less than half the total spine length (Figure 12a, ventral view details in annex 1).

Pectoral fin spine NYSM 19057 is curved along its distal half. The leading (anterior) edge is transversely rounded (Figures 12a, 13). Along the trailing edge, two rows of thorn-like denticles (see annex 1) extend from the apex to the mid-length of the spine. These rows are restricted to the curved portion of the spine. Despite lateral taphonomic compression, pectoral fin spine NYSM 19057 is asymmetrical (see annex 1).

The ornamentation of specimen NYSM 19051 consists of sub-parallel tuberculated ridges diverging from the leading edge (Figure 12e, 12f, 12g, 12h, 12i, 12j). Up to 14 ridges occur on each side of the spine proximally. The gap between ridges does not exceed the width of the tubercles and is ca. 1 mm deep. Toward the apex, ridges become smoother and individual tubercles are less distinct, whereas proximally the tubercle shapes are clearer. Each ridge bears 8 ± 1 tubercles per centimeter in specimens NYSM 19057 and NYSM 19051. The tubercles are diamond-shaped (Figure 12g) with concave edges, and each tubercle contacts the adjacent tubercle along the ridge. The apex of the tubercles is sharp, similar to an arrowhead, and no surface streaks are present. Tubercle size decreases distally to approximately one tier of proximal dimensions.

Dorsal fin spine morphology

Wellerodus priscus has one anterior dorsal fin spine that is shorter than the pectoral fin spine in specimen NYSM 19057. The dorsal fin spine of specimen NYSM 19051-2 reaches a maximum length of 65 mm and a maximum basal width of 9.5 mm, tapering distally to form an elongated triangular shape (see annex 1). The insertion zone is similar to that of the pectoral fin spines: it is 2 mm long with parallel longitudinal striations on the surface. An open, concave pulp cavity is present on the proximal portion of the trailing edge, extending for less than half the spine length. The complete dorsal fin spine NYSM 19051-2 is straight, with an angular leading edge and a trailing edge lacking denticule rows (see annex 1). Dorsal fin spines are symmetrical.

The ornamentation of dorsal fin spine consists of sub-parallel tuberculated ridges diverging from the leading edge. In the longest specimen (NYSM 19051-2), up to 11 ridges occur on each side of the spine (see annex 1). The gaps between ridges do not exceed the width of the tubercles and are less than 1 mm deep. Toward the apex (approximately the distal quarter), the ridges become smoother individual tubercles are no longer clearly distinguishable.

Each ridge bears 13 ± 1 tubercles per centimetre in the longest dorsal fin spine (see annex 1). The tubercles are conical with circular bases, and their surfaces bear fine longitudinally striations. Dorsal spine tubercles are clearly demarcated and do not fuse into continuous ridges. Some tubercles along the leading edge possess a lateral notch. The size of the tubercles decreases distally, reaching approximately one tier of their proximal dimensions.

Histology

Based on the palaeohistological sections and the micro-CT-scans, the tissue organization within the pectoral and dorsal fin spines of *Wellerodus priscus* varies between the proximal and distal regions.

The proximal part consists almost entirely of trabecular dentine (osteodentine) and is capped by a relatively thin layer of hypermineralized tissue covering the tops of the tubercles along the leading edge (Figure 12a, 12b). The trabecular dentine infill indicates substantial vascularization, at least within the first three proximal tiers of the spine. This trabecular dentine surrounds an open concave pulp cavity (Figure 12a, 12b) that extends up to the mid-length of the spine. Due to the state of preservation of the spine, dentine tubules are difficult to observe (see annex 1). No other tissue types were observed in the proximal section of the spine.

The distal part of the spine is more diversified histologically than the proximal part. It contains a smaller, central single pulp cavity surrounded by a circular layer of trabecular dentine (Figure 12c), which is itself encased by a layer of atrabecular dentine (Figure 12c). The outermost layer along the leading edge consists of more vascularized trabecular dentine layer compared to the internal layers, and this external layer extends into the tubercles (Figure 12d). A layer of hypermineralized tissue is also present (Figure 12d) thicker over the tubercles than in the proximal section, and restricted to the tubercles along the leading edge.

The distal portion of the spines shows a concentric organization of dentine layers, reflecting the layered deposition of tissue during growth.

Growth pattern

The growth of the spines occurs along two axes: longitudinal (lengthwise) and transverse (widthwise). Longitudinal growth primarily takes place at the proximal part, which is the most vascularized region of the spine (Figure 12a). Tissue production in this area includes the formation of tubercles and ensures the continuity of the tuberculated ridges.

Transverse (width) expansion is most pronounced in the proximal part but is not limited to it; the spine also expands in width toward the distal end. This expansion originates from the leading edge, where multiple ridge lines diverge. This expansion originates from the leading edge, where multiple ridge lines diverge. A clear growth pattern emerges along these divergence lines: a single ridge splits into two ridges at the leading edge (Figure 13). Of the two newly formed ridges, only one will diverge again, and this process continues in an alternating pattern: if the previous divergence occurred on the left side, the next occurs on the right side, and vice versa (Figure 13).

In total, up to eight divergences can be observed along the leading edge of a single spine. In specimen NYSM 19051, there are typically 4 to 6 tubercles between successive divergences. In specimen NYSM 19057, the number of tubercles varies between 4 and 6 along these intervals, with the observed sequence from proximal to distal being 6–6–5–4–6.

Discussion

The developmental pattern of the pectoral and dorsal fin spines of *Wellerodus priscus* exhibits a dual-axis growth pattern. Longitudinal growth occurs primarily at the proximal base near the insertion zone, while transverse growth is confined to the leading edge, as

indicated by divergences in the tuberculated ridges. Both growth axes are supported by the presence of highly vascularized tissues in their respective production areas. Fused tubercles at both the proximal and distal ends suggest that width expansion continues throughout the organism's lifetime, even after the formation of the proximal tubercles. Furthermore, width growth decreased distally, although it remained active, as evidenced by vascularized tissues localized to the tubercles at the leading edge near the apex.

A key aspect of this developmental pattern is the variation in axial growth rates, inferred from the number of tubercles between successive divergence zones. In the proximal production area, tubercles form regularly, with one tubercle emerging per ridge simultaneously. Divergence zones at the leading edge are likely to appear at regular intervals, assuming continuous growth. However, for specimen NYSM 19057, the number of tubercles between divergences varies, suggesting a slowdown in longitudinal growth, while width expansion continues at a constant rate. Alternatively, this could indicate an acceleration in longitudinal growth rates, as represented by the two series of six tubercles.

Even if transverse growth alters tubercle sequences over lifetime (e.g., through the splitting of tubercles rows), the proportion of successive tubercles would remain consistent, supporting the notion of non-constant growth rates along the two axes. If similar proportions of successive tubercles are found within a single individual in dorsal and pectoral spines, one can reconstruct spine growth curves, and potentially reveal autapomorphic spine characteristics, such as the ratio of successive tubercles, which may indicate spine maturity. This comparison could also help associating disarticulated spines with the same individual. Conversely, if the sequences differ among spines of the same individual, it could indicate distinct axial growth rates for each spine. Unfortunately, no sufficiently articulated specimens of *W. priscus* have been found to validate this hypothesis.

Among the rare basal shark species known from fin spines, some species exhibit similar ornamentation patterns. Among basal sharks, *W. priscus* shares developmental similarities with *Antarctilamna prisca* (Young, 1982) and certain fossil sharks from Bolivia (Ritcher *et al.*, 2017). The organization of the ridges, particularly in the divergence zones at

the leading edge, suggests conserved developmental features, although tubercle shape and arrangement differ among taxa. This similarity may strengthen the relationship among these species. By contrast, *Doliodus latispinosus*, as well as Permian shark such as *Sphenacanthus ignis* and *Bythiacanthus lopesi* (Figueroa & Gallo, 2017) display divergence zones in the ornamental ridges that indicate width expansion; however, these zones are confined to the base of the spine rather than the leading edge (Burrow *et al.*, 2017).

Silurian sinacanthid sharks, particularly *Sinacanthus*, display a different pattern: ridge divergences occur along the entire spine rather than being localized (Liu *et al.*, 2024). However, no evidence suggests that width growth in *Sinacanthus* species continues over time at the distal end because diverging tubercles are absent. These comparisons suggest a close developmental pattern between *W. priscus* and *A. prisca*, with more divergent growth patterns observed in *D. latispinosus* and sinacanthids.

Interestingly, *W. priscus* fin spine development resembles that of stem-chondrichthyans such as gyracanthid “acanthodians” (Gess & Burrow, 2023, Burrow *et al.*, 2008), which show similar ridge orientation and divergence zones along the leading edge. However, gyracanthids exhibit more extensive divergence areas on the leading edge. These similar developmental pattern in fin spine support a potential phylogenetic connection between early chondrichthyans and “acanthodians,” providing an additional support for their phylogenetic affinity (Chevrinais *et al.*, 2017). In order to test their resemblance, further comparative histological analyses will validate the presence of similar pattern of tissue organization.

Histologically, *W. priscus* shares features with xenacanth sharks, including the presence of trabecular dentine (Beck *et al.*, 2016, Soler-Gijon, 2004) but differs in growth pattern. Xenacanth spines are round in cross-section, have smooth external ornamentation, and exhibit prominent concentric growth lines around a larger central pulp cavity (Beck *et al.*, 2016, Soler-Gijon, 2004), features not observed in *W. priscus*. The concentric growth lines are not visible in *W. priscus* but highly likely considering the organisation of dentine

layer in the distal portion of the spine; as mentioned by Potvin-Leduc *et al.*, (2017) diagenetic transformation of the bony tissues from Cairo might have altered fine histological resolution.

W. priscus and some extant sharks such as heterodontiforms (Maisey, 1979; Tovar-Avila *et al.*, 2008) show similarities in internal spine organization, including a transitional layer or a discontinuity marked by less vascularized tissue, such as the atrabecular dentine layer observed in the distal portion of the spine of *W. priscus*. Nevertheless, comparisons with extant sharks remain limited due to the poorer preservation of fossil material compared to the fin spines available from extant taxa.

Potvin-Leduc *et al.*, (2017) suggested that some *W. priscus* material from the Cairo quarry might represent juvenile specimens. Notably, the histological structure of *W. priscus* spines resembles that of *Antarctilamna prisca*, except for the presence of hypermineralized layers (which occur only at tubercle tips in *W. priscus*), and a lamellar dentine layer surrounding the pulp cavity in *A. prisca* (Young, 1982). This difference could indicate that lamellar dentine forms later in development and may serve as a marker of spine maturity in adult specimens.

The characterization of the developmental pattern of *Wellerodus priscus* fin spines provides crucial insights into both growth dynamics and comparative anatomy. The dual-axis model supported by localized vascularized tissue production, highlights a complex and potentially variable growth system that likely reflects ontogenetic influences. Morphological and histological similarities with *A. prisca* (Young, 1982) suggest shared developmental patterns among certain early chondrichthyans, whereas contrasts with *Doliodus latispinosus*, *Sphenacanthus ignis*, and *Bythiacanthus lopesi* indicate distinct evolutionary pathways. Comparisons with Silurian sinacanthids and xenacanth sharks show greater divergence, while similarities with stem-chondrichthyans, such as gyracanthids, further support developmental conservation among basal chondrichthyans.

At the histological level, comparisons with Carboniferous, Permian, and extant chondrichthyans reveal common features, such as trabecular dentine, but differences in

growth modes—such as the absence of concentric growth lines in *W. priscus* —highlight distinct developmental strategies. The consistent organization of tubercles across taxa underscores the potential value of dermal structures for phylogenetic inference. With broader studies on additional early chondrichthyan spines, developmental patterns could refine assessments of morphological similarity (and homology) and consequently improve phylogenetic reconstructions, ultimately revealing a stronger signal in fin spines, which have traditionally been considered of limited taxonomic utility. Such approaches could reveal a stronger phylogenetic signal in fin spines, traditionally considered of limited taxonomic utility (Gess & Coates, 2015), and ultimately contribute to a more robust understanding of early chondrichthyan relationships.

Finally, the presence of two distinct growth axes in the fin spines of *Wellerodus priscus* — longitudinal elongation and transverse widening — can be interpreted as reflecting a modular developmental organization. Tissue production in the highly vascularized basal region appears to drive lengthwise elongation, while separate activity along the leading-edge ridges promotes width expansion. Such compartmentalized growth mirrors the modular organization observed in extant chondrichthyans, where different tissue zones (e.g., trabecular vs lamellar dentine, or cap vs body zones in tessellated cartilage) can grow at different rates or along independent axes (Jerve *et al.*, 2014). This developmental modularity provides a mechanistic explanation for the semi-independent control of spine morphology in Devonian sharks, linking histological processes to the macroscopic patterns of fin spine growth and ornamentation, and supporting a broader evo-devo perspective on early chondrichthyan skeletal evolution.

CHAPITRE 2

LES THELODONTES REDEFINISSENT L'ORIGINE DES CHONDRICHTHYENS ET L'EVOLUTION DES VERTEBRES BASAUX A MACHOIRES

2.1 RESUME EN FRANÇAIS DU DEUXIEME ARTICLE

Les vertébrés à mâchoires, ou gnathostomes, sont aujourd'hui représentés par deux lignées vivantes : les Ostéichthyens (poissons à nageoires rayonnées, dipneustes, coelacanthes et tétrapodes) et les Chondrichthyens (chimères, requins et raies). Deux grands groupes fossiles appartiennent également aux gnathostomes : les « placodermes », ou poissons cuirassés, et les « acanthodiens », souvent désignés comme des « requins aiguillonux ». Les relations phylogénétiques entre ces groupes vivants et fossiles, ainsi qu'avec les vertébrés sans mâchoires, ou « agnathes », font l'objet de débats depuis la fin du XIX^e siècle et aucun consensus n'a encore été atteint.

Les thélodontes, un groupe traditionnellement considéré comme composé de vertébrés sans mâchoires mais partageant plusieurs caractères avec les requins, ont notamment été peu étudiés. La plupart des cadres analytiques les ont placés loin des chondrichthyens, bien que certains auteurs les aient depuis longtemps considérés comme étroitement apparentés à ces derniers.

Nous avons construit un jeu de données morphologiques exhaustif comprenant 84 espèces de vertébrés à mâchoires et sans mâchoires, codées pour 792 caractères morphologiques et histologiques définis ontologiquement. Nous avons appliqué plusieurs approches phylogénétiques afin d'apporter un support concernant la relation entre les thélodontes et les chondrichthyens. Cette relation est systématiquement retrouvée dans l'ensemble des analyses

et fournit à ce jour la preuve la plus solide que l'origine évolutive des chondrichthyens est étroitement liée à l'histoire évolutive des thélodontes.

Cet article intitulé “*Thelodonts reshape the origin of sharks and jawed vertebrate evolution*” va être soumis dans la revue Nature au courant de l'année 2026. En tant que premier auteur, j'ai assemblé les données pour la matrice, codé la matrice, effectué les analyses, produits les figures ainsi que réalisé l'écriture du manuscrit. Michael Lee, le second auteur, a donné son aide pour la réalisation des analyses préliminaires. Richard Cloutier a supervisé le projet ainsi que fournis les corrections nécessaires pour la publication. Les résultats ont été présentés lors du « *International Symposium on Early and Lower Vertebrate* » à Rimouski en juin 2024 et à Berrechid au Maroc en 2026.

2.2 THELODONTS RESHAPE CHONDRICHTHYAN ORIGIN AND EARLY JAWED VERTEBRATE EVOLUTION

Abstract

Early Jawed vertebrates, or gnathostomes, are today represented by two living lineages: osteichthyans (ray-finned fishes, lungfishes, coelacanths, and tetrapods) and chondrichthyans (chimaeras, sharks, and rays). Two major fossil groups also belong to gnathostomes: “placoderms,” or armored fishes, and “acanthodians,” often referred to as “spiny sharks.” The phylogenetic relationships among these living and fossil groups, as well as with jawless vertebrates (“agnathans”), have been debated since the late nineteenth century, and no consensus has yet been reached.

Thelodonts, a group traditionally considered to consist of jawless vertebrates but sharing several features with sharks, have been comparatively understudied. Most analytical frameworks have placed them far from chondrichthyans, although some authors have long suggested a close relationship between the two groups.

We constructed a comprehensive morphological dataset comprising 84 species of jawed and jawless vertebrates, coded for 792 morphologically and histologically defined characters using an ontological framework. Multiple phylogenetic approaches were applied to assess the relationship between thelodonts and chondrichthyans. This relationship is consistently recovered across all analyses and currently provides the strongest evidence that the evolutionary origin of chondrichthyans is closely linked to the evolutionary history of thelodonts.

Introduction

Early vertebrate phylogeny and the transition from “agnathans” to gnathostomes have been investigated since the nineteenth century (Gegenbaur *et al.*, 1878; Balfour, 1881; de

Beer, 1937; Reif, 1982), with renewed attention in the early 2000s (Shubin, 2002; Kuratani, 2004; Shigetani *et al.*, 2005; Brazeau, 2009; Davis *et al.*, 2012; Brazeau & Friedman, 2014, 2015; Giles *et al.*, 2015; King *et al.*, 2017; Kuratani, 2021; Miyashita *et al.*, 2025). Gnathostomes are recognized as a monophyletic group comprising two extant lineages—Osteichthyes (bony fishes) and Chondrichthyes (cartilaginous fishes)—with an extinct assemblage, the “acanthodians” considered as stem-chondrichthyans (Brazeau & Friedman, 2015; Chevrinaiis *et al.*, 2017; Davis *et al.*, 2012; King *et al.*, 2017; Zhu *et al.*, 2021). Stem gnathostomes include “placoderms”, the extinct armored fishes (Goujet & Young, 2004; Brazeau, 2009; Young, 2010; King *et al.*, 2017). However, the origin and evolution of these major clades remain debated.

Two groups are pivotal to debates over early gnathostome evolution: the “placoderms” and “acanthodians”. The phylogenetic nature of “placoderms” has long time be regarded as monophyletic (Denison, 1978; Young, 1986). It has been contentious since the late twentieth century (Burrow & Turner, 1999; Goujet & Young, 2004; King *et al.*, 2017). In fact, since the 2000’s, they are interpreted as a paraphyletic assemblage (Friedman, 2007; Brazeau, 2009) but “placoderms” have occasionally been recovered as monophyletic (King *et al.*, 2017), though most recent analyses still resolve them as paraphyletic (Zhu *et al.*, 2021; Brazeau *et al.*, 2023). “Acanthodians” are now broadly accepted as a paraphyletic group within stem-chondrichthyans (Brazeau & Friedman, 2015; Rücklin *et al.*, 2021), although they share some features with osteichthyans (Brazeau & Friedman, 2015; Brazeau, 2009) and were once considered possible sister to both chondrichthyans and osteichthyans (Davis *et al.*, 2012). Today, “acanthodians” are considered as stem-chondrichthyans within the total-group chondrichthyans (Maisey *et al.*, 2017; Chevrinaiis *et al.*, 2017).

While overall interrelationships among crown gnathostomes are comparatively well resolved (Brazeau & Friedman, 2015; Brownstein, 2023; King *et al.*, 2017; Qiao *et al.*, 2016), identifying the closest “agnathan” relatives has proven more difficulties. The Osteostraci, jawless vertebrates with a headshield, have long been proposed as the sister group to gnathostomes (Forey & Janvier, 1993; Gagnier, 1993; Forey, 1995; Donoghue *et al.*, 2000;

Donoghue & Smith, 2001) and remain widely regarded as such (Shan *et al.*, 2020; Giammona, 2021; Miyashita *et al.*, 2025). On the other hand, the Galeaspids, another taxon of jawless vertebrates, endemic to China, have emerged as strong candidates, as the sister group to the total-group gnathostomes alongside Osteostraci (Gai & Zhu, 2012; Gai *et al.*, 2022), echoing earlier hypotheses (Janvier *et al.*, 1993; Min, 1992; Zhikun *et al.*, 2005; Janvier, 2008).

Despite extensive work on the “agnathan”–gnathostome transition, the Thelodonti has been largely absent from broader analyses. Most studies of early vertebrate phylogeny have excluded thelodonts (Qiao *et al.*, 2016; King *et al.*, 2017; Lu *et al.*, 2016) or treated them in isolation (Wilson & Märss, 2004; Donoghue & Smith, 2001), with only a few studies incorporating them directly (Donoghue & Keating, 2014; Qu *et al.*, 2013; Janvier, 2008; Cui *et al.*, 2019). Thelodonts, is ranging from the Late Ordovician to the Late Devonian (Sansom *et al.*, 1996; Märss & Karatajute-Talimaa, 2002; Märss *et al.*, 2007; Turner & Hairapetian, 2005; Hairapetian *et al.*, 2015). This group comprise ~147 recognized taxa (Turner, 1982; Märss *et al.*, 2007; Ferrón & Botella, 2017). Mostly known from isolated scales, about 29 species are represented by articulated material (Turner, 1982; Märss *et al.*, 2007; Ferrón & Botella, 2017).

Although usually placed crown-ward to the Osteostraci and the Galeaspids (Qu *et al.*, 2013; Janvier, 2008; Cui *et al.*, 2019), thelodonts share several gnathostome-like features, including a stomach chamber (Wilson & Märss, 2004), teeth and possible tooth whorls (de Brugghe & Janvier, 1993; Donoghue & Rücklin, 2016), non-imbricated shark-like scales (Turner, 1973), and paired pectoral appendages (Ferrón & Botella, 2017). Early suggestions that they were closely related to gnathostomes (Janvier, 1996; Turner, 1997) were based solely on scale morphology, predating more detailed analyses of denticles. Their mosaic of “agnathan” and chondrichthyan-like traits has since led to uncertainties concerning their phylogenetic nature.

Another enigmatic group, the Mongolepidida, further complicates chondrichthyan origins. First described in the late twentieth century (Karatajute-Talimaa, 1998; Sansom *et*

al., 1999), mongolepids have recently attracted renewed interest (Andreev *et al.*, 2016; Andreev *et al.*, 2020; Žigaitė *et al.*, 2011). Known only from scales, their phylogenetic position has been inferred exclusively from scale morphology and never tested within a broad gnathostome–agnathan framework (Andreev *et al.*, 2016). Their scale ultrastructure resembles that of early chondrichthyans, particularly the presence of polyodontode appositional growth (Andreev *et al.*, 2016). Stratigraphically, they occur from the Late Ordovician to the Late Silurian (Andreev *et al.*, 2017), leaving a ~20 Myr gap between the last mongolepids and stem chondrichthyans (excluding sinacanthids), and nearly 60 Myr with crown-chondrichthyans (Frey *et al.*, 2019; Coates *et al.*, 2017).

Here, we reassess early vertebrate phylogeny by incorporating both the Thelodonti and the mongolepids into the most comprehensive morphological dataset. We combine parsimony and Bayesian (tip-dated and undated) methods, standardize morphological characters using ontology-based vocabularies, we introduce new developmental characters from commonly preserved structures such as scales and fin spines. Our analyses recover a consistent and robust affinity between thelodonts and chondrichthyans, supporting a close relationship between these groups and positioning thelodonts as the nearest “agnathans” to gnathostomes and total-group chondrichthyans. Furthermore, mongolepids show affinities with chondrichthyans, but their signal is less stable, appearing morphologically close yet phylogenetically distant when tip-dating calibrations are applied.

Material & methods

Matrices

We compiled 320 taxa and 977 morphological characters into a supermatrix (Matrix 1). This supermatrix results from the integration of 18 previously published matrices used to investigate the interrelationships among gnathostomes and “agnathans”. The published matrices were selected to ensure comprehensive representation of the morphological, histological and anatomical features of the taxa relevant to our study. We incorporated five

matrices specifically focused on chondrichthyans (Grogan and Lund 2000, 2004, 2008, 2009; Grogan *et al.*, 2012). In addition, we included a matrix dedicated exclusively to thelodonts (Wilson & Märss, 2009). The remaining matrices are covering the gnathostomes, galeaspids, and osteostracans (Brazeau, 2009; Burrow & Turner, 2010; Chevrinais *et al.*, 2017; Coates *et al.*, 2017; Davis *et al.*, 2012; Dupret *et al.*, 2014; Giles *et al.*, 2015; King *et al.*, 2017; Long *et al.*, 2014; Lu *et al.*, 2016; Qiao *et al.*, 2016; Zhu *et al.*, 2009, 2013).

We reworked the initial supermatrix to generate two additional matrices. The matrix 2 includes 259 taxa and 792 morphological characters and retains only taxa with at least 2% of character completeness, as well as morphological characters that change fewer than 20 times across the simulated trees derived from Matrix 1. The matrix 3 comprises the same set of 792 morphological characters but includes only taxa with a minimum of 20% of completeness, resulting in a reduced dataset of 84 taxa.

For Matrix 3, we made exceptions for thelodonts and mongolepids, for which no species reaches 20% of completeness. For thelodonts, we selected the two most complete species, *Pezopallichthys ritchei* and *Furcacauda fredolhmae*. For mongolepids, we retained the five most complete species: *Tezakia hardingensis*, *Solinalepis levis*, *Canyonlepis smithae*, *Karksilepis parva*, and *Shiqianolepis hollandi*. Thelodonts consistently form a monophyletic group in our analyses, and therefore additional species were not required to test their phylogenetic signal, in contrast to mongolepids, for which broader sampling was necessary.

The matrices used to construct the supermatrix were carefully compiled, and each individual character was examined in order to avoid common issues associated with supermatrix construction, such as redundancy, homoplasy, and inadequate character definitions. All redundant characters—those describing identical phenotypic information using different formulations—were removed. We also reorganized the character classification by subdividing broader morphological categories into more precise character classes. In addition, several characters that reflected homoplastic conditions were excluded from the final dataset.

Taxa

The focus of our study is the total-group Chondrichthyes, comprising the stem chondrichthyans “acanthodians” and the crown group, including all putative known species. All included species range stratigraphically from the Middle Ordovician to the Late Devonian. The remaining taxa in this study were selected based on both their stratigraphic range and degree of anatomical completeness. For each major clade, we included the oldest known representatives and selected species that exhibit the highest levels of anatomical completeness.

In total, our dataset comprises 276 species of total-group chondrichthyans, 8 “placoderm” species, 12 osteichthyan species, 8 osteostracan species, 6 galeaspid species, and 10 thelodont species. We prioritized the most complete species available at the time of data compilation (up to 2021). In addition, we incorporated taxonomically controversial taxa such as *Entelognathus primordialis* and *Qilinyu rostrata*, two maxillate “placoderms” that play a key role in discussions of early gnathostome evolution. The complete list of taxa included in this study is provided in Annex 4.

Morphological characters

In total, 977 morphological characters were compiled in the supermatrix (full list in annex 2). We added 184 new morphological characters, indicated by the annotation (N) in Annex 2. These newly introduced characters were specifically designed to accommodate a dataset composed predominantly of hard tissues, such as scales, teeth, and fin spines. To this end, we focused on developing and incorporating characters that emphasize homologous conditions rather than homoplastic similarities.

The morphological character set encompasses skeletal histology, tooth ultrastructure and histology, sensory line systems, the neurocranium, external head structures, the axial

skeleton, vertebrae, fin spines, and scales. In all analyses, morphological characters were treated as unordered in order to provide the most objective assessment of interrelationships among gnathostomes and agnathans. Datasets were assembled in MorphoBank and then exported to Mesquite to accommodate the software requirements used in this study. The parameters and outcomes of each analysis are summarized in Table 1.

Standardisation

Numerous authors have emphasized that the construction of evolutionary units (characters) and the coding of putative homologous evolutionary units (character states) are key determinants of outcomes in cladistic analyses (Maddison, 1993; Pleijel, 1995; Wilkinson, 1995; Hawkins *et al.*, 1997; Strong & Lipscomb, 1999; Sereno, 2007; Brazeau, 2011; Simões *et al.*, 2017). To improve the clarity and consistency of morphological characters in the present study, we introduce a refined approach to phylogenetic character construction.

Morphological characters were defined as evolutionary units following a standardized format, based on methodologies proposed by Sereno (2007), Sprague *et al.* (2006), and Mungall *et al.* (2007), with the aim of producing characters that are universally interpretable and described using objective terminology. Each character was structured using locators, variables, and variable qualifiers to describe morphological features consistently across gnathostomes and agnathans. This approach was designed to (1) minimize subjective descriptions, (2) ensure the communicability and comparability of morphological data, and (3) facilitate the coding of evolutionary units.

Ontology

In addition to developing a standardized approach for constructing morphological characters, we paid particular attention to the vocabulary used in description. To ensure clear

interpretation and to avoid redundancy among morphological characters, we employed anatomical ontologies. Ontologies provide a controlled vocabulary that facilitates universal understanding of morphological structures. As different vocabularies are adapted to different taxonomic groups, we selected the UBERON (Mungall *et al.*, 2012) ontology to describe the morphological and anatomical structures included in our supermatrix.

UBERON was the most appropriate choice given the broad diversity of morphological and anatomical features represented across early vertebrates. This ontology allows the use of standardized, universally recognized terms to describe anatomical and morphological structures, with each term associated with a unique identifier listed in Annex 3. Consequently, this matrix represents, the first fully standardized morphological dataset designed to explore gnathostome and agnathan phylogeny in a comprehensive and objective manner.

Phylogenetic analyses

To investigate interrelationships among “agnathans” and gnathostomes with a particular emphasis on chondrichthyan affinities, we conducted a series of phylogenetic analyses aimed at capturing the most objective phylogenetic signal and producing the best-supported topologies. Currently, Maximum Parsimony (MP) and Bayesian inference are the subject of extensive methodological debate regarding their relative performance under different evolutionary scenarios (Lemmon, *et al.*, 2009; Wright & Hillis, 2014; Puttick *et al.*, 2017; Schrago *et al.*, 2018). To address this issue, we applied both methodologies within a comparative analytical framework.

We tested both approaches using the three matrices described above in order to evaluate the influence of taxon sampling and matrix completeness on the resolution of early vertebrate interrelationships. To further assess the robustness of the inferred topologies, we employed multiple outgroup configurations. This strategy allowed us to identify relationships among clades that are consistent regardless of outgroup choice.

In total, we performed MP and uncalibrated Bayesian analyses using seven alternative outgroups (galeaspids, osteostracans, thelodonts, “placoderms”, osteichthyans, chondrichthyans, and mongolepids) for each of the three matrices. This resulted in 42 inferred trees, which were subsequently used to generate phylogenetic network trees.

Parsimony

Parsimony analyses were conducted using TNT version 1.6 (Goloboff & Morales 2023). We employed a New Technology Search with 20 initial addition sequences, a minimum length hit of 10, Ratchet activated with 15 iterations, Drift activated with 15 iterations, and Tree Fusing enabled.

For each of the three matrices, we assessed the robustness of the resulting topologies by testing alternative outgroup selections. Each outgroup was chosen to represent a major early vertebrate clade. Accordingly, for each matrix, seven separate analyses were performed using different outgroups: *Ateleaspis tessellata* for the Osteostraci, *Doliodus latispinosus* for Chondrichthyes, *Hanyangaspis guodingshanensis* for Galeaspida, *Dicksonosteus arcticus* for “Placodermi”, *Styloichthys changae* for the Osteichthyes, *Solinalepis levis* for the Mongolepidida, and *Furcacauda fredolhmae* for the Thelodonti.

For each analysis, the most parsimonious trees were summarized using a 50% majority-rule consensus. Bootstrap resampling was subsequently performed to evaluate overall nodal support. All resulting trees are provided in Annex 5.

BEAST tip-dating

Bayesian tip-dating analyses were performed using BEAST2 version 2.7.7 (Bouckaert *et al.*, 2019), with XML input files generated in BEAUti, a software in BEAST2 package. The dataset was partitioned with all partitions sharing the same tree topology and clock

model. Each partition was assigned four gamma rate categories to accommodate among-character rate heterogeneity. We implemented an uncorrelated relaxed clock model that allows substitution rates to vary across lineages (Drummond *et al.*, 2006).

Two tree prior models were tested: the Fossilized Birth–Death (FBD) model (Heath *et al.*, 2014) and the Birth–Death Skyline (BDSKY) model (Stadler *et al.*, 2013), both of which are well suited to fossil morphological datasets characterized by temporal uncertainty and missing data. Results obtained under the BDSKY model are presented in Figure 14, whereas trees inferred using the FBD model are provided in Annex 6. In both cases, trees were rooted using galeaspids and osteostracans as outgroups.

Tip dating was calibrated using the mean age of each species based on its stratigraphic range, calculated from the minimum and maximum ages of its geological formation. Analyses were run for 270 million MCMC iterations to ensure adequate chain convergence. Trees were sampled using coupled Markov chain Monte Carlo (MCMC) procedures. The optimal topology was selected as the Maximum Clade Credibility (MCC) tree using the Mean Height option in TreeAnnotator, included in the BEAST package. Effective Sample Size (ESS) values indicated good mixing and convergence for all parameters and were assessed using Tracer version 1.7 (Rambaut *et al.*, 2018).

MrBayes

Because BEAST2 only allows Bayesian inference on time-calibrated phylogenies, we also explored tree topology using MrBayes version 3.2 (Ronquist *et al.*, 2012), which enables Bayesian phylogenetic analyses without temporal constraints. Analyses were conducted for each matrix and each outgroup configuration, using the same outgroups as in the Maximum Parsimony analyses.

For each analysis, Markov chain Monte Carlo (MCMC) simulations were run for 100 million iterations, with a burn-in fraction of 0.18 and a temperature parameter set to 0.1.

Resulting trees were summarized using both a strict consensus (selecting the topology with the highest posterior probability) and a 50% majority-rule consensus.

To evaluate overall support across analyses and outgroup selections, we computed a Bayes Index, which represents the mean posterior support across all branches of a given tree. Bayes Index results are presented in Table 1, and all resulting trees are provided in Annex 7.

Network Tree

A total of 42 undated trees (three matrices $\times$ seven outgroups, using both Maximum Parsimony and uncalibrated Bayesian approaches in MrBayes) were obtained from the non-time-calibrated analyses and are provided in Annex 8. For each analysis, summary trees were reconstructed using a 50% majority-rule consensus. From these trees, we aimed to extract the dominant phylogenetic signal shared among the different analytical conditions.

To visualize and compare conflicting phylogenetic signals among analyses, we conducted two phylogenetic network analyses using SplitsTree version 6.5.1 (Huson & Bryant, 2006, 2024). A single consensus network was generated using a threshold of 5% and reconstructed with the outline consensus network methods in Figure 15.

Results

Chondrichthyan origin

Crown chondrichthyans are represented by six species ranging from the Givetian (Middle Devonian) to the Famennian (Late Devonian). The most recent estimate for the crown-node origin of chondrichthyans is 389 Ma (Schnetzer *et al.*, 2024), based on diversity analyses. Our results instead suggest that the most recent common ancestor of crown chondrichthyans dates back to approximately 397 Ma, with a posterior support of 0.26 (Figure 14; Table 2). The phylogeny inferred under the Fossilized Birth–Death (FBD) model

indicates a slightly younger crown-node origin at 392 Ma, with a higher support value of 0.48, although this estimate excludes *Cladodoides wildungensis* (see Annex 7).

The taxa most closely related to the crown node include *Doliodus latispinosus* (the oldest known articulated putative chondrichthyan), *Gladbachus adentatus*, (a putative chondrichthyan), and *Karksilepis parva* (a mongolepid). These taxa are followed by the so-called MOTH species (i.e., *Obtusacanthus corroconis*, *Paucicanthus vaneltsi*, *Kathemacanthus rosulentus*, and *Brochoadmones milesi*). MOTH taxa have repeatedly been considered the closest stem chondrichthyans to the crown group (Hanke & Wilson 2010; Zhu *et al.*, 2013). Our analyses corroborate this hypothesis, with a node uniting crown chondrichthyans, putative chondrichthyans, and part of the MOTH assemblage supported by a posterior probability of 0.62.

Interrelationships within the paraphyletic assemblage traditionally referred to as “acanthodians” show variable support values. Among the 38 internal nodes, 18 exhibit posterior support ranging from 0.07 to 0.37, whereas 20 nodes are supported by values exceeding 0.39 (Figure 14). The most strongly supported clades comprising comprises *Cheiracanthus* species (support = 1.00), the *Diplacanthus* species (support = 1.00), and Escuminac “acanthodian” (i.e., *Triazeugacanthus* and *Homalacanthus*) (support = 0.93). The total-group Chondrichthyes, encompassing both “acanthodians” and crown-chondrichthyans, is recovered with strong support (0.96). These results reinforce the close evolutionary affinity between “acanthodians” and chondrichthyans, a relationship that is also consistently recovered in the consensus network analysis (Figure 15). Our findings therefore confirm that “acanthodians” belong unequivocally to the stem lineage of chondrichthyans.

Both the phylogenetic tree (Figure 14) and the consensus network (Figure 15) further support a close affinity between thelodonts and total-group chondrichthyans. The primary phylogenetic signal of all analyses links thelodonts with the total-group chondrichthyans. Thelodonts are recovered as a monophyletic group in all matrices and analytical frameworks. The node uniting thelodonts with total-group chondrichthyans is strongly supported (posterior probability = 0.82). In parsimony analyses, thelodonts are nested within crown

chondrichthyans (see Annex 5). The consensus network likewise reveals a strong affinity between thelodonts and chondrichthyans (Figure 15). These results indicate not only that thelodonts are closely related to chondrichthyans, but that they represent the closest known sister group to cartilaginous fishes within the total-group Chondrichthyes.

Mongolepids display a polyphyletic nature in tip-dated analyses. *Canyonlepis* and *Tezakia* are recovered as stem “placoderms”, *Solinalepis* and *Shiqianolepis* as stem thelodonts, and *Karksilepis parva* as a stem chondrichthyan. Given their broad stratigraphic range from the Ordovician to the Devonian, tip-dated phylogenies appear poorly suited for resolving mongolepid interrelationships. In contrast, consensus network analyses points toward a significant statistical affinity between mongolepids and chondrichthyans (Figure 15). Both parsimony and undated Bayesian analyses consistently place mongolepids as stem chondrichthyans, and in some cases within the crown group itself (see Annex 5).

Although our conclusions regarding mongolepids remain cautious, the combined evidence suggests that these taxa are closely related to chondrichthyans. However, the polyphyletic signal observed in tip-dated analyses introduces uncertainty regarding their precise phylogenetic position.

Gnathostomes

Osteichthyans constitute monophyletic group consistently recovered in Maximum Parsimony, Bayesian tip-dated, and Bayesian uncalibrated analyses with a robust and statistically significant support. Although this result is widely accepted in the literature, our analyses provide additional confirmation by recovering the crown-node Osteichthyes with maximum support (posterior probability = 1.00; Figure 14). Furthermore, our results suggest that osteichthyans originated around 430 Ma, as inferred from the estimated age of the crown node.

In addition, osteichthyans exhibit a strong phylogenetic affinity with “placoderms”. However, “placoderms” display a mixed phylogenetic signal across our analytical frameworks. Parsimony and Bayesian tip-dated analyses tend to recover “placoderms” as a monophyletic group, with the maxillate “placoderms” *Entelognathus primordialis* and *Qilinyu rostrata* occupying the most basal positions within the clade. In tip-dated analyses, this “placoderm” clade is supported by a posterior probability of 0.74, whereas parsimony analyses yield bootstrap values ranging from 42 to 50, depending on outgroup selection.

By contrast, Bayesian uncalibrated analyses recover a paraphyletic assemblage of “placoderms”, with maxillate placoderms resolved as stem osteichthyans. These conflicting results indicate that “placoderms” fail to exhibit a stable and unambiguous phylogenetic signal across methods. Nevertheless, “placoderms” consistently emerge as the closest relatives of osteichthyans. In Bayesian tip-dated analyses, “placoderms” and osteichthyans form a clade supported by a posterior probability of 0.71, while Bayesian uncalibrated analyses recover a similar association with an average support value of 0.70.

In contrast, parsimony analyses recover the traditional view of “placoderms” as the most basal gnathostomes, with an average bootstrap support of approximately 70. In the tip-dated phylogeny, “placoderms” show a crown-node support of 0.74, with an estimated origin around 445 Ma. The gnathostome crown node is calibrated at approximately 485 Ma.

“Agnathan” interrelationships

Osteostracans and galeaspids are consistently recovered as the most closely related “agnathan” groups across all analyses. In Bayesian uncalibrated phylogenies, their sister-group relationship is strongly supported, with average posterior probabilities of 0.95 with Matrix 3, 0.90 with Matrix 2, and 0.80 with Matrix 1. Parsimony analyses also recover this relationship, with bootstrap support averaging 75 in Matrix 3. As matrix size increases and overall completeness decreases, bootstrap support declines, with average values of 41 in

Matrix 2 and 34 in Matrix 1. Despite this reduction, the osteostracan–galeaspid relationship remains the most consistently supported “agnathan” association in all analyses.

In addition, both the osteostracans and the Galeaspids are consistently recovered as monophyletic groups. These results are further corroborated by the network analyses, which also recover a strong and stable association between these two clades (Figure 15).

Outgroup selection

Outgroup selection represents a critical issue in resolving the phylogenetic relationships among gnathostomes and “agnathans”. King *et al.* (2017) suggested, based on a comparable analytical framework, that outgroup choice in this context is largely non-informative. Our results corroborate this conclusion. Parsimony analyses using different outgroups fail to converge on a single optimal outgroup, and instead produce conflicting signals depending on the matrix and evaluation criterion.

For Matrix 3, unconventional results emerge: trees rooted with osteichthyans as the outgroup yield the highest average support values and the lowest total tree length, whereas the Osteostraci provide the best Consistency Index (CI) and the shortest branch lengths in the bootstrap consensus trees. In contrast, Bayes Index results do not favor either of these outgroups. Instead, the strict consensus tree yields the highest score when mongolepids are used as the outgroup, while the 50% majority-rule consensus favors galeaspids.

Similar inconsistencies are observed for the other matrices. For Matrix 2, parsimony analyses identify both osteostracans and thelodonts as equally optimal outgroups for the most parsimonious tree with the highest CI, whereas bootstrap analyses favor mongolepids. Bayesian uncalibrated analyses identify galeaspids as the optimal outgroup under the strict Bayes Index, and mongolepids under the 50% Bayes Index. For Matrix 1, several indices show a preference for thelodonts; however, mongolepids again yield the best tree length and

CI in bootstrap analyses. Additionally, Bayesian indices identify chondrichthyans as the optimal outgroup in both strict and majority-rule consensus trees.

Although certain outgroups score marginally better under specific indices, the differences among these values are consistently small and insufficient to be considered statistically meaningful. Consequently, no single outgroup emerges as clearly superior across methods, matrices, and evaluation metrics. Despite this ambiguity, osteostracans and galeaspids remain the most biologically and phylogenetically justified outgroup choices. Undated Bayesian and parsimony analyses rooted with these taxa consistently produce the most stable and interpretable topologies, which were therefore used to generate Figure 14.

Discussion

Early chondrichthyans reveal a close affinity with thelodonts, placing these supposedly agnathan fishes as a stem group of the total-group chondrichthyans. Thelodonts have long been characterized as an enigmatic group (Wilson & Märss, 2004) and remain poorly represented in recent phylogenetic analyses (Donoghue & Smith, 2001; Wilson & Märss, 2004; Donoghue & Rücklin, 2016), leading to a limited understanding of their interrelationships. Their systematic position has not been substantially updated in recent years, and thelodonts are often presented as more basal than osteostracans and galeaspids since their discovery (Donoghue & Rücklin, 2016). This phylogenetic placement has been controversial, and thelodonts have previously been suggested as the closest group to gnathostomes (Janvier, 1996, 1997). Our analyses support this hypothesis, as thelodonts emerge as the most closely related taxa to gnathostomes and even display a stronger affinity by appearing as the closest relatives of chondrichthyans. Thelodonts share several unique features with gnathostomes that are absent in other “agnathans”, such as the presence of a stomach chamber (Wilson & Caldwell, 1993) and the occurrence of teeth in *Loganellia scotica* as well as potential tooth whorls (der Brugghe & Janvier, 1993; Donoghue & Rücklin, 2016), even if this feature has been interpreted as convergent (Rücklin *et al.*, 2021).

Moreover, they share specific traits observed only in crown chondrichthyans, such as non-imbricated placoid scales (Turner, 1973; Žigaitė *et al.*, 2013). They also possess an unmineralized skeleton (Smith *et al.*, 1996), a condition characteristic of total-group chondrichthyans. Considering these shared features, we selected the two most complete thelodont species in the final tree presented in Figure 1, which represent the consistently monophyletic signal recovered for thelodonts across all analyses. *Loganellia scotica* was excluded to avoid bias from the controversial presence of teeth in this derived taxon. In addition, thelodonts exhibit a mosaic of ecological strategies, including strong swimmers, schooling forms, open-water taxa, and demersal species, suggesting a predatory lifestyle (Ferrón & Botella, 2017). They are retrieved in demersal environments such as caves, crevices, and rocky substrates rather than muddy or sandy settings, while some taxa were also strong-swimming pelagic species (Ferrón & Botella, 2017). We coded most thelodonts as having a terminal mouth position, a condition characteristic of most jawed vertebrates, whereas other agnathans such as osteostracans and galeaspids are primarily benthic taxa with ventral mouths (Sansom *et al.*, 2015). These ecological data, combined with morphological and anatomical traits, tend to reduce the gap between thelodonts and gnathostomes. One hypothesis emerging from these observations is that thelodonts may have possessed a primitive, unmineralized jaw, although this remains unsupported by the fossil record. While no direct fossil evidence currently supports this hypothesis, the strong phylogenetic signal placing thelodonts close to chondrichthyans is more parsimonious than invoking a secondary loss of jaws, given the importance of jaws as a key innovation in early vertebrate evolution (Brazeau & Friedman, 2015). Furthermore, thelodonts are predominantly known from isolated dermal elements, with only 29 of 147 species represented by partially articulated specimens (Turner, 1982; Märss *et al.*, 2007; Ferrón & Botella, 2017). Thelodonts thus represent the closest taxon to total-group chondrichthyans, and the specificities discussed above support this affinity. Nevertheless, caution is required when interpreting the potential presence of jaws. Although ecological, morphological, and anatomical evidence points toward the possibility of a primitive, unmineralized jaw in thelodonts, this hypothesis remains speculative. Thelodonts also display a relatively short temporal range in the fossil

record compared to chondrichthyans, which are continuously represented from the Devonian to the present. A key comparison may reveal a link between the rise of chondrichthyans in the Early Devonian (Schnetzer *et al.*, 2024) and the contemporaneous decline of thelodonts (Ferrón *et al.*, 2018). This pattern could reflect a phylogenetic relationship via a last common ancestor dating back to the Early Silurian, as supported by our phylogeny (Figure 14).

Crown chondrichthyans likely emerged during the Early Devonian, around 397 Ma (Table 2). Support for this node is relatively low, with a posterior probability of 0.26 (Table 2), but it nevertheless suggests an older origin for crown chondrichthyans than the previously proposed date of 392 Ma based on diversity analyses (Schnetzer *et al.*, 2024). Species assigned to the crown group are represented by a combination of dermal elements, including fin spines, scales, and teeth in *Antarctilamna prisca* (Young, 1982) and *Wellerodus priscus* (Potvin-Leduc *et al.*, 2015), as well as neurocranial components in *Cladodoides wildungensis* (Maisey, 2005; Ivanov, 2018) and *Tamiobatis vetustus* (Williams, 1998). All crown chondrichthyan taxa lack at least 75% of the total character coverage in the matrix, and the poor fossil preservation of chondrichthyans is the primary reason for the weak support of this node. A more strongly supported node (posterior probability 0.83) grouping putative chondrichthyans such as *Gladbachus adentatus* and *Doliodus latispinosus* provides additional support for their interpretation as the closest representatives of crown chondrichthyans. Although only calcified cartilage, and not prismatic cartilage, has been described in these taxa to date (Burrow & Desbiens, 2023; Coates *et al.*, 2018), we interpret *Doliodus latispinosus* and *Gladbachus adentatus* as the closest relatives of the crown group, followed closely by MOTH species. With respect to *Wellerodus priscus* and *Antarctilamna prisca*, all available characters support their assignment to crown chondrichthyans (Potvin-Leduc *et al.*, 2013; Burrow *et al.*, 2009), even though the presence of prismatic cartilage remains to be confirmed.

Beyond chondrichthyan interrelationships, our analyses recover a mixed signal regarding the systematic status of “placoderms”. The debate surrounding “placoderm” monophyly has been extensively discussed by King *et al.*, (2017) and Long and Trinajstić

(2024). At present, the paraphyletic interpretation of “placoderms” is the most widely accepted view (Brazeau & Friedman, 2015; Brazeau *et al.*, 2020), and their monophyly has been rejected by several studies (Brazeau, 2009; Dupret *et al.*, 2014; Qiao *et al.*, 2016). Our results provide a more nuanced perspective on placoderm affinities. Since the discovery of maxillate “placoderms” (Zhu *et al.*, 2013; Zhu *et al.*, 2016), their detailed anatomical investigation (Cui *et al.*, 2023; Li *et al.*, 2021), and their inclusion in early vertebrate phylogenies, “placoderms” have increasingly been regarded as potential stem osteichthyans (Janvier, 2024). In our tip-dated Bayesian analyses (Figure 14), “placoderms” are recovered as monophyletic, whereas uncalibrated Bayesian analyses provide stronger support for a paraphyletic assemblage, with *Entelognathus primordialis* and *Qilinyu rostrata* placed as stem osteichthyans. In contrast, parsimony analyses tend to recover a monophyletic “placoderm” clade, consistent with some recent phylogenetic results (Qiao *et al.*, 2016). The presence of maxillary systems is undoubtedly a key character supporting the placement of maxillate “placoderms” as stem osteichthyans. Moreover, when compared with galeaspids, osteostracans, and osteichthyans, “placoderms” fail to exhibit a consistent phylogenetic position across all analyses (see annexes). Rather than interpreting “placoderms” as basal gnathostomes, we favor their placement as stem osteichthyans sharing a common ancestor with osteichthyans. Osteichthyans themselves display a strongly supported monophyletic signal, and our analyses further reinforce this consensus, which is well established in the literature (Brazeau & Friedman, 2015). Given the robust monophyly of osteichthyans, our results highlight an additional aspect of their origin, namely a potential shared ancestry with placoderms. This interpretation is supported by both tip-dated and undated Bayesian analyses, whereas parsimony analyses place “placoderms” as stem gnathostomes.

Galeaspids and osteostracans represent the most strongly supported clade across all resulting trees in our analyses. They consistently exhibit the closest relationship to each other and are recovered together in every analysis. Our results confirm their monophyly and their position as stem gnathostomes, providing additional support for the widely accepted view in the literature (Forey & Janvier, 1993; Gagnier, 1993; Forey, 1995; Donoghue *et al.*, 2000; Donoghue & Smith, 2001; Sansom, 2009). These two groups also show the highest index

support as outgroups in our analyses, although they are closely followed by mongolepids (Table 1). Nevertheless, uncertainty remains regarding whether galeaspids or osteostracans are more closely related to gnathostomes. Galeaspids possess certain features, such as characteristics of the naso-hypophyseal complex, that could suggest a closer affinity to gnathostomes than osteostracans (Gai & Zhu, 2012). However, osteostracans are still commonly regarded as more closely related to jawed vertebrates than galeaspids (Shan *et al.*, 2020). In Figure 14, we deliberately constrained galeaspids and osteostracans as outgroups to ensure optimal representation of early vertebrate interrelationships, following an approach also adopted by Qiao *et al.*, (2016). These constraints do not affect the phylogenetic signal observed within gnathostome clades (see annexes).

CHAPITRE 3

DYNAMIQUE D'EVOLUTION DANS LA LIGNEE DES CHONDRICHTHYENS BASAUX

3.1 RESUME EN FRANÇAIS DU TROISIEME ARTICLE

Les chondrichthyens (requins, raies et chimères) occupent une place clé dans l'histoire évolutive des vertébrés à mâchoires, mais les modalités de leur évolution précoce restent mal comprises en raison d'un registre fossile fragmentaire et d'incertitudes phylogénétiques. Cette étude vise à caractériser les événements évolutifs ayant marqué l'origine et l'évolution initiale des chondrichthyens en combinant l'analyse des taux d'évolution morphologique, des dynamiques de diversification et de la disparité morphologique.

Nous avons analysé le jeu de données morphologiques le plus complet actuellement disponible pour les vertébrés paléozoïques, comprenant jusqu'à 320 taxons et 977 caractères, à partir de deux matrices : une matrice globale des gnathostomes fossiles et une matrice ciblée sur les chondrichthyens du groupe total. Des analyses phylogénétiques bayésiennes calibrées sur le temps ont été réalisées avec BEAST2 en utilisant le modèle Birth–Death Skyline Serial, complétées par des analyses de diversification avec BAMM-fossil et des analyses de disparité morphologique fondées sur des distances de Gower à travers des tranches temporelles du Silurien et du Dévonien.

Les résultats mettent en évidence un événement majeur de diversification à la racine des chondrichthyens du groupe total durant l'Ordovicien, suivi d'une phase prolongée de taux de diversification élevés sur environ 50 millions d'années. La lignée menant aux chondrichthyens présente également des taux d'évolution morphologique parmi les plus élevés de la phylogénie, structurés en phases successives d'accélération et de ralentissement.

Les analyses de disparité révèlent deux épisodes majeurs de disparification, au Praguien et au Famennien, suggérant que l'innovation morphologique a précédé et favorisé les phases ultérieures de diversification.

Dans l'ensemble, l'évolution précoce des chondrichthyens apparaît comme un processus complexe et étagé plutôt qu'une radiation brève, soulignant le rôle central de l'innovation morphologique dans leur succès évolutif.

Cet article intitulé “*Mode and tempo of chondrichthyan origin*” va être soumis dans la revue “*Nature ecology and evolution*” durant l'année 2026. En tant que premier auteur, j'ai réalisé les analyses, produits les figures, fais les interprétations et écrit le manuscrit. Richard Cloutier le second auteur a supervisé le projet. Une partie des résultats ont été présentés lors du « *International Symposium on Early and Lower Vertebrate* » à Berrechid au Maroc en février 2026.

3.2 MODE AND TEMPO OF CHONDRICHTHYAN ORIGIN

Abstract

Chondrichthyans (sharks, rays, and chimaeras) occupy a key position in the evolutionary history of jawed vertebrates, yet the dynamics of their early evolution remain poorly understood due to a fragmentary fossil record and persistent phylogenetic uncertainties. This study aims to characterize the evolutionary events that shaped the origin and early evolution of chondrichthyans by combining analyses of morphological evolutionary rates, diversification dynamics, and morphological disparity.

We analyzed the most comprehensive morphological dataset currently available for Paleozoic vertebrates, comprising up to 320 taxa and 977 characters, based on two matrices: a global matrix of fossil gnathostomes and a matrix focused on total-group chondrichthyans. Time-calibrated Bayesian phylogenetic analyses were conducted using BEAST2 under the

Birth–Death Skyline Serial model, complemented by diversification analyses with BAMM-fossil and morphological disparity analyses based on Gower distances across Silurian and Devonian time slices.

The results reveal a major diversification event at the root of total-group chondrichthyans during the Ordovician, followed by a prolonged phase of elevated diversification rates lasting approximately 50 million years. The lineage leading to chondrichthyans also exhibits some of the highest rates of morphological evolution within the phylogeny, structured into successive phases of acceleration and deceleration. Disparity analyses identify two major episodes of disparification, during the Pragian and Famennian, suggesting that morphological innovation preceded and facilitated subsequent phases of diversification.

Overall, the early evolution of chondrichthyans appears as a complex, stepwise process rather than a brief radiation, highlighting the central role of morphological innovation in their evolutionary success.

Introduction

Chondrichthyans are cartilaginous fishes represented today by sharks, skates, rays, and chimaeras (Long, 2025). They are characterized by the presence of prismatic cartilage, a distinctive histological feature of their endoskeleton (Dean *et al.*, 2005; Dean & Summers 2006). In the fossil record, the chondrichthyan stem group is largely composed of “acanthodians”, a paraphyletic assemblage of extinct jawed vertebrates that possessed fin spines but lacked prismatic cartilage (Brazeau 2009; Davis *et al.*, 2012). Together with early sharks, “acanthodians” constitute the total-group chondrichthyans (Chevrin *et al.*, 2017).

The evolutionary history of chondrichthyans likely extends back to the Ordovician, approximately 465 million years ago, based on the occurrence of mongolepids—putative chondrichthyan taxa known exclusively from isolated scales (Heinicke *et al.*, 2009; Andreev *et al.*, 2016). In contrast, the crown-group chondrichthyan node is currently calibrated at

around 397 million years ago (Flament *et al.*, in prep), leaving a temporal gap of nearly 70 million years between the earliest putative chondrichthyan remains and the emergence of the crown group. Although cartilaginous fishes experienced a marked increase in species richness during the Early Devonian (Schnetz *et al.*, 2024), major gaps in the fossil record obscure the early evolutionary history of the group. In particular, the interval between the first appearance of mongolepids in the Ordovician and the earliest “acanthodians” in the Late Silurian (Burrow & Rudkin, 2014), as well as the gap separating Silurian forms from the Devonian diversification, complicates interpretations of the tempo and mode of early chondrichthyan evolution.

Despite their importance for understanding early gnathostome evolution, chondrichthyans have rarely been investigated from the perspective of evolutionary and diversification rates. Most previous studies have focused on reconstructed species richness through time (Schnetz *et al.*, 2024), comparative anatomy and phylogenetic relationships (Davis *et al.*, 2012; Brazeau & Friedman, 2015; Chevrinais *et al.*, 2017), broad-scale patterns of morphological disparity during the radiation of gnathostomes (Anderson *et al.*, 2011), or large-scale phylogenetic analyses of evolutionary rates across vertebrates (King *et al.*, 2017). Consequently, no consensus has yet emerged regarding the origin and early evolutionary dynamics of chondrichthyans, although several authors have proposed that their history may involve one or more evolutionary radiations (Coates *et al.*, 2018; Schnetz *et al.*, 2024).

The mode and tempo of early chondrichthyan evolution remain difficult to resolve due to several factors. First, the fossil record of chondrichthyans is intrinsically biased by the poor preservation potential of their cartilaginous skeletons (Atake & Eames, 2021). As a result, articulated specimens are rare (Miller *et al.*, 2003; Frey *et al.*, 2019), and most fossil material consists of isolated hard tissues such as fin spines (Lebedev *et al.*, 2020; Andreev *et al.*, 2022), scales (Andreev *et al.*, 2015; Li *et al.*, 2021), and teeth (Derycke & Goujet, 2011; Martinez-Perez *et al.*, 2019). Second, “acanthodians”—key components of the stem-chondrichthyan lineage—exhibit a mosaic of characters shared with both osteichthyans and chondrichthyans (Brazeau & Friedman, 2015), which historically obscured the identity of the

last common ancestor of chondrichthyans. Although “acanthodians” are now consistently recovered as stem chondrichthyans in recent phylogenetic analyses (King *et al.*, 2017; Coates *et al.*, 2018; Chevrinai *et al.*, 2017), uncertainty persists regarding deeper relationships, with recent studies suggesting a close association between thelodonts and total-group chondrichthyans (Flament *et al.*, in prep).

Finally, the taxonomic attribution of early putative chondrichthyans remains problematic. Mongolepids represent the earliest potential record of chondrichthyans, yet their assignment is based solely on isolated scales, and their phylogenetic position remains uncertain, despite increasing support for their placement along the basal stem of total-group chondrichthyans (Flament *et al.*, in prep). Similarly, several Silurian taxa from China, including sinacanthid-like forms, remain ambiguously placed and may represent either early chondrichthyans or “acanthodians”.

Understanding the mode and tempo of early chondrichthyan evolution is therefore essential for clarifying the nature of their origin and early diversification. It has been suggested that chondrichthyans experienced two major radiations, one during the Early Devonian and another during the Early Carboniferous (Coates *et al.*, 2018; Schnetz *et al.*, 2024). However, these radiations have primarily been inferred from increases in species richness alone. Because evolutionary radiations can take multiple forms—including taxonomic diversification, rapid morphological evolution and increases in morphological disparity (Simões *et al.*, 2017)—disentangling the type of radiation experienced by chondrichthyans requires an integrative, multi-proxy approach.

Here, we aim to characterize the evolutionary events underlying the early history of chondrichthyans by jointly analyzing morphological evolutionary rates, diversification dynamics, and morphological disparity. We present the most comprehensive dataset assembled to date for early chondrichthyans and apply Bayesian statistical frameworks to infer phylogenetic relationships, evolutionary rates, and diversification shifts. In addition, we assess morphological disparity through time using the morphological matrix to capture changes in phenotypes. By integrating these complementary approaches, our study provides

robust evidence for a major evolutionary event at the root of the chondrichthyan stem lineage and offers new insights into the processes that shaped the early evolution of chondrichthyans

Material and Methods

Dataset

We used the morphological dataset of Flament *et al.*, (in prep.), which includes 320 taxa scored for 977 discrete morphological characters. The dataset encompasses a broad taxonomic and temporal sampling of early vertebrates, including galeaspids, osteostracans, “placoderms”, osteichthyans, thelodonts, “acanthodians”, and chondrichthyans, spanning the Ordovician to the Devonian. Taxon selection was primarily based on specimen completeness; however, for “acanthodians” and chondrichthyans, all currently known species within the targeted stratigraphic interval were included to maximize coverage of early cartilaginous fishes.

From this original matrix, we derived a reduced dataset focusing exclusively on total-group chondrichthyans. This modified matrix includes only “acanthodians” and chondrichthyans, with *Styloichthys changae* designated as the outgroup. The resulting dataset comprises 277 taxa and includes putative early chondrichthyans such as mongolepids, stem-chondrichthyans including MOTH taxa (e.g., *Brochoadmones milesi*, *Kathemacanthus rosulentus*), articulated forms such as *Doliodus latispinosus*, and more derived taxa representing crown-group chondrichthyans (e.g., *Ferromirum oukherbouchi*, *Cladodoides wildungensis*). Taxon age assignments follow Flament *et al.* (in prep.) and are based on original species descriptions and the stratigraphic ages of the corresponding geological formations.

Phylogenetic analysis

To estimate morphological evolutionary and diversification rates, and morphological disparity, we reconstructed two time-calibrated phylogenies based on the two datasets described above. Both phylogenies were inferred using an identical analytical framework to ensure methodological consistency.

Bayesian tip-dated phylogenetic analyses were performed using BEAST2 v2.7.7 (Bouckaert *et al.*, 2019). All priors and analytical settings were specified using BEAUti, included in the BEAST package. Phylogenetic reconstruction was conducted under the Birth–Death Skyline Serial (BDSKY) model (Stadler *et al.*, 2013), coupled with an optimized relaxed-clock model. The dataset was partitioned, and morphological evolution was modelled using the Lewis Mk model with four gamma rate categories, allowing for among-character rate heterogeneity.

The BDSKY model allows time to be divided into discrete intervals, enabling the estimation of extinction and diversification rates through time, which is not possible under the commonly used Fossilized Birth–Death (FBD) model (Heath *et al.*, 2014). To reduce temporal uncertainty associated with tip-dating, we applied most recent common ancestor (MRCA) priors to the clade uniting total-group chondrichthyans and thelodonts, as well as an ingroup prior excluding galeaspids and osteostracans, which were treated as outgroups. These constraints follow the phylogenetic hypotheses proposed by Flament *et al.* (in prep.).

Markov chain Monte Carlo (MCMC) analyses were run for 200 million generations. Convergence and mixing were assessed using Tracer v1.7.7 (Rambaut *et al.*, 2018), and all effective sample size (ESS) values exceeded 200. Maximum sum clade credibility (MSCC) trees were generated using TreeAnnotator, and the resulting time-calibrated phylogenies were visualized in FigTree v1.4.4 (Rambaut 2010). The final trees inferred from both datasets are provided in annex 9 and 10.

Morphological evolutionary rates analysis

Morphological evolutionary rates were initially extracted directly from the output files generated by the Bayesian analyses performed in BEAST2 under the Birth–Death Skyline Serial (BDSKY) model. Subsequent analyses and visualizations of these rates were conducted in R version 4.5 (R Core Team, 2021) using several dedicated packages to improve graphical representation and data handling. Thus, phylogenetic trees and associated evolutionary-rate data were processed using the packages *ggtree* (Yu *et al.*, 2017), *treeio* (Wang *et al.*, 2020), *ape* (Paradis & Schliep, 2019), and *stringr* (Wickham, 2025). All figures were produced using *ggplot2* (Wickham, 2016).

Morphological evolutionary rates were visualized using two complementary approaches. First, rates were mapped directly onto time-calibrated phylogenies using a colour gradient, in which branch-specific evolutionary rates were extracted and scaled from minimum to maximum values across the tree. Colour-mapped phylogenies are presented only for the complete dataset, as this allowed direct comparison of morphological evolutionary rates across major gnathostome groups and facilitated the identification of potential radiation events.

Secondly, evolutionary rates were plotted through time by calculating the mean age of each branch and associating it with the corresponding branch-specific evolutionary rate. These values were then plotted using *ggplot2* to generate temporal trends in morphological evolution. To capture continuous variations in evolutionary rates through time while minimizing noise, a locally estimated scatterplot smoothing (LOESS) regression was applied with a span parameter of 0.3.

Diversification analysis

We used Bayesian Analysis of Macroevolutionary Mixtures (BAMM), a Bayesian framework specifically developed to identify changes in diversification dynamics along phylogenies (Rabosky *et al.*, 2013). BAMM infers shifts in diversification rates that correspond to major evolutionary events in lineage accumulation. It has recently been extended to accommodate non-ultrametric phylogenies and to explicitly incorporate fossil data. This extension, referred to as BAMM-fossil, allows diversification rate estimation directly from time-calibrated phylogenies including extinct taxa (Mitchell *et al.*, 2019).

We applied the BAMM-fossil framework to our time-calibrated phylogenies and ran multiple independent Markov chain Monte Carlo (MCMC) analyses to ensure convergence toward the most probable diversification-rate shift configurations. A wide range of prior settings was explored to identify parameterizations best suited to our dataset. All analyses were run for 20 million generations, and convergence was assessed by examining effective sample size (ESS) values, which exceeded 200 for all parameters.

The resulting log files and event data were analysed in R using the package *bammtools* (Rabosky *et al.*, 2014) which is specifically designed to process and visualize BAMM output. Diversification dynamics were visualized as colour-mapped phylogenies, in which branch colours represent variation in diversification rates and highlight the location of the inferred shift, corresponding to a major diversification event.

Morphological disparity analysis

We conducted morphological disparity analyses to investigate whether the evolutionary history of chondrichthyans involved a rapid expansion of morphospace. We converted the morphological character matrices into distance matrices using Gower distances, which are well suited for discrete morphological datasets containing missing data. Disparity was then assessed through time by constructing time-calibrated plots representing normalized Gower

distances across successive geological intervals. Time slices correspond to individual stages of the Silurian and Devonian. Due to limited taxon completeness in the early part of the fossil record, disparity analyses could not be performed for intervals older than the Telychian stage for the complete matrix, and older than the Přídolí stage for the reduced matrix.

For each time slice, mean disparity values were calculated, resulting in a single data point per stage. To evaluate the sensitivity of disparity estimates to temporal binning, we performed complementary analyses using alternative time-slice durations.

All analyses were conducted in R version 4.5 (R Core Team 2021) using the following packages: *stringr* (Wickham, 2025), *ape* (Paradis & Schliep 2019), *cluster* (Maechler *et al.*, 2025), *disPRity* (Guillerme, 2018), and *treeio* (Wang *et al.*, 2020).

Results

Morphological evolutionary rates dynamic in the chondrichthyan lineage

Morphological evolutionary rates are displayed along each branch and lineage, revealing substantial heterogeneity across the phylogeny (Figure 16). Several branches exhibit elevated evolutionary rates, identifying candidate lineages associated with major evolutionary events such as adaptive radiation.

Our results display a rapidly evolving lineage leading to total-group chondrichthyans. Successive branches along the stem lineage of total-group chondrichthyans display among the highest evolutionary rates observed in the phylogeny. Three major nodes are followed by pronounced increases in evolutionary rates. The first corresponds to the gnathostome node, after which two major lineages diverge and exhibit elevated rates: one leading to the clade uniting thelodonts and total-group chondrichthyans, and the other leading to “placoderms” and osteichthyans.

Within the latter lineage, osteichthyans display the highest evolutionary rates observed in the entire phylogeny, reaching values of approximately 0.012, compared to 0.011 for the stem-chondrichthyan lineage. The lineage leading to total-group chondrichthyans exhibits a complex pattern of rate variation. The branch leading to thelodonts shows elevated evolutionary rates (>0.010), whereas a temporary slowdown is observed along the successive branches associated with mongolepids. Following the mongolepid node, evolutionary rates increase again to high values (~ 0.011) along the lineage leading to “acanthodians” and chondrichthyans, excluding mongolepids. Notably, the stem lineage of total-group chondrichthyans maintains evolutionary rates nearly twice the mean rate observed in other lineages (excluding osteichthyans) for approximately 50 million years.

For the colour-mapped phylogeny derived from the complete dataset (Figure 16), the LOESS-smoothed curve shows limited variation, with rates ranging between approximately 0.0050 and 0.0075 (Figure 17). A single peak is observed at the onset of the Emsian, suggesting a transient phase of accelerated morphological evolution. This peak is preceded by a prolonged interval of relatively low evolutionary rates extending from the Sheinwoodian to the Lochkovian. Overall, these results do not indicate a single, sharply defined interval of elevated evolutionary rates across all sampled taxa but instead suggest moderate variation with a notable increase during the Early Devonian.

In contrast, analyses based on the reduced dataset comprising 277 taxa reveal a different temporal pattern (Figure 17). From the Late Ordovician (Hirnantian) to the Lochkovian, evolutionary rates exhibit a long-term decreasing trend spanning approximately 50 million years, interrupted by a variation during the Homertian, corresponding to the appearance of multiple acanthodian lineages. The LOESS curve indicates the lowest mean evolutionary rates during the Lochkovian and Emsian, followed by a gradual increase from the Emsian to the Famennian, with evolutionary rates rising from approximately 0.003 to 0.004.

Diversification shift event at the chondrichthyan root

Across all analyses, and regardless of prior parameterization, a diversification-rate shift was consistently recovered at the root of the total-group chondrichthyans (Figure 18). Although prior specification can influence the placement and number of inferred shifts—particularly in phylogenies with fewer than 500 tips, where a single shift is generally expected—the location of this shift was repeatedly recovered across independent analyses.

The inferred diversification shift occurred during the Ordovician, approximately 477 million years ago, on the branch leading directly to total-group chondrichthyans, immediately after the node uniting thelodonts. This shift is strongly supported, as evidenced by convergence among independent Markov chain Monte Carlo (MCMC) runs and high effective sample size (ESS) values for all estimated parameters.

Following this shift, the lineage leading to total-group chondrichthyans exhibits the highest diversification rates observed across the entire phylogeny. Elevated diversification rates persist for approximately 50 million years, spanning from the early Ordovician (Floian) to the Late Silurian (Přídolí). From the Early Devonian (Lochkovian) onward, diversification rates along this lineage show a moderate decline but remain intermediate relative to other terminal lineages.

In contrast, other major gnathostome groups, including “placoderms”, osteichthyans, galeaspids, and osteostracans, consistently display lower diversification rates throughout the phylogeny, even if they are less represented taxonomically.

Morphological disparity reveals a disparification event

Morphological disparity analyses reveal distinct temporal trends within total-group chondrichthyans (Figure 19). An initial increase in morphological disparity is observed during the Pragian, followed by a sustained rise culminating in a pronounced increase toward the end of the Famennian, consistent with a major disparification event. This pattern indicates a progressive expansion of morphospace throughout the Late Devonian.

In contrast, results derived from the complete dataset comprising 320 taxa show a slightly different signal. In this analysis, peaks in morphological disparity are observed during both the Homeric and the Pragian, while disparity values during the Famennian remain comparable to those observed during earlier intervals. Despite these differences, both datasets consistently recover elevated levels of morphological disparity during the Pragian.

Taken together, these results suggest that total-group chondrichthyans experienced an early phase of disparification during the Pragian, followed by a period of relatively stable or slowly decreasing disparity, and culminating in a second disparification event near the end of the Devonian. Although increases in diversification rate and morphological disparity are often correlated (Simoes *et al.*, 2017), our results indicate that morphological disparity within total-group chondrichthyans continued to increase toward the Famennian, independent of any marked increase in diversification rates during this interval

Discussion

The stem-chondrichthyan lineage exhibits a remarkable combination of characteristics that are indicative of a major evolutionary event. Our results show that, regardless of osteichthyan lineage, the chondrichthyan stem lineage displays the highest morphological evolutionary rates among all lineages considered, reaching nearly twice the mean rate observed in other groups considering our dataset. This lineage maintains a sustained and elevated rate of morphological evolution over an interval of approximately 50 million years, interrupted only by a brief slowdown during the Floian–Dapingian interval (roughly three million years).

In addition to this prolonged phase of rapid morphological evolution, the lineage leading to the total-group chondrichthyans is associated with a major shift in diversification rate, followed by a sustained increase in lineage diversification. Furthermore, our results reveal a pronounced disparification event during the Famennian affecting chondrichthyans.

The pattern of morphological evolutionary rates (Figure 16) support the hypothesis that total-group chondrichthyans underwent rapid evolutionary change along their lineage. From the gnathostome node onward, several lineages exhibit elevated evolutionary rates, consistent with a major radiation triggered by the origin of jaws, a key evolutionary innovation. A noticeable slowdown in evolutionary rates occurs during the Floian and Dapingian. This decrease corresponds to the node represented by a scale (Figure 16), which marks the appearance of the earliest putative chondrichthyans, represented by mongolepids. From this node, the two subsequent branches mainly reflect additional nodes introduced to accommodate the various mongolepid taxa included in the matrix. Given the low diversity and fragmentary nature of the mongolepid fossil record (Andreev *et al.*, 2015; Andreev *et al.*, 2020), such a slowdown is entirely expected.

The following lineage supports this interpretation, as it exhibits nearly 20 million years of elevated morphological evolutionary rates, directly leading to the total-group chondrichthyan node. After this node, a subsequent lineage shows a decrease in evolutionary rate. Nevertheless, a final episode of rapid evolution is observed within the total-group

chondrichthyans. At this stage, a clear distinction emerges between more basal “acanthodians” exhibiting fewer chondrichthyan-like characters (e.g., Ischnacanthiformes) and more derived “acanthodians” occupying the stem-chondrichthyan position, such as the MOTM taxon *Brochoadmones milesi* and the well-known articulated form *Doliodus problematicus*. This final burst of rapid evolution further supports the conclusion that the lineage leading to crown chondrichthyans represents the fastest-evolving lineage within the total group, characterized by successive phases of accelerated morphological change.

Diversification analyses reveal a major rate shift at the root of chondrichthyans, occurring after the node including thelodonts. Although the method employed here (BAMM) has been the subject of longstanding debate (Meyer & Wiens, 2018; Meyer *et al.*, 2018), mainly due to concerns regarding Bayesian priors and MCMC calibration, the impact of these issues on our results is likely limited. We used a recent and improved version of BAMM specifically designed for calibrated fossil phylogenies based on morphological data. In addition, we tested multiple matrices and prior configurations to ensure convergence toward a single, robust diversification signal.

One frequently discussed limitation of BAMM concerns tree size. For phylogenies with fewer than 500 tips, it is generally recommended to model only a single major diversification shift, which is consistent with our analytical framework. While the disproportionate size of the total-group chondrichthyans relative to other groups may influence shift placement, reducing the number of chondrichthyan taxa prevents the detection of any diversification shift. We therefore argue that analyses based on larger datasets incorporating the diversity of galeaspid, osteostracans, “placoderms”, osteichthyans, and thelodonts would likely recover the same major diversification event at the root of chondrichthyans. Moreover, similar events would probably be detected at the root of osteichthyans, given the comparable patterns observed in their morphological evolutionary rates.

Disparification represents one form of pseudo-radiation that can characterize major evolutionary events within clades (Simões *et al.*, 2016). To date, total-group chondrichthyans have received little attention regarding hypotheses of morphological disparity, largely due to

their sparse fossil record and the scarcity of complete specimens suitable for geometric morphometric analyses. Using our dataset, we were able to calculate Gower distances for several time slices spanning the Late Silurian to the Late Devonian. Additional analyses using alternative temporal binning (e.g., 5- or 10-million-year intervals) yielded consistent results, revealing a significant increase in morphological disparity within chondrichthyans.

Furthermore, independent evidence indicates a second increase in chondrichthyan species richness during the Carboniferous (Schnetz *et al.*, 2024). In our dataset, Famennian terminal branches primarily correspond to derived crown-group chondrichthyans. Although species richness is lower than during the Early Devonian, the observed signal indicates increasing morphological divergence within the crown group, without a corresponding increase in diversification rate. We therefore propose that the Famennian disparification event preceded the Carboniferous rise in species richness. This pseudo-radiation may have played a crucial role in shaping chondrichthyan morphology and may have facilitated the subsequent diversification of the group by establishing key morphological innovations.

In conclusion, our analyses reveal that the evolutionary history of chondrichthyans is characterized by a unique combination of sustained high morphological evolutionary rates, a major diversification shift, and a pronounced disparification event. The stem lineage leading to total-group chondrichthyans represents the fastest-evolving trajectory among early gnathostomes, punctuated by successive phases of accelerated evolution rather than a single, brief radiation. This pattern supports the interpretation of chondrichthyan evolution as a stepwise process in which early morphological innovation preceded and potentially facilitated later increases in species richness. The Famennian disparification event, in particular, appears to have established key morphological novelties within crown-group chondrichthyans, setting the stage for their subsequent diversification during the Carboniferous. Together, these results highlight the central role of morphological innovation and disparity in shaping the early evolutionary success of chondrichthyans and underscore their importance for understanding major evolutionary transitions among early jawed vertebrates.

CHAPITRE 4

TABLEAUX ET FIGURES

4.1 TABLEAUX

Outgroup	MP Tree length	Consistency index (CI)	Sum of branch length	Average bootstrap tree support	Bootstrap Tree length	Bootstrap Tree CI	Bayes Index Strict	Bayes index 50%
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Matrix 1 - 320 Taxa / 977 Morphological Characters

Osteostracans	2721	0,3417	1263	7,1	3972	0,2341	0.1945	0.7485
Chondrichthyans	2718	0,3421	1306	7,1	3918	0,2373	0.1959	0.7746
Galeaspids	2717	0,3422	1286	7	3984	0,2334	0.1919	0.7307
Osteichthyans	2722	0,3416	1310	7	4120	0,2257	0.1918	0.7591
Mongolepids	2720	0,3419	1275	7,2	3880	0,2396	0.1906	0.7330
Thelodonts	2717	0,3422	1257	7,2	3890	0,239	0.1906	0.7529
« Placoderms »	2723	0,3415	1284	7,1	4087	0,2275	0.1950	0.7603

Matrix 2 - 259 Taxa / 792 Morphological Characters

Osteostracans	2282	0,3908	1040	8,6	3127	0,2852	0.1931	0.7422
Chondrichthyans	2285	0,3903	1051	8,7	3138	0,2842	0.1904	0.7339
Galeaspids	2287	0,39	995	8	3162	0,282	0.1981	0.7549
Osteichthyans	2285	0,3903	1031	8,7	3103	0,2874	0.1965	0.7460
Mongolepids	2285	0,3903	1036	8,8	3086	0,289	0.1961	0.7633
Thelodonts	2282	0,3908	1002	8,6	3106	0,2871	0.1975	0.7505
« Placoderms »	2283	0,3907	1054	8,3	3116	0,2862	0.1927	0.7376

Matrix 3 - 84 Taxa / 792 Morphological Characters

Osteostracans	1920	0,45	942	30,4	2064	0,4186	0.5816	0.7607
Chondrichthyans	1920	0,45	982	30,4	2080	0,4153	0.5738	0.7592
Galeaspids	1920	0,45	945	30,1	2080	0,4153	0.5869	0.7642
Osteichthyans	1920	0,45	938	30,5	2080	0,4153	0.5764	0.7622
Mongolepids	1920	0,45	976	30,4	2091	0,4131	0.5878	0.7602
Thelodonts	1920	0,45	979	30,3	2080	0,4153	0.5850	0.7631
« Placoderms »	1920	0,45	1002	30,5	2068	0,4177	0.5846	0.7640

Table 1: Resumed table of index and parameters from the resulting analyses made by Maximum Parsimony and Bayesian uncalibrated approaches for the three different matrices and the 7 outgroups for each. Each outgroup are shown and were tested for each matrix.

	% Node Support	Calibration (Mya)
Osteostraci	1	439
Galeaspids	0.98	447
« Placoderms »	0.74	443
Osteichthyans	1	428
Thelodonts	1	433
Total Group Chondrichthyans	0.96	441
Crown Chondrichthyans	0.26	397
Thelodonts and Total Group Chondrichthyans	0.82	468

Table 2: Resumed node support and calibration for the main origin of the various taxa analyzed in Figure 14.

4.2 FIGURES

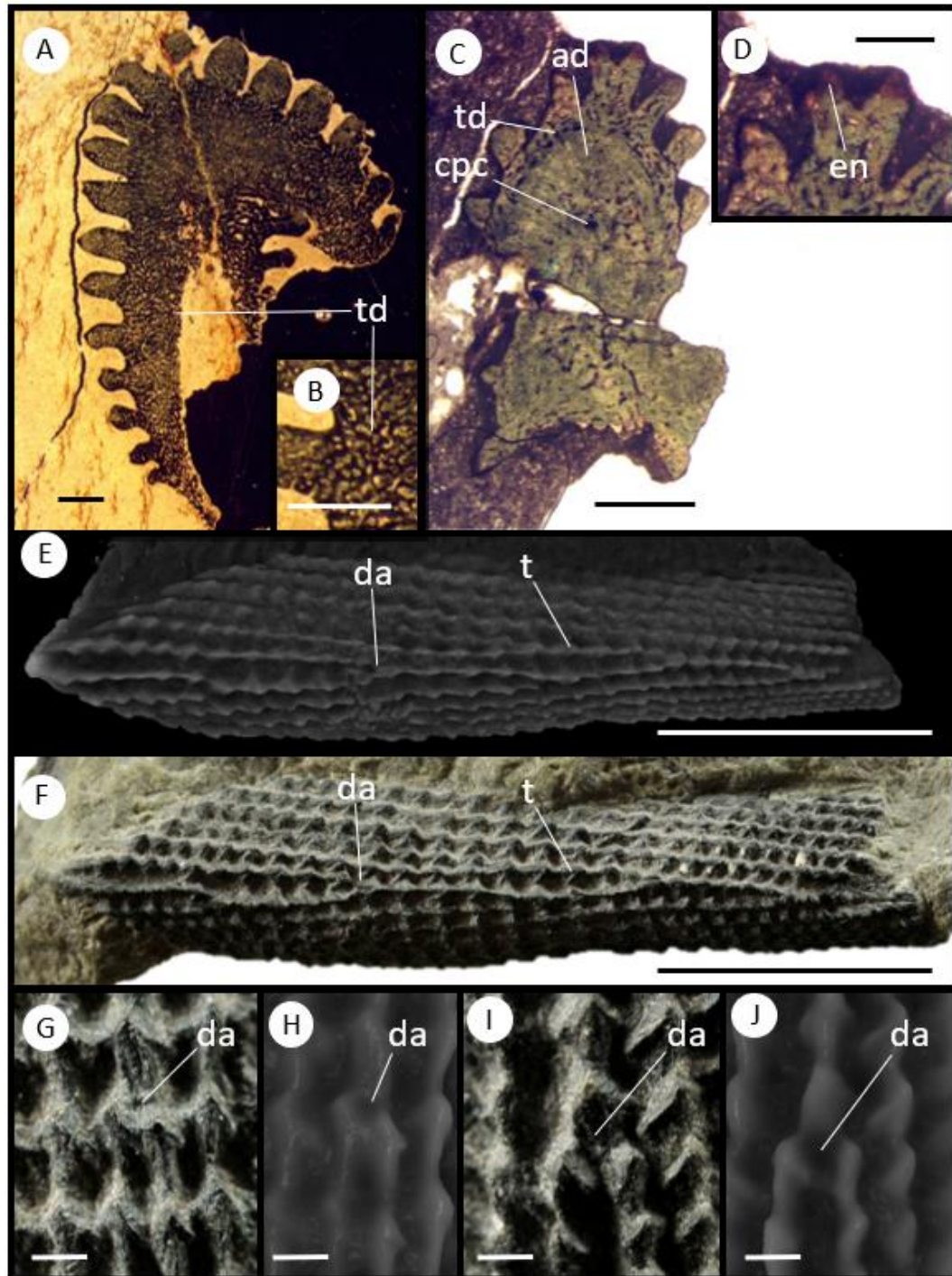


Figure 12: Middle Devonian shark, *Wellerodus priscus*, pectoral fin spines; (A) proximal section of a pectoral fin spine NYSM 19057; (B) NYSM 19057 close up proximal section; (C) NYSM 19057 distal section; (D) NYSM 19057 leading edge tubercles section; (E) NYSM 19051 from micro-CT scan tomography, dorsal view; (F) NYSM 19051 dorsal view; (G) fused tubercles at the leading edge of NYSM 19051; (H) fused tubercles at the leading edge of NYSM 19051 under tomography by micro CT-scan; (I) unfused tubercles at the leading edge of NYSM 19051; (J) unfused tubercles at the leading edge of NYSM19051 under tomography by micro-CT scan; abbreviations: ad, atrabecular dentine; cpc, central pulp cavity; da, divergence area; en, enameloid; t, tubercles; td, trabecular dentine. Scale bar (A), (C) = 1 mm; (B), (D) = 500 μ m; (E), (F) = 1 cm; (G), (H), (I), (J) = 1 mm.

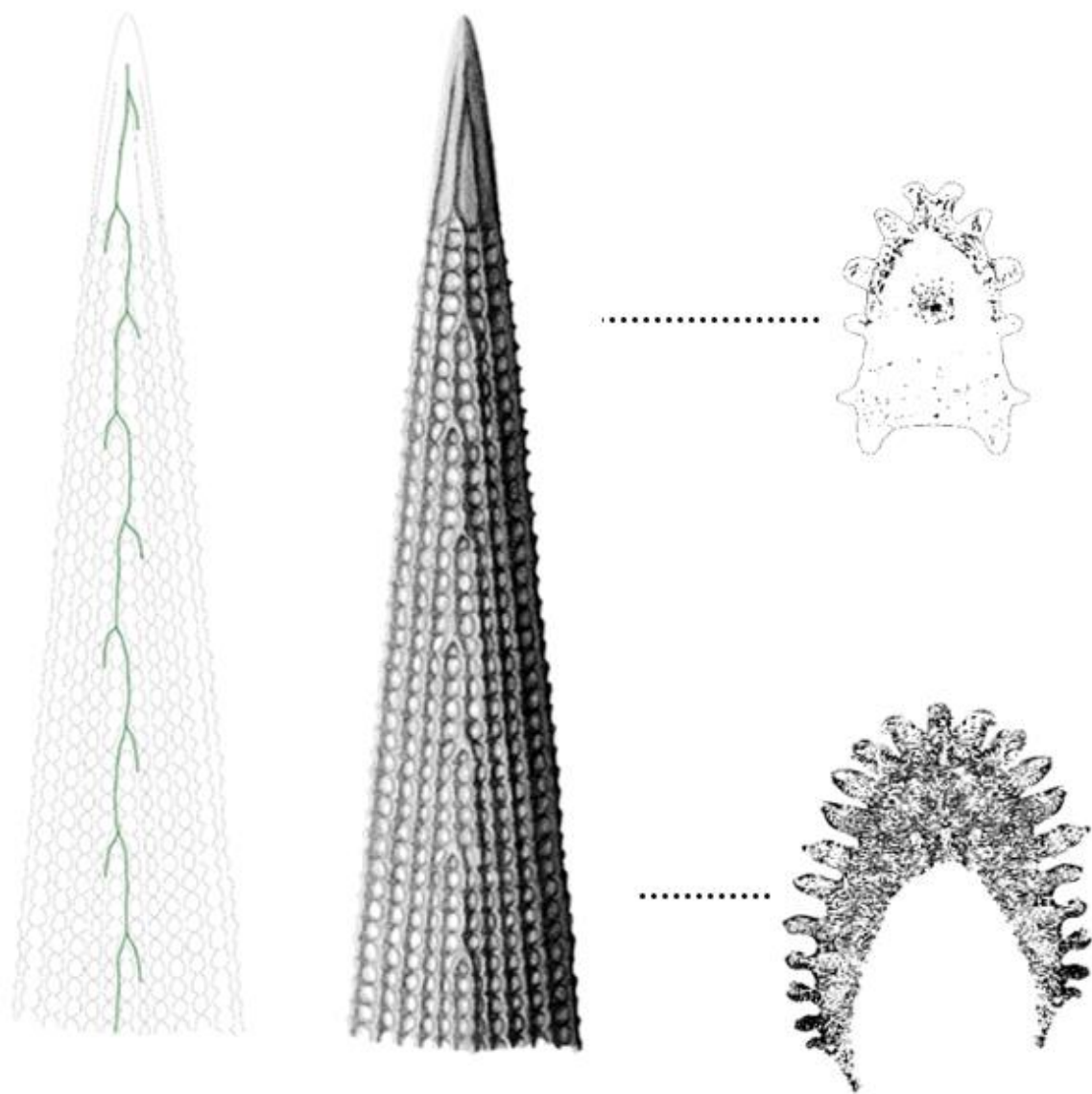


Figure 13: Reconstruction of *Wellerodus priscus* pectoral fin spine in dorsal view with proximal and distal cuts. The green line shows the divergences pattern of the tuberculated ornamentation.

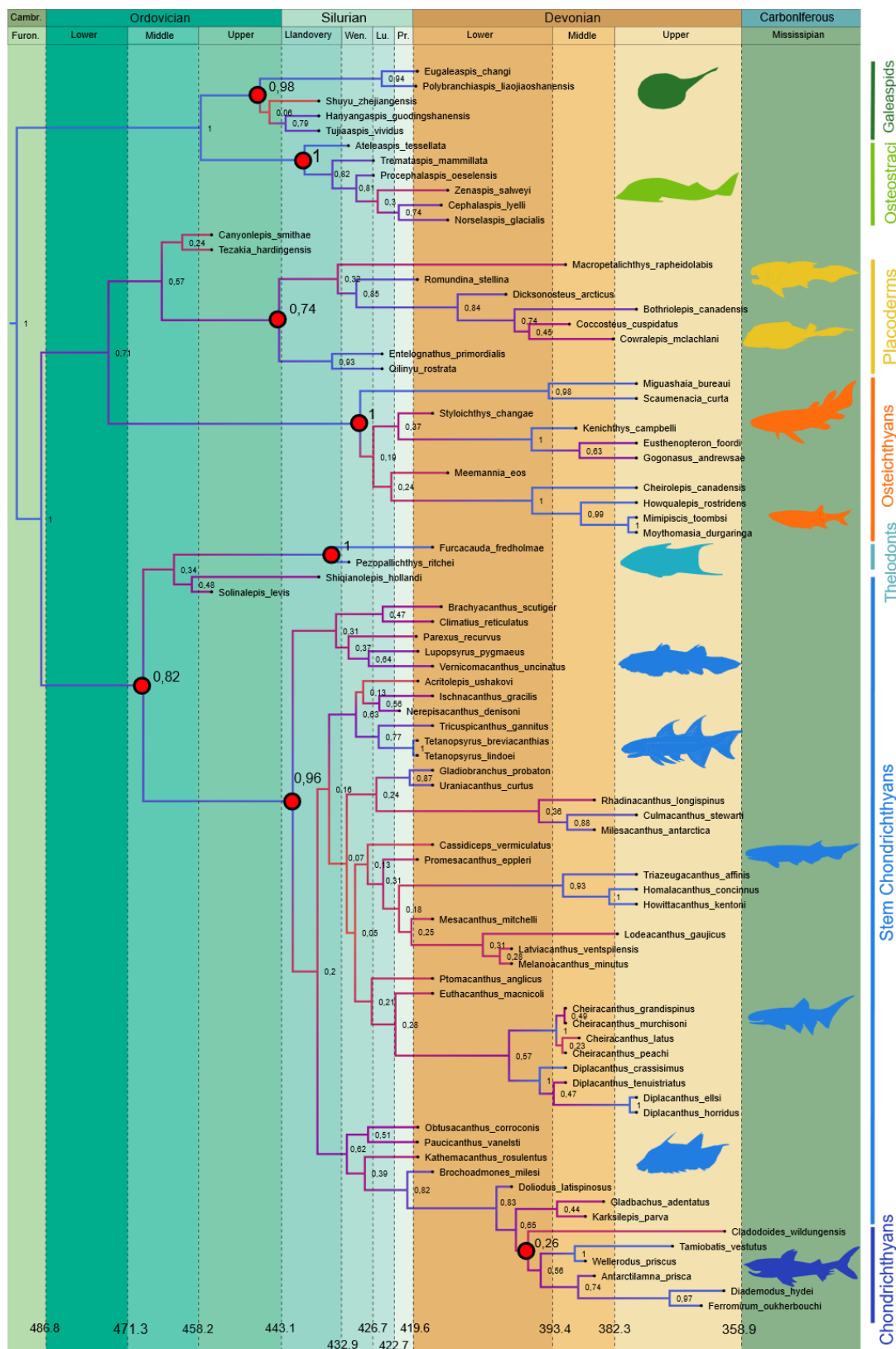


Figure 14: Bayesian Tip-dated phylogeny made from Matrix 3 with 84 taxa and 792 morphological characters.

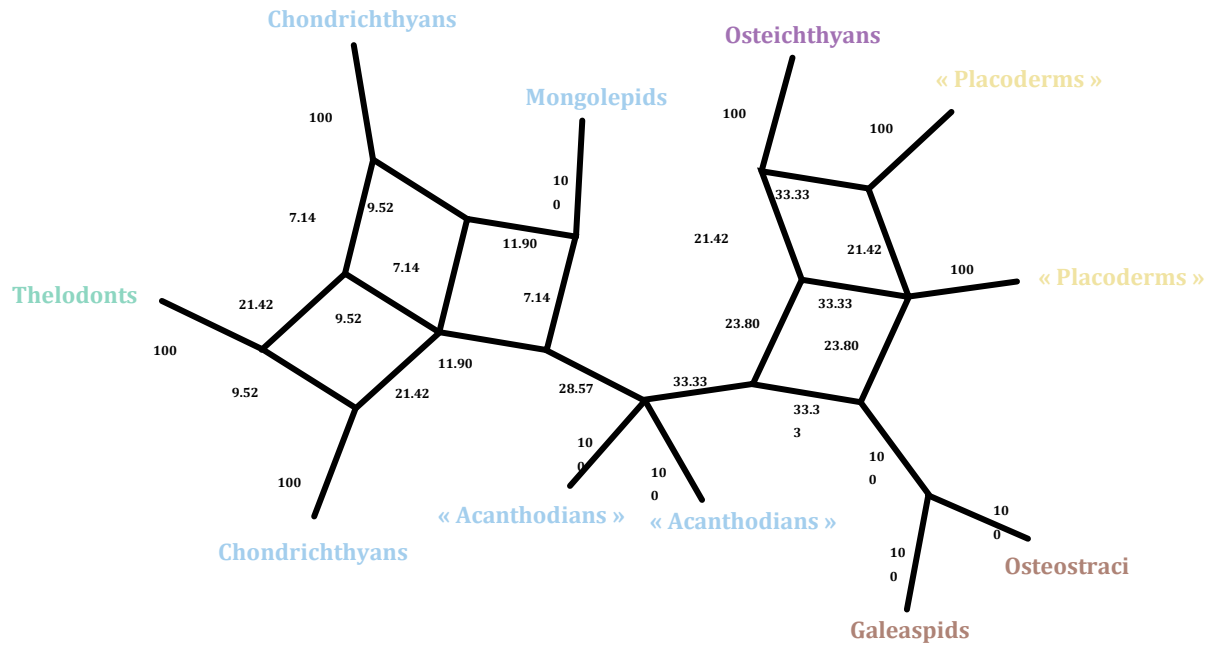


Figure 15: Consensus outline Tree with a threshold of 5% from Splitstree representing the interrelationships networks among gnathostomes and agnathans.

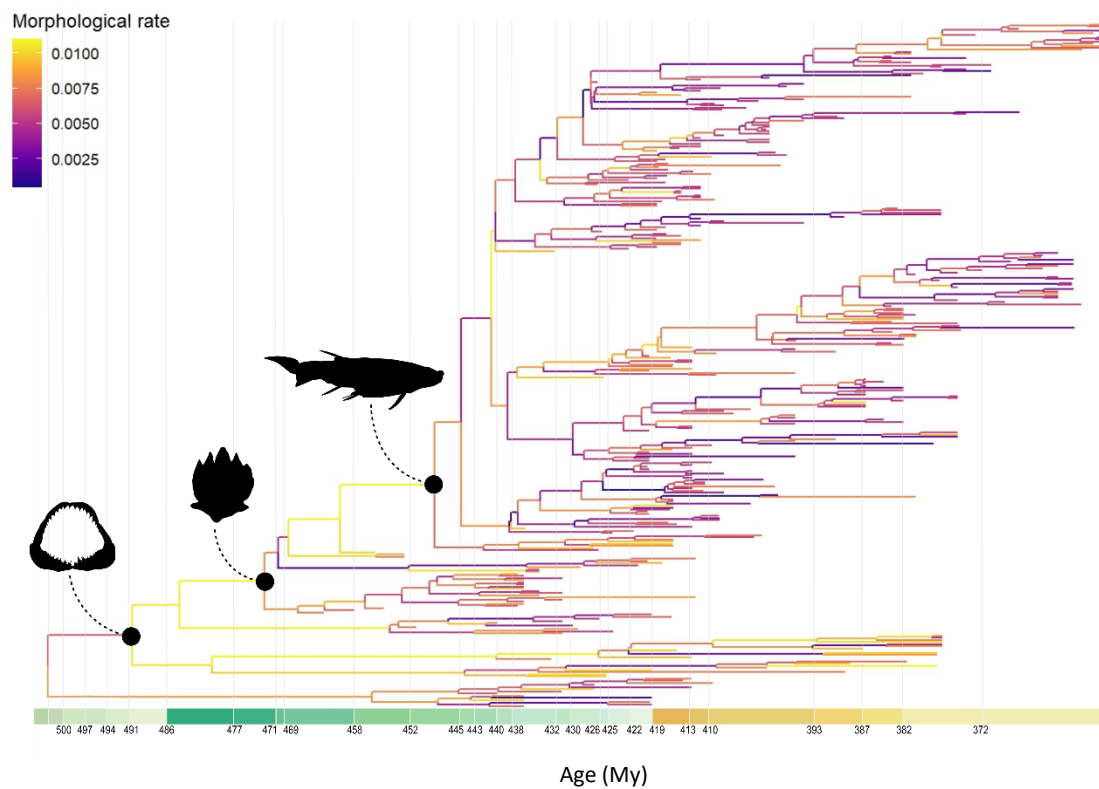


Figure 16: Time-calibrated phylogeny showing morphological rates across the various branches. The jaw represents the gnathostome node, the scale the total-group chondrichthyan node and the “acanthodian” the total-group chondrichthyan excluding mongolepids.

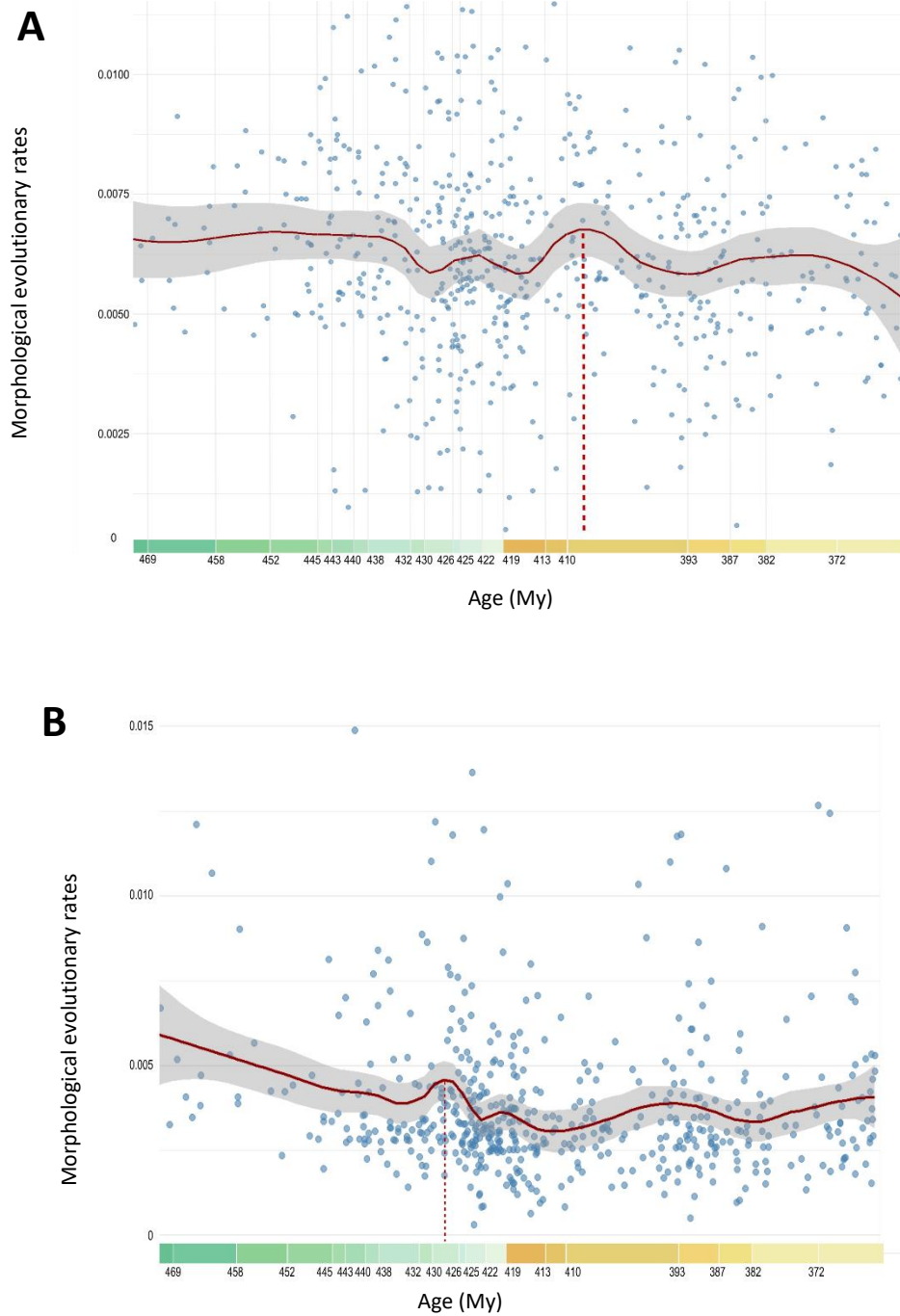


Figure 17: Morphological evolutionary rates through time. A is from the Matrix 1 with 320 taxa and 977 morphological characters and B is from the modified Matrix 1 with 277 taxa (Chondrichthyans only). Y axis displays morphological rate values and X axis the time.

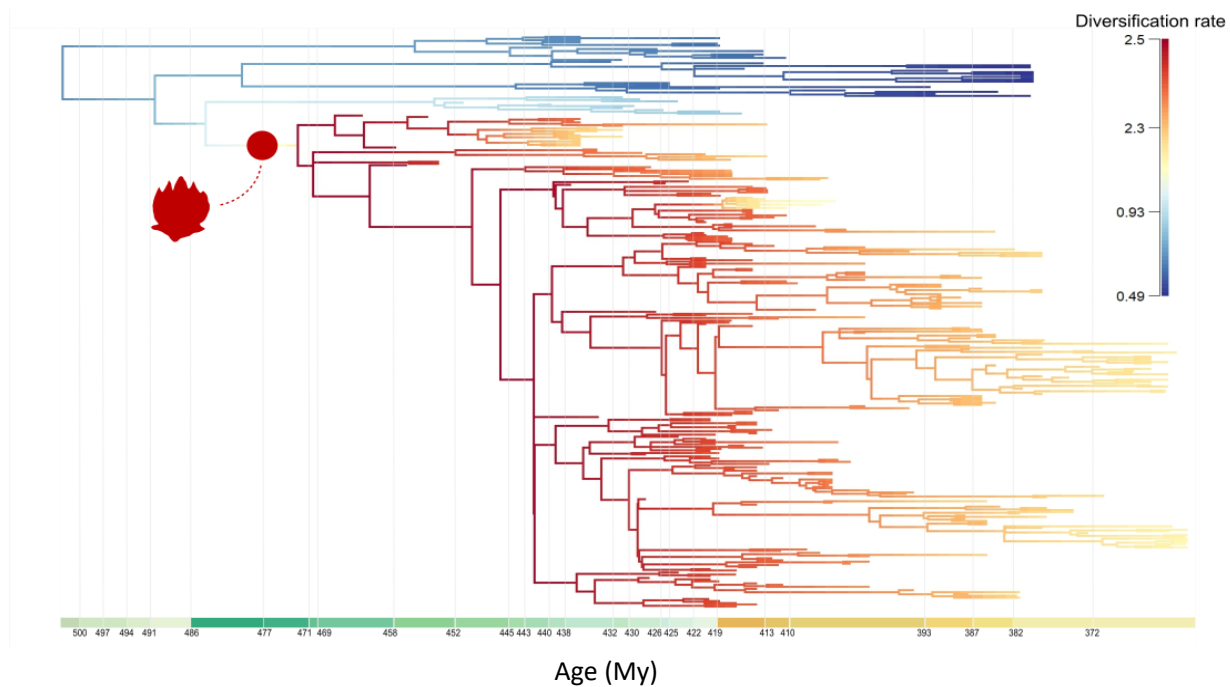


Figure 18: Time-calibrated phylogeny from BAMM analysis representing branches with estimated diversification rates. The red dot represents the shift event in diversification at the root of the total-group chondrichthyan.

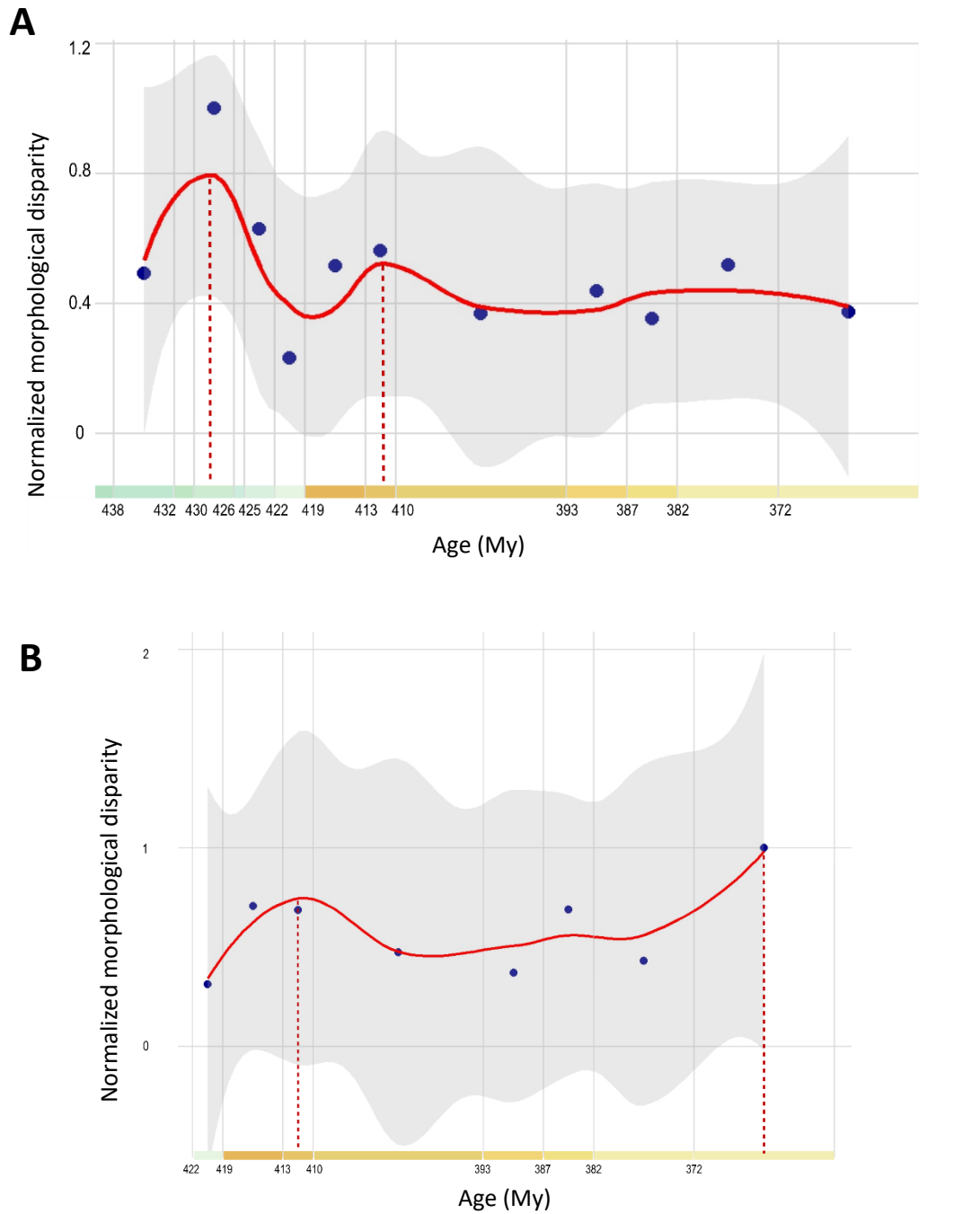


Figure 19: Disparity through time. On A the disparity through time from the Matrix 1 with 320 taxa and B shows from the matrix with 277 taxa (Chondrichthyans only). Y axis display normalized morphological disparity and X axis time.

CHAPITRE 5

PLAGIAT ET DROIT D'AUTEUR

L'étudiant qui ne respecte pas le droit d'auteur se rend coupable de plagiat et s'expose, en vertu de l'article 285 du règlement 6 : *Régime des études de cycles supérieurs*, à une sanction pouvant aller jusqu'à l'exclusion :

285. Tout acte (tentative, participation) de plagiat ou de fraude relatif à une activité ou à un programme peut entraîner, entre autres, une ou plusieurs des sanctions suivantes : a) l'annulation de l'épreuve ou du travail; b) l'échec de l'activité; c) la suspension pendant un ou plusieurs trimestres pour une durée ne pouvant excéder vingt-quatre (24) mois; d) la recommandation au Conseil de l'exclusion de l'Université pour une période ne pouvant excéder cinq (5) ans.

Pour obtenir plus d'information sur le droit d'auteur et pour prendre connaissance des questions courantes sur le sujet, consultez *Le guide du droit d'auteur* de l'Office de la propriété intellectuelle du Canada. Reportez-vous également à la *Politique sur la reconnaissance et la protection de la propriété intellectuelle de l'UQAR*.

CONCLUSION GÉNÉRALE

Cette thèse vise à réexaminer l'origine des chondrichthyens en proposant un cadre méthodologique renouvelé destiné à limiter les biais inhérents à la reconstruction des caractères morphologiques, à l'inférence phylogénétique et à l'interprétation des dynamiques macro-évolutives. Elle combine des analyses sur le développement de structure telle que les aiguillons de nageoires, les écailles ou encore les dents. Elle intègre également des analyses en histologie, sur la morphologie et l'anatomie des chondrichthyens basaux. L'ensemble de ces analyses est couplé à une approche phylogénétique multi-méthodologique, intégrant des phylogénies basées sur des modèles ou encore sur le maximum de parcimonie. Ce travail apporte une contribution significative à notre compréhension de l'évolution précoce des vertébrés à mâchoires et, plus spécifiquement, à l'étude des transitions évolutives majeures au sein de la lignée des chondrichthyens souches.

Le premier chapitre vise à décrire le schéma de développement des aiguillons de nageoires chez le chondrichthyen du Givétien moyen *Wellerodus priscus*. Cette étude contribue à fournir de nouveaux caractères morphologiques fondés sur des composantes développementales plutôt que sur des caractères strictement fonctionnels ou purement morphologiques dans le cadre des analyses phylogénétiques. Ce type d'approche n'a jamais été testé chez les représentants dévoniens de la lignée des chondrichthyens souches. En effet, les seuls taxons apparentés aux chondrichthyens ayant fait l'objet de telles analyses concernaient principalement des représentants plus récents, tels que les Holocéphales (Jerve *et al.*, 2014) ou encore les requins hétérodontiformes (Tovar-Avila *et al.*, 2008). De plus, le schéma de croissance des aiguillons de nageoires a été plus spécifiquement étudié chez des requins du Carbonifère (Soler-Gijon, 1999) et du Permien (Beck *et al.*, 2016).

Malgré la faible attention accordée aux structures dermiques chez les premiers chondrichthyens, ces structures fournissent des informations développementales précieuses (Cloutier, 2010 ; Cui *et al.*, 2021). Des caractéristiques telles que la morphologie (taille et

forme), l'ornementation et l'histologie des aiguillons de nageoires, en particulier les types de tissus et leur organisation, offrent des indications sur les schémas de croissance, même en l'absence d'une série ontogénétique (Jerve *et al.*, 2017 ; Maisey, 1979 ; Beck *et al.*, 2016). En combinant les analyses de ces caractéristiques, le schéma de développement des aiguillons de nageoires de *Wellerodus priscus* a révélé un mode de croissance à deux axes. Une croissance longitudinale se produit principalement à la base proximale de l'aiguillon, près de la zone d'insertion, tandis qu'une croissance transversale est constatée sur l'ensemble de l'aiguillon, comme l'indiquent les divergences des crêtes tuberculées qui recouvrent l'aiguillon. Les deux axes de croissance sont soutenus par la présence de tissus fortement vascularisés dans leurs zones de production respectives. Des tubercules fusionnés aux extrémités proximale et distale suggèrent que l'expansion en largeur se poursuit tout au long de la vie de l'organisme, même après la formation des tubercules proximaux. De plus, la croissance en largeur diminue distalement, bien qu'elle reste active, comme en témoignent les tissus vascularisés localisés dans les tubercules du bord antérieur près de l'apex.

Cette étude a proposé un schéma de développement des aiguillons de nageoires chez un chondrichthyen du Givétien moyen pouvant être comparé à des formes étroitement apparentées. Parmi ces proches parents figurent *Antarctilamna prisca* (Young, 1982) et certains requins fossiles de Bolivie (Ritcher *et al.*, 2017). Ils partagent des similarités d'ornementation en termes de zones de divergence dans les crêtes tuberculées ainsi qu'une composition histologique presque identique (Young, 1982 ; Ritcher *et al.*, 2017). Chez des formes moins similaires, mais toujours proches du point de vue des affinités phylogénétiques, on trouve *Doliodus latispinosus*, ainsi que des requins du Permien tels que *Sphenacanthus ignis* et *Bythiacanthus lopesi* (Figueroa & Gallo, 2017). Ceux-ci présentent des zones de divergence dans les crêtes ornementales indiquant une expansion en largeur ; toutefois, ces zones sont confinées à la base de l'aiguillon plutôt qu'au bord antérieur (Burrow *et al.*, 2017). Des formes plus éloignées sont représentées par les requins sinacanthidés du Silurien, en particulier *Sinacanthus*, qui présentent un schéma différent : les divergences des crêtes se produisent sur toute la longueur de l'aiguillon plutôt que d'être localisées (Liu *et al.*, 2024). En termes de comparaison, l'aspect majeur qui diffère concerne les divergences dans

l'ornementation de l'aiguillon de nageoire plutôt que la composition histologique, même chez d'autres formes précoces des chondrichthyens, tels que les formes énigmatiques de gyracanthides (Gess & Burrow, 2023 ; Burrow *et al.*, 2008).

Bien que notre étude propose un nouveau schéma de développement pour un chondrichthyen du Givétien moyen, elle met en évidence certaines limites. Nous avons exploré la composition histologique des aiguillons de nageoires pectorales d'une seule espèce. Malgré notre hypothèse quant au caractère juvénile des spécimens, nous manquons de preuves concernant le développement ontogénétique, notamment d'une séquence claire permettant de valider nos hypothèses sur le schéma de développement de l'aiguillon de nageoire. De plus, nous présentons des coupes histologiques pour une aiguillon de nageoire pectorale. Bien que nous ayons réalisé des scans micro-CT sur une aiguillon de nageoire dorsale, la résolution est insuffisante pour étendre nos hypothèses à cette dernière. Nos résultats suggèrent que l'ornementation constitue une composante importante de la caractérisation du schéma de développement, mais qu'elle représente également une potentielle variable homoplasique. Néanmoins, nos résultats suggèrent que chez *Wellerodus priscus*, le développement peut être exploré à travers cette composante, mais des analyses supplémentaires sont nécessaires sur d'autres chondrichthyens précoces afin de mieux supporter cette interprétation.

Le développement des aiguillons de nageoires chez les chondrichthyens n'a été étudié qu'au travers *Wellerodus priscus*, et nous manquons de données pour les autres chondrichthyens précoces. Dans ce chapitre, nous avons également considéré que les aspects développementaux constituent de meilleurs candidats pour refléter la nature homologue des caractères plutôt que des conditions homoplasiques. Néanmoins, nos résultats du premier chapitre ne permettent pas de valider cette hypothèse. La nature des caractères est principalement examinée dans le deuxième chapitre.

Le deuxième chapitre de cette thèse vise à intégrer les avancées réalisées dans la compréhension du développement des aiguillons de nageoires, et autres structures dermiques mentionnées, afin de les traduire en nouveaux caractères morphologiques dans le cadre de l'étude de l'origine des chondrichthyens. En effet, ce chapitre explore spécifiquement les

différentes hypothèses concernant l'origine des chondrichthyens. À savoir si les mongolépидидés sont des chondrichthyens précoces, si les thélodontes sont plus proches des chondrichthyens que ne le suggère leur position actuelle dans le groupe souche des gnathostomes, ou encore si l'origine des chondrichthyens du groupe-couronne est liée aux acanthodiens et si leur nœud de couronne est calibré autour de 390-400 millions d'années comme proposé dans la littérature récente (Coates *et al.*, 2018 ; Schnetz *et al.*, 2024 ; Janvier & Pradel, 2015). De plus, compte tenu de l'ampleur du jeu de données utilisé, nous explorons les relations internes entre les principaux groupes de gnathostomes du groupe-souche et du groupe-couronne. De cette manière, nous apportons des éléments supplémentaires en faveur de la nature phylogénétique des placodermes, qui reste débattue (Burrow & Turner, 1999 ; Goujet & Young, 2004 ; King *et al.*, 2017), ainsi que des relations des « agnathes » avec les gnathostomes, qui présentent encore des limites quant à l'identification du groupe le plus proche des gnathostomes (Forey & Janvier, 1993 ; Gagnier, 1993 ; Forey, 1995 ; Donoghue *et al.*, 2000 ; Donoghue & Smith, 2001 ; Gai & Zhu, 2012 ; Gai *et al.*, 2022).

L'intégration des caractères nouvellement définis dans une supermatrice morphologique à grande échelle comprenant 320 taxons et 977 caractères constitue une autre contribution centrale de cette thèse. Cette matrice, assemblée à partir de données précédemment publiées et de nouveaux caractères définis, a été rigoureusement standardisée afin de réduire la redondance, les ambiguïtés dans la description et les biais associés à des caractères morphologiques potentiellement homoplasiques. L'utilisation d'une syntaxe descriptive homogène et d'ontologies morphologiques visent à améliorer la reproductibilité analytique et la comparabilité des résultats, fournissant ainsi un outil durable pour les études futures des vertébrés paléozoïques.

Un point majeur qui n'a pas été développé dans cette thèse concerne l'ajout de caractères morphologiques supplémentaires à la matrice. Plusieurs caractères ont été ajoutés selon les mêmes principes que ceux des aiguillons de nageoires mais pour les écailles et les dents. Des caractères développementaux ont été ajoutés pour les écailles et concernent principalement l'ultrastructure de la couronne des écailles et l'organisation des odontodes. Concernant les dents, divers rapports de longueur entre la couronne et la racine ont été

ajoutés, ainsi que de nombreux caractères relatifs à l'organisation des cuspidés. De plus, plusieurs caractères néomorphiques cruciaux liés à la morphologie générale ont été introduits, tels que la présence de structures largement reconnues (par exemple, le maxillaire). Bien que la description et le cadre ne soient pas spécifiquement détaillés dans cette thèse, l'ajout de ces nouveaux caractères a été réalisé de manière rigoureuse sur la base du cadre utilisé pour l'aiguillon de nageoire de *Wellerodus priscus*, ce qui signifie que les caractéristiques morphologiques, ornementales, histologiques et anatomiques ont été prises en compte dans une approche développementale.

Les analyses phylogénétiques menées à l'aide de cette supermatrice, en utilisant à la fois des approches fondées sur la parcimonie et des approches bayésiennes, avec et sans calibration temporelle, révèlent un signal phylogénétique robuste concernant l'origine des chondrichthyens. En particulier, les résultats soutiennent fortement une affinité étroite entre les thélodontes et les chondrichthyens du groupe total, plaçant ces « agnathes » à squelette cartilagineux comme groupe frère, voire comme espèces souches, des chondrichthyens. Cette position remet en question la vision traditionnelle des thélodontes comme vertébrés sans mâchoires basaux et suggère qu'ils partagent plusieurs traits morphologiques et écologiques (Ferrón & Botella 2017) clés avec les chondrichthyens, absents chez les autres « agnathes ». Bien que spéculative au regard du registre fossile actuel, l'hypothèse d'une mâchoire primitive non minéralisée chez les thélodontes apparaît plus parcimonieuse qu'une perte secondaire des mâchoires, compte tenu de l'importance fonctionnelle majeure de cette innovation dans l'évolution des vertébrés (Brazeau & Friedman, 2015).

Cette thèse apporte également de nouveaux éclairages sur les relations internes des gnathostomes précoces. Les résultats confirment la monophylie des ostéichthyens et renforcent l'hypothèse d'une relation évolutive étroite entre les « placodermes » maxillés et les ostéichthyens, tout en mettant en évidence une instabilité persistante du signal phylogénétique concernant la monophylie versus la paraphylie des « placodermes ». En revanche, les galéaspides et les ostéostracés émergent systématiquement comme les groupes les mieux soutenus parmi les gnathostomes souches, occupant une position de groupes externes clés pour l'étude des vertébrés à mâchoires, comme le suppose de nombreuses

études de la littérature (Shan *et al.*, 2020 ; Giammona, 2021 ; Miyashita *et al.*, 2025 ; Gai & Zhu, 2012 ; Gai *et al.*, 2022). Ensemble, ces résultats illustrent à la fois les progrès permis par des jeux de données morphologiques enrichis et les limites inhérentes à l'interprétation de clades dominés par du matériel fossile fragmentaire.

Néanmoins, plusieurs limites ressortent de cette étude. L'objectif global était de fournir un nouveau jeu de données adapté aux analyses phylogénétiques des lignées de gnathostomes, avec un accent particulier sur la lignée des chondrichthyens. Dans cette optique, l'objectivité a été considérée comme essentielle. Cependant, plusieurs caractères manquent d'une description fondée sur des ontologies et ne s'inscrivent pas correctement dans le « Entity-Quality Formalism ». Ces caractères représentent moins de 10 % de la matrice globale, mais ils contribuent néanmoins à une moindre interopérabilité de l'ensemble et nécessitent probablement une refonte complète. De plus, la représentativité des taxons est inégale. La lignée des chondrichthyens est surreprésentée par rapport aux autres, ce qui pourrait influencer les résultats, notamment dans les analyses de type tip-dating. Par ailleurs, certains taxons clés manquent dans la matrice. En effet, malgré l'intégration de thélodontes encore peu représentés, de nombreux taxons tels que les hétérostracés, les pituriaspides et les anaspides ne sont pas inclus. La topologie des arbres obtenus pourrait être affectée par l'intégration de ces taxons, notamment en raison de la présence de structures comparables aux odontodes chez d'autres groupes d'« agnathes » (Grohgan *et al.*, 2015) et de la possible présence d'écailles placoides chez les hétérostracés (Keating *et al.*, 2015), susceptibles de produire un signal phylogénétique différent. Afin de pallier ces limites et de tester les relations phylogénétiques dans une perspective plus large, les hétérostracés, les anaspides et les pituriaspides devront être intégrés à la matrice, de même qu'un plus grand nombre de taxons pour les groupes déjà représentés.

Au-delà de la reconstruction phylogénétique, cette thèse inscrit l'origine des chondrichthyens dans un cadre macroévolutif plus large. Les analyses des taux d'évolution morphologique montrent que la lignée des chondrichthyens se distingue par des taux exceptionnellement élevés et soutenus sur 80 millions d'années. Ce qui en fait la trajectoire évolutive la plus rapide parmi les gnathostomes précoces (à l'exception de la lignée des

ostéichthyens). Cette dynamique ne se limite pas à un événement de radiation bref, mais reflète plutôt une succession de phases d'évolution accélérée, suggérant un processus progressif mais intense d'innovation morphologique.

Les analyses de diversification révèlent un changement majeur de taux à la base des chondrichthyens, indiquant une augmentation significative de la diversification des lignées après leur divergence des thélodontes. De plus, les analyses de disparité morphologique identifient un événement marqué de disparification durant le Famennien, survenant après les pics de taux évolutifs et de diversification. Ce décalage temporel suggère que l'augmentation de la disparité morphologique des chondrichthyens a précédé et potentiellement facilité la diversification taxonomique ultérieure, notamment au début du Carbonifère. Ainsi, l'histoire évolutive des chondrichthyens apparaît comme un exemple de pseudo-radiation, dans lequel l'innovation morphologique et la disparité jouent un rôle moteur distinct d'une simple augmentation de la richesse spécifique.

Malgré des résultats fortement étayés, plusieurs limites doivent être prises en compte. En effet, les taux d'évolution morphologique constituent l'un des points critiques. Afin d'évaluer correctement ces taux, leur comparaison pourrait révéler de nouvelles tendances si la représentativité des taxons était plus homogène (c'est-à-dire un nombre représentatif de la richesse spécifique pour chaque groupe). Par ailleurs, les taux de diversification ont été estimés à l'aide d'une technique récemment développée, appelée BAMM. Cette technique fait l'objet de diverses controverses (Meyer & Wiens, 2018 ; Meyer *et al.*, 2018), malgré l'intégration récente d'un cadre fossile (Mitchell *et al.*, 2019 ; Černý *et al.*, 2022). Une autre méthode aurait pu permettre de valider nos résultats, notamment des analyses supplémentaires dans BEAST2 avec découpage temporel (« time slice »). Concernant la mise en évidence d'un événement de disparification, il aurait été pertinent d'intégrer des formes du Carbonifère afin de vérifier si la tendance observée à la fin du Dévonien se maintient au Carbonifère inférieur.

Pris dans leur ensemble, les résultats de cette thèse soutiennent une vision de l'évolution des chondrichthyens comme un processus par étapes, caractérisé par une forte modularité développementale, des phases prolongées d'évolution morphologique rapide et

une diversification retardée. Cette perspective remet en question les modèles classiques de radiation adaptative rapide et souligne l'importance de considérer conjointement les dimensions phylogénétiques, développementales et macro-évolutives pour comprendre les grandes transitions évolutives.

De plus, cette thèse met en évidence le potentiel considérable des caractères développementaux et histologiques pour l'étude des vertébrés fossiles, en particulier dans les groupes où le squelette est soumis à de fortes variables taphonomiques le rendant incomplet ou biaisé. En proposant un cadre méthodologique intégratif et reproductible, ce travail ouvre de nouvelles perspectives pour des recherches futures visant à affiner la phylogénie des gnathostomes précoces, à tester plus explicitement les hypothèses d'homologie développementale et à mieux comprendre les mécanismes ayant conduit à l'émergence et au succès évolutif des chondrichthyens. En définitive, cette approche pourrait être étendue à d'autres clades fossiles, contribuant ainsi à une compréhension plus globale des processus structurant l'évolution du squelette et la biodiversité des vertébrés à travers les temps géologiques.

Plusieurs axes de cette thèse peuvent être améliorés à différents degrés. Afin d'aborder spécifiquement ces axes d'amélioration, plusieurs projets de suivi expérimental peuvent être envisagés. Le premier projet sera considéré comme un projet d'amélioration et visera à identifier les éléments pouvant être directement optimisés dans le jeu de données actuel et les méthodologies employées. Dans cette perspective, la liste des taxons et la reconstruction des caractères constituent les éléments principaux pouvant être améliorés aisément. L'un des points discutables de la matrice actuelle est l'inégale représentativité des groupes, bien que les méthodes utilisées permettent de produire des résultats robustes sans une égalité dans le nombre de taxons au sein des différents groupes. Nous avons mentionné précédemment que plusieurs taxons pourraient être ajoutés. Au-delà de cela, et compte tenu de la position systématique de plusieurs taxons de gnathostomes souches, tels que les galéaspides (Janvier *et al.*, 1993 ; Min, 1992 ; Zhikun *et al.*, 2005 ; Janvier, 2008), les ostéostracés (Forey & Janvier, 1993 ; Gagnier, 1993 ; Forey, 1995 ; Donoghue *et al.*, 2000 ; Donoghue & Smith, 2001), les hétérostracés (Randle & Sansom, 2017) et les thélodontes

(Donoghue & Keating, 2014 ; Qu *et al.*, 2013 ; Janvier, 2008 ; Cui *et al.*, 2019), il serait intéressant d'améliorer la résolution à la racine des vertébrés en incluant également les anaspides et le groupe controversé des conodontes (Ginot & Goudemand, 2020). Afin d'éviter tout biais lié à la représentativité des taxons, le même travail réalisé pour le groupe des chondrichthyens devrait être appliqué à l'ensemble des taxons de vertébrés connus, en intégrant tout le spectre des espèces connues du Cambrien au Carbonifère. En outre un inventaire exhaustif des espèces connues. Un travail considérable est nécessaire pour atteindre cet objectif, mais cela renforcerait probablement le signal phylogénétique des différents taxons ajoutés et permettrait de mieux soutenir les résultats obtenus. En plus de la représentativité des taxons, les caractères morphologiques nécessitent une refonte complète. Malgré la standardisation et l'ajout de nouveaux caractères morphologiques fondés sur le développement, un point intéressant reste à explorer : la construction d'une matrice reposant uniquement sur des caractères développementaux afin de tester la pertinence de ces derniers.

Le deuxième projet peut être considéré comme un projet d'approfondissement. L'une des limites identifiées pourrait être liée à l'échelle temporelle elle-même. Le signal des chondrichthyens du groupe-couronne est faiblement représenté et a fourni un soutien limité dans les analyses de type tip-dating. En étendant l'intervalle temporel jusqu'au Carbonifère, il serait également possible d'intégrer des « acanthodiens » dérivés, avec des espèces mieux connues, notamment en ce qui concerne leur neurocrâne (Brazeau, 2009). De plus, le Carbonifère est connu pour l'explosion de la diversité des chondrichthyens (Schnetz *et al.*, 2024), avec la diversification de taxons clés tels que les Holocephali et les Xenacanthiformes (Boivert *et al.*, 2019). De cette manière, il serait également possible d'intégrer davantage de taxons clés appartenant aux chondrichthyens du groupe-couronne. L'extension de l'échelle temporelle permettrait un meilleur suivi des taux d'évolution morphologique, des taux de diversification, et offrirait également la possibilité de valider les hypothèses de disparition au Dévonien supérieur et au Carbonifère inférieur. Il convient de noter que le jeu de données actuel intègre des espèces décrites avant 2021. Des taxons clés doivent encore être incorporés, tels que *Fanjingshania renovata* (Andreev *et al.*, 2022) ou *Qianodus duplicis*

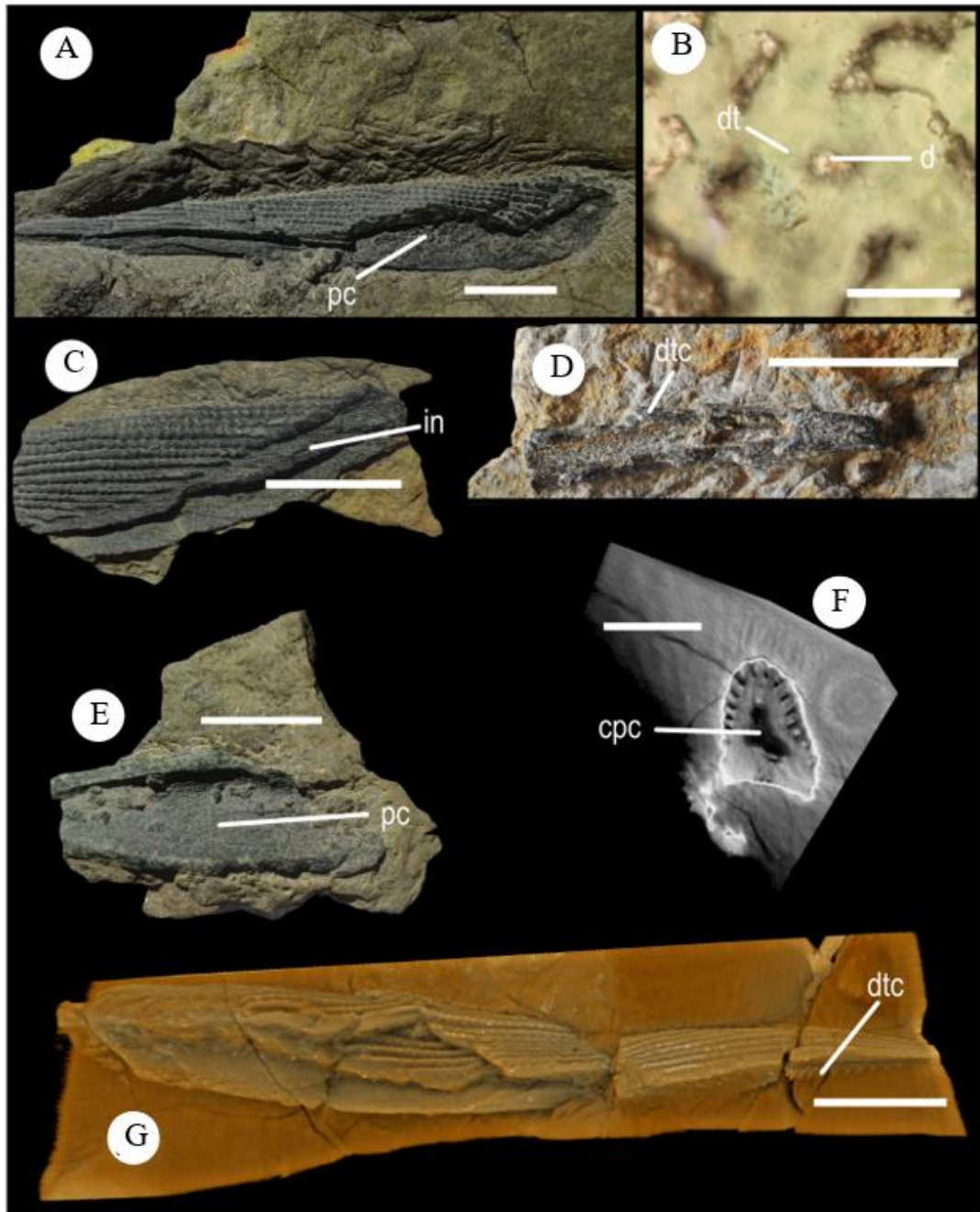
(Andreev *et al.*, 2022), afin d'évaluer les lacunes temporelles dans la lignée des chondrichthyens souches.

Un troisième projet, s'inscrivant également dans une perspective d'approfondissement, consisterait à explorer les facteurs abiotiques et biotiques de l'évolution dans la lignée des chondrichthyens souches. Les variations des courbes de diversité et de disparité enregistrées lors de la transition entre les chondrichthyens du Siluro-Dévonien et les chondrichthyens souches seraient comparées aux changements climatiques, géographiques et biotiques majeurs survenus entre 484 et 360 millions d'années afin d'établir des corrélations. Les dynamiques de diversification sont largement reconnues comme étant influencées à la fois par des facteurs biotiques (Van Valen, 1973) et abiotiques (Barnosky, 2001). Dans cette optique, plusieurs facteurs abiotiques (variables) pourraient avoir un impact significatif sur la transition entre les chondrichthyens du Siluro-Dévonien et les chondrichthyens souches, tels que la température moyenne globale basée sur les valeurs de $\delta^{18}\text{O}$ (Prokoph *et al.*, 2008), la concentration atmosphérique en O_2 (Scott & Glasspool, 2006 ; Berner, 2003), la fragmentation continentale (Zaffos *et al.*, 2017) et le niveau marin (Haq & Schutter, 2008). Ces facteurs abiotiques seraient modélisés à l'aide de variables telles que la variation de $\delta^{18}\text{O}$ au cours du temps, la concentration en O_2 au cours du temps ou les fluctuations du niveau marin. Par ailleurs, des facteurs biotiques tels les interactions écologiques (comme la compétition) ou l'apparition de nouveaux caractères augmentant la valeur adaptative des taxons pourraient également jouer un rôle déclencheur et seraient étudiés. Pour compléter une telle étude, une analyse paléogéographique des zones à forte diversité pourrait être corrélée à la phylogénie.

Enfin, un projet d'innovation pourrait émerger des bases posées dans cette thèse. La phylogénie en paléontologie est sujette à de nombreux biais liés aux fossiles et à la disponibilité des données morphologiques. Une nouvelle approche doit être explorée concernant la reconstruction des caractères et la standardisation des jeux de données. Un tel projet pourrait reposer sur le développement d'une nouvelle plateforme intégrative dédiée à la reconstruction des caractères, qui définirait précisément l'utilisation des caractères néomorphiques et transformationnels à l'aide de morphèmes spécifiques. Bien que certaines

plateformes existent déjà tel que Phenex (Balhoff *et al.*, 2010), celle-ci est incomplète et mal adapté pour les fossiles. Il est essentiel de centraliser ces données afin d'améliorer l'interopérabilité des caractères morphologiques afin d'assurer une meilleure inter communicabilité.

ANNEXES



Annex 1: Middle Devonian shark, *Wellerodus priscus*, fin spines remains; (A) Dorsal fin spine NYSM 19051-2 in lateral view, exposing central pulp cavity and external ornamentation; (B) Histological view of specimen NYSM 19057, showing a denteon with dentine tubules; (C) insertion zone of spine NYSM 19056 showing striation; (D) Ventral surface of pectoral fin spine NYSM 19060 showing thorn-like denticles; (E) Ventral surface exposing central pulp cavity in fin spine NYSM 19051-3; (F) CT-Scan middle section of fin pectoral fin spine NYSM 19057 exposing asymmetrical profil; (G) Complete fin spine NYSM 19057 before histological cuts. Abbreviations: cpc = central pulp cavity, d = denteon, dt = dentine tubule, dtc = denticles, in= insertion zone, pc = pulp cavity. Scale bar = 1 cm for (A), (C), (D), (E), (F), (G) and 100 μ m for (B).

Annex 2: character list

This annex aims to describe each morphological character used in the various matrices for this thesis. The morphological characters are split into various sections attributed to specific anatomical parts of early vertebrates. For each character, there are the number of the character, the standardized name of the character that follows the format described in the general introduction, the character states, the associated ontology identification, a description of the character if needed, and the corresponding number for the previous matrix if applicable. All new added characters are mentioned by a (N) before the name.

SKELETAL HISTOLOGY

1. Prismatic cartilage

Absent (0)

Present (1)

UBERON 0018352 Prismatic cartilage: Cartilage arranged into tesserae, blocks of calcified cartilage that fit together as tiles on a floor form a mosaic.

Zhu *et al.*, 2013 (1), Davis *et al.*, 2012 (1), Long *et al.*, 2014 (1), Dupret *et al.*, 2014 (1), Giles *et al.*, 2015 (1), Lu *et al.*, 2016 (1), Qiao *et al.*, 2016 (1), Chevrinais *et al.*, 2017 (1), King *et al.*, 2017 (1)

2. Prismatic cartilage, organisation of

Single monolayer (0)

Multiple monolayers (1)

Single polylayer (2)

Layers connected by a trough-stone (arrowed) (3)

Voussoirs (arrowed) forming and defining an arch (4)

UBERON 0018352 Prismatic cartilage: Cartilage arranged into tesserae, blocks of calcified cartilage that fit together as tiles on a floor form a mosaic.

Long *et al.*, 2014 (2), Giles *et al.*, 2015 (2), Lu *et al.*, 2016 (2), Qiao *et al.*, 2016 (253), King *et al.*, (2)

3. Perichondral bone

Present (0)

Absent (1)

UBERON 0008913 Perichondral bone: Bone element that is located on the surface of a cartilage element.

Grogan & Lund 2000, 2004, 2008, 2009, 2012 (0 in part), Brazeau 2009 (2), Davis *et al.*, (2), Zhu *et al.*, 2013 (2), Long *et al.*, 2014 (3), Dupret *et al.*, 2014 (2), Giles *et al.*, 2015 (3), Lu *et al.*, 2016 (3), Qiao *et al.*, 2016 (2), Chevriniais *et al.*, 2017 (2), King *et al.*, (3)

4. Endochondral bone

Absent (0)

Present (1)

UBERON 0002513 Endochondral bone: Replacement bone that forms within cartilage.

Zhu *et al.*, 2009 (30)

5. Endochondral ossification

Extensive (0)

Limited (1)

This refers to endochondral bone typified by a strongly developed and widely distributed spongiosa inside the interperichondral space – Brazeau (2009)

Brazeau 2009 (3), Davis *et al.*, 2012 (3), Zhu *et al.*, 2013 (3), Long *et al.*, 2014 (4), Giles *et al.*, 2015 (4), Lu *et al.*, 2016 (4), Qiao *et al.*, 2016 (3), Chevriniais *et al.*, 2017 (3), King *et al.*, 2017 (4)

6. Craniocervical region, dermal skeleton, type of bone

Cellular bone tissue (0)

Acellular bone tissue (1)

UBERON 0007811 Craniocervical region: The anteriormost subdivision of the body that includes the head, jaws, pharyngeal region and the neck (if present). In vertebrates this is the subdivision that includes the cervical vertebrae.

UBERON 0010364 Dermal skeleton: Skeletal subdivision that undergoes direct development and includes elements that either develop in association with the basement membrane of the ectoderm or are homologous with such elements; includes dermatocranium, components of the appendicular skeleton, teeth and tooth-like elements of the oropharynx, and integumentary elements.

UBERON 4000118 Cellular bone tissue: Mineralized bone tissue that always includes non-terminally differentiated osteoblasts and osteocytes

UBERON 4000122 Acellular bone tissue: Mineralized bone tissue that has terminally differentiated osteoblasts but lacks osteocytes.

Long *et al.*, 2014 (7), King *et al.*, 2017 (7)

7. Aspidin

Absent (0)

Present (1)

The term ‘aspidin’ was initially conceived to describe only the middle layer of the heterostracan dermal skeleton. Its use has subsequently been expanded to describe seemingly acellular dermal skeletal tissues in galeaspid, thelodont and anaspids, despite the fact that these tissues differ from aspidin *sensu stricto* both in terms of topology and histology. Details : aspidin developed around an extensive vascular network of anastomosing canals and/or interconnected polygonal cancellae. The cancellar trabecular walls are bipartite in

construction, consisting of lamellar layers (next to the vascular lumina) and a homogenous biomineral core. The lamellar tissue developed centripetally, resulting in constriction of the vascular spaces. The mineral matrix consists of elongate bundles (reflecting the fabric of the original collagen mesh) measuring 1–3 μm in diameter, which form a circumferential interlaced fabric enveloping the vascular spaces.

8. Galeaspidin

Absent (0)

Present (1)

Histological structure of the exoskeleton that shows a layer of small dermal units fused side by side and made up of horizontally zonated acellular bone.

Long *et al.*, 2014 (9), King *et al.*, 2017 (9)

9. Ganoine

Absent (0)

Present (1)

UBERON 4000104 Ganoine: Odontogenic tissue that is hypermineralized acellular, noncollagenous, covered by an epidermis and often deposited in multiple layers.

Zhu *et al.*, 2009 (149)

10. Dermal bones, enamel

Absent (0)

Present (1)

UBERON 0001752 Enamel: A dentine-like hypermineralized substance that covers the tooth tip. Enamel's primary mineral is hydroxylapatite, which is a crystalline calcium phosphate. Unlike dentin and bone, enamel does not contain collagen. Instead, it has two unique classes of proteins called amelogenins and enamelines.

UBERON 0008907 Dermal bone: Skeletal element that forms superficially in the organism, usually in association with the ectoderm.

Giles *et al.*, 2015 (5), Lu *et al.*, 2016 (5), Qiao *et al.*, 2016 (254), King *et al.*, 2017 (15)

11. Dermal skeleton, three layers

Absent (0)

Present (1)

UBERON 0010364 Dermal skeleton: Skeletal subdivision that undergoes direct development and includes elements that either develop in association with the basement membrane of the ectoderm or are homologous with such elements; includes dermatocranium, components of the appendicular skeleton, teeth and tooth-like elements of the oropharynx, and integumentary elements.

Long *et al.*, 2014 (6), King *et al.*, 2017 (6)

12. Sensory canals and vascular system, perforated horizontal lamina

Absent (0)

Present (1)

UBERON 2001612 Sensory canal: Multi-tissue structure that is a fluid-filled canal in the integument and usually dermal bones, and contains one or more neuromast organs.

Sensory canals usually communicate with the environment via pores in the sensory canal or at the distal ends of tubules, which extend from canal where pores would otherwise be.

Long *et al.*, 2014 (8), King *et al.*, 2017 (8)

13. Dermal armor, superficial glassy layer

Absent (0)

Present (1)

In some thyestiid Osteostraci, a layer of ‘enameloid’ is noted (Denison 1951b; Janvier 1985c) to occur overlaying the superficial/dentinous layer – King *et al.*, 2017

King *et al.*, 2017 (18)

DENTITION

14. Teeth

Absent (0)

Present (1)

Oral dermal tubercles exhibiting organised patterning – Brazeau 2009

Brazeau 2009 (42), Giles *et al.*, 2015 (78 modified), Lu *et al.*, 2016 (78 modified)

15. (N) Teeth morphotype, number of

1 (0)

2 (1)

3 (2)

4 (3)

16. Teeth, enameloid

Absent (0)

Present (1)

UBERON 0011692 Enameloid: Skeletal tissue that is hypermineralized and aprismatic and deposited by a combination of ameloblasts and odontoblasts that are excluded from the matrix. Enameloid develops from pre-enameloid tissue.

Giles *et al.*, 2015 (79), Lu *et al.*, 2016 (79), Qiao *et al.*, 2016 (284), King *et al.*, 2017 (365)

17. Teeth, enameloid layers

Present (0)

Absent (1)

UBERON 0011692 Enameloid: Skeletal tissue that is hypermineralized and aprismatic and deposited by a combination of ameloblasts and odontoblasts that are excluded from the matrix. Enameloid develops from pre-enameloid tissue.

Grogan & Lund 2000 (35 in part), 2004 (41 in part), 2008 (47 in part)

18. Teeth, enameloid layers, structure of

Radial crystallite (0)

Complex (1)

UBERON 0011692 Enameloid: Skeletal tissue that is hypermineralized and aprismatic and deposited by a combination of ameloblasts and odontoblasts that are excluded from the matrix. Enameloid develops from pre-enameloid tissue.

Grogan & Lund 2000 (35 in part), 2004 (41 in part), 2008 (47 in part)

19. Teeth, true enamel

Absent (0)

Present (1)

Zhu *et al.*, 2009 (153)

20. Teeth, acrodin

Absent (0)

Present (1)

UBERON 4300212 Acrodin: odontoid tissue forming a cap on teeth found in teeth of actinopterygian fishes.

Zhu *et al.*, 2009 (151), Zhu *et al.*, 2013 (140), Long *et al.*, 2014 (140), Dupret *et al.*, 2014 (140), Giles *et al.*, 2015 (80), Lu *et al.*, 2016 (80), Qiao *et al.*, 2016 (136), Chevrinais *et al.*, 2017 (140), Coates *et al.*, 2017 (7 modified), King *et al.*, 2017 (342)

21. Teeth, dentine

Present (0)

Absent (1)

UBERON 0001751 Dentine: Collagen-rich odontogenic tissue characteristic of teeth and tooth-like skeletal elements (e.g., odontodes); mature dentine is mineralized and develops from predentine tissue; often (but not always) tubular and acellular. Dentine is a bona fide vertebrate novelty, and dentine-secreting odontoblasts represent a cell type that is exclusively derived from the neural crest.

22. Teeth, orthodentine

Present (0)

Absent (1)

UBERON 4000097 Orthodentine: Odontoid tissue that typically contains tubules and is acellular.

Grogan & Lund 2000 (36), 2004 (42), 2008 (48), Grogan *et al.*, 2012 (59)

23. (N) Teeth, mesodentine

Present (0)

Absent (1)

24. (N) Teeth, semidentine

Present (0)

Absent (1)

25. (N) Teeth, metadentine

Present (0)

Absent (1)

26. Teeth, osteodentine

Absent (0)

Present (1)

Grogan & Lund 2000 (37), 2004 (43), 2008 (49), Grogan *et al.*, 2012 (60)

27. (N) Teeth, plicidentine

Absent (0)

Present (1)

Plicidentine is a structural term that refers to the infolding of the dentine around the pulp cavity

28. Teeth, plicidentine, structure of

Polyplocodont (0)

Dendrodont (1)

Plicidentine is a structural term that refers to the infolding of the dentine around the pulp cavity

Zhu *et al.*, 2009 (152), Zhu *et al.*, 2013 (141), Long *et al.*, 2014 (141), Dupret *et al.*, 2014 (141), Giles *et al.*, 2015 (86), Lu *et al.*, 2016 (86), Qiao *et al.*, 2016 (137), King *et al.*, 2017 (343)

29. (N) Teeth, root, basal line, shape of

Straight (0)

Concave (1)

Convex (2)

UBERON 0003677 Root: The part of a tooth that is implanted in the gum; the root is normally located below the neck of the tooth, covered by cementum rather than enamel, and attached by the periodontal ligament to the alveolar bone

30. (N) Teeth, root, realtive size of

Larger than crown (0)

Smaller than crown (1)

Equal (2)

UBERON 0003677 Root: The part of a tooth that is implanted in the gum; the root is normally located below the neck of the tooth, covered by cementum rather than enamel, and attached by the periodontal ligament to the alveolar bone

31. (N) Teeth, root, configuration of

Larger than deep (0)

Deeper than large (1)

Equal (2)

UBERON 0003677 Root: The part of a tooth that is implanted in the gum; the root is normally located below the neck of the tooth, covered by cementum rather than enamel, and attached by the periodontal ligament to the alveolar bone

32. (N) Teeth, root, pores

Absent (0)

Present (1)

UBERON 0003677 Root: The part of a tooth that is implanted in the gum; the root is normally located below the neck of the tooth, covered by cementum rather than enamel, and attached by the periodontal ligament to the alveolar bone

33. (N) Teeth, root, pores, position of

Restricted to inferior surface (0)

All around the root (1)

Labial side (2)

Lingual side (3)

UBERON 0003677 Root: The part of a tooth that is implanted in the gum; the root is normally located below the neck of the tooth, covered by cementum rather than enamel, and attached by the periodontal ligament to the alveolar bone

34. (N) Teeth, labial peg

Absent (0)

Present (1)

35. Pharyngeal teeth

Absent (0)

Present (1)

36. (N) Oral cavity teeth

Absent (0)

Present (1)

UBERON 0000167 Oral cavity teeth: Anatomical cavity at the start of the digestive tract that is enclosed by the mouth. The boundaries and contents vary depending on the species. In vertebrates, the boundaries are the oral opening, the cheeks, the palate and (if present) the palatoglossal arch.

37. Oral cavity teeth, organisation of

Homodont (0)

Heterodont (1)

UBERON 0000167 Oral cavity teeth: Anatomical cavity at the start of the digestive tract that is enclosed by the mouth. The boundaries and contents vary depending on the species. In vertebrates, the boundaries are the oral opening, the cheeks, the palate and (if present) the palatoglossal arch.

Grogan & Lund 2000 (26 modified), 2004 (32 modified), 2008 (40 modified), Grogan *et al.*, 2012 (51 modified).

38. Jaw skeleton, tooth families, number of

1 to 4 (0)

5 to 9 (1)

10 to 15 (2).

UBERON 0001708 Jaw skeleton: Subdivision of skeleton which includes upper and lower jaw skeletons.

Grogan & Lund 2000 (24 modified), 2004 (29)

39. Dentary teeth, position of

Reaching symphysis of dentary (0)

Not reaching symphysis (1)

UBERON 0011594 Dentary teeth: Tooth that is attached to a dentary/mandible.

Zhu *et al.*, 2009 (87), Zhu *et al.*, 2013 (200), Long *et al.*, 2014 (200), Dupret *et al.*, 2014 (200), Qiao *et al.*, 2016 (204), Chevrinais *et al.*, 2017 (200), King *et al.*, 2017 (347)

40. Dermal bone, teeth, ankylose of

Absent (0)

Present (1)

UBERON 0008907 Dermal bone: Skeletal element that forms superficially in the organism, usually in association with the ectoderm.

Brazeau 2009 (46), Davis *et al.*, 2012 (43), Zhu *et al.*, 2013 (43), Long *et al.*, 2014 (43), Dupret *et al.*, (2014), Giles *et al.*, 2015 (85), Lu *et al.*, 2016 (85), Qiao *et al.*, 2016 (42), Chevrinais *et al.*, 2017 (43), King *et al.*, 2017 (331)

41. Dermal bones lining the oral cavity, linear and subparallel ridges of remodeled denticles

Absent (0)

Present (1)

UBERON 0000167 Oral cavity teeth: Anatomical cavity at the start of the digestive tract that is enclosed by the mouth. The boundaries and contents vary depending on the species. In vertebrates, the boundaries are the oral opening, the cheeks, the palate and (if present) the palatoglossal arch

UBERON 0008907 Dermal bone: Skeletal element that forms superficially in the organism, usually in association with the ectoderm.

Zhu *et al.*, 2009 (97)

42. Tooth plates

Absent (0)

Present (1)

Coates *et al.*, 2017 (44)

43. Median labial element, upper tooth plates, grooved and curved

Absent (0)

Present (1)

King *et al.*, 2017 (390)

44. Vomerine tooth, fang

Absent (0)

Present (1)

UBERON 0004767 Vomerine tooth: A tooth that is on the vomer.

Zhu *et al.*, 2009 (63), Zhu *et al.*, 2013 (235), Long *et al.*, 2014 (235), Dupret *et al.*, 2014 (235), Qiao *et al.*, 2016 (225), King *et al.*, 2017 (360)

45. Cusp of tooth

Absent (0)

Present (1)

UBERON 0006844 Cusp of tooth: A raised area of the biting surface of a tooth

Grogan & Lund 2000 (30 in part), 2004 (36 in part)

46. Cusp of tooth, shape of

Sharp (0)

Rounded (1)

UBERON 0006844 Cusp of tooth: A raised area of the biting surface of a tooth

Grogan & Lund 2000 (31 in part), 2004 (37 in part)

47. Cusp of tooth, number of

1 (0)

2 to 3 (1)

4 to 7 (2)

more than 7 (3)

UBERON 0006844 Cusp of tooth: A raised area of the biting surface of a tooth

Grogan & Lund 2008 (36 modified), Grogan *et al.*, 2012 (47 modified).

48. Cusp of tooth, organisation of

Central bigger (0)

Lateral bigger (1)

Same size (2)

UBERON 0006844 Cusp of tooth: A raised area of the biting surface of a tooth

Grogan & Lund 2008 (33 modified), Grogan *et al.*, 2012 (45 modified)

49. Cusp of tooth, separation of

Distinctly separate on base (0)

Cusps basally confluent (1)

UBERON 0006844 Cusp of tooth: A raised area of the biting surface of a tooth

Grogan & Lund 2008 (38 modified), Grogan *et al.*, 2012 (44 modified)

50. (N) Cusp of tooth, ornamentation of

Striated (0)

Smooth (1)

Crenellated (2)

Ridged (3)

Vermiform striae/ridges (4)

UBERON 0006844 Cusp of tooth: A raised area of the biting surface of a tooth

51. (N) Cusp of tooth, relative size of

Biggest cusps of same size (0)

Biggest cusps of different size (1)

UBERON 0006844 Cusp of tooth: A raised area of the biting surface of a tooth

52. (N) Different size among cusp of tooth, number of

2 (0)

3 (1)

>3 (2)

UBERON 0006844 Cusp of tooth: A raised area of the biting surface of a tooth

53. (N) Main cusp of tooth, shape of

Straight (0)

Curved (1)

Sigmoidally curved (2)

UBERON 0006844 Cusp of tooth: A raised area of the biting surface of a tooth

54. (N) Cusp of tooth, crenulation of

Absent (0)

Present (1)

UBERON 0006844 Cusp of tooth: A raised area of the biting surface of a tooth

55. Teeth, crown and root, configuration of

Hypsodont (0)

Equal or subequal (1)

Brachydont (2)

UBERON 0003675 Crown: The portion of the tooth covered by enamel

UBERON 0003677 Root: The part of a tooth that is implanted in the gum; the root is normally located below the neck of the tooth, covered by cementum rather than enamel, and attached by the periodontal ligament to the alveolar bone

Grogan & Lund 2008 (37), Grogan *et al.*, 2012 (48)

56. (N) Teeth, root, lingual button

Absent (0)

Present (1)

UBERON 0003677 Root: The part of a tooth that is implanted in the gum; the root is normally located below the neck of the tooth, covered by cementum rather than enamel, and attached by the periodontal ligament to the alveolar bone

57. (N) Teeth, crown base, labial ridge

Absent (0)

Present (1)

UBERON 0003675 Crown: The portion of the tooth covered by enamel

58. Tooth whorls

Absent (0)

Present (1)

UBERON 0014682 Tooth whorl: A spirally arranged cluster of teeth.

Brazeau 2009 (43), Davis *et al.*, 2012 (40), Zhu *et al.*, 2013 (40), Long *et al.*, 2014 (40), Dupret *et al.*, 2014 (40), Giles *et al.*, 2015 (81), Lu *et al.*, 2016 (81), Qiao *et al.*, 2016 (39), Chevrinais *et al.*, 2017 (40), Coates *et al.*, 2017 (39), King *et al.*, 2017 (328)

59. Tooth whorls, base of

Single continuous plate (0)

Some or all whorls consist of separate tooth units (1)

UBERON 0014682 Tooth whorl: A spirally arranged cluster of teeth.

Brazeau 2009 (44), Davis *et al.*, 2012 (41), Zhu *et al.*, 2013 (41), Long *et al.*, 2014 (41), Dupret *et al.*, 2014 (41), Giles *et al.*, 2015 (82), Lu *et al.*, 2016 (82), Qiao *et al.*, 2016 (40), Chevrinais *et al.*, 2017 (41), Coates *et al.*, 2017 (40), King *et al.*, 2017 (329)

60. (N) Skeleton of lower jaw, tooth whorls

Absent (0)

Present (1)

UBERON 0003278 Skeleton of lower jaw: A subdivision of the skeleton that corresponds to the lower part of the mouth. The lower jaw skeleton includes the following elements, when present: lower jaw teeth, the mandible and other lower jaw bones, and Meckel's cartilage

UBERON 0014682 Tooth whorl: A spirally arranged cluster of teeth.

61. (N) Skeleton of upper jaw, tooth whorls

Absent (0)

Present (1)

UBERON 0003277 Skeleton of upper jaw: A subdivision of the skeleton that corresponds to the upper part of the mouth. The lower jaw skeleton includes the following elements, when present: upper jaw teeth, the maxilla and other upper jaw bones

UBERON 0014682 Tooth whorl: A spirally arranged cluster of teeth.

62. Tooth whorls, distribution of

Entire length of tooth row (0)

Restricted to symphyseal region (1)

UBERON 0014682 Tooth whorl: A spirally arranged cluster of teeth.

Giles *et al.*, 2015 (83), Lu *et al.*, 2016 (83), Coates *et al.*, 2017 (43 modified)

63. Adsymphysial tooth whorls, enlarged

Absent (0)

Present (1)

UBERON 0014682 Tooth whorl: A spirally arranged cluster of teeth.

Brazeau 2009 (45), Davis *et al.*, 2012 (42), Zhu *et al.*, 2013 (42), Long *et al.*, 2014 (42), Dupret *et al.*, 2014 (42), Qiao *et al.*, 2016 (41), Chevrinais *et al.*, 2017 (42), King *et al.*, 2017 (330)

64. Tooth whorls, multiple

Absent (0)

Present (1)

UBERON 0014682 Tooth whorl: A spirally arranged cluster of teeth.

Burrow & Turner 68 (modified)

65. (N) Tooth rows

Absent (0)

Present (1)

UBERON 0009678 Tooth row: Anatomical cluster consisting of adjacent teeth constituting a row.

66. (N) Tooth row, size gradient of

Absent (0)

Present (1)

UBERON 0009678 Tooth row: Anatomical cluster consisting of adjacent teeth constituting a row.

67. Jaw skeleton, tooth row, relative size of

> 50% of the mandible (0)

< 50% of the mandible (1).

UBERON 0009678 Tooth row: Anatomical cluster consisting of adjacent teeth constituting a row.

UBERON 0001708 Jaw skeleton: Subdivision of skeleton which includes upper and lower jaw skeletons.

UBERON 0001684 Mandible: A dentary bone that is the only bone in one of the lateral halves of the lower jaw skeleton

Grogan & Lund 2008 (30 modified), 2009 (30 modified), Grogan *et al.*, 2012 (42 modified)

68. (N) Outer dental arcade (Premaxilla, Dentary, Dentoangular, or Dentigerous jaw bone), tooth row

Absent (0)

Present (1)

UBERON 0009678 Tooth row: Anatomical cluster consisting of adjacent teeth constituting a row.

UBERON 0002244 Premaxilla: one of the bones of the upper jaw situated between and in front of the maxillae

UBERON 0004742 Dentary: the dentary is a dermal bone that forms the antero-lateral part of the lower jaw in fishes and amphibians, extending to the whole lower jaw in mammals

69. Outer dental arcade (Premaxilla, Dentary, Dentalosplenial, or Dentigerous jaw bone), tooth row, number of

One (0)

Two (1)

UBERON 0009678 Tooth row: Anatomical cluster consisting of adjacent teeth constituting a row.

UBERON 0002244 Premaxilla: one of the bones of the upper jaw situated between and in front of the maxillae

UBERON 0004742 Dentary: the dentary is a dermal bone that forms the antero-lateral part of the lower jaw in fishes and amphibians, extending to the whole lower jaw in mammals

King *et al.*, 2017 (80)

70. (N) Tooth rows, longitudinal ridge between

Absent (0)

Present (1)

UBERON 0009678 Tooth row: Anatomical cluster consisting of adjacent teeth constituting a row.

71. (N) Inner dental arcade (coronoid bone or palatine bone), tooth row

Absent (0)

Present (1)

UBERON 0001682 Palatine bone: a paired dermal bone situated in the mid-palate that helps form the hard palate

UBERON 0009678 Tooth row: Anatomical cluster consisting of adjacent teeth constituting a row.

72. (N) Inner dental arcade (coronoid bone or palatine bone), tooth row, number of

One (0)

Two (1)

UBERON 0001682 Palatine bone: a paired dermal bone situated in the mid-palate that helps form the hard palate

UBERON 0009678 Tooth row: Anatomical cluster consisting of adjacent teeth constituting a row.

73. Prearticular bone, teeth radial rows

Absent (0)

Present (1)

UBERON 0011637 Prearticular bone: Osseous element of intramembranous origin that extends along the lingual margin of Meckel's cartilage

UBERON 0009678 Tooth row: Anatomical cluster consisting of adjacent teeth constituting a row.

King *et al.*, 2017 (384)

74. Outer dental arcade, larger monolinear tooth row

Absent (0)

Present (1)

UBERON 0009678 Tooth row: Anatomical cluster consisting of adjacent teeth constituting a row.

Zhu *et al.*, 2009 (74)

75. Infraorbital sensory canal, supramaxillary sensory canal, joins of

Present (0)

Absent (1)

UBERON 2001811 Infraorbital sensory canal: Sensory canal lateral or ventral to and in close proximity to the otic and supraorbital sensory canals at their union. The infraorbital sensory canal is bilaterally paired and associated with the infraorbital bones.

UBERON 2001612 Sensory canal: multi-tissue structure that is a fluid-filled canal in the integument and usually dermal bones and contains one or more neuromast organs. Sensory canals usually communicate with the environment via pores in the sensory canal or at the distal ends of tubules, which extend from canal where pores would otherwise be.

Davis *et al.*, 2012 (17), Zhu *et al.*, 2013 (17), Long *et al.*, 2017 (17), Dupret *et al.*, 2014 (17), Giles *et al.*, 2015 (32), Lu *et al.*, 2016 (32), Qiao *et al.*, 2016 (16), Chevrinais *et al.*, 2017 (17), King *et al.*, 2017 (284)

76. (N) Infraorbital sensory canal

Absent (0)

Present (1)

UBERON 2001811 Infraorbital sensory canal: Sensory canal lateral or ventral to and in close proximity to the otic and supraorbital sensory canals at their union. The infraorbital sensory canal is bilaterally paired and associated with the infraorbital bones.

77. (N) Lateral dorsal sensory canal

Present (0)

Absent (1)

UBERON 2001612 Sensory canal: multi-tissue structure that is a fluid-filled canal in the integument and usually dermal bones and contains one or more neuromast organs. Sensory canals usually communicate with the environment via pores in the sensory canal or at the distal ends of tubules, which extend from canal where pores would otherwise be.

78. (N) Lateral transverse sensory canal

Present (0)

Absent (1)

UBERON 2001612 Sensory canal: multi-tissue structure that is a fluid-filled canal in the integument and usually dermal bones and contains one or more neuromast organs. Sensory canals usually communicate with the environment via pores in the sensory canal or at the distal ends of tubules, which extend from canal where pores would otherwise be.

79. (N) Lateral dorsal sensory canal, dorsal commissure

Absent (0)

Present (1)

UBERON 2001612 Sensory canal: multi-tissue structure that is a fluid-filled canal in the integument and usually dermal bones and contains one or more neuromast organs. Sensory canals usually communicate with the environment via pores in the sensory canal or at the distal ends of tubules, which extend from canal where pores would otherwise be.

80. (N) Infraorbital sensory canal, lateral transverse sensory canal, number of

<3 (0)

≥3 (1)

UBERON 2001612 Sensory canal: multi-tissue structure that is a fluid-filled canal in the integument and usually dermal bones and contains one or more neuromast organs. Sensory canals usually communicate with the environment via pores in the sensory canal or at the distal ends of tubules, which extend from canal where pores would otherwise be.

UBERON 2001811 Infraorbital sensory canal: Sensory canal lateral or ventral to and in close proximity to the otic and supraorbital sensory canals at their union. The infraorbital sensory canal is bilaterally paired and associated with the infraorbital bones.

81. (N) Lateral dorsal sensory canal, lateral transverse sensory canal, number of
- <5 (0)
- ≥5 (1)

UBERON 2001612 Sensory canal: multi-tissue structure that is a fluid-filled canal in the integument and usually dermal bones and contains one or more neuromast organs. Sensory canals usually communicate with the environment via pores in the sensory canal or at the distal ends of tubules, which extend from canal where pores would otherwise be.

82. Median dorsal sensory canal
- Present (0)
- Absent (1)

UBERON 2001612 Sensory canal: multi-tissue structure that is a fluid-filled canal in the integument and usually dermal bones and contains one or more neuromast organs. Sensory canals usually communicate with the environment via pores in the sensory canal or at the distal ends of tubules, which extend from canal where pores would otherwise be.

King *et al.*, 2017 (310)

83. Supraorbital sensory canal

Absent (0)

Present (1)

UBERON 2001810 Supraorbital sensory canal: sensory canal anterior to and in close proximity to the otic and infraorbital sensory canals. The supraorbital sensory canal is bilaterally paired. supraorbital canal

King *et al.*, 2017 (307)

84. Supraorbital sensory canal, course of

Between anterior and posterior nostril (0)

Anterior to both nostril (1)

UBERON 2001810 Supraorbital sensory canal: sensory canal anterior to and in close proximity to the otic and infraorbital sensory canals. The supraorbital sensory canal is bilaterally paired.

Zhu *et al.*, 2009 (109), Zhu *et al.*, 2013 (187), Long *et al.*, 2014 (187), Dupret *et al.*, (187), Qiao *et al.*, 2016 (192), Chevrinais *et al.*, 2017 (187), King *et al.*, 2017 (290)

85. Supraorbital sensory canal, shape of

Straight (0)

Lyre-shaped (1)

UBERON 2001810 Supraorbital sensory canal: sensory canal anterior to and in close proximity to the otic and infraorbital sensory canals. The supraorbital sensory canal is bilaterally paired.

Zhu *et al.*, 2009 (110), Zhu *et al.*, 2013 (188), Long *et al.*, 2014 (188), Dupret *et al.*, (188), Qiao *et al.*, 2016 (193), Chevrinais *et al.*, 2017 (188), King *et al.*, 2017 (291)

86. Supraorbital sensory canal, posterior end, position of

Extends back to level posterior/middle pit-lines (0)

Terminates anterior to level of posterior/middle pit-lines (1)

Extends posterior to pit-lines (2)

UBERON 2001810 Supraorbital sensory canal: sensory canal anterior to and in close proximity to the otic and infraorbital sensory canals. The supraorbital sensory canal is bilaterally paired.

Zhu *et al.*, 2009 (111), Zhu *et al.*, 2013 (189 modified), Long *et al.*, 2014 (189 modified), Dupret *et al.*, (189 modified), Qiao *et al.*, 2016 (194 modified), Chevrinais *et al.*, 2017 (189 modified), King *et al.*, 2017 (292)

87. Supraorbital sensory canal, infraorbital sensory canal, joins, position of

Anterior to supraoral sensory canal (0)

Posterior to supraoral sensory canal (1)

UBERON 2001810 Supraorbital sensory canal: sensory canal anterior to and in close proximity to the otic and infraorbital sensory canals. The supraorbital sensory canal is bilaterally paired.

UBERON 2001811 Infraorbital sensory canal: Sensory canal lateral or ventral to and in close proximity to the otic and supraorbital sensory canals at their union. The infraorbital sensory canal is bilaterally paired and associated with the infraorbital bones.

King *et al.*, 2017 (322)

88. (N) Supraorbital sensory canal, otic sensory canal, contact of

Absent (0)

Present (1)

UBERON 2001629 Otic sensory canal: sensory canal between and in close proximity posteriorly with the post-otic and preoperculo-mandibular sensory canals, and anteriorly with the supraorbital and infraorbital sensory canals. The otic sensory canal is bilaterally paired.

UBERON 2001810 Supraorbital sensory canal: sensory canal anterior to and in close proximity to the otic and infraorbital sensory canals. The supraorbital sensory canal is bilaterally paired.

89. Rostral plate, supraorbital sensory canal, infraorbital sensory canal, contact of

Present (0)

Absent (1)

UBERON 2001934 Rostral plate: dermal bone that is located on midline of snout in skin above mesethmoid and lateral ethmoid bones. Rostral plate bears type 1 odontodes and is unpaired

UBERON 2001810 Supraorbital sensory canal: sensory canal anterior to and in close proximity to the otic and infraorbital sensory canals. The supraorbital sensory canal is bilaterally paired.

UBERON 2001811 Infraorbital sensory canal: Sensory canal lateral or ventral to and in close proximity to the otic and supraorbital sensory canals at their union. The infraorbital sensory canal is bilaterally paired and associated with the infraorbital bones.

Zhu *et al.*, 2009 (113), Zhu *et al.*, 2013 (191), Long *et al.*, 2014 (191), Dupret *et al.*, (191), Qiao *et al.*, 2016 (196), Chevrinais *et al.*, 2017 (196), King *et al.*, 2017 (294)

90. Otic sensory canal, course of

Runs through skull roof (0)

Follows edge of skull roof (1)

UBERON 2001629 Otic sensory canal: sensory canal between and in close proximity posteriorly with the post-otic and preoperculo-mandibular sensory canals, and anteriorly with the supraorbital and infraorbital sensory canals. The otic sensory canal is bilaterally paired.

Zhu *et al.*, 2009 (114), Zhu *et al.*, 2013 (192), Long *et al.*, 2014 (192), Dupret *et al.*, (192), Qiao *et al.*, 2016 (197), Chevrinais *et al.*, 2017 (192), King *et al.*, 2017 (295)

91. Maxillary-premaxillary suture, infraorbital sensory canal, course of

Absent (0)

Present (1)

UBERON 0035884 Maxillary-premaxillary suture : A suture between the maxilla and premaxilla

UBERON 4200215 Suture : Line of junction between two parts immovably connected

Zhu *et al.*, 2009 (115 modified), Zhu *et al.*, 2013 (193 modified), Long *et al.*, 2014 (193 modified), Dupret *et al.*, (193 modified), Qiao *et al.*, 2016 (198 modified), Chevrinais *et al.*, 2017 (193 modified), King *et al.*, 2017 (296)

92. Maxilla, sensory canal or pit-line, association of

Absent (0)

Present (1)

UBERON 0002397 Maxilla: The bone which normally forms the lateral upper jaw in osteichthyans, including tetrapods.

UBERON 2001612 Sensory canal: multi-tissue structure that is a fluid-filled canal in the integument and usually dermal bones and contains one or more neuromast organs. Sensory canals usually communicate with the environment via pores in the sensory canal or at the distal ends of tubules, which extend from canal where pores would otherwise be.

Zhu *et al.*, 2009 (116), Zhu *et al.*, 2013 (194), Long *et al.*, 2014 (194), Dupret *et al.*, (194), Qiao *et al.*, 2016 (199), Chevrinais *et al.*, 2017 (194), King *et al.*, 2017 (297)

93. Most posterior infradentary, mandibular sensory canal, course of

Absent (0)

Present (1)

UBERON 2001814 Mandibular sensory canal: sensory canal anterior and ventral to and in close proximity with the preoperculo-mandibular sensory canal. The mandible sensory canal is bilaterally paired and associated with the angular and dentary bones.

Zhu *et al.*, 2009 (119), Zhu *et al.*, 2013 (217), Long *et al.*, 2014 (217), Dupret *et al.*, (217), Qiao *et al.*, 2016 (217), Chevrinais *et al.*, 2017 (217), King *et al.*, 2017 (298)

94. Dentary, mandibular sensory canal, course of

Present (0)

Absent (1)

UBERON 0004742 Dentary: the dentary is a dermal bone that forms the antero-lateral part of the lower jaw in fishes and amphibians, extending to the whole lower jaw in mammals

UBERON 2001814 Mandibular sensory canal: sensory canal anterior and ventral to and in close proximity with the preoperculo-mandibular sensory canal. The mandible sensory canal is bilaterally paired and associated with the angular and dentary bones.

Zhu *et al.*, 2009 (120), Zhu *et al.*, 2013 (218), Long *et al.*, 2014 (218), Dupret *et al.*, (218), Qiao *et al.*, 2016 (218), Chevrinais *et al.*, 2017 (218), King *et al.*, 2017 (299)

95. Supraorbital sensory canals, posterior pitlines, cross as an X

Absent (0)

Present (1)

UBERON 2001810 Supraorbital sensory canal: sensory canal anterior to and in close proximity to the otic and infraorbital sensory canals. The supraorbital sensory canal is bilaterally paired.

King *et al.*, 2017 (300)

96. Sensory canal, position of

Contained within the thickness of dermal bones (0)

Contained in prominent ridges on visceral surface of bone (1)

UBERON 2001612 Sensory canal: multi-tissue structure that is a fluid-filled canal in the integument and usually dermal bones and contains one or more neuromast organs. Sensory canals usually communicate with the environment via pores in the sensory canal or at the distal ends of tubules, which extend from canal where pores would otherwise be.

UBERON 0008907 Dermal bone: Skeletal element that forms superficially in the organism, usually in association with the ectoderm.

Brazeau 2009 (17), Giles *et al.*, 2015 (31), Lu *et al.*, 2016 (31), Qiao *et al.*, 2016 (266), King *et al.*, 2017 (301)

97. Postparietals, otic sensory canal, extension of

Absent (0)

Present (1)

UBERON 2001629 Otic sensory canal: sensory canal between and in close proximity posteriorly with the post-otic and preoperculo-mandibular sensory canals, and anteriorly with the supraorbital and infraorbital sensory canals. The otic sensory canal is bilaterally paired.

Giles *et al.*, 2015 (47), Lu *et al.*, 2016 (47), Qiao *et al.*, 2016 (273), King *et al.*, 2017 (303)

98. (N) Sel canals

Absent (0)

Present (1)

99. Sel canals, number of

Five (0)

Less than five (1)

King *et al.*, 2017 (91)

100. Sel canal #1, bifurcation of

Between orbit of skull and field (0)

Adjacent to field (1)

UBERON 0001697 Orbit of Skull: subdivision of skeleton that is an anterolateral part of the cranium and structurally supports the eye. Includes bones formed and located in sclerotic layer of eyeball

King *et al.*, 2017 (92)

101. Sensory canals, festooned pattern of

Absent (0)

Present (1)

UBERON 2001612 Sensory canal: multi-tissue structure that is a fluid-filled canal in the integument and usually dermal bones and contains one or more neuromast organs.

Sensory canals usually communicate with the environment via pores in the sensory canal or at the distal ends of tubules, which extend from canal where pores would otherwise be.

King *et al.*, 2017 (305)

102. Lateral transverse canals, branching end of

Absent (0)

Present (1)

King *et al.*, 2017 (308)

103. Supraorbital sensory canal, anterior portion of

Absent (0)

Present (1)

UBERON 2001810 Supraorbital sensory canal: sensory canal anterior to and in close proximity to the otic and infraorbital sensory canals. The supraorbital sensory canal is bilaterally paired.

King *et al.*, 2017 (309)

104. Postmarginal sensory canal

Absent (0)

Present (1)

UBERON 2001810 Supraorbital sensory canal: sensory canal anterior to and in close proximity to the otic and infraorbital sensory canals. The supraorbital sensory canal is bilaterally paired.

King *et al.*, 2017 (315)

105. Preopercular sensory canal

Absent (0)

Present (1)

UBERON 2001813 Preopercular sensory canal: Sensory canal lateral or ventral to and in close proximity with the otic and post-otic sensory canals at their union, and anteroventrally with the mandibular sensory canal. The preopercular sensory canal is bilaterally paired and associated with the preopercle bone.

King *et al.*, 2017 (316)

106. Preopercular sensory canal, main sensory canal, meeting of

Absent (0)

Present (1)

UBERON 2001813 Preopercular sensory canal: Sensory canal lateral or ventral to and in close proximity with the otic and post-otic sensory canals at their union, and anteroventrally with the mandibular sensory canal. The preopercular sensory canal is bilaterally paired and associated with the preopercle bone.

UBERON 2001612 Sensory canal: multi-tissue structure that is a fluid-filled canal in the integument and usually dermal bones and contains one or more neuromast organs.

Sensory canals usually communicate with the environment via pores in the sensory canal or at the distal ends of tubules, which extend from canal where pores would otherwise be.

King *et al.*, 2017 (317)

107. Supraoral sensory canal

Absent (0)

Present (1)

UBERON 2001612 Sensory canal: multi-tissue structure that is a fluid-filled canal in the integument and usually dermal bones and contains one or more neuromast organs. Sensory canals usually communicate with the environment via pores in the sensory canal or at the distal ends of tubules, which extend from canal where pores would otherwise be.

King *et al.*, 2017 (318)

108. P canal

Absent (0)

Present (1)

Extension of otic canal beyond infraorbital canal – King *et al.*, 2017

King *et al.*, 2017 (319)

109. Sensory line canal, course of

Passes between or beneath scales (0)

Passes over scales and/or is partially enclosed or surrounded by scales (1)

Perforates and passes through scales (2)

UBERON 2001612 Sensory canal: multi-tissue structure that is a fluid-filled canal in the integument and usually dermal bones and contains one or more neuromast organs. Sensory canals usually communicate with the environment via pores in the sensory canal or at the distal ends of tubules, which extend from canal where pores would otherwise be.

Brazeau 2009 (16 modified), Davis *et al.*, 2012 (15), Zhu *et al.*, 2013 (15), Long *et al.*, 2014 (15), Dupret *et al.*, 2014 (15), Giles *et al.*, (28 modified), Lu *et al.*, 2016 (28), Qiao *et al.*, 2016 (14), Chevrinais *et al.*, 2017 (15), Coates *et al.*, 2017 (16 modified), King *et al.*, 2017 (324)

110. Posterior dorsolateral plate, main sensory canal, dorsal branch

Absent (0)

Present (1)

UBERON 4300025 Posterior dorsolateral plate: Dermal bone that is part of the scapular complex in “placoderms”, located posterior to the main components of the complex

UBERON 2001612 Sensory canal: multi-tissue structure that is a fluid-filled canal in the integument and usually dermal bones and contains one or more neuromast organs. Sensory canals usually communicate with the environment via pores in the sensory canal or at the distal ends of tubules, which extend from canal where pores would otherwise be.

King *et al.*, 2017 (325)

111. Jugal sensory canal

Present (0)

Absent (1)

UBERON 2001612 Sensory canal: multi-tissue structure that is a fluid-filled canal in the integument and usually dermal bones and contains one or more neuromast organs. Sensory canals usually communicate with the environment via pores in the sensory canal or at the distal ends of tubules, which extend from canal where pores would otherwise be.

Zhu *et al.*, 2009 (117), Brazeau 2009 (18)

112. Sensory line canals

Open grooves in dermal bones (0)

Opening via tubular pores (1)

UBERON 2001612 Sensory canal: multi-tissue structure that is a fluid-filled canal in the integument and usually dermal bones and contains one or more neuromast organs. Sensory canals usually communicate with the environment via pores in the sensory canal or at the distal ends of tubules, which extend from canal where pores would otherwise be.

UBERON 0008907 Dermal bone: Skeletal element that forms superficially in the organism, usually in association with the ectoderm.

Brazeau 2009 (40)

113. Preopercular sensory canal, anterior portion of

Present (0)

Absent (1)

UBERON 2001813 Preopercular sensory canal: sensory canal lateral or ventral to and in close proximity with the otic and post-otic sensory canals at their union, and anteroventrally with the mandibular sensory canal. The preopercular sensory canal is bilaterally paired and associated with the preopercle bone.

Zhu *et al.*, 2009 (118), Zhu *et al.*, 2013 (195), Long *et al.*, 2014 (195), Dupret *et al.*, 2014 (195), Qiao *et al.*, 2016 (200)

114. Anterior pit-line, position of

On paired median skull roofing bones over the otico-occipital division of the neurocranium (0)

On paired median skull roofing bones over the sphenoid division of the neurocranium (1).

UBERON 0001703 Neurocranium: subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

Zhu *et al.*, 2009 (106), Zhu *et al.*, 2013 (184), Long *et al.*, 2014 (184), Dupret *et al.*, 2014 (184), Qiao *et al.*, 2016 (189), Chevrinais *et al.*, 2017 (184), King *et al.*, 2017 (287)

115. Postparietal/parietal (or central of “placoderms”), middle and posterior pit-lines, position of

Posteriorly situated (0)

Mesially situated (1)

Zhu *et al.*, 2009 (107), Zhu *et al.*, 2013 (185), Long *et al.*, 2014 (185), Dupret *et al.*, 2014 (185), Qiao *et al.*, 2016 (190), Chevrinais *et al.*, 2017 (185), King *et al.*, 2017 (288)

116. Main lateral line, posterior pit line, junction of

Closer to middle of vault of skull (0)

Closer to posterior margin of vault of skull (1)

UBERON 0004339 Vault of skull: upper part of skull, consisting of parietals, frontals, post-parietals, and in some species the squamosal and a portion of the alisphenoid.

Zhu *et al.*, 2013 (166), Long *et al.*, 2014 (166), Dupret *et al.*, 2014 (166), Qiao *et al.*, 2016 (175), Chevrinais *et al.*, 2017 (166), King *et al.*, 2017 (285)

117. Cheek, horizontal sensory pitline canal

Absent (0)

Present (1)

UBERON 0001567 Cheek : A fleshy subdivision of one side of the face bounded by an eye, ear and the nose.

King *et al.*, 2017 (314)

118. Semicircular pit line

Absent (0)

Present (1)

King *et al.*, 2017 (313)

119. Vault of skull, anterior pitline

Absent (0)

Present (1)

UBERON 0004339 Vault of skull: upper part of skull, consisting of parietals, frontals, post-parietals, and in some species the squamosal and a portion of the alisphenoid.

Giles *et al.*, 2015 (34), Lu *et al.*, 2016 (34), Qiao *et al.*, 2016 (267), King *et al.*, 2017 (302)

120. Posterior pitline, postmarginal sensory canal

Staggered (0)

Confluent (1)

UBERON 2001612 Sensory canal: multi-tissue structure that is a fluid-filled canal in the integument and usually dermal bones and contains one or more neuromast organs. Sensory canals usually communicate with the environment via pores in the sensory canal or at the distal ends of tubules, which extend from canal where pores would otherwise be.

King *et al.*, 2017 (321)

121. Body, lateral line system, arrangement of

Longitudinal lines (0)

Short segments forming right-angled network (1)

UBERON 0002540 Lateral line system: a line of sensory organs and associated structures along the sides of fish and amphibia that detect vibrations and pressure changes.

Wilson & Märss 2009 (52)

122. Infraorbital sensory canal

Crosses lateral field (0)

Does not cross lateral field (1)

UBERON 2001811 Infraorbital sensory canal: Sensory canal lateral or ventral to and in close proximity to the otic and supraorbital sensory canals at their union. The infraorbital sensory canal is bilaterally paired and associated with the infraorbital bones.

King *et al.*, 2017 (304)

123. Edge of marginal plate, infraorbital and cephalic main sensory canal groove, course of

Absent (0)

Present (1)

UBERON 2001811 Infraorbital sensory canal: Sensory canal lateral or ventral to and in close proximity to the otic and supraorbital sensory canals at their union. The infraorbital sensory canal is bilaterally paired and associated with the infraorbital bones.

UBERON 2001612 Sensory canal: multi-tissue structure that is a fluid-filled canal in the integument and usually dermal bones and contains one or more neuromast organs.

Sensory canals usually communicate with the environment via pores in the sensory canal or at the distal ends of tubules, which extend from canal where pores would otherwise be.

King *et al.*, 2017 (311)

124. Central sensory lines

Absent (0)

Present (1)

King *et al.*, 2017 (312)

125. Extrascapula, sensory canal commissure

Absent (0)

Present (1)

UBERON 2000663 Extrascapula: dermal canal-bearing bone placed at the dorso-posterior region of the skull roof, lying on the posterior region of the pterotic and parietals, or the pterotic and epioccipital, or on the pterotic, epioccipital and occipital bones.

UBERON 2001612 Sensory canal: multi-tissue structure that is a fluid-filled canal in the integument and usually dermal bones and contains one or more neuromast organs. Sensory canals usually communicate with the environment via pores in the sensory canal or at the distal ends of tubules, which extend from canal where pores would otherwise be.

King *et al.*, 20107 (323)

126. Posterior dorsolateral plate, sensory canal, sharp downward bend

Absent (0)

Present (1)

UBERON 4300025 Posterior dorsolateral plate: Dermal bone that is part of the scapular complex in “placoderms”, located posterior to the main components of the complex

UBERON 2001612 Sensory canal: multi-tissue structure that is a fluid-filled canal in the integument and usually dermal bones and contains one or more neuromast organs. Sensory canals usually communicate with the environment via pores in the sensory canal or at the distal ends of tubules, which extend from canal where pores would otherwise be.

King *et al.*, 2017 (326)

127. Head, sensory canal scales/plates

Unspecialized (0)

Apposed growth (1)

Paralleling canal (2)

Semicylindrical C-shaped ring scales (3).

UBERON 2001612 Sensory canal: multi-tissue structure that is a fluid-filled canal in the integument and usually dermal bones and contains one or more neuromast organs. Sensory canals usually communicate with the environment via pores in the sensory canal or at the distal ends of tubules, which extend from canal where pores would otherwise be.

Giles *et al.*, 2015 (61), Lu *et al.*, 2016 (61)

128. Supraorbital sensory canal, median commissure

Absent (0)

Present (1)

UBERON 2001810 Supraorbital sensory canal: sensory canal anterior to and in close proximity to the otic and infraorbital sensory canals. The supraorbital sensory canal is bilaterally paired.

Giles *et al.*, 2015 (45), Lu *et al.*, (45), Qiao *et al.*, 2016 (272)

129. Anterior pit line, position of

On postparietal (0)

On parietal (1)

Zhu *et al.*, 2009 (106), Lu *et al.*, 2016 (240), Qiao *et al.*, 2016 (326)

130. Pore clusters

Absent (0)

Present (1)

UBERON 0008915 Pore: anatomical space that is an opening, usually at the end of a canal or duct, on the surface of the integument or the lining of an internal anatomical space

King *et al.*, 2017 (267)

131. Pineal and parapineal tracts, paired

Absent (0)

Present (1)

UBERON 0034715 Pineal tract: a cranial nerve fiber tract that innervates the pineal body. This should be classified as an evaginated sensory afferents rather than cranial nerves, as they are part of the CNS

Lu *et al.*, 2016 (266), Qiao *et al.*, 2016 (334)

132. Endocranium

Unmineralized (0)

Mineralized (1)

Burrow & Turner 2010 (3)

133. Neurocranium, series of bilateral ossification

Absent (0)

Present (1)

UBERON 0001703 Neurocranium: subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

King *et al.*, 2017 (100)

134. Ethmoid and sphenoid regions, co-mineralisation of

Present (0)

Absent (1)

UBERON 0011241 Ethmoid region: The most anterior region of the braincase.
Provides structural support for peripheral olfactory organ

UBERON 0003111 Sphenoid region: Anatomical cluster that forms the floor and
sidewalls of the middle part of the cranium

Zhu *et al.*, 2009 (31), Brazeau 2009 (58)

135. Neurocranium, construction of

3 moieties, ethmosphenoid otic and occipital (0)

2 moieties, ethmosphenoid and oticooccipital (1)

Continuous vault (2)

Continuous vault + rhinocapsule (3)

UBERON 0001703 Neurocranium: subdivision of skeletal system that surrounds and
protects the brain. Includes the skull base, sensory capsules and the central part of the skull
roof.

Grogan & Lund 2008, 2009 (14), Grogan *et al.*, 2012 (20)

136. Neurocranium, consolidated bony plates

Absent (0)

Present (1)

UBERON 2002053 Bony plates: Dermal bone that is located on or subjacent to the surface anywhere on the body and that is not part of the general complement of scales, dermal bone of the dermatocranium, postcranial axial skeleton or paired fin skeleton. Bony plate may exist singly, or as unpaired or paired clusters or series.

UBERON 0001703 Neurocranium: Subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

Zhu *et al.*, 2009 (1)

137. Basicranium, morphology of

Platybasic (0)

Tropibasic (1)

UBERON 0002517 Basicranium: the base of skull is the most inferior area of the skull, composed of the endocranium and lower parts of the skull roof.

Brazeau 2009 (75), Davis *et al.*, 2012 (74), Zhu *et al.*, 2013 (74), Long *et al.*, 2014 (74), Dupret *et al.*, 2014 (74), Qiao *et al.*, 2016 (74), Chevrinais *et al.*, 2017 (74), Coates *et al.*, 2017 (116)

138. Basiphenoid bone, cranial cavity

Cranial cavity occupies full depth of sphenoid bone (0)

Cranial cavity dorsally restricted (1)

UBERON 0013411 Cranial cavity: Anatomical cavity that is the lumen of the skull and contains the brain.

UBERON 0006428 Basisphenoid bone: Part of the base of the cranium between the basioccipital and the presphenoid, which usually ossifies separately in the embryo or in the young and becomes a part of the sphenoid in the adult; in many animals it persists as a separate bone between the basioccipital bone and the presphenoidal bone.

UBERON 0001677 Sphenoid bone: An unpaired bone situated at the base of the skull in front of the temporal bone and basilar part of the occipital bone. The sphenoid bone is one of the seven bones that articulate to form the orbit. Its shape somewhat resembles that of a butterfly or bat with its wings extended

Giles *et al.*, 2015 (140), Lu *et al.*, 2016 (140), King *et al.*, 2017 (37)

139. Neurocranium, dorsal ridge

Absent (0)

Present (1)

UBERON 0001703 Neurocranium: subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

Davis *et al.*, 2012 (91), Zhu *et al.*, 2013 (91), Long *et al.*, 2014 (91), Dupret *et al.*, 2014 (91), Giles *et al.*, 2015 (160), Lu *et al.*, 2016 (160), Qiao *et al.*, 2016 (90), Chevrinais *et al.*, 2017 (91), King *et al.*, 2017 (52)

140. Neurocranium, opercular suspension

Absent (0)

Present (1)

UBERON 0001703 Neurocranium: subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

Brazeau 2009 (91), Zhu *et al.*, 2013 (229), Long *et al.*, 2014 (229), Durpet *et al.*, 2014 (229), Qiao *et al.*, 2016 (224), Chevrinais *et al.*, 2017 (229), King *et al.*, 2017 (70)

141. Neurocranium, vomeral area, grooves and raised areas

Absent (0)

Present (1)

UBERON 0001703 Neurocranium: subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

Zhu *et al.*, 2009 (64), Zhu *et al.*, 2013 (236), Long *et al.*, 2014 (236), Durpet *et al.*, 2014 (236), Qiao *et al.*, 2016 (226), Chevrinais *et al.*, 2017 (226), King *et al.*, 2017 (71)

142. Neurocranium, subcranial ridges

Absent (0)

Present (1)

UBERON 0001703 Neurocranium: subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

Giles *et al.*, 2015 (141), Lu *et al.*, 2016 (141), Qiao *et al.*, 2016 (298), King *et al.*, 2017 (80)

143. Tectum synoticum

Absent (0)

Present (1)

UBERON 0006605 Tectum synoticum: Unpaired thin dorsal sheet of cartilage that partially covers the posterior chondrocranium.

Giles *et al.*, 2015 (159), Lu *et al.*, 2016 (159), Qiao *et al.*, 2016 (300), King *et al.*, 2017 (82)

144. Branchial ridges

Present (0)

Absent (1)

Giles *et al.*, 2015 (166 modified), Lu *et al.*, 2016 (166 modified), Qiao *et al.*, 2016 (302 modified), King *et al.*, 2017 (84 modified).

145. Craniospinal process

Absent (0)

Present (1)

Giles *et al.*, 2015 (167), Lu *et al.*, 2016 (167), Qiao *et al.*, 2016 (303), King *et al.*, 2017 (85).

146. Sphenoid bone, prehypophysial portion, extension of

Absent (0)

Present (1)

UBERON 0001677 Sphenoid bone: An unpaired bone situated at the base of the skull in front of the temporal bone and basilar part of the occipital bone. The sphenoid bone is one of the seven bones that articulate to form the orbit. Its shape somewhat resembles that of a butterfly or bat with its wings extended

Brazeau 2009 (69), Davis *et al.*, 2012 (67), Zhu *et al.*, 2013 (67), Long *et al.*, 2014 (67), Dupret *et al.*, 2014 (67), Giles *et al.*, 2015 (135), Lu *et al.*, 2016 (135) Qiao *et al.*, 2016 (66), Chevrinais *et al.*, 2017 (67), King *et al.*, 2017 (31)

147. Median dorsal ridge anterior to endolymphatic fossa, shape of

Ungrooved (0)

Grooved (1)

Giles *et al.*, 2015 (161), Lu *et al.*, 2016 (161), Qiao *et al.*, 2016 (301), King *et al.*, 2017 (83)

148. Dermosphenotic, T-shaped

Absent (0)

Present (1)

UBERON 2001708 Dermosphenotic: Infraorbital that is the last bone of the infraorbital series, carrying the infraorbital canal, and sometimes also the supraorbital, temporal, and/or

preopercular canals. The dermosphenotic is sometimes sutured or fused completely to the skull, e.g. to the autosphenotic.

Zhu *et al.*, 2009 (13)

149. Dermal skull bones, endolymphatic ducts, oblique course of

Absent (0)

Present (1)

UBERON 0001860 Endolymphatic duct: The small membranous canal, connecting with both saccule and utricle of the membranous labyrinth, passing through the aqueduct of vestibule, and terminating in the endolymphatic sac

UBERON 0008907 Dermal bone: Skeletal element that forms superficially in the organism, usually in association with the ectoderm.

Brazeau 2009 (23), Davis *et al.*, 2012 (22), Zhu *et al.*, 2013 (22), Long *et al.*, 2014 (22), Dupret *et al.*, 2014 (22), Giles *et al.*, 2015 (39), Lu *et al.*, 2016 (39), Qiao *et al.*, 2016 (21), Chevrinais *et al.*, 2017 (22), King *et al.*, 2017 (155)

150. Ampula of Lorenzini

Absent (0)

Present (1)

UBERON 0008918 Ampula of Lorenzini: The ampullae of Lorenzini are special sensing organs called electroreceptors, forming a network of jelly-filled pores. Each ampulla consists of a canal opening to the surface by a pore in the skin and ending blindly in a cluster of small pockets full of special jelly. The ampullae are mostly clustered into groups inside

the body, each cluster having ampullae connecting with different parts of the skin, but preserving a left-right symmetry. The canal lengths vary from animal to animal, but the distribution of the pores is generally specific to each species. The ampullae pores are plainly visible as dark spots in the skin. They provide fish with a sixth sense capable of detecting electromagnetic fields as well as temperature gradients

Grogan & Lund 2000, 2004 (1 modified)

151. Extravisceral cephalic cartilages

Present (0)

Absent (1)

Grogan & Lund 2000 (13 modified), 2004 (17 modified), 2008 (18 modified), 2009 (19 modified), Grogan *et al.*, 2012 (25 modified).

152. Labyrinth cavity

Separated from the main neurocranial cavity by a cartilaginous or ossified capsular wall (0)

Skeletal capsular wall absent (1)

Davis *et al.*, 2012 (82), Zhu *et al.*, 2013 (82), Long *et al.*, 2014 (82), Dupret *et al.*, 2014 (82), Giles *et al.*, 2015 (148), Lu *et al.*, 2016 (148), Qiao *et al.*, 2016 (81), Chevrinais *et al.*, 2017 (82), Coates *et al.*, 2017 (98), King *et al.*, 2017 (44)

153. Suprapterygoid process

Absent (0)

Present (1)

King *et al.*, 2017 (109)

154. Neurocranium, outer wall, multiyared tesserae

Absent (0)

Present (1)

UBERON 0001703 Neurocranium: subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

Coates *et al.*, 2017 (2)

155. Preglenoid process

Absent (0)

Present (1)

Davis *et al.*, 2012 (52), Zhu *et al.*, 2013 (52), Long *et al.*, 2014 (52), Dupret *et al.*, 2014 (52), Giles *et al.*, 2015 (107), Lu *et al.*, 2016 (107), Qiao *et al.*, 2016 (51), Chevrinais *et al.*, 2017 (52), King *et al.*, 2017 (340)

156. Posterior myodome, medial recess

Absent (0)

Present (1)

UBERON 2001926 Posterior myodome: Fossa or chamber on posterior portion of orbital region of neurocranium that serves as attachment site for posterior extrinsic eye muscles.

King *et al.*, 2017 (90)

157. Labial pit

Absent (0)

Present (1)

Lu *et al.*, 2016 (249), King *et al.*, 2017 (385)

158. Parasphenoid, basipterygoid process, vertically oriented component

Absent (0)

Present (1)

UBERON 2001607 Basipterygoid process: Process that is the paired process of the parasphenoid that articulates with the suspensorium.

Davis *et al.*, 2012 (83), Zhu *et al.*, 2013 (83), Long *et al.*, 2014 (83), Dupret *et al.*, 2014 (83), Giles *et al.*, 2015 (149), Lu *et al.*, 2016 (149), Qiao *et al.*, 2016 (82), Chevrinais *et al.*, 2017 (83), King *et al.*, 2017 (45)

159. Basal/basipterygoid articulation, position of

Same anteroposterior level as hypophysial opening (0)

Anterior to hypophysial opening (1)

Brazeau 2009 (81), Davis *et al.*, 2012 (80), Zhu *et al.*, 2013 (80), Long *et al.*, 2014 (80), Dupret *et al.*, 2014 (80), Giles *et al.*, 2015 (146), Lu *et al.*, 2016 (146 modified), Qiao *et al.*, 2016 (79), Chevrinais *et al.*, 2017 (80), King *et al.*, 2017 (42)

160. Hyomandibular articulation, jugular groove, relative position of

Hyomandibular bone dorsal or same level (i.e. on bridge) (0)

Jugular vein passing dorsal or lateral to hyomandibular bone (1)

UBERON 0011606 Hyomandibular bone : Replacement bone that is bilaterally paired and (in teleosts) articulates with the neurocranium dorsally and the opercle posteriorly.

UBERON 0004711 Jugular vein : The jugular veins are veins that bring deoxygenated blood from the head back to the heart via the superior vena cava.

Qiao *et al.*, 2016 (324), King *et al.*, 2017 (89)

161. Hyomandibular bone, articulation facet, type of

Single-headed (0)

Double-headed (1)

UBERON 0011606 Hyomandibular bone : Replacement bone that is bilaterally paired and (in teleosts) articulates with the neurocranium dorsally and the opercle posteriorly.

Zhu *et al.*, 2009 (44), Zhu *et al.*, 2013 (227), Long *et al.*, 2014 (227), Dupret *et al.*, 2014 (227), Qiao *et al.*, 2016 (150), Chevrinais *et al.*, 2017 (227), King *et al.*, 2017 (63)

162. Ethmoid bone, palatoquadrate, articulation of

Absent (0)

Present (1)

UBERON 0001679 Ethmoid bone : A bone in the skull that separates the nasal cavity from the brain. As such, it is located at the roof of the nose, between the two orbits. The cubical bone is lightweight due to a spongy construction. The ethmoid bone is one of the bones that makes up the orbit of the eye

UBERON 0004752 Palatoquadrate cartilage: The dorsal component of the mandibular arch

King *et al.*, 2017 (122)

163. Palatobasal (or orbital) articulation, relative position of

Posterior to optic foramen (0)

Anterior to optic foramen (1)

UBERON 0005745 Optic foramen: An opening in the skull through which cranial nerve II passes.

Coates *et al.*, 2017 (71), King *et al.*, 2017 (123)

164. Suprapterygoid articulation

Absent (0)

Present (1)

Giles *et al.*, 2015 (147), Lu *et al.*, 2016 (147)

165. Basipterygoid process of parasphenoid, anterior expanded articular area

Absent (0)

Present (1)

UBERON 2001607 Basipterygoid process: Process that is the paired process of the parasphenoid that articulates with the suspensorium.

King *et al.*, 2017 (103)

166. Palatoquadrate, ethmoid bone articulation, relative position of

Placed on postnasal wall (0)

Extends posteriorly to the level of cranial N.II (1)

UBERON 0001679 Ethmoid bone: A bone in the skull that separates the nasal cavity from the brain. As such, it is located at the roof of the nose, between the two orbits. The cubical bone is lightweight due to a spongy construction. The ethmoid bone is one of the bones that makes up the orbit of the eye

UBERON 0004752 Palatoquadrate cartilage: The dorsal component of the mandibular arch.

UBERON 3000454 Postnasal wall: Paired, anteriorly concave structures that form the posterior limit of nasal capsule. It consists of two parts: a ventral piece, the lamina orbitonasalis, and a dorsal plate that is part of the tectum nasi

UBERON 0000941 Cranial nerve II: Cranial nerve fiber tract which is comprised of retinal ganglion cell axons running posterior medially towards the optic chiasm, at which some of the axons cross the midline and after which the structure is termed the optic tract. Transmits visual information from the retina to the brain

Zhu *et al.*, 2009 (35), Zhu *et al.*, 2013 (221), Long *et al.*, 2014 (221), Dupret *et al.*, 2014 (221), Qiao *et al.*, 2016 (242), Chevrinais *et al.*, 2017 (221), King *et al.*, 2017 (72)

167. Palatoquadrate, basitrabecular process articulation, position of

Postorbital (0)

Orbital (1)

Antorbital (2)

UBERON 3010092 Basitrabecular process: A process of the otic capsule that will bridge to the palatoquadrate basal process.

UBERON 0004752 Palatoquadrate cartilage: The dorsal component of the mandibular arch.

UBERON 0001697 Orbit of the skull: Subdivision of skeleton that is an anterolateral part of the cranium and structurally supports the eye. Includes bones formed and located in sclerotic layer of eyeball.

Grogan & Lund 2000 (11), 2004 (15), 2008 (13), 2009 (13), Grogan *et al.*, 2012 (19)

168. Rostral bar

Absent (0)

Present (1)

Coates *et al.*, 2017 (64)

169. Rostral plate, T-shaped

Absent (0)

Present (1)

UBERON 2001934 Rostral plate: dermal bone that is located on midline of snout in skin above mesethmoid and lateral ethmoid bones. Rostral plate bears type 1 odontodes and is unpaired

King *et al.*, 2017 (237)

170. Rostral process

Absent (0)

Present (1)

UBERON 3000547 Rostral process: Is a process of the nasal bone directed anteriorly towards the rostrum

King *et al.*, 2017 (99)

171. Rostral tubule

Absent (0)

Present (1)

UBERON 4300195 Rostral tubule: Consists of a set of tubuli occupying the space between the external dermal bones above the dorsal and anterior wall of the nasal capsule below.

Zhu *et al.*, 2009 (150), Zhu *et al.*, 2013 (142), Long *et al.*, 2014 (142), Dupret *et al.*, 2014 (142), Qiao *et al.*, 2016 (158), Chevrinais *et al.*, 2017 (142), King *et al.*, 2017 (67)

172. Neurocranial rostrum, extension of

Absent (0)

Present (1)

Grogan & Lund 2004 (30), 2008 (2), 2009 (2), Grogan *et al.*, 2012 (2)

173. Neurocranium, median rostral dorsal process

Absent (0)

Present (1)

UBERON 0001703 Neurocranium: subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

King *et al.*, 2017 (101)

174. Ethmoid bone, three pores, relative position of

Restricted to ethmosphenoid region (0)

Extends to otic region (1)

UBERON 0005928 External naris: A naris that provides one of the small external openings of the head that give passage to air for breathing.

UBERON 0001679 Ethmoid bone: A bone in the skull that separates the nasal cavity from the brain. As such, it is located at the roof of the nose, between the two orbits. The cubical bone is lightweight due to a spongy construction. The ethmoid bone is one of the bones that makes up the orbit of the eye

UBERON 0011287 Rostral organ: A putative electroreceptor organ located in the medial rostral cavity in the ethmoid portion of the chondrocranium of Coelacanth. It is surrounded by an insulating layer of adipose tissue and innervated by the superficial ophthalmic nerve.

UBERON 0003110 Otic region: Anatomical cluster that is a posterolateral part of the cranium and structurally supports the vestibuloauditory system.

Lu *et al.*, 2016 (263)

175. Rostral organ

Absent (0)

Present (1)

UBERON 0011287 Rostral organ: A putative electroreceptor organ located in the medial rostral cavity in the ethmoid portion of the chondrocranium of Coelacanth. It is surrounded by an insulating layer of adipose tissue and innervated by the superficial ophthalmic nerve.

King *et al.*, 2017 (107)

176. Neurocranium, prominent pre-orbital rostral expansion

Present (0)

Absent (1)

UBERON 0001703 Neurocranium: subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

Brazeau 2009 (61), Davis *et al.*, 2012 (58), Zhu *et al.*, 2013 (58), Long *et al.*, 2014 (58), Dupret *et al.*, 2014 (58), Giles *et al.*, 2015 (118), Lu *et al.*, 2016 (118), Qiao *et al.*, 2016 (57), Chevrinais *et al.*, 2017 (58)

177. Rostrum, basal plane

180° (0)

> 180° (1)

UBERON 7500071 Rostrum: An anatomical structure that protrudes from the head region. In vertebrates, this includes the part of the cranium (skull) in front of the zygomatic arches that also holds the teeth, palat, and nasal cavity. In invertebrates it is the forward extension of the carapace and/or the piercing mouthparts.

Grogan & Lund 2000 (4), 2004 (5), 2008 (4), 2009 (4)

178. Orbit of skull, anterolateral corners, nasal capsules, presence of

Absent (0)

Present (1)

UBERON 0006332 Nasal capsule: An embryonic cartilaginous frame, the nasal capsule, an evolutionary-conserved structure composed of ventral and dorsal components: the mesethmoid and ectethmoid cartilages, respectively.

UBERON 0001697 Orbit of skull: Subdivision of skeleton that is an anterolateral part of the cranium and structurally supports the eye. Includes bones formed and located in sclerotic layer of eyeball.

King *et al.*, 2017 (96)

179. Nasohypophysial opening, type of

Unconstricted (0)

Constriction between nasal and hypophysial divisions (1)

Split into nasal and hypophysial divisions (2)

King *et al.*, 2017 (228)

180. Nasal opening(s), position of

Dorsal placed between orbit of skull (0)

Ventral and anterior to orbit of skull (1)

UBERON 0001697 Orbit of Skull: subdivision of skeleton that is an anterolateral part of the cranium and structurally supports the eye. Includes bones formed and located in sclerotic layer of eyeball

Brazeau 2009 (59), Davis *et al.*, 2012 (56), Zhu *et al.*, 2013 (56), Long *et al.*, 2014 (56), Dupret *et al.*, 2014 (56), Giles *et al.*, 2015 (115), Lu *et al.*, 2016 (115), Qiao *et al.*, 2016 (55), Chevrinais *et al.*, 2017 (56), King *et al.*, 2017 (20)

181. Nasal sacs

Unpaired (0)

Paired (1)

King *et al.*, 2017 (130)

182. Ventral surface of nasal capsule, accessory processes, extension of

Absent (0)

Present (1)

UBERON 0006332 Nasal capsule: An embryonic cartilaginous frame, the nasal capsule, an evolutionary-conserved structure composed of ventral and dorsal components: the mesethmoid and ectethmoid cartilages, respectively.

King *et al.*, 2017 (124)

183. Nasal capsule, ventral face (in taxa with mineralized ethmoid bone)

Absent (0)

Present (1)

UBERON 0006332 Nasal capsule: An embryonic cartilaginous frame, the nasal capsule, an evolutionary-conserved structure composed of ventral and dorsal components: the mesethmoid and ectethmoid cartilages, respectively.

UBERON 0001679 Ethmoid bone : A bone in the skull that separates the nasal cavity from the brain. As such, it is located at the roof of the nose, between the two orbits. The cubical bone is lightweight due to a spongy construction. The ethmoid bone is one of the bones that makes up the orbit of the eye

Lu *et al.*, 2016 (264)

184. Roof of the endocranial space for telencephalon and olfactory tracts offset ventrally relative to level of midbrain

Absent (0)

Present (1)

UBERON 0002265 Olfactory tract: White matter tract that contains projections from the olfactory bulb to other parts of the brain.

UBERON 0001893 Telencephalon: Part of the forebrain consisting of paired olfactory bulbs and cerebral hemispheres.

UBERON 0001891 Midbrain: The midbrain is the middle division of the three primary divisions of the developing chordate brain or the corresponding part of the adult brain (in vertebrates, includes a ventral part containing the cerebral peduncles and a dorsal tectum containing the corpora quadrigemina and that surrounds the aqueduct of Sylvius connecting the third and fourth ventricles)

Coates *et al.*, 2017 (97)

185. Sinus superior

Absent (0)

Present (1)

Davis *et al.*, 2012 (86), Zhu *et al.*, 2013 (86), Long *et al.*, 2014 (86), Dupret *et al.*, 2014 (86), Giles *et al.*, 2015 (152), Lu *et al.*, 2016 (152), Qiao *et al.*, 2016 (85), Chevrinais *et al.*, 2017 (86), Coates *et al.*, 2017 (100), King *et al.*, 2017 (48)

186. (N) Internasal pits

Absent (0)

Present (1)

187. Internasal pits, shape of

Shallow paired pits with strong midline ridge (0)

Deep, pear-shaped pits (1)

Zhu *et al.*, 2009 (33 modified), Zhu *et al.*, 2013 (219 modified), Long *et al.*, 2014 (219 modified), Dupret *et al.*, 2014 (219 modified), Qiao *et al.*, 2016 (245 modified), Chevrinais *et al.*, 2017 (219 modified)

188. Ethmoid region, dorsoventrally lateral walls, elongation of

Absent (0)

Present (1)

UBERON 0011241 Ethmoid region: The most anterior region of the braincase.
Provides structural support for peripheral olfactory organ

Davis *et al.*, 2012 (73), Zhu *et al.*, 2013 (73), Long *et al.*, 2014 (73), Dupret *et al.*, 2014 (73), Qiao *et al.*, 2016 (72), chevrainais *et al.*, 2017 (73)

189. Neurocranium, ethmoid region, relative percentage of

<25% (0)

[25 - 40] % (1)

[40 - 50] % (2)

50% (3)

UBERON 0011241 Ethmoid region: The most anterior region of the braincase.
Provides structural support for peripheral olfactory organ

UBERON 0001703 Neurocranium: subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

Grogan & Lund 2000 (5), 2004 (6), 2008 (5), 2009 (5), Grogan *et al.*, 2012 (5)

190. Ethmoid region, keel

Absent (0)

Present (1)

UBERON 0011241 Ethmoid region: The most anterior region of the braincase.
Provides structural support for peripheral olfactory organ

UBERON 0018307 Keel: Ridge shaped projection, similar to the keel of a boat.

Brazeau 2009 (62), Davis *et al.*, 2012 (59), Zhu *et al.*, 2013 (59), Long *et al.*, 2014 (59), Giles *et al.*, 2015 (119), Lu *et al.*, 2016 (119), Qiao *et al.*, 2016 (58), Chevrinais *et al.*, 2017 (59), Coates *et al.*, 2017 (63), King *et al.*, 2017 (23)

191. Posterior neurocranium, optic tract level, ethmoid bone, division of

Absent (0)

Present (1)

UBERON 0001679 Ethmoid bone : A bone in the skull that separates the nasal cavity from the brain. As such, it is located at the roof of the nose, between the two orbits. The cubical bone is lightweight due to a spongy construction. The ethmoid bone is one of the bones that makes up the orbit of the eye

UBERON 0001703 Neurocranium : Subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

UBERON 1908 Optic tract : Diencephalic white matter (tract) which is comprised of retinal ganglion cell axons after which they have passed through the optic chiasm[ZFA].

Giles *et al.*, 2015 (121), Lu *et al.*, 2016 (121)

192. (N) Ethmosphenoid region

Absent (0)

Present (1)

193. Ethmoid region, contact in

Fissure (0)

Intracranial joint (1)

Continue (2)

Grogan *et al.*, 2012 (23)

194. Ethmoid commissure, course of

Middle portion through median rostral (0)

Sutural course (1)

Through bone center of premaxillary (2)

UBERON 4300241 Ethmoid commissure: Sensory canal that traverses the rostral bone.
ethmoid lateral line commissure

Zhu *et al.*, 2009 (105), Zhu *et al.*, 2013 (183), Long *et al.*, 2014 (183), Dupret *et al.*,
2014 (183), Qiao *et al.*, 2016 (188), Chevrin *et al.*, 2017 (183), King *et al.*, 2017 (286)

195. Ethmoid commissure, midline canal, fusion of

Absent (0)

Present (1)

UBERON 4300241 Ethmoid commissure: Sensory canal that traverses the rostral bone.
ethmoid lateral line commissure

King *et al.*, 2017 (320)

196. Orbit of skull, anterodorsal extremity, ophtalmic foramen and cranial interior,
communication of

Absent (0)

Present (1)

UBERON 0001697 Orbit of Skull: subdivision of skeleton that is an anterolateral part
of the cranium and structurally supports the eye. Includes bones formed and located in
sclerotic layer of eyeball

Coates *et al.*, 2017 (73)

197. Orbit of skull larger than otic capsule

Absent (0)

Present (1)

UBERON 0001697 Orbit of skull: Subdivision of skeleton that is an anterolateral part
of the cranium and structurally supports the eye. Includes bones formed and located in
sclerotic layer of eyeball.

UBERON 0004637 Otic capsule: The capsule surrounding the inner ear mechanism

Coates *et al.*, 2017 (80)

198. Neurocranium, orbit of skull, relative percentage of

[35 - 46] % (0)

>46% (1)

<35% (2)

UBERON 0001697 Orbit of Skull: subdivision of skeleton that is an anterolateral part of the cranium and structurally supports the eye. Includes bones formed and located in sclerotic layer of eyeball

UBERON 0001703 Neurocranium: subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

Grogan & Lund 2000 (6), 2004 (7), 2008 (6), 2009 (6), Grogan *et al.*, 2012 (6)

199. Postorbital arcade

Absent (0)

Present (1)

Coates *et al.*, 2017 (81)

200. Postorbital process

Dorsal protuberance (0)

Laterally distinct extended processes (1)

Dorsoventral ridge/postorbital wall (2)

UBERON 0013442 Postorbital process: The Postorbital Process marks the rear, upper edge of the eye socket and is a projection from the frontal bone.

Grogan *et al.*, 2012 (15 modified)

201. Postorbital pila ascending from basipterygoid process of parasphenoid to postorbital process

Absent (0)

Present (1)

UBERON 0013442 Postorbital process: The Postorbital Process marks the rear, upper edge of the eye socket and is a projection from the frontal bone.

UBERON 2001607 Basipterygoid process of parasphenoid : Process that is the paired process of the parasphenoid that articulates with the suspensorium.

Zhu *et al.*, 2013 (224), Long *et al.*, 2014 (224), Dupret *et al.*, 2014 (224), Chevrinais *et al.*, 2017 (224)

202. Posterior postorbital process and supravagal process

Absent (0)

Present (1)

UBERON 0013442 Postorbital process: The Postorbital Process marks the rear, upper edge of the eye socket and is a projection from the frontal bone.

Coates *et al.*, 2017 (88)

203. Postorbital cavity, development of

Absent (0)

Present (1)

Zhu *et al.*, 2013 (223), Long *et al.*, 2014 (223), Dupret *et al.*, 2014 (223), Qiao *et al.*, 2016 (220), Chevrinais *et al.*, 2017 (223)

204. Postorbital process, relative size of

Postorbital process and arcade width not more than maximum width of braincase (excluding arcade) (0)

Postorbital process and arcade width exceeds maximum width of braincase (1)

Postorbital process and arcade reduced to the dorsal part (2)

UBERON 0013442 Postorbital process: The Postorbital Process marks the rear, upper edge of the eye socket and is a projection from the frontal bone.

Coates *et al.*, 2017 (83)

205. Orbit of skull (dorsally facing), endocranium, lateral surround of

Present (0)

Absent (1)

UBERON 0001697 Orbit of Skull: subdivision of skeleton that is an anterolateral part of the cranium and structurally supports the eye. Includes bones formed and located in sclerotic layer of eyeball

Brazeau 2009 (68 modified), Davis *et al.*, 2012 (66), Zhu *et al.*, 2013 (66), Long *et al.*, 2014 (66), Dupret *et al.*, 2014 (66), Giles *et al.*, 2015 (130), Lu *et al.*, 2016 (130), Qiao *et al.*, 2016 (65), Chevrinais *et al.*, 2017 (66), King *et al.*, 2017 (30)

206. Orbit of skull, floor, fenestra nasobalis, opening of

Absent (0)

Present (1)

UBERON 3000166 Fenestra nasobasalis: Small opening at the anterior tip of the nasal capsule, on the floor of the cavum inferius. It is located medially to the base of the inferior prenasal cartilage and serves for the passage of the ramus medialis narium and arteria orbitonasalis. UBERON 0001697 Orbit of skull: Subdivision of skeleton that is an anterolateral part of the cranium and structurally supports the eye. Includes bones formed and located in sclerotic layer of eyeball

King *et al.*, 2017 (129)

207. Optic pedicel

Absent (0)

Present (1)

UBERON 0010326 Optic pedicel: Permanent cartilage structure projecting from the site of origin of the recti muscles. Supports eyeball and aids rotation

Coates *et al.*, 2017 (72)

208. Neurocranial wall, optic pedicel

Absent (0)

Present (1)

UBERON 0010326 Optic pedicel: Permanent cartilage structure projecting from the site of origin of the recti muscles. Supports eyeball and aids rotation

Zhu et al., 2009 (36), *Zhu et al.*, 2013 (222), *Long et al.*, 2014 (222), *Dupret et al.*, 2014 (222), *Giles et al.*, 2015 (131), *Lu et al.*, 2016 (131), *Qiao et al.*, 2016 (149), *Chevrinais et al.*, 2017 (222), *King et al.*, 2017 (62)

209. Optic pedicel, attachment

Absent (0)

Present (1)

UBERON 0010326 Optic pedicel: Permanent cartilage structure projecting from the site of origin of the recti muscles. Supports eyeball and aids rotation

Giles et al., 2015 (131), *Lu et al.*, 2016 (131)

210. Myodome for superior oblique extraocular muscle, position of

Posterior and dorsal to foramen for cranial nerve II (0)

Anterior and dorsal to foramen for cranial nerve II (1)

UBERON 0006321 Superior oblique extraocular muscle: The superior oblique muscle, or obliquus oculi superior, is a fusiform muscle in the upper, medial side of the orbit whose primary action is downward, lateral rotation of the eye. One of the extraocular muscles, the

superior oblique is the only muscle innervated by the trochlear nerve (the fourth cranial nerve).

Brazeau 2009 (63), Davis *et al.*, 2012 (60), Zhu *et al.*, 2013 (60), Long *et al.*, 2014 (60), Dupret *et al.*, 2014 (60), Giles *et al.*, 2015 (122), Lu *et al.*, 2016 (122), Qiao *et al.*, 2016 (59), Chevrinais *et al.*, 2017 (60), Coates *et al.*, 2017 (68), King *et al.*, 2017 (24)

211. Preorbital region between eyes and nasal capsule, extension of

Present (0)

Absent (1)

UBERON 0006332 Nasal capsule: An embryonic cartilaginous frame, the nasal capsule, an evolutionary-conserved structure composed of ventral and dorsal components: the mesethmoid and ectethmoid cartilages, respectively.

King *et al.*, 2017 (22)

212. Supraorbital shelf, convex lateral margin

Absent (0)

Present (1)

Brazeau 2009 (67), Davis *et al.*, 2012 (65), Zhu *et al.*, 2013 (65), Long *et al.*, 2014 (65), Dupret *et al.*, 2014 (65), Giles *et al.*, 2015 (129), Lu *et al.*, 2016 (129), Qiao *et al.*, 2016 (64), Chevrinais *et al.*, 2017 (65), Coates *et al.*, 2017 (69), King *et al.*, 2017 (29)

213. Processus supraorbitalis lateralis

Absent (0)

Present (1)

King et la. 2017 (110)

214. Tectum orbital

Absent (0)

Present (1)

UBERON 4300203 Tectum orbital: The dorsal portion of the endocranium that covers the orbital region

King *et al.*, 2017 (102)

215. Postorbital process

Absent (0)

Present (1)

UBERON 0013442 Postorbital process: The Postorbital Process marks the rear, upper edge of the eye socket and is a projection from the frontal bone.

Giles *et al.*, 2015 (132), Lu *et al.*, 2016 (132), Qiao *et al.*, 2016 (295), King *et al.*, 2017 (77)

216. Neurocranium, postorbital bone, relative percentage of

[25 - 40] % (0)

[15 - 25[% (1)

>40 % (2)

<15 % (3)

UBERON 0011169 Postorbital bone: The postorbital is one of the bones in vertebrate skulls which forms a portion of the dermal skull roof and, sometimes, a ring about the orbit. Generally, it is located behind the postfrontal and posteriorly to the orbital fenestra. In some vertebrates, the postorbital is fused with the postfrontal to create a postorbitofrontal.

UBERON 0001703 Neurocranium: Subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

Grogan & Lund 2000 (7), 2004 (8), 2008 (7), 2009 (7), Grogan *et al.*, 2012 (7)

217. Postorbital process, palatoquadrate cartilage, articulation of

Absent (0)

Present (1)

UBERON 0013442 Postorbital process: the Postorbital Process marks the rear, upper edge of the eye socket and is a projection from the frontal bone.

UBERON 0004752 Palatoquadrate cartilage: The dorsal component of the mandibular arch.

Davis *et al.*, 2012 (81), Zhu *et al.*, 2013 (81), Long *et al.*, 2014 (81), Dupret *et al.*, 2014 (81), Qiao *et al.*, 2016 (80), Chevrinais *et al.*, 2017 (81), Coates *et al.*, 2017 (82), King *et al.*, 2017 (43)

218. Posterior postorbital process

Absent (0)

Present (1)

UBERON 0013442 Postorbital process: the Postorbital Process marks the rear, upper edge of the eye socket and is a projection from the frontal bone.

Zhu *et al.*, 2013 (230), Long *et al.*, 2014 (230), Dupret *et al.*, 2014 (230), Chevrinais *et al.*, 2017 (230)

219. Postorbital pillar

Absent (0)

Present (1)

Zhu *et al.*, 2009 (37)

220. (N) Basitrabecular process

Present (0)

Absent (1)

UBERON 3010092 Basitrabecular process: A process of the otic capsule that will bridge to the palatoquadrate basal process

221. Basitrabecular process, position of

In line with post orbit edge/postorbital (0)

Flared ventrolateral to postorbital (1)

Flared anteroventrolaterally (2)

UBERON 3010092 Basitrabecular process: A process of the otic capsule that will bridge to the palatoquadrate basal process

Grogan & Lund 2000 (11 modified), 2004 (15 modified), 2008 (12 modified), 2009 (12 modified), Grogan *et al.*, 2012 (18 modified).

222. Occipital arch, otic capsule, relative posterolateral extension of

Absent (0)

Present (1)

UBERON 0004637 Otic capsule: The capsule surrounding the inner ear mechanism

UBERON 3010142 Occipital arch: Posterior chondrocranium forming ventral and lateral margins of foramen magnum, medial to otic capsules.

Coates *et al.*, 2017 (92)

223. Palatoquadrate articulation, bulbous otic and auxiliary condyle

Absent (0)

Present (1)

King *et al.*, 2017 (128)

224. Otic capsule, accessory fenestration

Absent (0)

Present (1)

UBERON 0004637 Otic capsule : The capsule surrounding the inner ear mechanism

Zhu *et al.*, 2009 (49)

225. Otic process

Absent (0)

Present (1)

Zhu *et al.*, 2009 (53), Zhu *et al.*, 2013 (232), Long *et al.*, 2014 (232), Dupret *et al.*, 2014 (232), Chevriniais *et al.*, 2017 (232)

226. Transverse otic process

Present (0)

Absent (1)

Giles *et al.*, 2015 (125), Lu *et al.*, 2016 (125), Qiao *et al.*, 2016 (293), King *et al.*, 2017 (75)

227. Transverse otic process, extension of

Not extending in front of orbit of skull (0)

Extending in front of orbit of skull (1)

UBERON 0001697 Orbit of Skull: subdivision of skeleton that is an anterolateral part of the cranium and structurally supports the eye. Includes bones formed and located in sclerotic layer of eyeball

King *et al.*, 2017 (95)

228. Endocranial cavity (infill) anterior to otic capsules smoothly convex dorsally and anteriorly

Absent (0)

Present (1)

UBERON 0004637 Otic capsule : The capsule surrounding the inner ear mechanism

Coates *et al.*, 2017 (95)

229. Neurocranium, preotic part, ventral rounded process

Absent (0)

Present (1)

UBERON 0001703 Neurocranium: subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

King *et al.*, 2017 (116)

230. Dorsal otic ridge, horizontal crest

Absent (0)

Present (1)

Coates *et al.*, 2017 (108), King *et al.*, 2017 (118)

231. Periotic process

Absent (0)

Present (1)

Coates *et al.*, 2017 (89), King *et al.*, 2017 (117)

232. Lateral otic process

Absent (0)

Present (1)

Brazeau 2009 (88), Davis *et al.*, 2012 (93), Zhu *et al.*, 2013 (93), Long *et al.*, 2014 (93), Dupret *et al.*, 2014 (93), Chevrinais *et al.*, 2017 (93), Coates *et al.*, 2017 (90)

233. Postotic process

Absent (0)

Present (1)

Coates *et al.*, 2017 (93)

234. Endolymphatic duct of supraotic cavity

Absent (0)

Present (1)

UBERON 0001860 Endolymphatic duct: The small membranous canal, connecting with both saccule and utricle of the membranous labyrinth, passing through the aqueduct of vestibule, and terminating in the endolymphatic sac

Zhu *et al.*, 2009 (54)

235. Otic roof and otic floor, relative position of

Parallel (0)

Convex posterodorsally (1)

Dorsal overhangs ventral margin (2)

Grogan *et al.*, 2012 (9)

236. Sphenoid-otic junction, dermal cranial joint

Absent (0)

Present (1)

Zhu *et al.*, 2009 (21), Brazeau 2009 (64), Zhu *et al.*, 2013 (147), Long *et al.*, 2014 (147), Dupret *et al.*, 2014 (147), Giles *et al.*, 2015 (46), Lu *et al.*, 2016 (46), Qiao *et al.*, 2016 (141), Chevrinais *et al.*, 2017 (147), Coates *et al.*, 2017 (25), King *et al.*, 2017 (170)

237. Process forming part or complete wall of jugular groove or canal projecting from otic capsule wall

Absent (0)

Present (1)

UBERON 0004637 Otic capsule : The capsule surrounding the inner ear mechanism

Davis *et al.*, 2013 (94), Zhu *et al.*, 2013 (94), Long *et al.*, 2014 (94), Dupret *et al.*, 2014 (94), Chevrinais *et al.*, 2017 (94)

238. Metotic fissure

Absent (0)

Present (1)

UBERON 0018339 Metotic fissure: An embryonic fissure between the otic capsule and the arches which develop into the occipital bones. The fissure may persist into adulthood. It is also referred to as the 'lateral otic fissure' The metotic fissure opens into the vestibular fontanelle, if the fontanelle is present.

Brazeau 2009 (93), Davis *et al.*, 2012 (97), Zhu *et al.*, 2013 (97), Long *et al.*, 2014 (97), Dupret *et al.*, 2014 (97), Giles *et al.*, 2015 (170), Lu *et al.*, 2016 (170), Qiao *et al.*, 2016 (93), Chevrinais *et al.*, 2017 (97), Coates *et al.*, 2017 (113), King *et al.*, 2017 (55)

239. Metotic fissure, condition of

Dorsally open (0)

Continuous with ventral otic fissure (1)

Continuous with ventral occipital fissure (2)

Fused (3)

UBERON 0018339 Metotic fissure: An embryonic fissure between the otic capsule and the arches which develop into the occipital bones. The fissure may persist into adulthood. It is also referred to as the 'lateral otic fissure' The metotic fissure opens into the vestibular fontanelle, if the fontanelle is present.

Grogan *et al.*, 2012 (22 modified)

240. Sub-otic occipital fossa

Absent (0)

Present (1)

Coates *et al.*, 2017 (91)

241. Number of marginal bones alongside paired median skull roofing bones over the otico-occipital division of neurocranium

1 (0)

>2 (1)

UBERON 0001703 Neurocranium: Subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

Zhu *et al.*, 2009 (27), Zhu *et al.*, 2013 (161), Long *et al.*, 2014 (161) Dupret *et al.*, 2014 (161), Giles *et al.*, 2015 (48), Lu *et al.*, 2016 (48), Qiao *et al.*, 2016 (143), Chevrinais *et al.*, 2017 (161), King *et al.*, 2017 (172)

242. Roof of otico-occipital, anterolateral fenestra

Absent (0)

Present (1)

King *et al.*, 2017 (111)

243. Occipital joint fissure

Open fissure (0)

Immobile / Fusion (1)

Grogan & Lund 2008 (15)

244. Occipital facets, paired

Absent (0)

Present (1)

Giles *et al.*, 2015 (177), Lu *et al.*, 2016 (177), Qiao *et al.*, 2016 (305), King *et al.*, 2017 (87)

245. Rear of otic capsules, ventral portion of occipital arch, wedged between

Absent (0)

Present (1)

UBERON 3010142 Occipital arch: Posterior chondrocranium forming ventral and lateral margins of foramen magnum, medial to otic capsules.

UBERON 0004637 Otic capsule : The capsule surrounding the inner ear mechanism

Coates *et al.*, 2017 (119)

246. Otic capsules, dorsal portion of occipital arch, wedged between

Absent (0)

Present (1)

UBERON 3010142 Occipital arch: Posterior chondrocranium forming ventral and lateral margins of foramen magnum, medial to otic capsules.

UBERON 0004637 Otic capsule : The capsule surrounding the inner ear mechanism

Coates *et al.*, 2017 (120)

247. Roof of the posterior tectum, nuchal crest, anteroposterior elongation and extension of

Absent (0)

Present (1)

UBERON 4300127 Nuchal crest: Bony protuberance on the external surface of the occipital bone

Coates *et al.*, 2017 (121)

248. External (horizontal) semicircular canal

Absent (0)

Present (1)

UBERON 0001840 Semicircular canal: One of three half-circular, interconnected tubes located inside each ear.

Brazeau 2009 (83), Davis *et al.*, (85), Zhu *et al.*, 2013 (85), Long *et al.*, 2014 (85), Dupret *et al.*, 2014 (85), Giles *et al.*, 2015 (151), Lu *et al.*, 2016 (151), Qiao *et al.*, 2016 (84), Chevrinais *et al.*, 2017 (85), King *et al.*, 2017 (47)

249. External (horizontal) semicircular canal, join of

Joins the vestibular region dorsal to posterior ampulla (0)

Joins level with posterior ampulla (1)

UBERON 0001840 Semicircular canal: One of three half-circular, interconnected tubes located inside each ear.

Davis *et al.*, (87), Zhu *et al.*, 2013 (87), Long *et al.*, 2014 (87), Dupret *et al.*, 2014 (87), Giles *et al.*, 2015 (153), Lu *et al.*, 2016 (153), Qiao *et al.*, 2016 (86), Chevrinais *et al.*, 2017 (87), King *et al.*, 2017 (49)

250. Roof of skeletal cavity for cerebellum and mesencephalon significantly higher than dorsal most level of semicircular canals

Absent (0)

Present (1)

UBERON 0001840 Semicircular canal : One of three half-circular, interconnected tubes located inside each ear

UBERON 0002037 Cerebellum: Part of the metencephalon that lies in the posterior cranial fossa behind the brain stem

Coates *et al.*, 2017 (96)

251. Subcircular foramen endolymphaticum

Absent (0)

Present (1)

Coates *et al.*, 2017 (107)

252. Crus commune, anterior and posterior semicircular canals, connection of

Present (0)

Absent (1)

UBERON 0005600 Crus commune: A region formed by non-ampulated ends of posterior and superior semicircular canals of vestibular apparatus in inner ear.

UBERON 0001840 Semicircular canal: One of three half-circular, interconnected tubes located inside each ear

Coates *et al.*, 2017 (99)

253. Angle of external semicircular canal in lateral view, straight line projected through canal intersects anterior ampulla, external ampullae, and base of foramen magnum

Absent (0)

Present (1)

UBERON 0001840 Semicircular canal: One of three half-circular, interconnected tubes located inside each ear.

UBERON 0003687 Foramen magnum: In anatomy, in the occipital bone, the foramen magnum is one of the several oval or circular apertures in the base of the skull, through which the medulla oblongata (an extension of the spinal cord) enters and exits the skull vault. Apart from the transmission of the medulla oblongata and its membranes, the foramen magnum transmits the Spinal Accessory nerve, vertebral arteries, the anterior and posterior spinal arteries, the membrana tectoria and alar ligaments.

Coates *et al.*, 2017 (101)

254. Left and right external semicircular canals approach or meet the posterodorsal midline of hindbrain roof

Absent (0)

Present (1)

UBERON 0002028 Hindbrain: The most posterior of the three principal regions of the brain

UBERON 0001840 Semicircular canal: One of three half-circular, interconnected tubes located inside each ear.

Coates *et al.*, 2017 (102)

255. Horizontal semicircular canal in dorsal view, relative position of

Medial to path of jugular vein (0)

Dorsal to jugular vein (1)

UBERON 0004711 Jugular vein: The jugular veins are veins that bring deoxygenated blood from the head back to the heart via the superior vena cava.

UBERON 0001840 Semicircular canal: One of three half-circular, interconnected tubes located inside each ear.

Giles *et al.*, 2015 (154), Lu *et al.*, 2016 (154), Qiao *et al.*, 2016 (299), King *et al.*, 2017 (81)

256. Endoskeletal cranial joint

Absent (0)

Present (1)

UBERON 4300202 Endoskeletal cranial joint: The braincase of most plesiomorphic sarcopterygians is divided by the intracranial point into ethmosphenoid and otic-occipital portions each covered by dermal bones. The function of the joint is presumably to increase the gape of the mouth rapidly during opening phases.

Davis *et al.*, 2012 (61), Zhu *et al.*, 2013 (61), Long *et al.*, 2014 (61), Dupret *et al.*, 2014 (61), Giles *et al.*, 2015 (123), Lu *et al.*, 2016 (123), Qiao *et al.*, 2016 (60), Chevrinais *et al.*, 2017 (61), King *et al.*, 2017 (25)

257. Endoskeletal cranial joint, orientation of

Vertical or anteroventrally slanting (0)

Posteroventrally slanting (1)

UBERON 4300202 Endoskeletal cranial joint: The braincase of most plesiomorphic sarcopterygians is divided by the intracranial point into ethmosphenoid and otic-occipital portions each covered by dermal bones. The function of the joint is presumably to increase the gape of the mouth rapidly during opening phases.

Zhu *et al.*, 2009 (43)

258. Sphenoid-otic junction, dermal intracranial joint

Absent (0)

Present (1)

UBERON 4100113 dermal intracranial joint: Hinge in the skull skeleton to allow for kinetic movement of different parts.

Giles *et al.*, 2015 (46), Lu *et al.*, 2016 (46)

259. Lateral commissure, position of

Overlying root of trigeminal nerve (0)

Posterior to root of trigeminal nerve (1)

UBERON 4300134 Lateral commissure: Region of the braincase which bears the facets for the hyomandibula in fishes. This region disappears in the origin of tetrapods and the space it occupied comes to contribute to the fenestra vestibuli.

UBERON 0001645 Trigeminal nerve: Cranial nerve that has three branches - the ophthalmic (supplying the skin of the nose and upper jaw), the maxillary and the mandibular (supplying the lower jaw).

Zhu et al., 2009 (46)

260. Ventral cranial fissure

Absent (0)

Present (1)

Brazeau 2009 (92), Davis *et al.*, 2012 (96), Zhu *et al.*, 2013 (96), Long *et al.*, 2014 (96), Dupret *et al.*, 2014 (96), Giles *et al.*, 2015 (168), Lu *et al.*, 2016 (168), Qiao *et al.*, 2016 (92), Chevrinais *et al.*, 2017 (96), Coates *et al.*, 2017 (111), King *et al.*, 2017 (54)

261. Vestibular fontanelles, ventral cranial fissure, connection of

Absent (0)

Present (1)

UBERON 0002221 Fontanelle: Anatomical structure that is a membranous gap between bones of the skull.

Zhu et al., 2009 (48), Brazeau 2009 (96), Davis *et al.*, 2012 (98), Zhu *et al.*, 2013 (98), Long *et al.*, 2014 (98), Dupret *et al.*, 2014 (98), Giles *et al.*, 2015 (171), Lu *et al.*, 2016 (171), Qiao *et al.*, 2016 (94), Chevrinais *et al.*, 2017 (98), King *et al.*, 2017 (56)

262. Ventral fissure, anterior margin, course of

Straight (0)

Sinusoidal (1)

King *et al.*, 2017 (127)

263. Ethmosphenoid joint/fissure, type of

Open fissure (0)

Immobile / fusion (1)

Mobile joint (2)

Grogan & Lund 2008 (16), 2009 (17)

264. Optic fissure

Present (0)

Absent (1)

UBERON 0005412 Groove that is in the developing ventral optic cup and through which blood vessels pass to the enclosed mesenchyme

Long *et al.*, 2014 (255), Dupret *et al.*, 2014 (255), Qiao *et al.*, 2016 (247), Chevrinais *et al.*, 2017 (255), King *et al.*, 2017 (73)

265. Anterior neurocranium opening, type of

Closed (0)

Open (1)

Precerebral fontanelle (2)

UBERON 0001703 Neurocranium: subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

Grogan & Lund 2000 (3), 2004 (4), 2008 (3), 2009 (3)

266. Neurocranium, hypophysial opening

Absent (0)

Present (1)

UBERON 0001703 Neurocranium: subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

King *et al.*, 2017 (114)

267. Basicranial fenestra

Absent (0)

Present (1)

UBERON 3000037 Basicranial fenestra: Ventral opening of the neurocranium.

Zhu *et al.*, 2009 (52), Zhu *et al.*, 2013 (231), Long *et al.*, 2014 (231), Dupret *et al.*, 2014 (231), Giles *et al.*, 2015 (169), Lu *et al.*, 2016 (169), Qiao *et al.*, 2016 (151), Chevrinais *et al.*, 2017 (231), King *et al.*, 2017 (64)

268. Fenestra ventrolateralis

Absent (0)

Present (1)

Zhu *et al.*, 2009 (34), Zhu *et al.*, 2013 (220), Long *et al.*, 2014 (220), Dupret *et al.*, 2014 (220), Qiao *et al.*, 2016 (219), Chevrinais *et al.*, 2017 (220)

269. Subpituitary fenestra

Absent (0)

Present (1)

Brazeau 2009 (66), Davis *et al.*, 2012 (64), Zhu *et al.*, 2013 (64), Long *et al.*, 2014 (64), Dupret *et al.*, 2014 (64), Giles *et al.*, 2015 (128), Lu *et al.*, 2016 (128), Qiao *et al.*, 2016 (63), Chevrinais *et al.*, 2017 (64), King *et al.*, 2017 (28)

270. Perilymphatic fenestra

Absent (0)

Present (1)

Coates *et al.*, 2017 (103), King *et al.*, 2017 (119)

271. Precerebral fontanelle

Absent (0)

Present (1)

UBERON 0018351 Precerebral fontanelle: The lack of chondrification of the anterior wall of the cranial cavity in front of the pineal foramen

Brazeau 2009 (56), Davis *et al.*, 2012 (54), Zhu *et al.*, 2013 (54), Long *et al.*, 2014 (54), Giles *et al.*, 2015 (109), Lu *et al.*, 2016 (109), Qiao *et al.*, 2016 (53), Chevrinais *et al.*, 2017 (54), Coates *et al.*, 2017 (62), King *et al.*, 2017 (19)

272. Precerebral fontanelle, type of

Open (0)

Closed (1)

UBERON 0018351 Precerebral fontanelle: The lack of chondrification of the anterior wall of the cranial cavity in front of the pineal foramen

Grogan *et al.*, 2012 (3)

273. Posterior fontanelle

Absent (0)

Present (1)

UBERON 0006683 Posterior fontanelle: A gap between bones in the skull at the junction of the sagittal suture and lambdoidal suture.

Brazeau 2009 (85), Davis *et al.*, 2012 (89), Zhu *et al.*, 2013 (89), Long *et al.*, 2014 (89), Dupret *et al.*, 2014 (89), Giles *et al.*, 2015 (157), Lu *et al.*, 2016 (157), Qiao *et al.*, 2016 (88), Chevrinais *et al.*, 2017 (89), Coates *et al.*, 2017 (105), King *et al.*, 2017 (50)

274. Posterior fontanelle, shape of

As long as broad (0)

Longer than wide, slot-shaped (1)

UBERON 0006683 Posterior fontanelle: A gap between bones in the skull at the junction of the sagittal suture and lambdoidal suture.

Brazeau 2009 (86), Davis *et al.*, 2012 (90), Zhu *et al.*, 2013 (90), Long *et al.*, 2014 (90), Dupret *et al.*, 2014 (90), Giles *et al.*, 2015 (158), Lu *et al.*, 2016 (158), Qiao *et al.*, 2016 (89), Chevrinais *et al.*, 2017 (90), King *et al.*, 2017 (51)

275. Posterior fontanelle, connection of

Connected to persistent metotic fissure (0)

Tectum synoticum separates fontanelle from fissure (1)

UBERON 0006685 Posterior fontanelle: A gap between bones in the skull at the junction of the sagittal suture and lambdoidal suture.

UBERON 0018339 Metotic fissure: An embryonic fissure between the otic capsule and the arches which develop into the occipital bones. The fissure may persist into adulthood.

It is also referred to as the 'lateral otic fissure' The metotic fissure opens into the vestibular fontanelle, if the fontanelle is present.

UBERON 0006605 Tectum synoticum: Unpaired thin dorsal sheet of cartilage that partially covers the posterior chondrocranium. Posterior fontanelle : occipital fontanelle, fonticulus posterior, posterior fontanelle of skull

Coates *et al.*, 2017 (106)

276. Vestibular fontanelles

Absent (0)

Present (1)

Zhu *et al.*, 2009 (48), Brazeau 2009 (96), Davis *et al.*, 2012 (98), Zhu *et al.*, 2013 (98), Long *et al.*, 2014 (98), Dupret *et al.*, 2014 (98), Giles *et al.*, 2015 (171), Lu *et al.*, 2016 (171), Qiao *et al.*, 2016 (94), Chevrinais *et al.*, 2017 (98), King *et al.*, 2017 (56)

277. Posttemporal fossae

Absent (0)

Present (1)

UBERON 2001753 Posttemporal fossae: Fossa where the exoccipital forms the medial portion and the epioccipital forms the lateral margin. The posttemporal fossa in most species has two openings separated by the epioccipital bridge. temporal groove

King *et al.*, 2017 (106)

278. Endolymphatic or parietal fossa

Absent (0)

Present (1)

Coates *et al.*, 2017 (110)

279. Spino-occipital nerve foramina

Two or more aligned horizontally (0)

One or two dorsoventrally offset (1)

Brazeau 2009 (95), Davis *et al.*, 2012 (100), Zhu *et al.*, 2013 (100), Long *et al.*, 2014 (100), Dupret *et al.*, 2014 (100), Giles *et al.*, 2015 (173), Lu *et al.*, 2016 (173), Qiao *et al.*, 2016 (96), Chevrinais *et al.*, 2017 (100), King *et al.*, 2017 (58)

280. Posterior jugular opening, ramus hyomandibularis of facial nerve (N. VII), exit of

Absent (0)

Present (1)

UBERON 3010720 Ramus hyomandibularis: the posttrematic branch of the facial nerve, both motor and sensory in function.

UBERON 0001647 Facial nerve: Cranial nerve that branches into the supraorbital (supplying the skin of the eye region and the lateral line organs here), the palatine (to the roof of the buccal cavity), and the hyomandibular (dividing into the jugular and mental branches).

Brazeau 2009 (72), Davis *et al.*, 2012 (70), Zhu *et al.*, 2013 (70), Long *et al.*, 2014 (70), Dupret *et al.*, 2014 (70), Qiao *et al.*, 2016 (69), Chevrinais *et al.*, 2017 (70), Coates *et al.*, 2017 (87), King *et al.*, 2017 (33)

281. Facial nerve (N. VII), main trunk, course of

Elongate and passes anterolaterally through orbital floor (0)

Stout, divides within otic capsule at the level of the transverse otic wall (1)

UBERON 0001647 Facial nerve: Cranial nerve that branches into the supraorbital (supplying the skin of the eye region and the lateral line organs here), the palatine (to the roof of the buccal cavity), and the hyomandibular (dividing into the jugular and mental branches).

UBERON 0004637 Otic capsule: The capsule surrounding the inner ear mechanism.

Brazeau 2009 (71), Davis *et al.*, 2012 (69), Zhu *et al.*, 2013 (69), Long *et al.*, 2014 (69), Dupret *et al.*, 2014 (69), Giles *et al.*, 2015 (137), Lu *et al.*, 2016 (137), Qiao *et al.*, 2016 (68), Chevrinais *et al.*, 2017 (69)

282. Single posterior foramen for jugular canal and ramus hyomandibularis of facial nerve N.VII

Absent (0)

Present (1)

UBERON 3010720 Ramus hyomandibularis: the posttrematic branch of the facial nerve, both motor and sensory in function.

UBERON nerve: Facial nerve : Cranial nerve that branches into the supraorbital (supplying the skin of the eye region and the lateral line organs here), the palatine (to the roof of the buccal cavity), and the hyomandibular (dividing into the jugular and mental branches).

Zhu *et al.*, 2009 (47)

283. Glossopharyngeal nerve (N. IX) exit, position of

Foramen situated posteroventral to otic capsule and anterior to metotic fissure (0)

Through metotic fissure (1)

UBERON 0001649 Glossopharyngeal nerve: Cranial nerve that branches into the ramus communicans (to the skin), the pretrematic (to the walls of the pharynx and mouth, viscerosensory fibers), and the larval post-trematic branch (lost in the adult).

UBERON 0004637 Otic capsule: The capsule surrounding the inner ear mechanism.

UBERON 0018339 Metotic fissure: An embryonic fissure between the otic capsule and the arches which develop into the occipital bones. The fissure may persist into adulthood. It is also referred to as the 'lateral otic fissure' The metotic fissure opens into the vestibular fontanelle, if the fontanelle is present

Brazeau 2009 (73), Davis *et al.*, 2012 (71), Zhu *et al.*, 2013 (71), Long *et al.*, 2014 (71), Dupret *et al.*, 2014 (71), Giles *et al.*, 2015 (139), Lu *et al.*, 2016 (139), Qiao *et al.*, 2016 (70), Chevrin *et al.*, 2017 (71), Coates *et al.*, 2017 (115 modified), King *et al.*, 2017 (34)

284. Profundus and trigeminal nerves, relation of

Emerge from cranial cavity separately from the trigeminal nerve (0)

Emerge from cranial cavity together with the trigeminal nerve (1)

UBERON 0001645 Trigeminal nerve: Cranial nerve that has three branches - the ophthalmic (supplying the skin of the nose and upper jaw), the maxillary and the mandibular (supplying the lower jaw).

King *et al.*, 2017 (94)

285. Trigemino-facial recess

Absent (0)

Present (1)

Davis *et al.*, 2012 (88), Zhu *et al.*, 2013 (88), Long *et al.*, 2014 (88), Giles *et al.*, 2015 (156), Lu *et al.*, 2016 (156), Chevriniais *et al.*, 2017 (88)

286. Vagal process

Forked (0)

Unforked (1)

King *et al.*, 2017 (97)

287. Paravagal fossa

Absent (0)

Present (1)

King *et al.*, 2017 (98)

288. Basicranial cartilage, canal for efferent pseudobranchial artery

Absent (0)

Present (1)

UBERON 2005011 Pseudobranchial artery: A vascular loop attached to the efferent part of the mandibular arch that forms at 3.5 dpf

Brazeau 2009 (80), Davis *et al.*, 2012 (79), Zhu *et al.*, 2013 (79), Long *et al.*, 2014 (79), Dupret *et al.*, 2014 (79), Giles *et al.*, 2015 (145), Lu *et al.*, 2016 (145), Qiao *et al.*, 2016 (75), Chevrinais *et al.*, 2017 (79), Coates *et al.*, 2017 (76), King *et al.*, 2017 (39)

289. Basicranial cartilage, canal for lateral dorsal aorta

Absent (0)

Present (1)

UBERON 0005805 Dorsal aorta: The dorsal aorta is a blood vessel in a single-pass circulatory system that carries oxygenated blood from the gills to the rest of the body. In a single-pass circulatory system blood passes once through the heart to supply the body once.

Brazeau 2009 (78), Davis *et al.*, 2012 (77), Zhu *et al.*, 2013 (77), Long *et al.*, 2014 (77), Dupret *et al.*, 2014 (77), Giles *et al.*, 2015 (143), Lu *et al.*, 2016 (143), Qiao *et al.*, 2016 (77), Chevrinais *et al.*, 2017 (77), King *et al.*, 2017 (40)

290. Basioccipital region, canal for dorsal aorta, enclose of

Absent (0)

Present (1)

UBERON 0005805 Dorsal aorta: The dorsal aorta is a blood vessel in a single-pass circulatory system that carries oxygenated blood from the gills to the rest of the body. In a single-pass circulatory system blood passes once through the heart to supply the body once.

Zhu *et al.*, 2009 (51)

291. Pituitary vein canal, relative position of

Dorsal to level of basipterygoid process of parasphenoid (0)

Flanked posteriorly by basipterygoid process of parasphenoid (1)

UBERON 2001607 Basipterygoid processs of parasphenoid : Process that is the paired process of the parasphenoid that articulates with the suspensorium.

Davis *et al.*, 2012 (84), Zhu *et al.*, 2013 (84), Long *et al.*, 2014 (84), Dupret *et al.*, 2014 (84), Giles *et al.*, 2015 (150), Lu *et al.*, 2016 (150), Qiao *et al.*, 2016 (83), Chevrinais *et al.*, 2017 (84), King *et al.*, 2017 (46)

292. Lateral cranial canal

Absent (0)

Present (1)

Zhu *et al.*, 2009 (55), Zhu *et al.*, 2013 (233), Long *et al.*, 2014 (233), Dupret *et al.*, 2014 (233), Giles *et al.*, 2015 (155), Lu *et al.*, 2016 (155), Qiao *et al.*, 2016 (152), Chevrinais *et al.*, 2017 (233), King *et al.*, 2017 (65)

293. Basicranium, midline canal for dorsal aorta

Absent (0)

Present (1)

UBERON 0005805 Dorsal aorta: The dorsal aorta is a blood vessel in a single-pass circulatory system that carries oxygenated blood from the gills to the rest of the body. In a single-pass circulatory system blood passes once through the heart to supply the body once.

UBERON 0002517 Basicranium : The base of skull is the most inferior area of the skull, composed of the endocranium and lower parts of the skull roof.

Zhu *et al.*, 2013 (234), Long *et al.*, 2014 (234), Dupret *et al.*, 2014 (234), Giles *et al.*, 2015 (179), Lu *et al.*, 2016 (180), Qiao *et al.*, 2016 (153), Chevrinais *et al.*, 2017 (234), King *et al.*, 2017 (66)

294. Hypotic lamina (and dorsally directed glossopharyngeal canal)

Absent (0)

Present (1)

Davis *et al.*, 2012 (103), Zhu *et al.*, 2013 (103), Long *et al.*, 2014 (103), Dupret *et al.*, 2014 (103), Giles *et al.*, 2015 (180), Lu *et al.*, 2016 (180), Qiao *et al.*, 2016 (99), Chevrinais *et al.*, 2017 (103), Coates *et al.*, 2017 (114), King *et al.*, 2017 (61)

295. Parasphenoid, buccohypophysial canal, condition of

Single (0)

Paired (1)

UBERON 0004745 Parasphenoid: A tooth- or denticle-covered plate which is attached to the sphenoid stem

Giles *et al.*, 2015 (114), Lu *et al.*, 2016 (114), Qiao *et al.*, 2016 (292), King *et al.*, 2017 (74)

296. Postorbital process, jugular vein

Absent (0)

Present (1)

UBERON 0004711 Jugular vein: The jugular veins are veins that bring deoxygenated blood from the head back to the heart via the superior vena cava.

UBERON 0013442 Postorbital process: The Postorbital Process marks the rear, upper edge of the eye socket and is a projection from the frontal bone

Giles *et al.*, 2015 (133), Lu *et al.*, 2016 (133), Qiao *et al.*, 2016 (296), King *et al.*, 2017 (78)

297. Notochordal canal aperture, relative size of

Smaller than foramen magnum (0)

Equal or larger than foramen magnum (1)

UBERON 0013704 Notochordal canal: A tubular passage that extends from the primitive pit into the head process during the early stages of embryonic development in mammals. It perforates the splanchnopleure layer so that the yolk sac and the amnion are connected temporarily.

UBERON 0003687 Foramen magnum: In anatomy, in the occipital bone, the foramen magnum is one of the several oval or circular apertures in the base of the skull, through which the medulla oblongata (an extension of the spinal cord) enters and exits the skull vault. Apart from the transmission of the medulla oblongata and its membranes, the foramen magnum transmits the Spinal Accessory nerve, vertebral arteries, the anterior and posterior spinal arteries, the membrana tectoria and alar ligaments.

Giles *et al.*, 2015 (178), Lu *et al.*, 2016 (178), Qiao *et al.*, 2016 (306), King *et al.*, 2017 (88)

298. Otic region, jugular vein

Present (0)

Absent (1)

UBERON 0004711 Jugular vein: The jugular veins are veins that bring deoxygenated blood from the head back to the heart via the superior vena cava.

UBERON 0003110 Otic region: Anatomical cluster that is a posterolateral part of the cranium and structurally supports the vestibuloauditory system

Giles *et al.*, 2015 (126 modified), Lu *et al.*, 2016 (126 modified), Qiao *et al.*, 2016 (294 modified), King *et al.*, 2017 (76 modified)

299. Supraorbital shelf, series of perforations for innervation of supraorbital sensory canal

Absent (0)

Present (1)

UBERON 2001810 Supraorbital sensory canal: Sensory canal anterior to and in close proximity to the otic and infraorbital sensory canals. The supraorbital sensory canal is bilaterally paired.

Giles *et al.*, 2015 (134), Lu *et al.*, 2016 (134), Qiao *et al.*, 2016 (297), King *et al.*, 2017 (79)

300. Neurocranium, endolymphatic ducts, orientation of

Posterodorsally angled tubes (0)

Tubes oriented vertically through median endolymphatic fossa (1)

UBERON 0001860 Endolymphatic duct: The small membranous canal, connecting with both saccule and utricle of the membranous labyrinth, passing through the aqueduct of vestibule, and terminating in the endolymphatic sac

UBERON 0001703 Neurocranium: Subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

Brazeau 2009 (87), Davis *et al.*, 2012 (92), Zhu *et al.*, 2013 (92), Long *et al.*, 2014 (92), Dupret *et al.*, 2014 (92), Giles *et al.*, 2015 (162), Lu *et al.*, 2016 (162), Qiao *et al.*, 2016 (91), Chevrinais *et al.*, 2017 (92), Coates *et al.*, 2017 (104), King *et al.*, 2017 (53)

301. Bucco-hypophyseal duct, condition of

Open (0)

Closed (1)

Coates *et al.*, 2017 (74)

302. Dorsal ridge divided posteriorly by an anteroposteriorly elongate recess enclosing the exits of the endolymphatic ducts

Absent (0)

Present (1)

UBERON 0001860 Endolymphatic duct: The small membranous canal, connecting with both saccule and utricle of the membranous labyrinth, passing through the aqueduct of vestibule, and terminating in the endolymphatic sac

Coates *et al.*, 2017 (109)

303. Marginal vein

Absent (0)

Present (1)

King *et al.*, 2017 (93)

304. Cranioquadrate passage, jugular vein, course of

Absent (0)

Present (1)

UBERON 0004711 Jugular vein : The jugular veins are veins that bring deoxygenated blood from the head back to the heart via the superior vena cava.

King *et al.*, 2017 (126)

305. Dorsal aorta into lateral dorsal aorta, division of

Posterior to occipital level (0)

Anterior to occipital level (1)

UBERON 0005805 Dorsal aorta: The dorsal aorta is a blood vessel in a single-pass circulatory system that carries oxygenated blood from the gills to the rest of the body. In a single-pass circulatory system blood passes once through the heart to supply the body once.

Coates *et al.*, 2017 (118)

306. Internal carotid artery, entrance of

Entering single or paired openings in the basicranium from a posterolateral angle (0)

Entering basicranial opening(s) head-on from an extreme, lateral angle (1)

Not entering basicranium (2)

UBERON 0001532 Internal carotid artery: A terminal branch of the left or right common carotid artery which supplies oxygenated blood to the brain and eyes Internal carotid artery

Coates *et al.*, 2017 (75)

307. Orbit of skull, internal carotid artery and efferent pseudobranchial artery, meeting of

Absent (0)

Present (1)

UBERON 0001532 / "Internal carotid artery: A terminal branch of the left or right common carotid artery which supplies oxygenated blood to the brain and eyes

UBERON 0001697 Orbit of skull : Subdivision of skeleton that is an anterolateral part of the cranium and structurally supports the eye. Includes bones formed and located in sclerotic layer of eyeball.

UBERON 2005011 Pseudobranchial artery: A vascular loop attached to the efferent part of the mandibular arch

King *et al.*, 2017 (125)

308. Ascending basisphenoid, internal carotid artery, crossed of

Absent (0)

Present (1)

UBERON 0001532 Internal carotid artery: A terminal branch of the left or right common carotid artery which supplies oxygenated blood to the brain and eyes

Brazeau 2009 (76), Davis *et al.*, 2012 (75), Zhu *et al.*, 2013 (75), Long *et al.*, 2014 (75), Dupret *et al.*, 2014 (75), Giles *et al.*, 2015 (142), Lu *et al.*, 2016 (142), Qiao *et al.*, 2016 (74), Chevrinais *et al.*, 2017 (75), Coates *et al.*, 2017 (77), King *et al.*, 2017 (38)

309. Ventral notch between parachordals

Absent (0)

Present (1)

Brazeau 2009 (97), Davis *et al.*, 2012 (101), Zhu *et al.*, 2013 (101), Long *et al.*, 2014 (101), Dupret *et al.*, 2014 (101), Giles *et al.*, 2015 (174), Lu *et al.*, 2016 (174), Qiao *et al.*, 2016 (97), Chevrinais *et al.*, 2017 (101), King *et al.*, 2017 (59)

310. Parachordal, shape of

Flat (0)

Keeled with sloping lateral margins (1)

Brazeau 2009 (98), Davis *et al.*, 2012 (102), Zhu *et al.*, 2013 (102), Long *et al.*, 2014 (102), Dupret *et al.*, 2014 (102), Giles *et al.*, 2015 (175), Lu *et al.*, 2016 (175), Qiao *et al.*, 2016 (98), Chevrinais *et al.*, 2017 (102), King *et al.*, 2017 (60)

311. Parachordal plates

Separated from the otic capsule by cartilage or a persistent fissure (0)

Sutured or co-mineralised with the otic capsule (1)

UBERON 0004637 Otic capsule: The capsule surrounding the inner ear mechanism.

Zhu *et al.*, 2009 (50), King *et al.*, 2017 (105)

312. Parachordal/occipital region, stalk-shaped

Absent (0)

Present (1)

UBERON 0005902 Occipital region: Anatomical cluster that is located in the posterior region of the cranium and forms the margin of the foramen magnum and occipital condyles.

Giles *et al.*, 2015 (179), Lu *et al.*, 2016 (179), Qiao *et al.*, 2016 (304), King *et al.*, 2017 (86)

313. Cranial notochord, unconstricted

Absent (0)

Present (1)

UBERON 0002328 Notochord: A flexible rod-shaped body found in embryos of all chordates. It is composed of cells derived from the mesoderm and defines the primitive axis of the embryo. In some chordates, it persists throughout life as the main axial support of the body, while in most vertebrates it becomes the nucleus pulposus of the intervertebral disc. The notochord is found ventral to the neural tube.

Zhu *et al.*, 2009 (40), Zhu *et al.*, 2013 (225), Long *et al.*, 2014 (225), Dupret *et al.*, 2014 (225), Qiao *et al.*, 2016 (221), Chevrinais *et al.*, 2017 (225), King *et al.*, 2017 (68)

314. Sphenoid bone, descending process (with its posterior extremity lacking periosteal lining)

Absent (0)

Present (1)

UBERON 0001677 Sphenoid bone: An unpaired bone situated at the base of the skull in front of the temporal bone and basilar part of the occipital bone. The sphenoid bone is one

of the seven bones that articulate to form the orbit. Its shape somewhat resembles that of a butterfly or bat with its wings extended

Zhu *et al.*, 2009 (41), Zhu *et al.*, 2013 (226), Long *et al.*, 2014 (226), Dupret *et al.*, 2014 (226), Qiao *et al.*, 2016 (222), Chevrinais *et al.*, 2017 (226), King *et al.*, 2017 (69)

315. Notochord stopped by occipital cotylus

Absent (0)

Present (1)

UBERON 0002328 Notochord: A flexible rod-shaped body found in embryos of all chordates. It is composed of cells derived from the mesoderm and defines the primitive axis of the embryo. In some chordates, it persists throughout life as the main axial support of the body, while in most vertebrates it becomes the nucleus pulposus of the intervertebral disc. The notochord is found ventral to the neural tube.

King *et al.*, 2017 (120)

316. Basicranial surface, spiracular groove

Absent (0)

Present (1)

Brazeau 2009 (65), Davis *et al.*, 2012 (62), Zhu *et al.*, 2013 (62), Long *et al.*, 2014 (62), Dupret *et al.*, 2014 (62), Giles *et al.*, 2015 (124), Lu *et al.*, 2016 (124), Qiao *et al.*, 2016 (61), Chevrinais *et al.*, 2017 (62), Coates *et al.*, 2017 (78), King *et al.*, 2017 (26)

317. Lateral commissure, spiracular groove

Absent (0)

Present (1)

UBERON 4300134 Lateral commissure: Region of the braincase which bears the facets for the hyomandibula in fishes. This region disappears in the origin of tetrapods and the space it occupied comes to contribute to the fenestra vestibuli

Davis *et al.*, 2012 (63), Zhu *et al.*, 2013 (63), Long *et al.*, 2014 (63), Dupret *et al.*, 2014 (63), Giles *et al.*, 2015 (124), Lu *et al.*, 2016 (127), Qiao *et al.*, 2016 (62), Chevrinais *et al.*, 2017 (63), King *et al.*, 2017 (27)

318. Jugular canal, lateral or transverse wall of jugular canal, spiracular groove

Absent (0)

Present (1)

Coates *et al.*, 2017 (79)

319. Prespiracular dental plate

Absent (0)

Present (1)

King *et al.*, 2017 (108)

320. Bar across spiracular groove

Absent (0)

Present (1)

King *et al.*, 2017 (113)

321. Endoskeletal spiracular canal

Open (0)

Partial enclosure or spiracular bar (1)

Complete enclosure in canal (2)

Lu *et al.*, 2016 (268), Qiao *et al.*, 2016 (335)

322. Consolidated cheek bones

Absent (0)

Present (1)

Brazeau 2009 (25), Davis *et al.*, 2012 (24), Zhu *et al.*, 2013 (24), Long *et al.*, 2014 (24), Dupret *et al.*, 2014 (24), Giles *et al.*, 2015 (53), Lu *et al.*, 2016 (53), Qiao *et al.*, 2016 (23), Chevrinais *et al.*, 2017 (24), Coates *et al.*, 2017 (24), King *et al.*, 2017 (157)

323. Cheek bones, division of

Undivided (0)

Divided (i.e., squamosal and preopercular) (1)

Giles *et al.*, 2015 (54), Lu *et al.*, 2016 (54), Qiao *et al.*, 2016 (278), King *et al.*, 2017 (214)

324. Cheek bones, foramina

Absent (0)

Present (1)

King *et al.*, 2017 (264)

325. Suspensorium

Autodiastyly (0)

Hyostyly (1)

Amphistyly (2)

Holostyly (3)

Methyostyly (4)

UBERON 0003108 Suspensorium : (1) the arrangement of bones which supports the jaw from the braincase; (2) in teleost fish, a large, usually triangular, bone which supports the jaw. The teleost suspensorium is formed by fusion of various elements which vary among different taxa.

Grogan & Lund 2000 (12), 2004 (16), 2008 (17), 2009 (18) Grogan *et al.*, 2012 (24)

326. (N) Mouth, position of

Superior (0)

Inferior (1)

Terminal (2)

Protrusible (3)

Oblique (4)

Ventral (5)

UBERON 0000165 Mouth: The proximal portion of the digestive tract, containing the oral cavity and bounded by the oral opening. In vertebrates, this extends to the pharynx and includes gums, lips, tongue and parts of the palate. Typically also includes the teeth, except where these occur elsewhere

327. Submarginal articulation

Absent (0)

Present (1)

UBERON 0004905 Articulation: Anatomical cluster that connects two or more adjacent skeletal elements or hardened body parts.

King *et al.*, 2017 (250)

328. Cheek, posterodorsal plate, enlarged of

Absent (0)

Present (1)

UBERON 0001567 Cheek: A fleshy subdivision of one side of the face bounded by an eye, ear and the nose.

Brazeau 2009 (29)

329. Skeletal oral margin, organisation of

Premandibular or labial complex (0)

Premaxilla, (maxilla), dentary (1)

Supra and infragnathals (2)

Palatoquadrate cartilage and Meckel's cartilage (3)

Palatoquadrate cartilage and meckelian bone (4)

UBERON 0002244 Premaxilla: One of the bones of the upper jaw situated between and in front of the maxilla

UBERON 0002397 Maxilla: The bone which normally forms the lateral upper jaw in osteichthyans, including tetrapods.

UBERON 0004742 Dentary: The dentary is a dermal bone that forms the antero-lateral part of the lower jaw in fishes and amphibians, extending to the whole lower jaw in mammals

UBERON 0004752 Palatoquadrate cartilage: The dorsal component of the mandibular arch.

UBERON 0003107 Meckel's cartilage: Meckel's cartilage is the bilaterally paired, rod-like, cartilaginous ventral component of the lower jaw, or ventral mandibular arch. It is typically resorbed in adults.

UBERON 4200250 Meckelian bone: The ossification of the Meckel's cartilage."

Grogan *et al.*, 2012 (27)

330. (N) External naris

Absent (0)

Present (1)

UBERON 0005928 External naris: A naris that provides one of the small external openings of the head that give passage to air for breathing

331. Anterior naris, position of

Facial (0)

At oral margin (1)

Lu *et al.*, 2016 (261)

332. Preorbital process of premaxilla, posterior naris, enclose of

Absent (0)

Present (1)

UBERON 0002244 Maxilla: One of the bones of the upper jaw situated between and in front of the maxillae

Zhu *et al.*, 2009 (9)

333. Orbit of skull and posterior naris, association of

Present (0)

Absent (1)

UBERON 0001697 Orbit of skull: Subdivision of skeleton that is an anterolateral part of the cranium and structurally supports the eye. Includes bones formed and located in sclerotic layer of eyeball.

Zhu *et al.*, 2009 (8 modified), Zhu *et al.*, 2013 (152 modified), Long *et al.*, 2014 (152 modified), Dupret *et al.*, 2014 (152 modified), Giles *et al.*, 2015 (116 modified), Lu *et al.*, 2016 (116 modified), Qiao *et al.*, 2016 (142 modified), Chevrinais *et al.*, 2017 (152 modified), King *et al.*, 2017 (171 modified)

334. Posterior naris, position of

Facial (0)

At margin oral cavity (1)

Palatal (2)

Lu *et al.*, 2016 (262), Qiao *et al.*, 2016 (332)

335. Posterior naris, position of

External far from jaw margin (0)

External close to jaw margin (1)

Zhu *et al.*, 2009 (7), Zhu *et al.*, 2013 (153), Long *et al.*, 2014 (153), Dupret *et al.*, 2014 (153), Qiao *et al.*, 2016 (163), Chevrinais *et al.*, 2017 (153), King *et al.*, 2017 (181)

336. Maxilla

Absent (0)

Present (1)

UBERON 0002397 Maxilla: The bone which normally forms the lateral upper jaw in osteichthyans, including tetrapods.

Lu *et al.*, 2016 (247)

337. Maxilla, shape of

Splint-shaped (0)

Cleaver-shaped (1)

UBERON 0002397 Maxilla: The bone which normally forms the lateral upper jaw in osteichthyans, including tetrapods.

Zhu *et al.*, 2013 (180), Long *et al.*, 2014 (180), Dupret *et al.*, 2014 (180), Giles *et al.*, 2015 (90), Lu *et al.*, 2016 (90)

338. Posterior margin of cheek, maxilla, contribution of

Present (0)

Absent (1)

UBERON 0002397 Maxilla: The bone which normally forms the lateral upper jaw in osteichthyans, including tetrapods

UBERON 0001567 Cheek: A fleshy subdivision of one side of the face bounded by an eye, ear and the nose.

Zhu *et al.*, 2009 (81), Zhu *et al.*, 2013 (182), Long *et al.*, 2014 (182), Dupret *et al.*, 2014 (182), Giles *et al.*, 2015 (59), Lu *et al.*, 2016 (59), Qiao *et al.*, 2016 (146), Chevrinais *et al.*, 2017 (182), King *et al.*, 2017 (176)

339. Maxilla, ventral margin, shape of

Straight (0)

Curved (1)

UBERON 0002397 Maxilla : The bone which normally forms the lateral upper jaw in osteichthyans, including tetrapods

Zhu *et al.*, 2009 (80), Zhu *et al.*, 2013 (181), Long *et al.*, 2014 (181), Dupret *et al.*, 2014 (181), Qiao *et al.*, 2016 (187), Chevrinais *et al.*, 2017 (181), King *et al.*, 2017 (201)

340. Maxilla, orbital process

Absent (0)

Present (1)

UBERON 0002397 Maxilla: The bone which normally forms the lateral upper jaw in osteichthyans, including tetrapods

King *et al.*, 2017 (282)

341. Contact between most posterior major bone of cheek bearing preopercular sensory canal and maxilla

Present (0)

Absent (1)

UBERON 0002397 Maxilla: The bone which normally forms the lateral upper jaw in osteichthyans, including tetrapods.

UBERON 0001567 Cheek: A fleshy subdivision of one side of the face bounded by an eye, ear and the nose.

UBERON 2001813 Preopercular sensory canal: Sensory canal lateral or ventral to and in close proximity with the otic and post-otic sensory canals at their union, and anteroventrally with the mandibular sensory canal. The preopercular sensory canal is bilaterally paired and associated with the preopercle bone.

King *et al.*, 2017 (265)

342. Sclerotic plates

Absent (0)

Present (1)

Chevrainais *et al.*, 2017 (259)

343. Sclerotic plates, number of

≤4 (0)

>4 (1)

Zhu *et al.*, 2009 (57), Zhu *et al.*, 2013 (170), Long *et al.*, 2014 (170), Dupret *et al.*, 2014 (170), Qiao *et al.*, 2016 (241), Chevrinais *et al.*, 2017 (170), King *et al.*, 2017 (204)

344. Sclerotic ring

Absent (0)

Present (1)

UBERON 0007804 Sclerotic ring: Sclerotic rings are rings of bone found in the eyes of several groups of vertebrate animals, except for mammals and crocodilians. They can be made up of single bones or small bones together. They are believed to have a role in supporting the eye, especially in animals whose eyes are not spherical, or which live underwater. Fossil sclerotic rings are known for a variety of extinct animals, including ichthyosaurs, pterosaurs, and dinosaurs, but are often not preserved

Giles *et al.*, 2015 (52), Lu *et al.*, 2016 (52), Qiao *et al.*, 2016 (277), King *et al.*, 2017 (213)

345. Vault of skull, sclerotic ring, incorporation of

Absent (0)

Present (1)

UBERON 0007804 Sclerotic ring: Sclerotic rings are rings of bone found in the eyes of several groups of vertebrate animals, except for mammals and crocodilians. They can be made up of single bones or small bones together. They are believed to have a role in supporting the eye, especially in animals whose eyes are not spherical, or which live underwater. Fossil sclerotic rings are known for a variety of extinct animals, including ichthyosaurs, pterosaurs, and dinosaurs, but are often not preserved

UBERON 0004339 Vault of skull: upper part of skull, consisting of parietals, frontals, post-parietals, and in some species the squamosal and a portion of the alisphenoid.

King *et al.*, 2017 (244)

346. Preorbital depression

Absent (0)

Present (1)

King *et al.*, 2017 (246)

347. Preorbital recess

Absent (0)

Present (1)

King *et al.*, 2017 (247)

348. Preorbital recess, position of

Restricted to premedian plate (0)

Extends to lateral plates (1)

King *et al.*, 2017 (248)

349. Orbit of skull, location of

Dorsal (0)

Lateral (1)

UBERON 0001697 Orbit of skull: Subdivision of skeleton that is an anterolateral part of the cranium and structurally supports the eye. Includes bones formed and located in sclerotic layer of eyeball.

Wilson & Märss 2009 (37)

350. Supraorbital bone

Absent (0)

Present (1)

UBERON 2000691 Supraorbital bone: Dermal bone that is part of the dorsal or upper border or antero-dorsal border of the orbit. The supraorbital bone may contact the orbital margin of the frontal bone medially, the antorbital antero-ventrally and the dermosphenotic posteriorly. The supraorbital bone does not carry sensory canals. The supraorbital bone is paired

Zhu *et al.*, 2009 (10), Zhu *et al.*, 2013 (154), Long *et al.*, 2014 (154), Dupret *et al.*, 2014 (154), Qiao *et al.*, 2016 (164), Chevrinais *et al.*, 2017 (154), King *et al.*, 2017 (182)

351. Supraorbital bone, number of

1 (0)

2 (1)

>2 (2)

UBERON 2000691 Supraorbital bone: Dermal bone that is part of the dorsal or upper border or antero-dorsal border of the orbit. The supraorbital bone may contact the orbital margin of the frontal bone medially, the antorbital antero-ventrally and the dermosphenotic posteriorly. The supraorbital bone does not carry sensory canals. The supraorbital bone is paired

King *et al.*, 2017 (262)

352. Supraorbital cartilage

Present (0)

Absent (1)

Grogan & Lund 2000 (2), Grogan & Lund 2004 (2), Grogan *et al.*, 2012 (4)

353. Suborbital bone, cutaneous sense organ

Absent (0)

Present (1)

King *et al.*, 2017 (240)

354. Postsuborbital bone, cutaneous sense organ

Absent (0)

Present (1)

King *et al.*, 2017 (241)

355. Paraorbital plate separating suborbital bone from orbit of skull

Absent (0)

Present (1)

UBERON 0001697 Orbit of skull: Subdivision of skeleton that is an anterolateral part of the cranium and structurally supports the eye. Includes bones formed and located in sclerotic layer of eyeball.

King *et al.*, 2017 (253)

356. Supraorbital bone, preorbital bone and nasal bone, fusion of

Unfused (0)

Fused (1)

UBERON 2000691 Supraorbital bone: Dermal bone that is part of the dorsal or upper border or antero-dorsal border of the orbit. The supraorbital bone may contact the orbital margin of the frontal bone medially, the antorbital antero-ventrally and the dermosphenotic posteriorly. The supraorbital bone does not carry sensory canals. The supraorbital bone is paired.

UBERON 0001681 Nasal bone: One of two small oblong bones, varying in size and form in different individuals; they are placed side by side at the middle and upper part of the face, and form, by their junction, 'the bridge' of the nose[WP]. Paired dermal bones, likened to a bone tube, positioned lateral to the supraethmoid. Nasal bones are transversed by the anterior most part of the supraorbital canals and bear one neuromast foramen in zebrafish[ZFA].

357. Lacrimal

Absent (0)

Present (1)

UBERON 3010146 Lacrimal: Investing bone in non-teleosts associated with nasolacrimal duct and lying between pars facialis of maxilla and prefrontal and sometimes nasal.

King *et al.*, 2017 (257)

358. Lacrimal notch

Absent (0)

Present (1)

UBERON 3010146 Lacrimal: Investing bone in non-teleosts associated with nasolacrimal duct and lying between pars facialis of maxilla and prefrontal and sometimes nasal.

King *et al.*, 2017 (280)

359. Lacrimal, posterior naris, posterior enclose of

Absent (0)

Present (1)

UBERON 3010146 Lacrimal: Investing bone in non-teleosts associated with nasolacrimal duct and lying between pars facialis of maxilla and prefrontal and sometimes nasal.

Zhu *et al.*, 2009 (58), Zhu *et al.*, 2013 (172), Long *et al.*, 2014 (172), Dupret *et al.*, 2014 (172), Qiao *et al.*, 2016 (179), Chevrinais *et al.*, 2017 (172), King *et al.*, 2017 (192)

360. (N) Circumorbital bones

Absent (0)

Present (1)

361. Circumorbital bones, shape of

Interlocking plates with pronounced crescentic margins (0)

Scale-like (1)

Anterior plate greatly enlarged (2)

Brazeau 2009 (28)

362. Circumorbital scales/bones, relative size of

Smaller than head scales (0)

Same size as head scales (1)

Anterior or posterior larger than head scales (2)

Burrow & Turner 2100 (1)

363. Circumorbital ossification, series of

Absent (0)

Present (1)

Brazeau 2009 (17)

364. Tectal plate

Absent (0)

Present (1)

Zhu *et al.*, 2009 (15), Zhu *et al.*, 2013 (156), Long *et al.*, 2014 (156), Dupret *et al.*, 2014 (156), Qiao *et al.*, 2016 (166), Chevrinais *et al.*, 2017 (156), King *et al.*, 2017 (184)

365. (N) Jugal bone

Absent (0)

Present (1)

UBERON 0001683 Jugal bone: The quadrilateral bone that forms the prominence of the cheek.

366. Jugal bone, anterior margin, notch

Absent (0)

Present (1)

UBERON 0001683 Jugal bone: The quadrilateral bone that forms the prominence of the cheek.

King *et al.*, 2017 (275)

367. Postorbital bone

Absent (0)

Present (1)

UBERON 0011169 Postorbital bone : The postorbital is one of the bones in vertebrate skulls which forms a portion of the dermal skull roof and, sometimes, a ring about the orbit. Generally, it is located behind the postfrontal and posteriorly to the orbital fenestra. In some vertebrates, the postorbital is fused with the postfrontal to create a postorbitofrontal.

King *et al.*, 2017 (279)

368. Quadratojugal bone

Absent (0)

Present (1)

UBERON 0011267 Quadratojugal bone: The quadratojugal is a small jaw bone that is present in most amphibians, reptiles, and birds, but has been lost in mammals. It is connected to the jugal as well as other bones, though these may vary with species. The quadratojugal bone is a small bone between the cheek and otic notch

King *et al.*, 2017 (276)

369. Bone bearing both quadratojugal pit-line and preopercular sensory canal

Absent (0)

Present (1)

UBERON 2001813 Preopercular sensory canal: Sensory canal lateral or ventral to and in close proximity with the otic and post-otic sensory canals at their union, and anteroventrally with the mandibular sensory canal. The preopercular sensory canal is bilaterally paired and associated with the preopercle bone. May be continuous with the otic and post-otic sensory canals at their union.

Zhu *et al.*, 2009 (61), Zhu *et al.*, 2013 (175), Long *et al.*, 2014 (175), Dupret *et al.*, 2014 (175), Qiao *et al.*, 2016 (182), Chevrin *et al.*, 2017 (175), King *et al.*, 2017 (197)

370. Subsquamals

Absent (0)

Present (1)

Giles *et al.*, 2015 (55), Lu *et al.*, 2016 (55), Qiao *et al.*, 2016 (279), King *et al.*, 2017 (215)

371. (N) Preopercle

Absent (0)

Present (1)

Preopercle: UBERON 2000264 Dermal bone that is part of the opercular series and bears the preopercular sensory canal. The preopercle is a paired bone and typically L-shaped, with the horizontal limb overlying the interopercle and the vertical limb overlying the opercle

372. Preopercle, shape of

Rhombic (0)

Bar-shaped (1)

Preopercle: UBERON 2000264 Dermal bone that is part of the opercular series and bears the preopercular sensory canal. The preopercle is a paired bone and typically L-shaped, with the horizontal limb overlying the interopercle and the vertical limb overlying the opercle

Giles *et al.*, 2015 (56), Lu *et al.*, 2016 (56), Qiao *et al.*, 2016 (280), King *et al.*, 2017 (216)

373. Preopercular sensory canal, exit of

Canal exits the dorso-posterior margin of the preopercular (0)

Canal exits at the antero-dorsal margin of the preopercular (1)

Canal exits the anterior margin of the preopercular at half-length (2)

UBERON 2001813 Preopercular sensory canal: Sensory canal lateral or ventral to and in close proximity with the otic and post-otic sensory canals at their union, and anteroventrally with the mandibular sensory canal. The preopercular sensory canal is bilaterally paired and associated with the preopercle bone.

Chevrainais *et al.*, 2017 (195)

374. Preoperculosubmandibular

Absent (0)

Present (1)

Lu *et al.*, 2016 (244), Qiao *et al.*, 2016 (328)

375. Preopercle, anterior extension of

Absent (0)

Present (1)

UBERON 2001813 Preopercular sensory canal: Sensory canal lateral or ventral to and in close proximity with the otic and post-otic sensory canals at their union, and anteroventrally with the mandibular sensory canal. The preopercular sensory canal is bilaterally paired and associated with the preopercle bone.

Zhu *et al.*, 2009 (59), Zhu *et al.*, 2013 (173), Long *et al.*, 2014 (173), Dupret *et al.*, 2014 (173), Qiao *et al.*, 2016 (180), Chevrinais *et al.*, 2017 (173), King *et al.*, 2017 (195)

376. Preopercular sensory canal, cheek bones, number of

One (0)

Two (1)

UBERON 0001567 Cheek: A fleshy subdivision of one side of the face bounded by an eye, ear and the nose.

UBERON 2001813 Preopercular sensory canal: Sensory canal lateral or ventral to and in close proximity with the otic and post-otic sensory canals at their union, and anteroventrally with the mandibular sensory canal. The preopercular sensory canal is bilaterally paired and associated with the preopercle bone. UBERON 0001683 Jugal bone: The quadrilateral bone that forms the prominence of the cheek.

Zhu *et al.*, 2009 (60), Zhu *et al.*, 2013 (174), Long *et al.*, 2014 (174), Dupret *et al.*, 2014 (174), Qiao *et al.*, 2016 (181), Chevrinais *et al.*, 2017 (174), King *et al.*, 2017 (196)

377. Dermohyal

Absent (0)

Present (1)

Zhu *et al.*, 2009 (62), Zhu *et al.*, 2013 (176), Long *et al.*, 2014 (176), Dupret *et al.*, 2014 (176), Qiao *et al.*, 2016 (183), Chevrinais *et al.*, 2017 (176), King *et al.*, 2017 (198)

378. Prelateral plate

Absent (0)

Present (1)

King *et al.*, 2017 (251)

379. Lateral plate

Absent (0)

Present (1)

Zhu *et al.*, 2013 (157), Long *et al.*, 2014 (157), Dupret *et al.*, 2014 (157), Qiao *et al.*, 2016 (167), Chevrinais *et al.*, 2017 (157), King *et al.*, 2017 (185)

380. Marginal plate, mesial lamina

Absent (0)

Present (1)

King *et al.*, 2017 (254)

381. Posterior dorsolateral plate

Absent (0)

Present (1)

UBERON 4300025 Posterior dorsolateral plate: Dermal bone that is part of the scapular complex in “placoderms”, located posterior to the main components of the complex.

Giles *et al.*, 2015 (187), Lu *et al.*, 2016 (187), Qiao *et al.*, 2016 (308), King *et al.*, 2017 (436)

382. Posterior dorsolateral plate and prelateral plate, overlap of

Simple (0)

Insertion (1)

UBERON 4300025 Posterior dorsolateral plate: Dermal bone that is part of the scapular complex in “placoderms”, located posterior to the main components of the complex.

King *et al.*, 2017 (437)

383. Below mediodorsal plate, posterior dorsolateral plates, contact of

Absent (0)

Present (1)

UBERON 4300025 Posterior dorsolateral plate : Dermal bone that is part of the scapular complex in “placoderms”, located posterior to the main components of the complex.

King *et al.*, 2017 (438)

384. Posterior dorsolateral plate, externe exposition of

Absent (0)

Present (1)

UBERON 4300025 Posterior dorsolateral plate : Dermal bone that is part of the scapular complex in “placoderms”, located posterior to the main components of the complex.

King *et al.*, 2017 (439)

385. Mediodorsal plate, posterior produced spine

Absent (0)

Present (1)

King *et al.*, 2017 (440)

VAULT OF SKULL

386. (N) Dermatocranium, distinct dermal bones

Absent (0)

Present (1)

UBERON Dermatocranium: 0003113 Subdivision of skeleton that includes all dermal bones in the cranial skeleton

UBERON 0008907 Dermal bone: Skeletal element that forms superficially in the organism, usually in association with the ectoderm.

387. Dermatocranium, undifferentiated plates or tesseræ

Absent (0)

Present (1)

UBERON Dermatocranium: 0003113 Subdivision of skeleton that includes all dermal bones in the cranial skeleton

Brazeau 2009 (19 modified), Davis *et al.*, 2012 (18), Zhu *et al.*, 2013 (18), Long *et al.*, 2014 (18), Dupret *et al.*, 2014 (18), Giles *et al.*, 2015 (33), Lu *et al.*, 2016 (33), Chevrinais *et al.*, 2017 (18), Qiao *et al.*, 2016 (17), Coates *et al.*, 2017 (18), King *et al.*, 2017 (151)

388. Snout region, composition of

Not fragmented into mosaic of plates (0)

Fragmented into mosaic of plates (1)

UBERON 0006333 Snout: Surface structure that is the region of the head in front of and between the orbits, and above the lower jaw. Nares are located on the snout

King *et al.*, 2017 (259)

389. Head, shape of

Broad, rectangular (0)

Conical, tapered (1)

Bluntly rounded (2)

Barrel-shaped (3).

UBERON 0000033 Head: The head is the anterior-most division of the body

Wilson & Märss 2009 (40)

390. (N) Dermatocranium, odontode scales

Absent (0)

Present (1)

UBERON 0003113 Dermatocranium: Subdivision of skeleton that includes all dermal bones in the cranial skeleton

UBERON 0000041 Odontode scale: Multi-tissue structure composed of enameloid, dentine surrounding a pulp cavity, and bone of attachment anchoring the element into the dermis

391. (N) Dermatocranium, radial denticules

Absent (0)

Present (1)

UBERON 0003113 Dermatocranium: Subdivision of skeleton that includes all dermal bones in the cranial skeleton

392. (N) Dermatocranium, conical scales

Absent (0)

Present (1)

UBERON 0003113 Dermatocranium: Subdivision of skeleton that includes all dermal bones in the cranial skeleton

393. Head tesserae

Absent (0)

Present (1)

Brazeau 2009 (20 modified), Davis *et al.*, 2012 (19 modified), Long *et al.*, 2014 (19 modified), Dupret *et al.*, 2014 (19 modified), Giles *et al.*, 2015 (35 modified), Lu *et al.*, 2016 (35 modified), Qiao *et al.*, 2016 (18 modified), Chevrinai *et al.*, 2017 (19 modified), Coates *et al.*, 2017 (19 modified), King *et al.*, 2017 (152 modified)

394. Dermatocranium, tesseræ, shape of

Polygonal plates (0)

Microsquamose, not larger than body scales (1)

UBERON 0003113 Dermatocranium: Subdivision of skeleton that includes all dermal bones in the cranial skeleton

Brazeau 2009 (20 modified), Davis *et al.*, 2012 (19 modified), Long *et al.*, 2014 (19 modified), Dupret *et al.*, 2014 (19 modified), Giles *et al.*, 2015 (35 modified), Lu *et al.*, 2016 (35 modified), Qiao *et al.*, 2016 (18 modified), Chevrinais *et al.*, 2017 (19 modified), Coates *et al.*, 2017 (19 modified), King *et al.*, 2017 (152 modified)

395. Dorsal midline of dermatocranium, series of paired median skull roofing bones, meet of

Absent (0)

Present (1)

UBERON 0003113 Dermatocranium: Subdivision of skeleton that includes all dermal bones in the cranial skeleton

UBERON 0003129 Skull: Anatomical structure that is part of the head consisting entirely of cranium and mandible

Brazeau 2009 (24), Davis *et al.*, 2012 (23), Long *et al.*, 2014 (23), Dupret *et al.*, 2014 (23), Giles *et al.*, 2015 (43), Lu *et al.*, 2016 (43), Qiao *et al.*, 2016 (22), Chevrinais *et al.*, 2017 (23), Coates *et al.*, 2017 (20), King *et al.*, 2017 (156)

396. Anteriorly directed adductor fossae between neurocranium and vault of skull

Absent (0)

Present (1)

UBERON 0001703 Neurocranium: Subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

UBERON 0004339 Vault of skull: Upper part of skull, consisting of parietals, frontals, post-parietals, and in some species the squamosal and a portion of the alisphenoid

Lu *et al.*, 2016 (256)

397. Vault of skull, posterior margin, unpaired median bone, contribution of

Absent (0)

Present (1)

UBERON 0004339 Vault of skull: Upper part of skull, consisting of parietals, frontals, post-parietals, and in some species the squamosal and a portion of the alisphenoid

Zhu *et al.*, 2013 (163), Long *et al.*, 2014 (163), Dupret *et al.*, 2014 (163), Qiao *et al.*, 2016 (172), Chevrinais *et al.*, 2017 (163)

398. Vault of skull, endolymphatic ducts, opening of

Present (0)

Absent (1)

UBERON 0001860 Endolymphatic duct: The small membranous canal, connecting with both saccule and utricle of the membranous labyrinth, passing through the aqueduct of vestibule, and terminating in the endolymphatic sac.

UBERON 0004339 Vault of skull: Upper part of skull, consisting of parietals, frontals, post-parietals, and in some species the squamosal and a portion of the alisphenoid.

Brazeau 2009 (22), Davis *et al.*, 2012 (21), Zhu *et al.*, 2013 (21), Long *et al.*, 2014 (21), Dupret *et al.*, 2014 (21), Giles *et al.*, 2015 (38), Lu *et al.*, 2016 (38), Qiao *et al.*, 2016 (20), Chevrinais *et al.*, 2017 (21), King *et al.*, 2017 (154)

399. Vault of skull, posterior descending lamina

Absent (0)

Present (1)

UBERON 0004339 Vault of skull : Upper part of skull, consisting of parietals, frontals, post-parietals, and in some species the squamosal and a portion of the alisphenoid.

King *et al.*, 2017 (252)

400. Vault of skull, posterior margin, shape of

Embayed (0)

Straight (1)

Convex (2)

UBERON 0004339 Vault of skull : Upper part of skull, consisting of parietals, frontals, post-parietals, and in some species the squamosal and a portion of the alisphenoid.

Zhu *et al.*, 2009 (26)

401. Paired skull roofing bones, suture, shape of

Straight (0)

Sinusoidal (1)

Giles *et al.*, 2015 (49), Lu *et al.*, 2016 (49), Qiao *et al.*, 2016 (274), King *et al.*, 2017
(210)

402. Headshield

Present (0)

Absent (1)

403. Posterior part of headshield, enlarged tubercles, symmetrical pattern of

Absent (0)

Present (1)

King *et al.*, 2017 (236)

404. Headshield enclosed posteriorly behind oralobranchial chamber

Absent (0)

Present (1)

King *et al.*, 2017 (235)

405. Headshield, dorsal spinal process

Absent (0)

Present (1)

King *et al.*, 2017 (231)

406. Cranial spines

Absent (0)

Present (1)

Giles *et al.*, 2015 (36), Lu *et al.*, 2016 (36), Qiao *et al.*, 2016 (268), King *et al.*, 2017 (206)

407. Cranial spines, organisation of

Multicuspid (0)

Monocuspid (1)

Giles *et al.*, 2015 (36), Lu *et al.*, 2016 (36), Qiao *et al.*, 2016 (268), King *et al.*, 2017 (206)

408. Dermal neck-joint

Absent (0)

Present (1)

UBERON 4300029 Dermal neck joint: Dermal articulation between skull and shoulder girdle localized to paired dermal neck-joint between anterior dorsolateral plate (ADL) and paranuchal (PNu) plates in “placoderms”

Zhu *et al.*, 2013 (168), Long *et al.*, 2014 (168), Dupret *et al.*, 2014 (168), Qiao *et al.*, 2016 (177), Chevrinais *et al.*, 2017 (168), King *et al.*, 2017 (192)

409. Dermal neck-joint, type of

Sliding, dermal shoulder girdle plate with flat articular flange (0)

Ginglymoid, dermal shoulder girdle plate with condyle or bone fossa (1)

UBERON 4300029 Dermal neck joint: Dermal articulation between skull and shoulder girdle localized to paired dermal neck-joint between anterior dorsolateral plate (ADL) and paranuchal (PNu) plates in “placoderms”.

UBERON 0009979 Condyle: An articular prominence of a bone, typically present in pairs, resembling a pair of knuckles.

UBERON 0004704 Bone fossa: A depression or hollow in a bone

Zhu *et al.*, 2013 (169), Long *et al.*, 2014 (169), Dupret *et al.*, 2014 (169), Giles *et al.*, 2015 (60), Lu *et al.*, 2016 (60), Qiao *et al.*, 2016 (144), Chevrinais *et al.*, 2017 (169), King *et al.*, 2017 (173)

410. Dermatocranium cover, extent of

Complete (0)

Incomplete (scale-free and elsewhere) (1)

UBERON 0003113 Dermatocranium: Subdivision of skeleton that includes all dermal bones in the cranial skeleton

Brazeau 2009 (21), Davis *et al.*, 2012 (20), Zhu *et al.*, 2013 (20), Long *et al.*, 2014 (20), Dupret *et al.*, 2014 (20), Giles *et al.*, 2015 (37), Lu *et al.*, 2016 (37), Qiao *et al.*, 2016 (19), Chevrinais *et al.*, 2017 (20), King *et al.*, 2017 (153)

411. Dermatocranium, ornamentation of

Smooth (0)

Parallel, vermiform ridges (1)

Concentric ridges (2)

Tuberculate (3)

Giles *et al.*, 2015 (29), Lu *et al.*, 2016 (29), Qiao *et al.*, 2016 (265), King *et al.*, 2017 (205)

412. Outer dental arcade, dermal plates

Only with denticles (0)

With monolinear tooth row (1)

UBERON 0009678 Tooth row: Anatomical cluster consisting of adjacent teeth constituting a row.

Zhu *et al.*, 2013 (198), Long *et al.*, 2014 (198), Dupret *et al.*, 2014 (198), Qiao *et al.*, 2016 (202) Chevrinais *et al.*, 2017 (198), Coates *et al.*, 2017 (49), King *et al.*, 2017 (202)

413. (N) Premaxilla

Absent (0)

Present (1)

UBERON 0002244 Premaxilla: One of the bones of the upper jaw situated between and in front of the maxillae

414. Premaxilla, position of

Extends under orbits of skull (0)

Restricted anterior to orbit of skull (1)

UBERON 0002244 Premaxilla: One of the bones of the upper jaw situated between and in front of the maxillae

UBERON 0001697 Orbit of skull: Subdivision of skeleton that is an anterolateral part of the cranium and structurally supports the eye. Includes bones formed and located in sclerotic layer of eyeball

Giles *et al.*, 2015 (89), Lu *et al.*, 2016 (89), Qiao *et al.*, 2016 (286), King *et al.*, 2017 (217)

415. Premaxilla and orbit of skull, contact of

Absent (0)

Present (1)

UBERON 0002244 Premaxilla: One of the bones of the upper jaw situated between and in front of the maxillae

UBERON 0001697 Orbit of skull: Subdivision of skeleton that is an anterolateral part of the cranium and structurally supports the eye. Includes bones formed and located in sclerotic layer of eyeball.

Zhu *et al.*, 2013 (178), Long *et al.*, 2014 (178), Dupret *et al.*, 2014 (178), Qiao *et al.*, 2016 (185), Chevrinaiis *et al.*, 2017 (178), King *et al.*, 2017 (200)

416. Premaxilla and posterior naris, contact of

Absent (0)

Present (1)

UBERON 0002244 Premaxilla: One of the bones of the upper jaw situated between and in front of the maxillae

King *et al.*, 2017 (272)

417. Premaxilla, inturned symphysial processes

Absent (0)

Present (1)

UBERON 0002244 Premaxilla: One of the bones of the upper jaw situated between and in front of the maxillae

Zhu *et al.*, 2013 (177), Long *et al.*, 2014 (177), Dupret *et al.*, 2014 (177), Qiao *et al.*, 2016 (184), Chevrinais *et al.*, 2017 (177), King *et al.*, 2017 (199)

418. Premaxilla, preorbital process

Absent (0)

Present (1)

UBERON 0002244 Premaxilla: One of the bones of the upper jaw situated between and in front of the maxillae

Zhu *et al.*, 2009 (78), Zhu *et al.*, 2013 (179), Long *et al.*, 2014 (179), Dupret *et al.*, 2014 (179), Qiao *et al.*, 2016 (186), Chevrinais *et al.*, 2017 (197)

419. Premaxilla, enlarged anterior tooth

Absent (0)

Present (1)

UBERON 0002244 Premaxilla: One of the bones of the upper jaw situated between and in front of the maxillae

King *et al.*, 2017 (379)

420. (N) Rostral plate

Absent (0)

Present (1)

UBERON 2001934 Rostral plate: dermal bone that is located on midline of snout in skin above mesethmoid and lateral ethmoid bones. Rostral plate bears type 1 odontodes and is unpaired

421. Headshield, median rostral plate, extension of

Absent (0)

Present (1)

UBERON 2001934 Rostral plate: dermal bone that is located on midline of snout in skin above mesethmoid and lateral ethmoid bones. Rostral plate bears type 1 odontodes and is unpaired

King *et al.*, 2017 (218)

422. Prerostral plate

Absent (0)

Present (1)

King *et al.*, 2017 (269)

423. Postrostral plate

Absent (0)

Present (1)

Zhu *et al.*, 2009 (2)

424. Median rostral, tooth

Absent (0)

Present (1)

Zhu *et al.*, 2009 (75), Zhu *et al.*, 2013 (199), Long *et al.*, 2014 (199), Dupret *et al.*, 2014 (199), Qiao *et al.*, 2016 (203), Chevrinais *et al.*, 2017 (199), King *et al.*, 2017 (346)

425. Postrostral plate, composition of

Mosaic of bones (0)

Large median plate with smaller additive bones (1)

Single median plate (2)

Zhu *et al.*, 2009 (2)

426. Vault of skull, external naris, enclose of

Present (0)

Absent (1)

UBERON 0005928 External naris: A naris that provides one of the small external openings of the head that give passage to air for breathing.

UBERON 0004339 Vault of skull: Upper part of skull, consisting of parietals, frontals, post-parietals, and in some species the squamosal and a portion of the alisphenoid.

King *et al.*, 2017 (256)

427. Ethmoid plate, toothplate (supragnathals or vomers), pair of

Absent (0)

Present (1)

UBERON 0002396 Vomer: The triangular flat bone of the nasal septum.

Giles *et al.*, 2015 (91), Lu *et al.*, 2016 (91), Qiao *et al.*, 2016 (287), King *et al.*, 2017 (367)

428. Posterior superognathal, vertical pipe-like ridges

Absent (0)

Present (1)

King *et al.*, 2017 (373)

429. Anterior supragnathals, fusion of

Absent (0)

Present (1)

King *et al.*, 2017 (372)

430. Supragnathal, durophagous occlusal surface

Absent (0)

Present (1)

Long *et al.*, 2014 (257), Qiao *et al.*, 2016 (249), King *et al.*, 2017 (364)

431. (N) Nasal bone

Absent (0)

Present (1)

UBERON 0001681 Nasal bone: One of two small oblong bones, varying in size and form in different individuals; they are placed side by side at the middle and upper part of the face, and form, by their junction, 'the bridge' of the nose[WP]. Paired dermal bones, likened to a bone tube, positioned lateral to the supraethmoid. Nasal bones are transversed by the anterior most part of the supraorbital canals and bear one neuromast foramen in zebrafish[ZFA].

432. Nasal bone, number of

>2 (0)

≤2 (1)

UBERON 0001681 Nasal bone: One of two small oblong bones, varying in size and form in different individuals; they are placed side by side at the middle and upper part of the

face, and form, by their junction, 'the bridge' of the nose[WP]. Paired dermal bones, likened to a bone tube, positioned lateral to the supraethmoid. Nasal bones are transversed by the anterior most part of the supraorbital canals and bear one neuromast foramen in zebrafish[ZFA].

Zhu *et al.*, 2009 (4), Zhu *et al.*, 2013 (149), Long *et al.*, 2014 (149), Dupret *et al.*, 2014 (149), Qiao *et al.*, 2016 (160), Chevrinais *et al.*, 2017 (149), King *et al.*, 2017 (178)

433. Nasal bone, mesial margin, notch of

Absent (0)

Present (1)

UBERON 0001681 Nasal bone: One of two small oblong bones, varying in size and form in different individuals; they are placed side by side at the middle and upper part of the face, and form, by their junction, 'the bridge' of the nose[WP]. Paired dermal bones, likened to a bone tube, positioned lateral to the supraethmoid. Nasal bones are transversed by the anterior most part of the supraorbital canals and bear one neuromast foramen in zebrafish[ZFA].

Zhu *et al.*, 2009 (3), Zhu *et al.*, 2013 (150), Long *et al.*, 2014 (150), Dupret *et al.*, 2014 (150), Qiao *et al.*, 2016 (161), Chevrinais *et al.*, 2017 (150), King *et al.*, 2017 (179)

434. External nasal opening, type of

Single (0)

Median paired (1)

King *et al.*, 2017 (227)

435. Unpaired median skull roofing bone anterior to the level of nasal capsules

Absent (0)

Present (1)

UBERON 0006332 Nasal capsule: An embryonic cartilaginous frame, the nasal capsule, an evolutionary-conserved structure composed of ventral and dorsal components: the mesethmoid and ectethmoid cartilages, respectively.

Zhu *et al.*, 2013 (148), Long *et al.*, 2014 (148), Dupret *et al.*, 2014 (148), Qiao *et al.*, 2016 (159), Chevrinais *et al.*, 2017 (148), Coates *et al.*, 2017 (21), King *et al.*, 2017 (177)

436. Nasal bone and premaxillary, contact of

Absent (0)

Present (1)

UBERON 0001681 Nasal bone: One of two small oblong bones, varying in size and form in different individuals; they are placed side by side at the middle and upper part of the face, and form, by their junction, 'the bridge' of the nose

UBERON 0002244 Premaxilla: One of the bones of the upper jaw situated between and in front of the maxillae

Zhu *et al.*, 2009 (3)

437. Internasal groove

Absent (0)

Present (1)

Coates *et al.*, 2017 (65)

438. Dermintermedial process

Absent (0)

Present (1)

Zhu *et al.*, 2009 (6), Zhu *et al.*, 2013 (151), Long *et al.*, 2014 (151), Dupret *et al.*, 2014 (151), Qiao *et al.*, 2016 (162), Chevrinais *et al.*, 2017 (151), Coates *et al.*, 2017 (66), King *et al.*, 2017 (180)

439. Cutaneous sense organ on vault of skull posterior to orbit of skull

Absent (0)

Present (1)

UBERON 0004339 Vault of skull: Upper part of skull, consisting of parietals, frontals, post-parietals, and in some species the squamosal and a portion of the alisphenoid.

UBERON 0001697 Orbit of skull: Subdivision of skeleton that is an anterolateral part of the cranium and structurally supports the eye. Includes bones formed and located in sclerotic layer of eyeball.

King *et al.*, 2017 (242)

440. Parietal and supraorbital, contact of

Present (0)

Absent (1)

Zhu *et al.*, 2009 (12)

441. Parietal

Absent (0)

Present (1)

442. Parietals (preorbitals of “placoderms”), pineal foramen, surround of

Absent (0)

Present (1)

Zhu *et al.*, 2009 (20), Zhu *et al.*, 2013 (159), Long *et al.*, 2014 (159), Dupret *et al.*, 2014 (159)

443. Canal-bearing bone of vault of skull extends far past posterior margin of parietals

Absent (0)

Present (1)

UBERON 0004339 Vault of skull: upper part of skull, consisting of parietals, frontals, post-parietals, and in some species the squamosal and a portion of the alisphenoid.

Lu *et al.*, 2016 (238), Qiao *et al.*, 2016 (325)

444. Parietal, anterior margin

Between or in front orbit of skull (0)

Same level as posterior margin of orbit of skull (1)

Posterior to orbit of skull (2)

UBERON 0001697 Orbit of skull: Subdivision of skeleton that is an anterolateral part of the cranium and structurally supports the eye. Includes bones formed and located in sclerotic layer of eyeball.

Zhu *et al.*, 2009 (16)

445. Vault of skull, anterior edge, parietal or preorbital plates

Absent (0)

Present (1)

UBERON 0004339 Vault of skull: Upper part of skull, consisting of parietals, frontals, post-parietals, and in some species the squamosal and a portion of the alisphenoid

King *et al.*, 2017 (243)

446. Anterior to parietal and pineal foramen, median dermal bone

Absent (0)

Present (1)

UBERON 0008907 Dermal bone: Skeletal element that forms superficially in the organism, usually in association with the ectoderm.

King *et al.*, 2017 (258)

447. Parietal and post-parietals, relative length of

Parietal portion longer as postparietal portion (0)

Parietal portion longer than postparietal portion (1)

Parietal portion shorter than postparietal portion (2)

UBERON 0004339 Vault of skull: Upper part of skull, consisting of parietals, frontals, post-parietals, and in some species the squamosal and a portion of the alisphenoid.

Zhu *et al.*, 2009 (24)

448. (N) Postparietal

Absent (0)

Present (1)

449. Lateral side of postparietals, dermal bones, number of

2 (0)

1 (1)

>2 (2)

UBERON 0004339 Vault of skull: Upper part of skull, consisting of parietals, frontals, post-parietals, and in some species the squamosal and a portion of the alisphenoid.

UBERON 0008907 Dermalbone: Skeletal element that forms superficially in the organism, usually in association with the ectoderm.

Giles *et al.*, 2015 (48), Lu *et al.*, 2016 (48)

450. Dermal intracranial joint, postparietals and parietals, participation of

Smooth (0)

Jagged (1)

UBERON 4100113 Dermal intracranial joint: Hinge in the skull skeleton to allow for kinetic movement of different parts.

Zhu *et al.*, 2009 (22)

451. Intertemporal bone

Absent (0)

Present (1)

Zhu *et al.*, 2009 (14)

452. Interparietal bone

Absent (0)

Present (1)

UBERON 0002229 Interparietal bone: The bone of the cranium that lies above and anterior to the occipital bone.

King *et al.*, 2017 (271)

453. (N) Supratemporal bone

Absent (0)

Present (1)

454. Supratemporal bone, postparietal, contact of

Absent (0)

Present (1)

King *et al.*, 2017 (273)

455. Supratemporal bone, nasal bone, contact of

Absent (0)

Present (1)

UBERON 0001681 Nasal bone: One of two small oblong bones, varying in size and form in different individuals; they are placed side by side at the middle and upper part of the face, and form, by their junction, 'the bridge' of the nose[WP]. Paired dermal bones, likened to a bone tube, positioned lateral to the supraethmoid. Nasal bones are transversed by the anterior most part of the supraorbital canals and bear one neuromast foramen in zebrafish[ZFA].

King *et al.*, 2017 (274)

456. (N) Supratemporal series, lateral series of lateral dermal bones, contact of

Absent (0)

Present (1)

UBERON 0008907 Dermal bone: Skeletal element that forms superficially in the organism, usually in association with the ectoderm.

457. Supratemporal bones, lateral series of dermal bones, number of

1 (0)

2 (1)

UBERON 0008907 Dermal bone: Skeletal element that forms superficially in the organism, usually in association with the ectoderm.

King *et al.*, 2017 (263)

458. Extratemporal bone

Absent (0)

Present (1)

UBERON 4100119 Extratemporal bone : Skull bone in the posterior half of the cranium, bordering the squamosal and opercular.

Zhu et al., 2009 (28)

459. B-bone

Absent (0)

Present (1)

King et al., 2017 (261)

460. Pineal foramen

Present (0)

Absent (1)

Zhu et al., 2009 (17)

461. Anterior dorsal (pineal) fontanelle

Absent (0)

Present (1)

UBERON 0002221 Fontanelle: Anatomical structure that is a membranous gap between bones of the skull

Brazeau 2009 (84)

462. Pineal eminence (in taxa lacking pineal foramen)

Absent (0)

Present (1)

Zhu *et al.*, 2009 (18), Lu *et al.*, 2016 (239)

463. Pineal foramen or eminence, dermal bone, association of

Contributes to orbital margin (plate excluded from orbital margin by skull roofing bones) (0)

Plate bordered laterally by skull roofing bones (1)

Giles *et al.*, 2015 (42), Lu *et al.*, 2016 (42), Qiao *et al.*, 2016 (270), King *et al.*, 2017 (208)

464. Behind pineal foramen, transverse external groove

Absent (0)

Present (1)

King *et al.*, 2017 (255)

465. Pineal foramen or eminence, location of

Same level as posterior margin of orbit of skull (0)

Posterior to orbit of skull (1)

UBERON 0001697 Orbit of Skull: subdivision of skeleton that is an anterolateral part of the cranium and structurally supports the eye. Includes bones formed and located in sclerotic layer of eyeball

Zhu *et al.*, 2009 (19), Zhu *et al.*, 2013 (158), Long *et al.*, 2014 (158), Dupret *et al.*, 2014 (158), Qiao *et al.*, 2016 (168), Chevrinais *et al.*, 2017 (158), King *et al.*, 2017 (186)

466. Paired pineal plates, ornamentation of

Absent (0)

Present (1)

Burrow & Turner 2010 (47)

467. Spiracle (sensu Vertebrata)

Absent (0)

Present (1)

UBERON 0010019 Spiracle (sensu Vertebrata): A small hole behind each eye that opens to the mouth in some fish. In the primitive jawless fish, the first gill opening immediately behind the mouth is essentially similar to the other gill openings.

Chevrinais *et al.*, 2017 (160)

468. Spiracle (sensu Vertebrata) bounded by bones carrying otic sensory canal

Absent (0)

Present (1)

UBERON 0010019 Spiracle (sensu Vertebrata) : A small hole behind each eye that opens to the mouth in some fish. In the primitive jawless fish the first gill opening immediately behind the mouth is essentially similar to the other gill openings.

UBERON 0004339 Vault of skull: Upper part of skull, consisting of parietals, frontals, post-parietals, and in some species the squamosal and a portion of the alisphenoid.

UBERON 2001629 Otic sensory canal: Sensory canal between and in close proximity posteriorly with the post-otic and preoperculo-mandibular sensory canals, and anteriorly with the supraorbital and infraorbital sensory canals. The otic sensory canal is bilaterally paired.

Chevrinais *et al.*, 2017 (160)

469. Vault of skull, spiracle, enclose of

Absent (0)

Present (1)

UBERON 0010019 Spiracle (sensu Vertebrata): A small hole behind each eye that opens to the mouth in some fish. In the primitive jawless fish the first gill opening immediately behind the mouth is essentially similar to the other gill openings.

UBERON 0004339 Vault of skull: Upper part of skull, consisting of parietals, frontals, post-parietals, and in some species the squamosal and a portion of the alisphenoid.

Zhu *et al.*, 2009 (25), Zhu *et al.*, 2013 (160), Long *et al.*, 2014 (160), Dupret *et al.*, 2014 (160), Qiao *et al.*, 2016 (170), Chevrinais *et al.*, 2017 (160), King *et al.*, 2017 (188)

470. (N) Nuchal plate

Absent (0)

Present (1)

UBERON 2001815 Nuchal plate: Dermal bone that is a bony expansion in the integument anterior to or flanking the dorsal fin that is part of and at the distal end of a supraneural or dorsal fin proximal radial.

471. Nuchal plate, orbital facets

Absent (0)

Present (1)

UBERON 2001815 Nuchal plate: Dermal bone that is a bony expansion in the integument anterior to or flanking the dorsal fin that is part of and at the distal end of a supraneural or dorsal fin proximal radial.

King *et al.*, 2017 (249)

472. Nuchal or centronuchal plate and paired preorbital plates, contact of

Absent (0)

Present (1)

UBERON 2001815 Nuchal plate: Dermal bone that is a bony expansion in the integument anterior to or flanking the dorsal fin that is part of and at the distal end of a supraneural or dorsal fin proximal radial.

Zhu *et al.*, 2013 (164), Long *et al.*, 2014 (164), Dupret *et al.*, 2014 (164), Qiao *et al.*, 2016 (173), Chevriniais *et al.*, 2017 (164), King *et al.*, 2017 (190)

473. Nuchal plate, posterior pit line canals and supraorbital sensory canals, course of

Converging but not meeting (0)

Crossing as an X in bone (1)

UBERON 2001815 Nuchal plate: Dermal bone that is a bony expansion in the integument anterior to or flanking the dorsal fin that is part of and at the distal end of a supraneural or dorsal fin proximal radial.

UBERON 2001810 Supraorbital sensory canal: Sensory canal anterior to and in close proximity to the otic and infraorbital sensory canals. The supraorbital sensory canal is bilaterally paired.

Long *et al.*, 2014 (256), Qiao *et al.*, 2016 (248)

474. Ventral surface of nuchal plate, paired pits

Absent (0)

Present (1)

UBERON 2001815 Nuchal plate: Dermal bone that is a bony expansion in the integument anterior to or flanking the dorsal fin that is part of and at the distal end of a supraneural or dorsal fin proximal radial

Giles *et al.*, 2015 (51), Lu *et al.*, 2016 (51), Qiao *et al.*, 2016 (276), King *et al.*, 2017 (212)

475. Endolymphatic duct, relation of

With nuchal plate (0)

With bones flanking the nuchal plate (e.g., paranuchals) (1)

UBERON 0001860 Endolymphatic duct: The small membranous canal, connecting with both saccule and utricle of the membranous labyrinth, passing through the aqueduct of vestibule, and terminating in the endolymphatic sac.

UBERON 2001815 Nuchal plate: Dermal bone that is a bony expansion in the integument anterior to or flanking the dorsal fin that is part of and at the distal end of a supraneural or dorsal fin proximal radial.

Giles *et al.*, 2015 (40), Lu *et al.*, 2016 (40), Qiao *et al.*, 2016 (269), King *et al.*, 2017 (207)

476. Centronuchal plate

Absent (0)

Present (1)

King *et al.*, 2017 (238)

477. (N) Paranuchal plate

Absent (0)

Present (1)

478. Posterior process of the paranuchal plate behind the nuchal plate (dorsal face)

Absent (0)

Present (1)

UBERON 2001815 Nuchal plate: Dermal bone that is a bony expansion in the integument anterior to or flanking the dorsal fin that is part of and at the distal end of a supraneural or dorsal fin proximal radial.

Zhu *et al.*, 165 (2013), Long *et al.*, 2014 (165), Dupret *et al.*, 2014 (165), Qiao *et al.*, 2016 (174), Chevrinais *et al.*, 2017 (165)

479. Paranuchal, number of

One pair (0)

Two pairs (1)

Zhu *et al.*, 2013 (162), Long *et al.*, 2014 (162), Dupret *et al.*, 2014 (162), Qiao *et al.*, 2016 (171), Chevrinais *et al.*, 2017 (162)

480. Posterolateral corners of nuchal plate, medial processes of paranuchal, overlap of

Absent (0)

Present (1)

UBERON 2001815 Nuchal plate: Dermal bone that is a bony expansion in the integument anterior to or flanking the dorsal fin that is part of and at the distal end of a supraneural or dorsal fin proximal radial.

Giles *et al.*, 2015 (50), Lu *et al.*, 2016 (50), Qiao *et al.*, 2017 (275), King *et al.*, 2017 (211)

481. (N) Extrascapula

Absent (0)

Present (1)

UBERON 2000663 Extrascapula: Dermal canal-bearing bone placed at the dorso-posterior region of the skull roof, lying on the posterior region of the pterotic and parietals, or the pterotic and epioccipital, or on the pterotic, epioccipital and occipital bones.

482. Extrascapula, organisation of

Uneven (0)

Paired (1)

UBERON 2000663 Extrascapula: Dermal canal-bearing bone placed at the dorso-posterior region of the skull roof, lying on the posterior region of the pterotic and parietals, or the pterotic and epioccipital, or on the pterotic, epioccipital and occipital bones.

Zhu *et al.*, 2009 (29), Zhu *et al.*, 2013 (167), Long *et al.*, 2014 (167), Dupret *et al.*, 2014 (167), Qiao *et al.*, 2016 (176), Chevrinais *et al.*, 2017 (167), King *et al.*, 2017 (191)

483. Extrascapula, number of

One pair (0)

Two pairs (1)

UBERON 2000663 Extrascapula: Dermal canal-bearing bone placed at the dorso-posterior region of the skull roof, lying on the posterior region of the pterotic and parietals, or the pterotic and epioccipital, or on the pterotic, epioccipital and occipital bones.

King *et al.*, 2017 (277)

484. (N) Premedian plate

Absent (0)

Present (1)

485. Median dorsal plate

Absent (0)

Present (1)

UBERON 4200102 Median dorsal plate: Dermal armour plate that is situated behind the head and constitute the dorsal most portion of the dermal shoulder girdle.

Brazeau 2009 (103), Davis *et al.*, 2012 (108), Zhu *et al.*, 2013 (108), Long *et al.*, 2014 (108), Dupret *et al.*, 2014 (108), Giles *et al.*, 2015 (186), Lu *et al.*, 2016 (186), Qiao *et al.*, 2016 (104), Chevrinais *et al.*, 2017 (108), King *et al.*, 2017 (425)

486. Median dorsal plate, number of

1 (0)

2 (1)

3 (2)

UBERON 4200102 Median dorsal plate : Dermal armour plate that is situated behind the head and constitute the dorsal most portion of the dermal shoulder girdle.

King *et al.*, 2017 (445)

487. Median dorsal plate, opening

Absent (0)

Present (1)

UBERON 4200102 Median dorsal plate: Dermal armour plate that is situated behind the head and constitute the dorsal most portion of the dermal shoulder girdle.

King *et al.*, 2017 (226)

488. Median dorsal plate, opening, shape of

Transvers slit-like (0)

Oval-like (1)

Slender longitudinal oval (2)

UBERON 4200102 Median dorsal plate : Dermal armour plate that is situated behind the head and constitute the dorsal most portion of the dermal shoulder girdle.

King *et al.*, 2017 (233)

489. Premedian plate, inner surface, rostrocaudal groove

Absent (0)

Present (1)

King *et al.*, 2014 (245)

490. Median field

Present (0)

Absent (1)

King *et al.*, 2017 (223)

491. Median field, pineal plate or foramen, separation of

Absent (0)

Present (1)

King *et al.*, 2017 (224)

492. External endolymphatic duct openings and median field, relative position of

Internal (0)

External (1)

UBERON 0001860 Endolymphatic duct : The small membranous canal, connecting with both saccule and utricle of the membranous labyrinth, passing through the aqueduct of vestibule, and terminating in the endolymphatic sac.

King *et al.*, 2017 (225)

493. Lateral fields

Present (0)

Absent (1)

King *et al.*, 2017 (219)

494. Lateral fields, division of

None (0)

One (1)

Two (2)

King *et al.*, 2017 (220)

495. Pectoral sinus, lateral fields, posterior extension of

Absent (0)

Present (1)

King *et al.*, 2017 (221)

496. Cornua, lateral fields, extension of

Absent (0)

Present (1)

King *et al.*, 2017 (222)

497. Cornual extensions

Absent (0)

Present (1)

King *et al.*, 2017 (229)

498. Cornual extension, spines

Absent (0)

Present (1)

King *et al.*, 2017 (234)

PALATE

499. Labial cartilages, bilateral series of

Absent (0)

Present (1)

UBERON 0018333 Labial cartilage: Distinct cartilage around the jaws of elasmobranchs.

King *et al.*, 2017 (393)

500. Sublingual rod

Absent (0)

Present (1)

King *et al.*, 2017 (149)

501. Autopalatine and quadrate bone, mineralization of

Comineralized (0)

Separate mineralizations (1)

UBERON 2000620 Autopalatine: Endochondral bone that is part of the antero-lateral region of the palate. Commonly, it articulates with the maxilla anterolaterally and with the ethmoidal region medially. It may also articulate with the dermopalatine ventro-laterally and with the entopterygoid posteriorly. The autopalatine is paired.

UBERON 0006597 Quadrate bone: Ossified pars articularis of the palatoquadrate cartilage.

Giles *et al.*, 2015 (97), Lu *et al.*, 2016 (97), Qiao *et al.*, 2016 (290), King *et al.*, 2017 (370)

502. Upper jaw cartilage, mineralization of

None (0)

Single (1)

Multiple macroelements (2)

Burrow & Turner 2010 (15)

503. Quadrate bone and mandible, articulation, position of

Orbital (0)

Postorbital (1)

Antorbital (2)

UBERON 0006597 Quadrate bone: Ossified pars articularis of the palatoquadrate cartilage. UBERON 0001684 Mandible: A dentary bone that is the only bone in one of the lateral halves of the lower jaw skeleton

Grogan & Lund 2000 (18)

504. (N) Basal process of palatoquadrate

Present (0)

Absent (1)

UBERON 3000036 Basal process of palatoquadrate: Process that extends medially from the ventromedial corner of the palatoquadrate cartilage and articulates or fuses to the anterior wall of the otic capsule via the basitrabecular process.

505. (N) Basal process of palatoquadrate, fusion of

Fused (0)

Unfused (1)

UBERON 3000036 Basal process of palatoquadrate: Process that extends medially from the ventromedial corner of the palatoquadrate cartilage and articulates or fuses to the anterior wall of the otic capsule via the basitrabecular process.

506. Palatoquadrate cartilage and postorbital process, articulation of

Absent (0)

Present (1)

UBERON 0004752 Palatoquadrate cartilage: The dorsal component of the mandibular arch.

UBERON 0013442 Postorbital process: The Postorbital Process marks the rear, upper edge of the eye socket and is a projection from the frontal bone.

Grogan & Lund 2000 (8), 2004 (12), 2008 (10), 2009 (10)

507. Palatoquadrate cartilage and postorbital process, articulation, position of

Ventral to postorbital process (0)

Posterior to postorbital process (1)

At otic level (2)

UBERON 0004752 Palatoquadrate cartilage: The dorsal component of the mandibular arch.

UBERON 0013442 Postorbital process: The Postorbital Process marks the rear, upper edge of the eye socket and is a projection from the frontal bone.

Grogan & Lund 2000 (9), 2004 (13), 2008 (11), 2009 (11), Grogan *et al.*, 2012 (16)

508. Palatoquadrate cartilage and postorbital process, articulation, direction of

Anteriorly (0)

Laterally (1)

Dorsally (2)

UBERON 0004752 Palatoquadrate cartilage: The dorsal component of the mandibular arch.

UBERON 0013442 Postorbital process: The Postorbital Process marks the rear, upper edge of the eye socket and is a projection from the frontal bone.

Coates *et al.*, 2017 (53)

509. Palatoquadrate, basipterygoid articulation, fenestration

Absent (0)

Present (1)

UBERON 0004752 Palatoquadrate cartilage: The dorsal component of the mandibular arch.

Brazeau 2009 (53), Davis *et al.*, 2012 (49), Zhu *et al.*, 2013 (49), Long *et al.*, 2014 (49), Dupret *et al.*, 2014 (49), Giles *et al.*, 2015 (103), Lu *et al.*, 2016 (103), Qiao *et al.*, 2016 (48), Chevrinais *et al.*, 2017 (49), King *et al.*, 2017 (337)

510. Palatoquadrate cartilage, suprapterygoid articulation

Single (0)

Double (1)

UBERON 0004752 Palatoquadrate cartilage: The dorsal component of the mandibular arch.

Brzeau 2009 (51)

511. Palatoquadrate cartilage (and associated cheek plate where present), position of

Entirely suborbital (0)

With a postorbital extension (1)

UBERON 0004752 Palatoquadrate cartilage: The dorsal component of the mandibular arch.

Giles *et al.*, 2015 (95), Lu *et al.*, 2016 (95), Qiao *et al.*, 2016 (289)

512. (N) Vomer

Absent (0)

Present (1)

UBERON 0002396 Vomer: The triangular flat bone of the nasal septum.

513. Vomer, posterior process

Absent (0)

Present (1)

UBERON 0002396 Vomer: The triangular flat bone of the nasal septum.

King *et al.*, 2017 (375)

514. (N) Vomer, anterior process

Absent (0)

Present (1)

UBERON 0002396 Vomer: The triangular flat bone of the nasal septum.

515. Choana

Absent (0)

Present (1)

King *et al.*, 2017 (260)

516. Palatine bone, number of

1 (0)

2 (1)

≥3 (2)

UBERON 0001682 Palatine bone: A paired dermal bone situated in the mid-palate

Lu *et al.*, 2016 (258), King *et al.*, 2017 (378)

517. (N) Palatoquadrate

Absent (0)

Present (1)

518. Palatoquadrate cartilage and neurocranium, relation between

Unfused (0)

Fused (1)

UBERON 0004752 Palatoquadrate cartilage: The dorsal component of the mandibular arch.

UBERON 0001703 Neurocranium: Subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

Giles *et al.*, 2015 (101), Lu *et al.*, 2016 (101), Qiao *et al.*, 2016 (291), Coates *et al.*, 2017 (54), King *et al.*, 2017 (371)

519. Palatoquadrate surface, mineralization of

Unmineralized (0)

Granular mineralization (1)

Perichondrally ossified (2)

Burrow & Turner 2010 (8)

520. Palatoquadrate, anteriad

Separate (0)

Median Symphysis (1)

Parallel (parasymphysial) extension (2)

Grogan & Lund 2000 (14), 2004 (18), 2008 (19), 2009 (20)

521. Palatoquadrate, otic process, shape of

Slight postorbital (0)

Dorsally recurved (1)

Posteriorly extended (2)

Dorsally expanded (3)

Grogan & Lund 2000 (15), 2004 (19), 2008 (20), 2009 (21), Grogan *et al.*, 2012 (29)

522. Palatoquadrate, ethmoid support

Absent (0)

Present (1)

UBERON 0004752 Palatoquadrate cartilage: The dorsal component of the mandibular arch.

Grogan *et al.*, 2012 (12)

523. Palatoquadrate, ethmoid support, type of

Ethmoid articulation (0)

Ethmoid ligament (1)

Ethmoid fusion (2)

UBERON 0004752 Palatoquadrate cartilage: The dorsal component of the mandibular arch.

Grogan *et al.*, 2012 (12)

524. Palatoquadrate, basal support

Absent (0)

Present (1)

UBERON 0004752 Palatoquadrate cartilage: The dorsal component of the mandibular arch.

Grogan *et al.*, 2012 (13)

525. Palatoquadrate, basal support, type of.

Basitrabecular process articulation (0)

Baistrabecular postorbital process articulation (1)

Basal process of palatoquadrate/basipterygoid ligament (2)

Orbitostyly (3)

Fused (4)

UBERON 0004752 Palatoquadrate cartilage: The dorsal component of the mandibular arch.

UBERON 3000036 Basal process of palatoquadrate: Process that extends medially from the ventromedial corner of the palatoquadrate cartilage and articulates or fuses to the anterior wall of the otic capsule via the basitrabecular process.

UBERON 0013442 Postorbital process: The Postorbital Process marks the rear, upper edge of the eye socket and is a projection from the frontal bone.

UBERON 3010092 Basitrabecular process: A process of the otic capsule that will bridge to the palatoquadrate basal process

Grogan *et al.*, 2012 (13)

526. Palatoquadrate, posterior support

Absent (0)

Present (1)

UBERON 0004752 Palatoquadrate cartilage: The dorsal component of the mandibular arch.

527. Palatoquadrate, posterior support, type of

Otic wall (0)

Hyomandibular and postorbital process articulation (1)

Hyomandibular bone only (2)

Bony palate sutured to hyomandibular bone (3)

Fused (4).

UBERON 0004752 Palatoquadrate cartilage: The dorsal component of the mandibular arch.

UBERON 0011606 Hyomandibular bone: Replacement bone that is bilaterally paired and (in teleosts) articulates with the neurocranium dorsally and the opercle posteriorly

UBERON 0013442 Postorbital process: The Postorbital Process marks the rear, upper edge of the eye socket and is a projection from the frontal bone

Grogan *et al.*, 2012 (14)

528. Palatoquadrate cartilage, ventromedial fossa

Present (0)

Absent (1)

UBERON 0004752 Palatoquadrate cartilage: The dorsal component of the mandibular arch.

Coates *et al.*, 2017 (51)

529. Palatoquadrate cartilage, insertion area for jaw adductor muscles

Ventral (0)

Lateral (1)

UBERON 0004752 Palatoquadrate cartilage: The dorsal component of the mandibular arch.

Brazeau 2009 (50), Davis *et al.*, 2012 (47), Zhu *et al.*, 2013 (47), Long *et al.*, 2013 (47), Dupret *et al.*, 2014 (47), Giles *et al.*, 2015 (99), Lu *et al.*, 2016 (99), Qiao *et al.*, 2016 (46), Chevrinais *et al.*, 2017 (47), King *et al.*, 2017 (335)

530. Palatoquadrate cartilage, medial face, oblique ridge or groove

Absent (0)

Present (1)

UBERON 0004752 Palatoquadrate cartilage: The dorsal component of the mandibular arch.

Brazeau 2009 (52), Davis *et al.*, 2012 (48), Zhu *et al.*, 2013 (48), Long *et al.*, 2013 (48), Dupret *et al.*, 2014 (48), Giles *et al.*, 2015 (102), Lu *et al.*, 2016 (102), Qiao *et al.*, 2016 (47), Chevrinais *et al.*, 2017 (48), Coates *et al.*, 2017 (52), King *et al.*, 2017 (336)

531. Palatoquadrate, metapterygoid fenestration (anterodorsal portion)

Absent (0)

Present (1)

UBERON 2000240 Metapterygoid: Endochondral bone that forms the posteriormost element of the palatal complex. It overlies the quadrate and symplectic, posteriorly it articulates with the hyomandibula and anteriorly with the entopterygoid and ectopterygoid. It curves dorsally to form the posteroventral surface of the orbit. The metapterygoid is paired.

Brazeau 2009 (54), Davis *et al.*, 2012 (50), Zhu *et al.*, 2013 (50), Long *et al.*, 2013 (50), Dupret *et al.*, 2014 (50), Giles *et al.*, 2015 (104), Lu *et al.*, 2016 (104), Qiao *et al.*, 2016 (49), Chevrinais *et al.*, 2017 (50), King *et al.*, 2017 (338)

532. Palatoquadrate and dermal cheek bones, contact of

Continuous contact of metapterygoid and autopalatine (0)

Metapterygoid and autopalatine contacts separated by gap between commissural lamina of palatoquadrate and cheeks bones (1).

UBERON 2000620 Autopalatine: Endochondral bone that is part of the antero-lateral region of the palate. Commonly, it articulates with the maxilla anterolaterally and with the ethmoidal region medially. It may also articulate with the dermopalatine ventro-laterally and with the entopterygoid posteriorly. The autopalatine is paired.

UBERON 2000240 Metapterygoid: Endochondral bone that forms the posteriormost element of the palatal complex. It overlies the quadrate and symplectic, posteriorly it articulates with the hyomandibula and anteriorly with the entopterygoid and ectopterygoid. It curves dorsally to form the posteroventral surface of the orbit. The metapterygoid is paired." Autopalatine : palatines

Zhu *et al.*, 2013 (215), Long *et al.*, 2014 (215), Dupret *et al.*, 2014 (215), Qiao *et al.*, 2016 (243), Chevrinais *et al.*, 2017 (215), King *et al.*, 2017 (361)

533. Fenestra in palatoquadrate marking position of basal articulation

Absent (0)

Present (1)

Zhu *et al.*, 2009 (72)

534. Palatoquadrate, adductor fossa, relative size of

Over half the length of the upper jaw (0)

Less than half the length of the upper jaw (1)

Burrow & Turner 2010 (9)

535. (N) Palatoquadrate, occlusal bone

Absent (0)

Present (1)

536. Palatoquadrate, occlusal bone, kind of

Dentigerous dermal bone (0)

Toothless plate (1)

Burrow & Turner 2010 (14)

537. Palatoquadrate, processus ascendens

Absent (0)

Present (1)

King *et al.*, 2017 (389)

538. Anterior portion of palatoquadrate, two divergent processes, extension of

Absent (0)

Present (1)

King *et al.*, 2017 (391)

539. (N) Entopterygoid

Absent (0)

Present (1)

UBERON 2000657 Entopterygoid: Dermal bone that forms the ventro-medial part of the palate and the antero-ventral and ventral wall of the orbit. The entopterygoid is a paired bone

540. Entopterygoids, organisation of

Separated across midline (0)

Contact along midline (1)

UBERON 2000657 Entopterygoid: Dermal bone that forms the ventro-medial part of the palate and the antero-ventral and ventral wall of the orbit. The entopterygoid is a paired bone

Lu *et al.*, 2016 (259)

541. Entopterygoids, proportion of

Anterior end level with processus ascendens (0)

Anterior end anterior to processus ascendens (1)

UBERON 2000657 Entopterygoid: Dermal bone that forms the ventro-medial part of the palate and the antero-ventral and ventral wall of the orbit. The entopterygoid is a paired bone

King *et al.*, 2017 (377)

542. Parasphenoid, basipterygoid process, shape of

Knob-like process (0)

Developed as a platform (1)

UBERON 0004745 Parasphenoid: A tooth- or denticle-covered plate which is attached to the sphenoid stem

UBERON 2001607 Basipterygoid process of parasphenoid: Process that is the paired process of the parasphenoid that articulates with the suspensorium.

Zhu *et al.*, 2009 (38)

543. Metapterygoid, developed medial ventral protrusion (i.e., commissural lamina sensu stricto)

Absent (0)

Present (1)

UBERON 2000240 Metapterygoid : Endochondral bone that forms the posteriormost element of the palatal complex. It overlies the quadrate and symplectic, posteriorly it articulates with the hyomandibula and anteriorly with the entopterygoid and ectopterygoid. It curves dorsally to form the posteroventral surface of the orbit. The metapterygoid is paired.

Zhu *et al.*, 2013 (216), Long *et al.*, 2014 (216), Dupret *et al.*, 2014 (216), Qiao *et al.*, 2014 (244), Chevrinaiis *et al.*, 2017 (216), King *et al.*, 2017 (362)

544. (N) Ectopterygoid bone

Absent (0)

Present (1)

UBERON 0011634 Ectopterygoid: A palatal bone which -- like many palatal bones -- may originally have developed as a dermal bone replacing part of the palatoquadrate, the primitive upper jaw. Like the palatine (also called dermopalatine), the ectopterygoid replaces the middle part of the autopalatine. It may be serially homologous with the palatine(s), but is somewhat specialized, being the last (most posterior in palatal view) of the series and bordering the fossa for the jaw muscles. In a typical tetrapod it abuts the palatine anteriorly, the maxilla laterally, the pterygoid or the fossa mandibularis medially, and the fossa posteriorly.

545. (N) Ectopterygoid bone, fang pair

Absent (0)

Present (1)

UBERON 0011634 Ectopterygoid: A palatal bone which -- like many palatal bones -- may originally have developed as a dermal bone replacing part of the palatoquadrate, the primitive upper jaw. Like the palatine (also called dermopalatine), the ectopterygoid replaces the middle part of the autopalatine. It may be serially homologous with the palatine(s), but is somewhat specialized, being the last (most posterior in palatal view) of the series and

bordering the fossa for the jaw muscles. In a typical tetrapod it abuts the palatine anteriorly, the maxilla laterally, the pterygoid or the fossa mandibularis medially, and the fossa posteriorly.

546. Ectopterygoid, fang pair, number of

1 (0)

2 (1)

UBERON 0011634 Ectopterygoid: A palatal bone which -- like many palatal bones -- may originally have developed as a dermal bone replacing part of the palatoquadrate, the primitive upper jaw. Like the palatine (also called dermopalatine), the ectopterygoid replaces the middle part of the autopalatine. It may be serially homologous with the palatine(s), but is somewhat specialized, being the last (most posterior in palatal view) of the series and bordering the fossa for the jaw muscles. In a typical tetrapod it abuts the palatine anteriorly, the maxilla laterally, the pterygoid or the fossa mandibularis medially, and the fossa posteriorly.

King *et al.*, 2017 (376)

547. Parasphenoid

Absent (0)

Present (1)

UBERON 0004745 Parasphenoid: A tooth- or denticle-covered plate which is attached to the sphenoid stem

Brazeau 2009 (57), Davis *et al.*, 2012 (55), Zhu *et al.*, 2013 (55), Long *et al.*, 2014 (55), Dupret *et al.*, 2014 (55), Giles *et al.*, 2015 (110), Lu *et al.*, 2016 (110), Qiao *et al.*, 2016 (54), Chevrinais *et al.*, 2017 (55), Coates *et al.*, 2017 (61), King *et al.*, 2017 (131)

548. Parasphenoid, shape of

Lozenge-shaped (0)

Splint-shaped (1)

UBERON 0004745 Parasphenoid: A tooth- or denticle-covered plate which is attached to the sphenoid stem

Zhu *et al.*, 2009 (68), Giles *et al.*, 2015 (111), Lu *et al.*, 2016 (111)

549. Parasphenoid, position of

Protruding forward into ethmoid region of endocranium (0)

Behind ethmoid region (1)

UBERON 0004745 Parasphenoid: A tooth- or denticle-covered plate which is attached to the sphenoid stem

UBERON 0011241 Ethmoid region: The most anterior region of the braincase. Provides structural support for peripheral olfactory organ.

UBERON 0001703 Neurocranium: Subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

Zhu *et al.*, 2009 (65), Zhu *et al.*, 2013 (237), Long *et al.*, 2014 (237), Dupret *et al.*, 2014 (237), Qiao *et al.*, 2016 (227), Chevrinais *et al.*, 2017 (237), King *et al.*, 2017 (135)

550. Parasphenoid, multifid anterior margin

Absent (0)

Present (1)

UBERON 0004745 Parasphenoid: A tooth- or denticle-covered plate which is attached to the sphenoid stem

Zhu *et al.*, 2009 (69), Zhu *et al.*, 2013 (241), Long *et al.*, 2014 (241), Dupret *et al.*, 2014 (241), Giles *et al.*, 2015 (112), Lu *et al.*, 2016 (112), Qiao *et al.*, 2016 (156), Chevrinais *et al.*, 2017 (241), King *et al.*, 2017 (134)

551. Parasphenoid, anterior, divergent lateral margins

Absent (0)

Present (1)

UBERON 0004745 Parasphenoid: A tooth- or denticle-covered plate which is attached to the sphenoid stem

Zhu *et al.*, 2013 (242), Qiao *et al.*, 2016 (229)

552. Parasphenoid, spiracular groove

Absent (0)

Present (1)

UBERON 0004745 Parasphenoid: A tooth- or denticle-covered plate which is attached to the sphenoid stem

Zhu *et al.*, 2009 (66), Zhu *et al.*, 2013 (238), Long *et al.*, 2014 (238), Dupret *et al.*, 2014 (238), Qiao *et al.*, 2016 (228), Chevrinais *et al.*, 2017 (238), King *et al.*, 2017 (136)

553. Parasphenoid, denticulated field, position of

Terminates at or anterior to level of foramina for internal carotid arteries (0)

Extends posterior to foramina for internal carotid arteries (1)

UBERON 0004745 Parasphenoid: A tooth- or denticle-covered plate which is attached to the sphenoid stem

Zhu *et al.*, 2009 (71), Zhu *et al.*, 2013 (243), Long *et al.*, 2014 (243), Dupret *et al.*, (243), Qiao *et al.*, 2016 (230), Chevrinais *et al.*, 2017 (243), King *et al.*, 2017 (137)

554. Parasphenoid, four carotid foramina

Absent (0)

Present (1)

UBERON 0004745 Parasphenoid: A tooth- or denticle-covered plate which is attached to the sphenoid stem

King *et al.*, 2017 (138)

555. (N) Parasphenoid, posterior, position of

Restricted to ethmosphenoid region (0)

Extends to otic region (1)

UBERON 0004745 Parasphenoid: A tooth- or denticle-covered plate which is attached to the sphenoid stem

556. Parasphenoid, ascending process

Absent (0)

Present (1)

UBERON 0004745 Parasphenoid: A tooth- or denticle-covered plate which is attached to the sphenoid stem

Zhu *et al.*, 2009 (67), Zhu *et al.*, 2013 (239), Long *et al.*, 2014 (239), Dupret *et al.*, 2014 (249), Giles *et al.*, 2015 (113), Lu *et al.*, 2016 (113), Qiao *et al.*, 2016 (154), Chevrinais *et al.*, 2017 (239), King *et al.*, 2017 (132)

557. (N) Buccopharyngeal/palatal denticles

Absent (0)

Present (1)

558. Buccopharyngeal/palatal denticles, type of

Simple (0)

Compound (1)

Grogan & Lund 2008 (27), 2009 (28), Grogan *et al.*, 2012 (40)

559. Pharyngeal toothplates consolidated into one to three large posterior plates, and one to three smaller anterior tooth plates, occupying each quadrant of the jaw

Absent (0)

Present (1)

UBERON 2001647 Pharyngeal toothplates: Dermal bone of the pharyngeal arches usually bearing teeth.

Coates *et al.*, 2017 (45)

560. Median rostral, tooth

Absent (0)

Present (1)

Zhu *et al.*, 2009 (75), Zhu *et al.*, 2013 (199), Long *et al.*, 2014 (199), Dupret *et al.*, 2014 (199), Qiao *et al.*, 2016 (203), Chevrinais *et al.*, 2017 (199), King *et al.*, 2017 (346)

561. Mandibular mineralization, type of

Perichondral bones (0)

Random tesserae (1)

Calcified cartilage (2)

Prismatic cartilage (3)

UBERON 0008913 Perichondral bone: Bone element that is located on the surface of a cartilage element.

UBERON 0001995 Fibrocartilage: Cartilage tissue intermediate between hyaline cartilage and dense connective tissue; contains of abundant collagen fibers; chondrocytes often arranged in columns.

UBERON 0018352 Prismatic cartilage: Cartilage arranged into tesserae, blocks of calcified cartilage that fit together as tiles on a floor form a mosaic. Found only in chondrichthyans.

Grogan & Lund 2000 (16), 2004 (21), 2008 (22), 2009 (23), Grogan *et al.*, 2012 (32)

562. Jaw skeleton

Absent (0)

Present (1)

UBERON 0001708 Jaw skeleton: Subdivision of skeleton which includes upper and lower jaw skeletons.

Long *et al.*, 2014 (254), Dupret *et al.*, 2014 (254), Qiao *et al.*, 2016 (246), King *et al.*, 2017 (363)

563. Mandibular squamation

Absent (0)

Present (1)

564. Mandibular squamation, repartition of

Generalized (0)

Posterior specialization (1)

Longitudinal specialization (plates) (2)

Grogan & Lund 2004 (59), 2008 (65), Grogan *et al.*, 2012 (78)

565. Jaw cartilage, occlusal portion, dermal bones

Absent (0)

Present (1)

UBERON 0008907 Dermalbone: Skeletal element that forms superficially in the organism, usually in association with the ectoderm

Coates *et al.*, 2017 (47)

566. Jaw skeleton, articulation of

Absent (0)

Present (1)

UBERON 0001708 Jaw skeleton: Subdivision of skeleton which includes upper and lower jaw skeletons.

Chevrinais *et al.*, 2017 (254)

567. Palatoquadrate, lower jaw articulation, type of

Single condyle-socket articulation (0)

Double articulation (1)

No articulatory projections (2)

Burrow & Turner 2010 (19)

568. Jaw articulation located in rearmost extremity of mandible

Absent (0)

Present (1)

UBERON 0001708 Jaw skeleton: Subdivision of skeleton which includes upper and lower jaw skeletons.

UBERON 0004905 Articulation: Anatomical cluster that connects two or more adjacent skeletal elements or hardened body parts.

UBERON 0001684 Mandible: A dentary bone that is the only bone in one of the lateral halves of the lower jaw skeleton.

Davis *et al.*, 2012 (53), Zhu *et al.*, 2013 (53), Long *et al.*, 2014 (53), Dupret *et al.*, 2014 (53), Giles *et al.*, 2015 (108), Lu *et al.*, 2016 (108), Qiao *et al.*, 2016 (52), Chevrinains *et al.*, 2017 (53), Coates *et al.*, 2017 (56), King *et al.*, 2017 (341)

569. Symplectic articulation

Absent (0)

Present (1)

UBERON 2000692 Symplectic: Replacement bone that is bilaterally paired and articulates with the hyomandibula and the quadrate.

UBERON 0004905 Articulation: Anatomical cluster that connects two or more adjacent skeletal elements or hardened body parts.

King *et al.*, 2017 (388)

570. Mandibular arch articulation, position of

Terminal (0)

Subterminal (1)

Giles *et al.*, 2015 (96), Lu *et al.*, 2016 (96)

571. Infradentary bones

Absent (0)

Present (1)

Zhu *et al.*, 2013 (204), Long *et al.*, 2014 (204), Dupret *et al.*, 2014 (204), Qiao *et al.*, 2016 (106), Chevrinais *et al.*, 2017 (204), King *et al.*, 2017 (349)

572. Infradentary bones, number of

1 (0)

2 (1)

>2 (2)

King *et al.*, 20117 (381)

573. Infradentary bones, extend of

Along much of ventral margin of dentary (0)

Restricted to posterior half of dentary (1)

UBERON 0004742 Dentary: The dentary is a dermal bone that forms the antero-lateral part of the lower jaw in fishes and amphibians, extending to the whole lower jaw in mammals.

Giles *et al.*, 2015 (93), Lu *et al.*, 2016 (93), Qiao *et al.*, 2016 (288), King *et al.*, 2017 (368)

574. Infradentary, foramina

Present (0)

Absent (1)

Zhu *et al.*, 2009 (85), Zhu *et al.*, 2013 (205), Long *et al.*, 2014 (205), Dupret *et al.*, 2014 (205), Qiao *et al.*, 2016 (207), Chevrinais *et al.*, 2017 (205), King *et al.*, 2017 (350)

575. Maxilla and dentary tooth-bearing bones

Absent (0)

Present (1)

UBERON 0004742 Dentary: The dentary is a dermal bone that forms the antero-lateral part of the lower jaw in fishes and amphibians, extending to the whole lower jaw in mammals

UBERON 0002397 Maxilla: The bone which normally forms the lateral upper jaw in osteichthyans, including tetrapods.

Brazeau 2009 (47), Davis *et al.*, 2012 (45), Zhu *et al.*, 2013 (45), Long *et al.*, 2014 (45), Dupret *et al.*, 2014 (45), Giles *et al.*, 2015 (88), Lu *et al.*, 2016 (88), Qiao *et al.*, 2016 (44), Chevrinais *et al.*, 2017 (45), King *et al.*, 2017 (333)

576. Dentary, length of

Constitutes more than half of jaw length (0)

Half the length of jaw or less (1)

UBERON 0004742 Dentary: The dentary is a dermal bone that forms the antero-lateral part of the lower jaw in fishes and amphibians, extending to the whole lower jaw in mammals

Lu *et al.*, 2016 (248)

577. Splenial bone

Absent (0)

Present (1)

UBERON 0011635 Splenial bone: The splenial is a small bone in the lower jaw of reptiles, amphibians and birds, usually located on the lingual side (closest to the tongue) between the angular and suprangular.

Zhu *et al.*, 2009 (88)

578. Postsplenial

Absent (0)

Present (1)

UBERON 4300199 Postsplenial: Dermal bone of the lower jaw.

Zhu *et al.*, 2009 (89)

579. Surangular

Absent (0)

Present (1)

UBERON 0011636 Surangular bone: The surangular is a dermal bone of the lower jaw. It typically covers much of the dorsal and lateral surface of the posterior jaw and variably extends onto the medial (inside) surface. The surangular articulates with and supports the articular, which forms the jaw joint with the quadrate in most vertebrates and is in turn supported by the angular. More distally, the surangular bridges the mandibular fenestra, if one is present. It may also bear a raised dorsal coronoid process, an important attachment site for the mandibular adductors. At its distal (or rostral) end, the surangular meets the dentary, the main tooth-bearing bone of the lower jaw in most vertebrates.

Zhu *et al.*, 2009 (90)

580. Median gular plate

Absent (0)

Present (1)

UBERON 2002089 Gular plate: Dermal bone located on the ventral surface of the skull and positioned between the two rami of the lower jaw. Anteriorly the gular attaches to the symphysis of the lower jaw through fibrous connective tissue. The gular is an unpaired median bone.

Zhu *et al.*, 2009 (102), Zhu *et al.*, 2013 (196), Long *et al.*, 2014 (196), Dupret *et al.*, 2014 (196), Giles *et al.*, 2015 (67), Lu *et al.*, 2016 (67), Qiao *et al.*, 2016 (135), Chevrinais *et al.*, 2017 (196), King *et al.*, 2017 (169)

581. Lateral gular plates

Absent (0)

Present (1)

UBERON 2002089 Gular plate: Dermal bone located on the ventral surface of the skull and positioned between the two rami of the lower jaw. Anteriorly the gular attaches to the symphysis of the lower jaw through fibrous connective tissue. The gular is an unpaired median bone.

Brazeau 2009 (38), Burrow & Turner 2010 (66), Davis *et al.*, 2012 (35), Zhu *et al.*, 2013 (35), Long *et al.*, 2014 (35), Dupret *et al.*, 2014 (35), Giles *et al.*, 2015 (68), Lu *et al.*, 2016 (68), Qiao *et al.*, 2016 (34), Chevrinais *et al.*, 2017 (35), Coates *et al.*, 2017 (28), King *et al.*, 2017 (167)

582. Lateral gular plates, size of

Extending more than half the jaw length (0)

Restricted to the anterior third of the jaw (no longer than width of three or four branchiostegals) (1)

UBERON 2002089 Gular plate: Dermal bone located on the ventral surface of the skull and positioned between the two rami of the lower jaw. Anteriorly the gular attaches to the symphysis of the lower jaw through fibrous connective tissue. The gular is an unpaired median bone.

Zhu *et al.*, 2009 (103), Brazeau 2009 (39), Davis *et al.*, 2012 (36), Zhu *et al.*, 2013 (36), Long *et al.*, 2014 (36), Dupret *et al.*, 2014 (36), Giles *et al.*, 2015 (71), Lu *et al.*, 2016 (71), Qiao *et al.*, 2016 (35), Chevrinais *et al.*, 2017 (36), King *et al.*, 2017 (168)

583. Coronoid bone

Absent (0)

Present (1)

Zhu *et al.*, 2009 (93), King *et al.*, 2017 (382)

584. Coronoid bone, number of

>3 (0)

3 (1)

Zhu *et al.*, 2009 (93), Zhu *et al.*, 2013 (201), Long *et al.*, 2014 (201), Dupret *et al.*, 2014 (201), Giles *et al.*, 2015 (106), Lu *et al.*, 2016 (106), Qiao *et al.*, 2016 (147), Chevrinais *et al.*, 2017 (201), King *et al.*, 2017 (344)

585. Coronoid bone, fang

Absent (0)

Present (1)

Zhu *et al.*, 2009 (94), Zhu *et al.*, 2013 (202), Long *et al.*, 2014 (202), Dupret *et al.*, 2014 (202), Giles *et al.*, 2015 (94), Lu *et al.*, 2016 (94), Qiao *et al.*, 2014 (147), Chevrinais *et al.*, 2017 (202), King *et al.*, 2017 (345)

586. Coronoid bone, posterior, shape of

Similar to anterior coronoid forms (0)

Forms expanded coronoid process (1)

Lu *et al.*, 2016 (253)

587. Coronoid bones, marginal denticle band

Absent (0)

Present (1)

588. (N) Coronoid bone, posterior, fang pair

Absent (0)

Present (1)

589. Coronoid bone, posterior, fang pair, number of

1 (0)

2 (1)

King *et al.*, 2017 (383)

590. (N) Prearticular bone

Absent (0)

Present (1)

UBERON 0011637 Prearticular bone: Osseous element of intramembranous origin that extends along the lingual margin of Meckel's cartilage

591. Prearticular bone, symphysis

Absent (0)

Present (1)

UBERON 0011637 Prearticular bone: Osseous element of intramembranous origin that extends along the lingual margin of Meckel's cartilage.

UBERON 0002216 Symphysis: Cartilaginous joint in which the articulating bones or cartilages are connected by fibrocartilage

Lu *et al.*, 2016 (250)

592. (N) Prearticular bone and jaw symphysis, contact of

Absent (0)

Present (1)

UBERON 0011637 Prearticular bone: Osseous element of intramembranous origin that extends along the lingual margin of Meckel's cartilage.

593. Prearticular bone and dentary, contact of

Present (0)

Absent (1)

UBERON 0011637 Prearticular bone: Osseous element of intramembranous origin that extends along the lingual margin of Meckel's cartilage.

UBERON 0004742 Dentary: The dentary is a dermal bone that forms the antero-lateral part of the lower jaw in fishes and amphibians, extending to the whole lower jaw in mammals

Zhu *et al.*, 2009 (98), Zhu *et al.*, 2013 (211), Long *et al.*, 2014 (211), Dupret *et al.*, 2014 (211), Qiao *et al.*, 2016 (213), Chevrinais *et al.*, 2017 (211), King *et al.*, 2017 (356)

594. (N) Adsymphyseal cartilage(s)

Absent (0)

Present (1)

595. Adsymphyseal cartilage(s), extension of

Anteriorly extended (0)

Posteriorly extended (1)

Grogan & Lund 2000 (17)

596. (N) Parasymphysial plate

Absent (0)

Present (1)

UBERON 4200245 Parasymphysial plate: Bone, often with tooth attachments, on the lingual side of the anterior of the lower jaw

597. Parasymphysial plate, type of

Detachable tooth whorl (0)

With posterior corner, sutured to coronoid, denticulated or with tooth row (1)

UBERON 4200245 Parasymphysial plate: Bone, often with tooth attachments, on the lingual side of the anterior of the lower jaw

Zhu *et al.*, 2009 (91), Zhu *et al.*, 2013 (209), Long *et al.*, 2014 (209), Dupret *et al.*, 2014 (209), Qiao *et al.*, 2016 (211), Chevrinais *et al.*, 2017 (209), King *et al.*, 2017 (354)

598. Mandible, symphyseal region, ventromesially directed flange

Absent (0)

Present (1)

UBERON 0001684 Mandible: A dentary bone that is the only bone in one of the lateral halves of the lower jaw skeleton.

Zhu *et al.*, 2009 (83), Zhu *et al.*, 2013 (206), Long *et al.*, 2014 (206), Dupret *et al.*, 2014 (206), Qiao *et al.*, 2016 (208), Chevrinais *et al.*, 2017 (206), King *et al.*, 2017 (351)

599. (N) Lower symphysial element

Present (0)

Absent (1)

600. Lower symphysial element, position of

Between mandibles (0)

Extended anteriorly (1)

Grogan & Lund 2004 (23), 2004 (24), 2009 (25)

601. (N) Lower symphysial tooth whorls

Absent (0)

Present (1)

UBERON 0014682 Tooth whorls: A spirally arranged cluster of teeth.

602. (N) Lower symphysial tooth whorls, organisation of

Paired only (0)

Median + 5-6 pairs (1)

Median + 3-4 pairs (2)

Median + 2 pairs (3)

Median + 1 pair (4)

Median only (5)

UBERON 0014682 Tooth whorls: A spirally arranged cluster of teeth.

603. Lower symphysial family

Generalized (0)

Prominent (1)

Whorl (2)

Fused plate (3)

Grogan & Lund 2000 (28), 2004 (34), 2008 (41), Grogan *et al.*, 2012 (52)

604. (N) Lower symphysial cartilage(s)

Present (0)

Absent (1)

605. Lower symphysial cartilage(s), number of

>2 (0)

≤2 (1)

Grogan *et al.*, 2012 (35)

606. Lower symphyseal cartilage, V-shaped

Present (0)

Absent (1)

Grogan *et al.*, 2012 (36)

607. Mandibular symphysis, fusion of

Absent (0)

Present (1)

UBERON 0006606 Mandibular symphysis: A cartilaginous joint that connects left and right mandibles/dentary bones. Mandibular symphysis is unpaired.

Coates *et al.*, 2017 (59)

608. Mandibular symphysis, type of

Mobile symphyseal cartilage(s) (0)

Symphysis fused to Meckel's cartilage (1)

Ligamentous mandibular junction (2)

UBERON 0006606 Mandibular symphysis: A cartilaginous joint that connects left and right mandibles/dentary bones. Mandibular symphysis is unpaired.

Grogan *et al.*, 2012 (31)

609. Upper parasymphysial cartilage(s)

Present (0)

Absent (1)

Grogan & Lund 2004 (22), 2008 (23), 2009 (24)

610. Upper parasymphysial cartilage(s), extension of

Anteriorly extended (0)

Posteriorly extended (1)

Grogan & Lund 2004 (22), 2008 (23), 2009 (24)

611. Upper parasymphysial family

Generalized (0)

Prominent (1)

Whorl (2)

Fused plate (3)

Grogan & Lund 2000 (29), 2004 (35), 2004 (42), Grogan *et al.*, 2012 (54)

612. (N) Meckel's cartilage

Absent (0)

Present (1)

UBERON 0003107 Meckel's cartilage: Meckel's cartilage is the bilaterally paired, rod-like, cartilaginous ventral component of the lower jaw, or ventral mandibular arch. It is typically resorbed in adults.

613. (N) Meckelian bone

Absent (0)

Present (1)

UBERON 4200250 Meckelian bone: The ossification of the Meckel's cartilage.

614. Meckel's cartilage, mineralization of

Unmineralized (0)

Granular mineralization (1)

Perichondrally ossified (2)

UBERON 0003107 Meckel's cartilage: Meckel's cartilage is the bilaterally paired, rod-like, cartilaginous ventral component of the lower jaw, or ventral mandibular arch. It is typically resorbed in adults.

Burrow & Turner 2010 (10)

615. Meckel's cartilage, prearticular "coronoid" flange

Absent (0)

Present (1)

UBERON 0003107 Meckel's cartilage: Meckel's cartilage is the bilaterally paired, rod-like, cartilaginous ventral component of the lower jaw, or ventral mandibular arch. It is typically resorbed in adults.

Burrow & Turner 2010 (11)

616. Meckelian bone exposed immediately anterior to first coronoid

Present (0)

Absent (1)

UBERON 4200250 Meckelian bone: The ossification of the Meckel's cartilage.

Zhu *et al.*, 2009 (99), Zhu *et al.*, 2013 (212), Long *et al.*, 2017 (212), Dupret *et al.*, 2014 (212), Qiao *et al.*, 2016 (214), Chevrinais *et al.*, 2017 (212), King *et al.*, 2017 (357)

617. Meckelian bone or cartilage, dorsal process

Absent (0)

Present (1)

UBERON 4200250 Meckelian bone: The ossification of the Meckel's cartilage.

UBERON 0003107 Meckel's cartilage: Meckel's cartilage is the bilaterally paired, rod-like, cartilaginous ventral component of the lower jaw, or ventral mandibular arch. It is typically resorbed in adults.

Brazeau 2009 (55), Davis *et al.*, 2012 (51), Zhu *et al.*, 2013 (51), Long *et al.*, 2014 (51), Dupret *et al.*, 2014 (51), Giles *et al.*, 2015 (105), Lu *et al.*, 2016 (105), Qiao *et al.*, 2016 (50), Chvevrinais *et al.*, 2017 (51), King *et al.*, 2107 (339)

618. Flange like extension of mandible composed of prearticular bone and Meckelian bone

Absent (0)

Present (1)

UBERON 4200250 Meckelian bone: The ossification of the Meckel's cartilage.

UBERON 0011637 Prearticular bone: Osseous element of intramembranous origin that extends along the lingual margin of Meckel's cartilage.

Zhu *et al.*, 2009 (84), Zhu *et al.*, 2013 (207), Long *et al.*, 2014 (207), Dupret *et al.*, 2014 (207), Qiao *et al.*, 2016 (209), Chevrinais *et al.*, 2017 (207), King *et al.*, 2017 (352)

619. Meckel's cartilage or Meckelian bone and quadrate bone articulation, position of

Postorbital (0)

Orbital (1)

Preorbital (2)

UBERON 4200250 Meckelian bone: The ossification of the Meckel's cartilage.

UBERON 0003107 Meckel's cartilage: Meckel's cartilage is the bilaterally paired, rod-like, cartilaginous ventral component of the lower jaw, or ventral mandibular arch. It is typically resorbed in adults.

UBERON 0006597 Quadrate bone: Ossified pars articularis of the palatoquadrate cartilage.

Grogan & Lund 2004 (20), 2008 (21), Grogan & Lund 2009 (22), Grogan *et al.*, 2012 (30)

620. Meckel's cartilage and palatoquadrate cartilage, scalloped oral margin

Absent (0)

Present (1)

UBERON 0003107 Meckel's cartilage: Meckel's cartilage is the bilaterally paired, rod-like, cartilaginous ventral component of the lower jaw, or ventral mandibular arch. It is typically resorbed in adults

UBERON 0004752 Palatoquadrate cartilage: The dorsal component of the mandibular arch.

Coates *et al.*, 2017 (58)

621. (N) Meckel's cartilage, dermal cover

Absent (0)

Present (1)

UBERON 0003107 Meckel's cartilage: Meckel's cartilage is the bilaterally paired, rod-like, cartilaginous ventral component of the lower jaw, or ventral mandibular arch. It is typically resorbed in adults.

622. Meckel's cartilage, dermal cover, type of

Monodontode scales (0)

Polygonal or plate-like scales (1)

UBERON 0003107 Meckel's cartilage: Meckel's cartilage is the bilaterally paired, rod-like, cartilaginous ventral component of the lower jaw, or ventral mandibular arch. It is typically resorbed in adults.

Burrow & Turner 2010 (12)

623. (N) Meckel's cartilage, occlusal bone

Absent (0)

Present (1)

UBERON 0003107 Meckel's cartilage: Meckel's cartilage is the bilaterally paired, rod-like, cartilaginous ventral component of the lower jaw, or ventral mandibular arch. It is typically resorbed in adults.

624. Meckel's cartilage, occlusal bone, type of

Dentigerous dermal bone (0)

Toothless plate (1)

UBERON 0003107 Meckel's cartilage: Meckel's cartilage is the bilaterally paired, rod-like, cartilaginous ventral component of the lower jaw, or ventral mandibular arch. It is typically resorbed in adults.

Burrow & Turner 2010 (13)

625. Dental trough or sulcus adjacent to oral rim on Meckel's cartilage and palatoquadrate

Absent (0)

Present (1)

UBERON 0003107 Meckel's cartilage: Meckel's cartilage is the bilaterally paired, rod-like, cartilaginous ventral component of the lower jaw, or ventral mandibular arch. It is typically resorbed in adults.

Coates *et al.*, 2017 (57)

626. Meckel's cartilage and palatoquadrate, mesial surface, dermal plates

Absent (0)

Present (1)

UBERON 0003107 Meckel's cartilage: Meckel's cartilage is the bilaterally paired, rod-like, cartilaginous ventral component of the lower jaw, or ventral mandibular arch. It is typically resorbed in adults.

Zhu *et al.*, 2013 (213), Long *et al.*, 2014 (213), Dupret *et al.*, 2014 (213), Qiao *et al.*, 2016 (215), Chevrinais *et al.*, 2017 (213), Coates *et al.*, 2017 (60), King *et al.*, 2017 (358)

627. Jaw cartilage, oral dermal tubercles borne

Absent (0)

Present (1)

Brazeau 2009 (41), Davis *et al.*, 2012 (39), Zhu *et al.*, 2013 (39), Long *et al.*, 2014 (39), Dupret *et al.*, 2014 (39), Giles *et al.*, 2015 (77), Lu *et al.*, 2016 (77), Qiao *et al.*, 2016 (38), Chevrinais *et al.*, 2017 (39), Coates *et al.*, 2017 (37), King *et al.*, 2017 (327)

628. Curved infragnathal, flat non-biting region

Absent (0)

Present (1)

King *et al.*, 2017 (374)

629. Skeleton of lower jaw, biconcave glenoid

Absent (0)

Present (1)

UBERON 0003278 Skeleton of lower jaw: A subdivision of the skeleton that corresponds to the lower part of the mouth. The lower jaw skeleton includes the following elements, when present: lower jaw teeth, the mandible and other lower jaw bones, and Meckel's cartilage.

Zhu *et al.*, 2013 (214), Long *et al.*, 2014 (214), Dupret *et al.*, 2014 (214), Qiao *et al.*, 2016 (216), Chevrinais *et al.*, 2017 (214), King *et al.*, 2017 (359)

630. Retroarticular process

Absent (0)

Present (1)

UBERON 3000543 Retroarticular process: Bony process that is part of the articular and is the point of insertion of the m. interhuoideus posterior

Lu *et al.*, 2016 (254), King *et al.*, 2017 (387)

631. Submandibular bone

Absent (0)

Present (1)

Zhu *et al.*, 2009 (104), King *et al.*, 2017 (387)

632. Outer dental arcade, dermal bone

Absent (0)

Present (1)

UBERON 0008907 Dermalbone: Skeletal element that forms superficially in the organism, usually in association with the ectoderm

Zhu *et al.*, 2009 (73)

633. Parotic dental plate

Absent (0)

Present (1)

King *et al.*, 2017 (139)

OPERCULAR SERIES

634. Branchial chamber, opercular cover, type of

Complete or partial (0)

Separate gill covers and gill slits (1)

Davis *et al.*, 2012 (32), Zhu *et al.*, 2013 (32), Long *et al.*, 2014 (32), Dupret *et al.*, 2014 (32), Qiao *et al.*, 2016 (31), Chevrinais *et al.*, 2017 (32), King *et al.*, 2017 (165)

635. Opercle (submarginal), ossification of

Absent (0)

Present (1)

UBERON:2000250 Opercle: Dermal bone that forms the postero-dorsal part of the opercular series. The opercle articulates with the hyomandibula antero-dorsally and with the subopercle ventrally. The opercle is a paired bone. The opercle is usually a large, flat bone that may be partially covered by the posterior region of the preopercle.

Brazeau 2009 (36), Davis *et al.*, 2012 (33), Zhu *et al.*, 2013 (33), Long *et al.*, 2014 (33), Dupret *et al.*, 2014 (33), Giles *et al.*, 2015 (69), Lu *et al.*, 2016 (69), Qiao *et al.*, 2016 (32), Chevrinais *et al.*, 2017 (33), Coates *et al.*, 2017 (27).

636. Accessory operculum

Absent (0)

Present (1)

King *et al.*, 2017 (278)

637. Branchiostegal ray, imbrication of

Absent (0)

Present (1)

UBERON 2000476 Branchiostegal ray: Dermal bone that is a flattened element that supports the branchiostegal membrane. Branchiostegal rays are generally present in a series articulating ventrally or ventro-medially with the anterior and posterior ceratobranchials whereas the most posterior ray articulates with the subopercle. The branchiostegal ray is paired. Although the branchiostegals are articulated or attached to the hyoid arch, they belong to the opercular series. Branchiostegal rays are of variable shape and number and their homology is problematic. Usually they are numbered from anterior to posterior elements, instead from posterior to anteriorly considering that the last element of the series is consistently associated to the subopercle.

Brazeau 2009 (35), Davis *et al.*, 2012 (31), Zhu *et al.*, 2013 (31), Long *et al.*, 2014 (31), Dupret *et al.*, 2014 (31), Giles *et al.*, 2015 (66), Lu *et al.*, 2016 (66), Qiao *et al.*, 2016 (30), Chevrinais *et al.*, 2017 (31), King *et al.*, 2017 (164)

638. Branchiostegal ray series

Absent (0)

Present (1)

UBERON 2002101 Branchiostegal ray series: Anatomical cluster that consists of the branchiostegal rays within an individual.

Brazeau 2009 (31), Davis *et al.*, 2012 (27), Zhu *et al.*, 2013 (27), Long *et al.*, 2014 (27), Giles *et al.*, 2015 (62), Lu *et al.*, 2016 (62), Qiao *et al.*, 2016 (26), Chevrinais *et al.*, 2017 (27), Coates *et al.*, 2017 (26), King *et al.*, 2017 (160)

639. Skeleton of lower jaw, ventral margin, branchiostegal ray series

Absent (0)

Present (1)

UBERON 0003278 Skeleton of lower jaw: A subdivision of the skeleton that corresponds to the lower part of the mouth. The lower jaw skeleton includes the following elements, when present: lower jaw teeth, the mandible and other lower jaw bones, and Meckel's cartilage.

UBERON 2002101 Branchiostegal ray series: Anatomical cluster that consists of the branchiostegal rays within an individual.

Brazeau 2009 (32), Burrow & Turner 2010 (5), Davis *et al.*, 2012 (28), Zhu *et al.*, 2013 (28), Long *et al.*, 2014 (28), Dupret *et al.*, 2014 (28), Giles *et al.*, 2015 (63), Lu *et al.*, 2016 (63), Qiao *et al.*, 2016 (27), Chevrinais *et al.*, 2017 (28), King *et al.*, 2017 (161)

640. Branchiostegal ray, shape of

Plate-like (0)

Ribbon-like (1)

Filamentous (2)

UBERON 2000476 Branchiostegal ray: Dermal bone that is a flattened element that supports the branchiostegal membrane. Branchiostegal rays are generally present in a series articulating ventrally or ventro-medially with the anterior and posterior ceratobranchials whereas the most posterior ray articulates with the subopercle. The branchiostegal ray is paired. Although the branchiostegals are articulated or attached to the hyoid arch, they belong to the opercular series. Branchiostegal rays are of variable shape and number and their homology is problematic. Usually they are numbered from anterior to posterior elements, instead from posterior to anteriorly considering that the last element of the series is consistently associated to the subopercle.

Brazeau 2009 (33), Burrow & Turner 2010 (5), Davis *et al.*, 2012 (29), Zhu *et al.*, 2013 (29), Long *et al.*, 2014 (29), Dupret *et al.*, 2014 (29), Giles *et al.*, 2015 (64), Lu *et al.*, 2016 (64), Qiao *et al.*, 2016 (28), Chevrinais *et al.*, 2017 (29), King *et al.*, 2017 (162)

641. Ossified branchiostegal ray, ornamentation of

Present (0)

Absent (1)

UBERON 2000476 Branchiostegal ray: Dermal bone that is a flattened element that supports the branchiostegal membrane. Branchiostegal rays are generally present in a series articulating ventrally or ventro-medially with the anterior and posterior ceratobranchials whereas the most posterior ray articulates with the subopercle. The branchiostegal ray is

paired. Although the branchiostegals are articulated or attached to the hyoid arch, they belong to the opercular series. Branchiostegal rays are of variable shape and number and their homology is problematic. Usually they are numbered from anterior to posterior elements, instead from posterior to anteriorly considering that the last element of the series is consistently associated to the subopercle.

Brazeau 2009 (34), Davis *et al.*, 2012 (30), Zhu *et al.*, 2013 (30), Long *et al.*, 2014 (30), Dupret *et al.*, 2014 (30), Giles *et al.*, 2015 (65), Lu *et al.*, 2016 (65), Qiao *et al.*, 2016 (29), Chevrinais *et al.*, 2017 (30), King *et al.*, 2017 (163)

642. Branchiostegal rays per side, number of

>10 (0)

2 to 10 (1)

1 (2)

UBERON 2000476 Branchiostegal ray: Dermal bone that is a flattened element that supports the branchiostegal membrane. Branchiostegal rays are generally present in a series articulating ventrally or ventro-medially with the anterior and posterior ceratobranchials whereas the most posterior ray articulates with the subopercle. The branchiostegal ray is paired. Although the branchiostegals are articulated or attached to the hyoid arch, they belong to the opercular series. Branchiostegal rays are of variable shape and number and their homology is problematic. Usually they are numbered from anterior to posterior elements, instead from posterior to anteriorly considering that the last element of the series is consistently associated to the subopercle.

Zhu *et al.*, 2009 (101), King *et al.*, 2017 (266)

HYOID ARCH

643. Neurocranium, hyomandibular bone, articulation of

Present (0)

Absent (1)

UBERON 0001703 Neurocranium: Subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

UBERON 0011606 Hyomandibular bone: Replacement bone that is bilaterally paired and (in teleosts) articulates with the neurocranium dorsally and the opercle posteriorly.

King *et al.*, 2017 (121)

644. Neurocranium, hyoid arch articulation, type of

Single (0)

Double (1)

UBERON 0001703 Neurocranium: Subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof

Giles *et al.*, 2015 (165), Lu *et al.*, 2016 (165)

645. Hyoid arch articulation, position of

On lateral commissure (0)

On otic capsule wall (1)

UBERON 4300134 Lateral commissure: Region of the braincase which bears the facets for the hyomandibula in fishes. This region disappears in the origin of tetrapods and the space it occupied comes to contribute to the fenestra vestibuli.

UBERON 0004637 Otic capsule: The capsule surrounding the inner ear mechanism.

Zhu *et al.*, 2009 (45), Brazeau 2009 (90), Zhu *et al.*, 2013 (228), Long *et al.*, 2014 (228), Dupret *et al.*, 2014 (228), Qiao *et al.*, 2016 (223), Chevrinais *et al.*, 2017 (228)

646. Neurocranium, hyomandibular bone articulation, position of

Anterior position suborbital (0)

Posterior position behind orbit (1)

UBERON 0001703 Neurocranium: Subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

UBERON 0011606 Hyomandibular bone: Replacement bone that is bilaterally paired and (in teleosts) articulates with the neurocranium dorsally and the opercle posteriorly

UBERON 0001697 Orbit of skull: Subdivision of skeleton that is an anterolateral part of the cranium and structurally supports the eye. Includes bones formed and located in sclerotic layer of eyeball.

Brazeau 2009 (89), Davis *et al.*, 2012 (95), Zhu *et al.*, 2013 (95), Long *et al.*, 2014 (95), Dupret *et al.*, 2014 (95), Giles *et al.*, 2015 (163), Lu *et al.*, 2016 (163), Qiao *et al.*, 2016 (76), Chevrinais *et al.*, 2017 (95), King *et al.*, 2017 (369)

647. Skeletal labyrinth, hyomandibular bone articulation, relative position of

Anterior or lateral to skeletal labyrinth (0)

At level of posterior semicircular canal (1)

UBERON 0001840 Semicircular canal: One of three half-circular, interconnected tubes located inside each ear

UBERON 0011606 Hyomandibular bone: Replacement bone that is bilaterally paired and (in teleosts) articulates with the neurocranium dorsally and the opercle posteriorly.

Giles *et al.*, 2015 (164), Lu *et al.*, 2016 (164)

648. Hyomandibular bone, foramen

Absent (0)

Present (1)

UBERON 0011606 Hyomandibular bone: Replacement bone that is bilaterally paired and (in teleosts) articulates with the neurocranium dorsally and the opercle posteriorly.

Lu *et al.*, 2016 (245)

649. Epihyal, contribution of

Opercular support (0)

Mandibular support (1)

Grogan & Lund 2000 (20), 2004 (25), 2008 (26), 2009 (27), Grogan *et al.*, 2012 (38)

650. Interhyal

Absent (0)

Present (1)

Davis *et al.*, 2012 (38), Zhu *et al.*, 2013 (38), Long *et al.*, 2014 (38), Dupret *et al.*, 2014 (38), Giles *et al.*, 2015 (74), Lu *et al.*, 2016 (74), Qiao *et al.*, 2016 (37), Chevrinais *et al.*, 2017 (38), Coates *et al.*, 2017 (30), King *et al.*, 2017 (141)

651. Basihyal

Absent (0)

Present (1)

Davis *et al.*, 2012 (37), Zhu *et al.*, 2013 (37), Long *et al.*, 2014 (37), Dupret *et al.*, 2014 (37), Giles *et al.*, 2015 (73), Lu *et al.*, 2016 (73), Qiao *et al.*, 2016 (36), Chevrinais *et al.*, 2017 (37), Coates *et al.*, 2017 (32), King *et al.*, 2017 (140)

652. Hypohyal

Absent (0)

Present (1)

Giles *et al.*, 2016 (75), Lu *et al.*, 2016 (75), Qiao *et al.*, 2016 (282), Coates *et al.*, 2017 (31), King *et al.*, 2017 (144)

653. Urohyal

Absent (0)

Present (1)

UBERON 2000452 Urohyal : Tendon bone that forms in the tendon of the sternohyoid muscles ventral to the anterior end of copula 1. The urohyal associates by ligaments to the ventral hypohyals or it articulates with the ventral hypohyals. The urohyal is an unpaired bone.

Giles *et al.*, 2015 (76), Lu *et al.*, 2016 (76), Qiao *et al.*, 2016 (283), King *et al.*, 2017 (145)

BRANCHIAL ARCHES

654. Gill arches, extend of

Restricted to region under neurocranium (0)

Extend posterior to neurocranium (1)

UBERON 0001703 Neurocranium: Subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

Giles *et al.*, 2015 (72), Lu *et al.*, 2016 (72), Qiao *et al.*, 2016 (281), King *et al.*, 2017 (143)

655. Gill opening, number of

Single opercular valve (0)

Separate gill openings (1)

UBERON 2002057 Gill opening: anatomical space that is the external opening of a gill slit connecting the pharyngeal cavity to the exterior. Gill opening is usually paired and located on the lateral or ventral surfaces of the head.

Grogan & Lund 2000 (19), 2004 (24), 2008 (25), 2009 (26)

656. Gill openings, type of

Membraneous opercular valve (0)

Bony opercular valve (1)

UBERON 2002057 Gill opening: anatomical space that is the external opening of a gill slit connecting the pharyngeal cavity to the exterior. Gill opening is usually paired and located on the lateral or ventral surfaces of the head.

Grogan *et al.*, 2012 (37)

657. Gills, position of

Mostly beneath otico-occipital region (0)

Posterior to occipital region (1)

Coates *et al.*, 2017 (29)

658. Oralobranchials, cover of

Tesserae (0)

Plates (1)

King *et al.*, 2017 (232)

659. Oralobranchial chamber, interbranchial ridges, disposition of

Oligobranchiate (0)

Orthobranchiate (1)

Nectaspidiform (2)

King *et al.*, 2017 (146)

660. Branchial fossae, number of

1 to 7 (0)

8 to 17 (1)

> 17 (2)

King *et al.*, 2017 (147)

661. Branchial chamber, relative length of

Compact, shorter than jaw (0)

Elongate, longer than jaw (1)

Burrow & Turner 2010 (7)

662. Branchial denticles

Present (0)

Absent (1)

Grogan & Lund 2000 (21), 2004 (26), Burrow & Turner 2010 (67)

663. Branchial vascularization perforates postbranchial lamina

Present (0)

Absent (1)

UBERON 4200016 Postbranchial lamina: Medial facing projection or surface on the anterior (cranial) region of the cleithrum that is often textured or denticled. This process has two primary functions: 1) its shape enhances the vertical strength of the cleithrum and 2) it forms the edge of the gill chamber and helps to direct water after it has passed over the gills

Brazeau 2009 (122)

664. Branchial row (where known), course of

Horizontal (0)

Oblique (1)

Wilson & Märss 2009 (41)

665. Basibranchial element

Unpaired (0)

Paired (1)

UBERON 0013746 Basibranchial element: Endochondral element that is ventral, median, and associated with a single pharyngeal arch in the pharyngeal arch 3-7 skeleton.

King *et al.*, 2017 (148)

666. Hypobranchial element, direction of

Directed anteriorly (0)

Hypobranchials of second and more posterior gill arches directed posteriorly (1)

UBERON 2001893 Hypobranchial element: Skeletal element that is bilaterally paired and articulates medially with a median skeletal element and laterally with a ceratobranchial element.

Coates *et al.*, 2017 (36)

667. Pharyngobranchial element

Absent (0)

Present (1)

UBERON 2001909 Pharyngobranchial element : Skeletal element of the branchial arches located medial to the epibranchials.

Coates *et al.*, 2017 (33)

668. Pharyngobranchial element, direction of

Anteriorly (0)

Posteriorly (1)

UBERON 2001909 Pharyngobranchial element : Skeletal element of the branchial arches located medial to the epibranchials.

Coates *et al.*, 2017 (35)

669. Supra- and infra- pharyngobranchials, separation of

Absent (0)

Present (1)

UBERON 2001858 Suprapharyngobranchial: A pharyngobranchial bone that articulates with the neurocranium dorsally and epibranchial 1 and pharyngobranchial 2 ventrally; lies dorsal to other elements of the dorsal portions of the branchial arches. Articulates with the exoccipital or prootic depending on taxon.

UBERON 2001909 Pharyngobranchial element: Skeletal element of the branchial arches located medial to the epibranchials.

Coates *et al.*, 2017 (34)

PECTORAL FINS AND GIRDLE

670. Pectoral girdle skeleton, position of

Mostly endoskeletal (0)

Mostly exoskeletal (1)

UBERON 0007831 Pectoral girdle skeleton: A subdivision of a limb or fin skeleton consisting of bones which connects the upper limb or fin to the axial skeleton on each side. It consists of the clavicle and scapula in humans and, in those species with three bones in the pectoral girdle, the coracoid. Some mammalian species (e.g. the dog and the horse) have only the scapula. In humans, the only joints between the shoulder girdle and axial skeleton are the sternoclavicular joints on each side. No joint exists between each scapula and the rib cage; instead, the muscular connection between the two permits relatively great mobility of the shoulder girdle in relation to the pelvic girdle. In those species having only the scapula, no joint exists between the forelimb and the thorax, the only attachment being muscular.

Grogan & Lund 2000 (45), 2004 (69), 2008 (75), Grogan *et al.*, 2012 (88)

671. Pectoral girdle skeleton, type of

Macromeric dermal pectoral girdle (0)

Micromeric or lacking dermal skeleton entirely (1)

UBERON 0007831 Pectoral girdle skeleton: A subdivision of a limb or fin skeleton consisting of bones which connects the upper limb or fin to the axial skeleton on each side.

It consists of the clavicle and scapula in humans and, in those species with three bones in the pectoral girdle, the coracoid. Some mammalian species (e.g. the dog and the horse) have only the scapula. In humans, the only joints between the shoulder girdle and axial skeleton are the sternoclavicular joints on each side. No joint exists between each scapula and the rib cage; instead, the muscular connection between the two permits relatively great mobility of the shoulder girdle in relation to the pelvic girdle. In those species having only the scapula, no joint exists between the forelimb and the thorax, the only attachment being muscular.

Coates *et al.*, 2017 (127)

672. Pectoral fin, endoskeletal support, number of

Multiple elements articulating with girdle (0)

Single element ("humerus") articulating with girdle (1)

UBERON 0000151 Pectoral fin: Paired fin that is located in the thoracic region of the body.

Zhu *et al.*, 2009 (130), Zhu *et al.*, 2013 (250), Long *et al.*, 2014 (250), Dupret *et al.*, 2015 (250), Giles *et al.*, 2015 (201), Lu *et al.*, 2016 (201), Qiao *et al.*, 2016 (233), Chevrinais *et al.*, 2017 (250), King *et al.*, 2017 (409)

673. Pectoral girdle skeleton, median dorsal surface, pronounced internal crista

Absent (0)

Present (1)

UBERON 0007831 Pectoral girdle skeleton: A subdivision of a limb or fin skeleton consisting of bones which connects the upper limb or fin to the axial skeleton on each side.

It consists of the clavicle and scapula in humans and, in those species with three bones in the pectoral girdle, the coracoid. Some mammalian species (e.g. the dog and the horse) have only the scapula. In humans, the only joints between the shoulder girdle and axial skeleton are the sternoclavicular joints on each side. No joint exists between each scapula and the rib cage; instead, the muscular connection between the two permits relatively great mobility of the shoulder girdle in relation to the pelvic girdle. In those species having only the scapula, no joint exists between the forelimb and the thorax, the only attachment being muscular.

Brazeau 2009 (104), Davis *et al.*, 2012 (109), Zhu *et al.*, 2013 (109), Long *et al.*, 2014 (109), Dupret *et al.*, 2014 (2014), Giles *et al.*, 2015 (188), Lu *et al.*, 2016 (188), Qiao *et al.*, 2016 (105), Chevrinais *et al.*, 2017 (109), King *et al.*, 2017 (426)

674. Dermal shoulder girdle, composition of

Ventral and dorsal (scapular) components (0)

Ventral components only (1)

Brazeau 2009 (100), Davis *et al.*, 2012 (105), Zhu *et al.*, 2013 (105), Long *et al.*, 2014 (105), Dupret *et al.*, 2014 (105), Giles *et al.*, 2015 (182), Lu *et al.*, 2016 (182), Qiao *et al.*, 2016 (101), Chevrinais *et al.*, 2017 (105), King *et al.*, 2017 (422)

675. Dermal shoulder girdle, forming a complete ring around the trunk

Present (0)

Absent (1)

Brazeau 2009 (101), Davis *et al.*, 2012 (106), Zhu *et al.*, 2013 (106), Long *et al.*, 2014 (106), Dupret *et al.*, 2014 (106), Giles *et al.*, 2015 (184), Lu *et al.*, 2016 (184), Qiao *et al.*, 2016 (102), Chevrinais *et al.*, 2017 (106), King *et al.*, 2017 (423)

676. Pectoral fenestra completely encircled by dermal shoulder armour

Present (0)

Absent (1)

UBERON 3000779 Pectoral fenestra: Ovoid space on the pectoral girdle limited anteriorly by the procoracoid, medially by the epicoracoid, and posteriorly by the coracoid

Brazeau 2009 (102), Davis *et al.*, 2012 (107), Zhu *et al.*, 2013 (107), Long *et al.*, 2014 (107), Dupret *et al.*, 2014 (107), Giles *et al.*, 2015 (185), Lu *et al.*, 2016 (185), Qiao *et al.*, 2016 (103), Chevrinais *et al.*, 2017 (107), King *et al.*, 2017 (424)

677. (N) Scapula

Absent (0)

Present (1)

UBERON 0006849 Scapula: Endochondral bone that is dorsoventrally compressed and provides attachment site for muscles of the pectoral appendage

678. Scapular infundibulum

Absent (0)

Present (1)

Giles *et al.*, 2015 (190), Lu *et al.*, 2016 (190), Qiao *et al.*, 2016 (309), King *et al.*, 2017 (413)

679. Scapular process

Skeletal link to neurocranium (0)

Adjacent to neurocranium (1)

Distant from neurocranium (2)

UBERON 4200123 Scapular process: The dorsal extension of the scapulocoracoid above the level of the glenoid region in basal gnathostomes.

Grogan & Lund 2008 (73)

680. Scapular process and coracoid bone, mineralization of

Comineralised (0)

Separate mineralization (1)

UBERON 4200123 Scapular process: The dorsal extension of the scapulocoracoid above the level of the glenoid region in basal gnathostomes.

UBERON 0004743 Coracoid bone: endochondral bone that is paired and forms part of the socket for the humerus in tetrapods and acts as base of the pectoral fin in fish.

Brazeau 2009 (106)

681. Scapular blade, internal surface, mineralisation of

Mineralised all around (0)

Unmineralised on internal face forming a hemicylindrial cross-section (1)

UBERON 1500000 Scapular blade: Enlarged and broad extension of the scapula distal to the glenoid region that conforms to the contour of the ribs. Origin for the major shoulder muscles including the deltoid group.

Brazeau 2009 (111), Davis *et al.*, 2012 (116), Zhu *et al.*, 2013 (116), Long *et al.*, 2014 (116), Dupret *et al.*, 2014 (116), Giles *et al.*, 2015 (197), Lu *et al.*, 2016 (197), Qiao *et al.*, 2016 (112), Chevrinais *et al.*, 2017 (116), King *et al.*, 2017 (404)

682. Shoulder endoskeleton, scapular process

Absent (0)

Present (1)

UBERON 4200123 Scapular process: The dorsal extension of the scapulocoracoid above the level of the glenoid region in basal gnathostomes.

Davis *et al.*, 2012 (110), Zhu *et al.*, 2013 (110), Long *et al.*, 2014 (110), Dupret *et al.*, 2014 (110), Giles *et al.*, 2015 (191), Lu *et al.*, 2016 (191), Qiao *et al.*, 2016 (106), Chevrinais *et al.*, 2017 (110), King *et al.*, 2017 (398)

683. Separate scapular ossification, ventral margin

Horizontal (0)

Angled (1)

Brazeau 2009 (107), Davis *et al.*, 2012 (111), Zhu *et al.*, 2013 (111), Long *et al.*, 2014 (111), Dupret *et al.*, 2014 (111), Giles *et al.*, 2015 (192), Lu *et al.*, 2016 (192), Qiao *et al.*, 2016 (107), Chevrinais *et al.*, 2017 (111), King *et al.*, 2017 (399)

684. Scapular process, cross section, shape of

Flattened or ovate (0)

Subcircular (1)

UBERON 4200123 Scapular process: The dorsal extension of the scapulocoracoid above the level of the glenoid region in basal gnathostomes.

Brazeau 2009 (108), Davis *et al.*, 2012 (112), Zhu *et al.*, 2013 (112), Long *et al.*, 2014 (112), Dupret *et al.*, 2014 (112), Giles *et al.*, 2015 (193), Lu *et al.*, 2016 (193), Qiao *et al.*, 2016 (108), Chevrinais *et al.*, 2017 (112), King *et al.*, 2017 (400)

685. Scapular process, posterodorsal angle

Absent (0)

Present (1)

UBERON 4200123 Scapular process: The dorsal extension of the scapulocoracoid above the level of the glenoid region in basal gnathostomes.

Davis *et al.*, 2012 (114), Zhu *et al.*, 2013 (114), Long *et al.*, 2014 (114), Dupret *et al.*, 2014 (114), Giles *et al.*, 2015 (195), Lu *et al.*, 2016 (195), Qiao *et al.*, 2016 (110), Chevrinais *et al.*, 2017 (114), Coates *et al.*, 2017 (128), King *et al.*, 2017 (402)

686. Scapular process, endoskeletal postbranchial lamina

Present (0)

Absent (1)

UBERON 4200016 Postbranchial lamina: Medial facing projection or surface on the anterior (cranial) region of the cleithrum that is often textured or denticled. This process has two primary functions: 1) its shape enhances the vertical strength of the cleithrum and 2) it forms the edge of the gill chamber and helps to direct water after it has passed over the gills

UBERON 4200123 Scapular process: The dorsal extension of the scapulocoracoid above the level of the glenoid region in basal gnathostomes.

Brazeau 2009 (110), Davis *et al.*, 2012 (115), Zhu *et al.*, 2013 (115), Long *et al.*, 2014 (115), Dupret *et al.*, 2014 (115), Giles *et al.*, 2015 (196), Lu *et al.*, 2016 (196), Qiao *et al.*, 2016 (111), Chevrinais *et al.*, 2017 (115), King *et al.*, 2017 (403)

687. Subscapular foramen

Absent (0)

Present (1)

UBERON 2001735 Scapular foramen: Foramen that is located in the scapula. The scapular foramen is paired and formed by a ring of bone

Zhu *et al.*, 2009 (129), Zhu *et al.*, 2013 (249), Long *et al.*, 2014 (249), Dupret *et al.*, 2014 (249), Qiao *et al.*, 2016 (237), Chevrinais *et al.*, 2017 (249), King *et al.*, 2017 (411)

688. Anocleithrum

Element developed as postcleithrum (0)

Element developed as anocleithrum (*sensu stricto*) (1)

UBERON 4000160 Anocleithrum: Dermal bone of pectoral girdle that is dorsal to and articulates with the cleithrum.

UBERON 2000410 Postcleithrum: Dermal bone placed postero-medially to the supracleithrum and/or cleithrum

Brazeau 2009 (122), Zhu *et al.*, 2013 (245), Long *et al.*, 2014 (245), Dupret *et al.*, 2014 (245), Qiao *et al.*, 2016 (232), Chevrinais *et al.*, 2017 (245), King *et al.*, 2017 (430)

689. Anocleithrum (*sensu stricto*), position of

Exposed (0)

Subdermal (1)

UBERON 4000160 Anocleithrum: Dermal bone of pectoral girdle that is dorsal to and articulates with the cleithrum.

King *et al.*, 2017 (446)

690. Dorsal cleithrum (AL of the Placodermi) ventral cleithrum (AVL of the Placodermi) and pectoral spine (SP of the Placodermi)

Not fused (0)

Fused (1)

UBERON 4300015 Ventral cleithrum & UBERON 4300014 Dorsal cleithrum: In “placoderms” there are large overlapping plates which completely encircle the body and

superficially may be matched with those in osteichthyans (Stensio, 1959; Forey, 1980; Jarvik, 1980). Thus, the anterior median ventral, anteroventral and anterior lateral of “placoderms” lie in the same positions as the interclavicle, clavicle (ventral cleithrum) and cleithrum (dorsal cleithrum) of osteichthyans.

Zhu *et al.*, 2009 (123), Zhu *et al.*, 2013 (246), Long *et al.*, 2014 (246), Dupret *et al.*, 2014 (246), Qiao *et al.*, 2016 (234), King *et al.*, 2017 (431)

691. Presupracleithrum

Absent (0)

Present (1)

UBERON 4200115 Presupracleithrum: An skeletal element of the upper pectoral girdle overlapped by the opercular and posttemporal bones

Zhu *et al.*, 2009 (121), Zhu *et al.*, 2013 (244), Long *et al.*, 2014 (244), Dupret *et al.*, 2014 (244), Qiao *et al.*, 2016 (231), Chevrinais *et al.*, 2017 (244), King *et al.*, 2017 (203)

692. Cleithrum

Absent (0)

Present (1)

UBERON 0004741 Cleithrum: Dermal bone on the margin of the scapula. The cleithrum is attached to the skull in fishes, but free from the latter in amphibians and disappears early in the evolution of reptiles.

Chevrinais *et al.*, 2017 (246)

693. Clavicle bone and cleithrum, relationship of

Ascending process of clavicle bone overlapping cleithrum (0)

Ascending process of clavicle bone wrapping round anterior edge of cleithrum, overlapping it both laterally and mesially (1)

UBERON 0001105 Clavicle bone: A paired dermal or endochondral bone that is part of the pectoral girdle. The clavicle may be in contact with the interclavicle or coracoid and forms an attachment site for pectoral musculature

UBERON 0004741 Cleithrum: Dermal bone on the margin of the scapula. The cleithrum is attached to the skull in fishes, but free from the latter in amphibians and disappears early in the evolution of reptiles

Zhu *et al.*, 2009 (126), Zhu *et al.*, 2013 (247), Long *et al.*, 2014 (247), Dupret *et al.*, 2014 (247), Qiao *et al.*, 2016 (235), Chevrinais *et al.*, 2017 (247), King *et al.*, 2017 (432)

694. Cleithrum, dorsal end

Pointed (0)

Rounded (1)

UBERON 0004741 Cleithrum: Dermal bone on the margin of the scapula. The cleithrum is attached to the skull in fishes, but free from the latter in amphibians and disappears early in the evolution of reptiles

Zhu *et al.*, 2009 (124)

695. Cleithrum, number of

2 (0)

1 (1)

UBERON 0004741 Cleithrum: Dermal bone on the margin of the scapula. The cleithrum is attached to the skull in fishes, but free from the latter in amphibians and disappears early in the evolution of reptiles

Chevrainais *et al.*, 2017 (246)

696. Extracleithrum

Absent (0)

Present (1)

UBERON 4200022 Extracleithrum: Narrow bone that lies ventral to the level of insertion of the pectoral fin and is sutured to the posterior edges of both the clavicle and cleithrum.

King *et al.*, 2017 (448)

697. (N) Clavicle bone

Absent (0)

Present (1)

UBERON 0001105 Clavicle bone: A paired dermal or endochondral bone that is part of the pectoral girdle. The clavicle may be in contact with the interclavicle or coracoid and forms an attachment site for pectoral musculature

698. Clavicle bone/interolateral plates, relative size of

Same size or bigger than cleithrum (0)

Smaller than cleithrum (1)

UBERON 4300023 Interolateral plate: Dermal bone that is part of the scapular complex in “placoderms” and located anterior to the anterior ventrolateral (AVL) plate

UBERON 0004741 Cleithrum: Dermal bone on the margin of the scapula. The cleithrum is attached to the skull in fishes, but free from the latter in amphibians and disappears early in the evolution of reptiles

King *et al.*, 2017 (443)

699. Interclavicle

Absent (0)

Present (1)

UBERON 0011655 Interclavicle: dermal bone of pectoral girdle that is median and ventral in position.

Zhu *et al.*, 2009 (127)

700. (N) Coracoid bone

Absent (0)

Present (1)

UBERON 0004743 Coracoid bone: Endochondral bone that is paired and forms part of the socket for the humerus in tetrapods and acts as base of the pectoral fin in fish.

701. Coracoid process of scapula

Absent (0)

Present (1)

UBERON 0006633 Coracoid process of scapula: A process of the scapula in most mammals representing the remnant of the coracoid bone of lower vertebrates that has become fused with the scapula.

Brazeau 2009 (112), Davis *et al.*, 2012 (117), Zhu *et al.*, 2013 (117), Long *et al.*, 2014 (117), Dupret *et al.*, 2014 (117), Giles *et al.*, 2015 (198), Lu *et al.*, 2016 (198), Qiao *et al.*, 2016 (113), Chevrinai *et al.*, 2017 (117), King *et al.*, 2017 (405)

702. Procoracoid element, separation of

Absent (0)

Present (1)

UBERON 0011248 Procoracoid element: Endochondral element of pectoral girdle, positioned posterior to the clavicle and anterior to the coracoid.

Burrow & Turner 2010 (52)

703. Procoracoid element, mineralization of

Absent (0)

Present (1)

UBERON 0011248 Procoracoid element: Endochondral element of pectoral girdle, positioned posterior to the clavicle and anterior to the coracoid.

Brazeau 2009 (114), Davis *et al.*, 2012 (118), Zhu *et al.*, 2013 (118), Long *et al.*, 2014 (118), Dupret *et al.*, 2014 (118), Giles *et al.*, 2015 (199), Lu *et al.*, 2016 (199), Qiao *et al.*, 2016 (114), Chevrinais *et al.*, 2017 (118), King *et al.*, 2017 (406)

704. (N) Scapulocoracoid

Absent (0)

Present (1)

UBERON 0004753 Scapulocoracoid: Skeletal element that consists of the scapula and the coracoid

705. Scapulocoracoid surface, mineralization of

Non-mineralized (0)

Granular mineralization (1)

Perichondrally ossified (2)

UBERON 0004753 Scapulocoracoid: Skeletal element that consists of the scapula and the coracoid

Burrow & Turner 2010 (51)

706. Scapulocoracoid, triradiate

Absent (0)

Present (1)

UBERON 0004753 Scapulocoracoid: Skeletal element that consists of the scapula and the coracoid

Zhu *et al.*, 2009 (128), Zhu *et al.*, 2013 (248), Long *et al.*, 2014 (248), Dupret *et al.*, 2014 (248), Qiao *et al.*, 2016 (236), Chevrinais *et al.*, 2017 (248), King *et al.*, 2017 (410)

707. Scapulocoracoid, trailing edge, flange

Absent (0)

Present (1)

UBERON 0004753 Scapulocoracoid: Skeletal element that consists of the scapula and the coracoid

Brazeau 2009 (109), Davis *et al.*, 2012 (113), Zhu *et al.*, 2013 (113), Long *et al.*, 2014 (113), Dupret *et al.*, 2014 (113), Giles *et al.*, 2015 (194), Lu *et al.*, 2016 (194), Qiao *et al.*, 2016 (109), Chevrinais *et al.*, 2017 (113), King *et al.*, 2017 (401)

708. Scapulocoracoid, horizontal plate

Absent (0)

Present (1)

UBERON 0004753 Scapulocoracoid: Skeletal element that consists of the scapula and the coracoid

King *et al.*, 2017 (419)

709. Scapulocoracoid elements

Single, with U-shaped shaft cross section and wide base (0)

Single element, shaft with circular cross section (1)

Single elements, circular cross section shaft plus wide posteriro flange (2)

Two growth centres, ventral portion relatively flat and below level of pectoral fin (3)

Triangular element, oval cross-section (4)

UBERON 0004753 Scapulocoracoid: Skeletal element that consists of the scapula and the coracoid

Burrow & Turner 2010 (53)

710. Scapulocoracoid, fin base articulation, type of

Stenobasal (deeper than wide) (0)

Eurybasal (wider than deep) (1)

UBERON 0004753 Scapulocoracoid: Skeletal element that consists of the scapula and the coracoid

Brazeau 2009 (113), Davis *et al.*, 2012 (119), Zhu *et al.*, 2013 (119), Long *et al.*, 2014 (119), Dupret *et al.*, 2014 (119), Giles *et al.*, 2015 (200), Lu *et al.*, 2016 (200), Qiao *et al.*, 2016 (115), Chevrinais *et al.*, 2017 (119), King *et al.*, 2017 (407)

711. Pectoral propterygium

Absent (0)

Present (1)

Zhu *et al.*, 2009 (131), Zhu *et al.*, 2013 (251), Long *et al.*, 2014 (251), Dupret *et al.*, 2014 (251), Qiao *et al.*, 2016 (238), Chevrinais *et al.*, 2017 (251), King *et al.*, 2017 (412)

712. Propterygium, perforation of

Absent (0)

Present (1)

Brazeau 2009 (116), Davis *et al.*, 2012 (120), Zhu *et al.*, 2013 (120), Long *et al.*, 2014 (120), Dupret *et al.*, 2014 (120), Giles *et al.*, 2015 (206), Lu *et al.*, 2016 (206), Qiao *et al.*, 2016 (116), Chevrinais *et al.*, 2017 (120), King *et al.*, 2017 (408)

713. Propterygium, distal articulation

With fin rays (0)

With a second enlarged plate (1)

No articulation (2)

King *et al.*, 2017 (420)

714. Metapterygial whip

Absent (0)

Present (1)

Coates *et al.*, 2017 (130)

715. Metapterygial axis, mesomeres, number of

≤ 5 (0)

≥ 6 (1)

UBERON 0012079 Metapterygial axis: Proximodistal trajectory through a metapterygium

Giles *et al.*, 2015 (204), Lu *et al.*, 2016 (204), Qiao *et al.*, 2016 (311), King *et al.*, 2017 (415)

716. Pectoral post-metapterygial axis

Absent (0)

Present (1)

UBERON 0012079 Metapterygial axis: Proximodistal trajectory through a metapterygium

Grogan & Lund 2000 (52), 2004 (74), 2008 (80), Grogan *et al.*, 2012 (93)

717. Pectoral post-metapterygial axis elements, number of

≤ 4 (0)

> 4 (1)

UBERON 0012079 Metapterygial axis: Proximodistal trajectory through a metapterygium

Grogan & Lund 2000 (52), 2004 (74), 2008 (80), Grogan *et al.*, 2012 (93)

718. Humerus, entepicondyle

Present (0)

Absent (1)

UBERON 0006806 Entepicondyle of humerus: A bony projection on the distal epiphysis of the humerus that is the attachment site for the flexor muscles of the manus. This condyle faces posteriorly (for sprawling tetrapods) or medially (for erect tetrapods).

King *et al.*, 2017 (418)

719. Prepectoral spine

Absent (0)

Present (1)

UBERON 4200110 Prepectoral spine: Spine located anterior to the pectoral fin.

Brazeau 2009 (128), Burrow & Turner 2010 (44), Davis *et al.*, 2012 (131), Zhu *et al.*, 2013 (131), Long *et al.*, 2014 (131), Dupret *et al.*, 2014 (131), Giles *et al.*, 2015 (220), Lu *et al.*, 2016 (220), Qiao *et al.*, 2016 (127), Chevrinais *et al.*, 2017 (131), King *et al.*, 2017 (461)

720. (N) Prepectoral spine, number of

One pair (0)

Two pairs (1)

Three pairs or more (2)

UBERON 4200110 Prepectoral spine: Spine located anterior to the pectoral fin.

721. Prepectoral spine, insertion of

Free in skin (0)

Fused to ornamented dermal plates (1)

UBERON 4200110 Prepectoral spine: Spine located anterior to the pectoral fin.

Burrow & Turner 2010 (44)

722. Prepectoral spine form "necklace"

Absent (0)

Present (1)

UBERON 4200110 Prepectoral spine: Spine located anterior to the pectoral fin.

King *et al.*, 2017 (483)

723. Pectoral fin, radial support

> 50 % on anterior basals (0)

> 50 % on metapterygium (1)

> 50 % on postmetapterygial axis (2)

UBERON 0000151 Pectoral fin: Paired fin that is located in the thoracic region of the body.

Grogan & Lund 2000 (49), 2004 (71), 2008 (77), Grogan *et al.*, 2012 (90)

724. Suprabranchial fins

Absent (0)

Present (1)

UBERON 4000182 Suprabranchial fin: Paired fin that is a bilaterally paired anterior outgrowth located high on the side of the animal, not far behind the orbit, with the posterior extremity corresponding with the expected posterior end of the branchial region.

Wilson & Märss 2009 (44)

725. Pectoral fins

Absent (0)

Present (1)

UBERON 0000151 Pectoral fin: Paired fin that is located in the thoracic region of the body.

Brazeau 2009 (115)

726. Pectoral fins, surface of

rays' of subparallel scale rows (0)

Fleshy base of scale covered skin (1)

Dermal plates (2)

UBERON 0000151 Pectoral fin: Paired fin that is located in the thoracic region of the body.

Wilson & Märss 2009 (45)

727. Pectoral fin, articulation of

Monobasal (0)

Polybasal (1)

UBERON 0000151 Pectoral fin: Paired fin that is located in the thoracic region of the body.

Giles *et al.*, 2015 (201), Lu *et al.*, 2016 (201)

728. Pectoral fin, basals, number of

≥ 3 (0)

2 (1)

UBERON 0000151 Pectoral fin: Paired fin that is located in the thoracic region of the body.

Giles *et al.*, 2015 (202), Lu *et al.*, 2016 (202), Qiao *et al.*, 2016 (310), King *et al.*, 2017 (414)

729. Pectoral fin, position of

Ventrolateral (0)

Mid-lank (1)

Nape of the neck (2)

UBERON 0000151 Pectoral fin: Paired fin that is located in the thoracic region of the body.

Grogan & Lund 2000 (46), 2004 (68), 2008 (74), Grogan *et al.*, 2012 (87)

730. Pectoral fins completely covered in macromeric dermal armour

Absent (0)

Present (1)

UBERON 0000151 Pectoral fin: Paired fin that is located in the thoracic region of the body.

Brazeau 2009 (120), Davis *et al.*, 2012 (124), Zhu *et al.*, 2013 (124), Long *et al.*, 2014 (124), Dupret *et al.*, 2014 (124), Giles *et al.*, 2015 (211), Lu *et al.*, 2016 (211), Qiao *et al.*, 2016 (120), Chevrinais *et al.*, 2017 (124), King *et al.*, 2017 (427)

731. Pectoral fin, filamentous extension (from axillary region)

Absent (0)

Present (1)

UBERON 0000151 Pectoral fin: Paired fin that is located in the thoracic region of the body.

Giles *et al.*, 2015 (207), Lu *et al.*, 2016 (207), Qiao *et al.*, 2016 (313), King *et al.*, 2017 (417)

732. Armoured pectoral fin, joint

Absent (0)

Present (1)

UBERON 0000151 Pectoral fin: Paired fin that is located in the thoracic region of the body.

King *et al.*, 2017 (441)

733. Pectoral fin spines

Absent (0)

Present (1)

UBERON 2001787 Pectoral fin spine: Pectoral-fin lepidotrichium 1 with mostly co-ossified and unsegmented hemitrichia that form a stiff and usually thick shaft and enlarged basal processes that moveably articulate with the pectoral girdle. The pectoral fin spine may also result from the fusion of several lepidotrichia that form a stiff shaft.

Coates *et al.*, 2017 (138)

734. (N) Pectoral fin spine, denticles

Absent (0)

Present (1)

UBERON 2001787 Pectoral fin spine: Pectoral-fin lepidotrichium 1 with mostly co-ossified and unsegmented hemitrichia that form a stiff and usually thick shaft and enlarged basal processes that moveably articulate with the pectoral girdle. The pectoral fin spine may also result from the fusion of several lepidotrichia that form a stiff shaft.

735. (N) Pectoral fin spine, denticles, type of

Retrorse (0)

Straight (1)

UBERON 2001787 Pectoral fin spine: Pectoral-fin lepidotrichium 1 with mostly co-ossified and unsegmented hemitrichia that form a stiff and usually thick shaft and enlarged basal processes that moveably articulate with the pectoral girdle. The pectoral fin spine may also result from the fusion of several lepidotrichia that form a stiff shaft.

736. (N) Pectoral fin spines, denticle rows, number of

1 (0)

2 (1)

UBERON 2001787 Pectoral fin spine: Pectoral-fin lepidotrichium 1 with mostly co-ossified and unsegmented hemitrichia that form a stiff and usually thick shaft and enlarged basal processes that moveably articulate with the pectoral girdle. The pectoral fin spine may also result from the fusion of several lepidotrichia that form a stiff shaft.

737. (N) Pectoral fin spine, paired

Absent (0)

Present (1)

UBERON 2001787 Pectoral fin spine: Pectoral-fin lepidotrichium 1 with mostly co-ossified and unsegmented hemitrichia that form a stiff and usually thick shaft and enlarged basal processes that moveably articulate with the pectoral girdle. The pectoral fin spine may also result from the fusion of several lepidotrichia that form a stiff shaft.

738. Pectoral fin spine, denticles, position of

Along trailing edge (0)

Along leading edge (1)

UBERON 2001787 Pectoral fin spine: Pectoral-fin lepidotrichium 1 with mostly co-ossified and unsegmented hemitrichia that form a stiff and usually thick shaft and enlarged basal processes that moveably articulate with the pectoral girdle. The pectoral fin spine may also result from the fusion of several lepidotrichia that form a stiff shaft.

Burrow & Turner 2010 (45)

739. (N) Pectoral fin spine, denticles, extension of

Restricted to distal part (0)

Extend for most of spine length (1)

UBERON 2001787 Pectoral fin spine: Pectoral-fin lepidotrichium 1 with mostly co-ossified and unsegmented hemitrichia that form a stiff and usually thick shaft and enlarged

basal processes that moveably articulate with the pectoral girdle. The pectoral fin spine may also result from the fusion of several lepidotrichia that form a stiff shaft.

740. Pectoral fin spine, shape of

Not bivalve-like (0)

Bivalve-like (1)

UBERON 2001787 Pectoral fin spine: Pectoral-fin lepidotrichium 1 with mostly co-ossified and unsegmented hemitrichia that form a stiff and usually thick shaft and enlarged basal processes that moveably articulate with the pectoral girdle. The pectoral fin spine may also result from the fusion of several lepidotrichia that form a stiff shaft.

King *et al.*, 2017 (449)

741. Pectoral fin spine, curvature of

Curved for most of its lengths (0)

Straight (1)

Plate-like (2)

UBERON 2001787 Pectoral fin spine: Pectoral-fin lepidotrichium 1 with mostly co-ossified and unsegmented hemitrichia that form a stiff and usually thick shaft and enlarged basal processes that moveably articulate with the pectoral girdle. The pectoral fin spine may also result from the fusion of several lepidotrichia that form a stiff shaft.

Burrow & Turner 2010 (46)

742. (N) Pectoral fin spine, ornamentation of

Striated (0)

Ribbed (1)

Tuberculated ribs (2)

Smooth (3)

UBERON 2001787 Pectoral fin spine: Pectoral-fin lepidotrichium 1 with mostly co-ossified and unsegmented hemitrichia that form a stiff and usually thick shaft and enlarged basal processes that moveably articulate with the pectoral girdle. The pectoral fin spine may also result from the fusion of several lepidotrichia that form a stiff shaft.

743. (N) Pectoral fin spine, ribs/stries, orientation of

Converged on leading edge (0)

Parallel to the leading edge (1)

UBERON 2001787 Pectoral fin spine: Pectoral-fin lepidotrichium 1 with mostly co-ossified and unsegmented hemitrichia that form a stiff and usually thick shaft and enlarged basal processes that moveably articulate with the pectoral girdle. The pectoral fin spine may also result from the fusion of several lepidotrichia that form a stiff shaft.

744. (N) Pectoral fin spine, ribs/stries per side, number of

1 to 5 (0)

6 to 10 (1)

>10 (2)

UBERON 2001787 Pectoral fin spine: Pectoral-fin lepidotrichium 1 with mostly co-ossified and unsegmented hemitrichia that form a stiff and usually thick shaft and enlarged basal processes that moveably articulate with the pectoral girdle. The pectoral fin spine may also result from the fusion of several lepidotrichia that form a stiff shaft.

745. (N) Pectoral fin spine, ribs or stries, organisation of

Subparallel with divergences (0)

Parallel without divergences (1)

UBERON 2001787 Pectoral fin spine: Pectoral-fin lepidotrichium 1 with mostly co-ossified and unsegmented hemitrichia that form a stiff and usually thick shaft and enlarged basal processes that moveably articulate with the pectoral girdle. The pectoral fin spine may also result from the fusion of several lepidotrichia that form a stiff shaft.

746. (N) Pectoral fin spine, ribs/stries divergences, position of

Restricted to leading edge (0)

Not restricted to leading edge (1)

UBERON 2001787 Pectoral fin spine: Pectoral-fin lepidotrichium 1 with mostly co-ossified and unsegmented hemitrichia that form a stiff and usually thick shaft and enlarged basal processes that moveably articulate with the pectoral girdle. The pectoral fin spine may also result from the fusion of several lepidotrichia that form a stiff shaft.

747. (N) Pectoral fin spine, insertion, size of

<25% of its length (0)

>25% of its length (1)

UBERON 2001787 Pectoral fin spine: Pectoral-fin lepidotrichium 1 with mostly co-ossified and unsegmented hemitrichia that form a stiff and usually thick shaft and enlarged basal processes that moveably articulate with the pectoral girdle. The pectoral fin spine may also result from the fusion of several lepidotrichia that form a stiff shaft.

748. (N) Pectoral fin spine, insertion surface, ornamentation of

Same as exerted surface (0)

Longitudinal striations (1)

Full-length parallel grooves and ridges (2)

Smooth (3)

UBERON 2001787 Pectoral fin spine: Pectoral-fin lepidotrichium 1 with mostly co-ossified and unsegmented hemitrichia that form a stiff and usually thick shaft and enlarged basal processes that moveably articulate with the pectoral girdle. The pectoral fin spine may also result from the fusion of several lepidotrichia that form a stiff shaft.

749. (N) Pectoral fin spine, smooth apex

Absent (0)

Present (1)

UBERON 2001787 Pectoral fin spine: Pectoral-fin lepidotrichium 1 with mostly co-ossified and unsegmented hemitrichia that form a stiff and usually thick shaft and enlarged basal processes that moveably articulate with the pectoral girdle. The pectoral fin spine may also result from the fusion of several lepidotrichia that form a stiff shaft.

750. (N) Pectoral fin spine, cavity

Open for less than half spine length (0)

Open for more than half spine length (1)

UBERON 2001787 Pectoral fin spine: Pectoral-fin lepidotrichium 1 with mostly co-ossified and unsegmented hemitrichia that form a stiff and usually thick shaft and enlarged basal processes that moveably articulate with the pectoral girdle. The pectoral fin spine may also result from the fusion of several lepidotrichia that form a stiff shaft.

751. Pectoral fin spine, attachment of

Not attached to dermal plates (0)

Firmly attached to ornamented dermal plates (1)

UBERON 2001787 Pectoral fin spine: Pectoral-fin lepidotrichium 1 with mostly co-ossified and unsegmented hemitrichia that form a stiff and usually thick shaft and enlarged basal processes that moveably articulate with the pectoral girdle. The pectoral fin spine may also result from the fusion of several lepidotrichia that form a stiff shaft.

Burrow & Turner 2010 (50)

752. Pectoral fin spine and scapulocoracoid, association of

Loosely associated, movable joint (0)

Firmly fixed, fin spine held erect (1)

UBERON 2001787 Pectoral fin spine: Pectoral-fin lepidotrichium 1 with mostly co-ossified and unsegmented hemitrichia that form a stiff and usually thick shaft and enlarged basal processes that moveably articulate with the pectoral girdle. The pectoral fin spine may also result from the fusion of several lepidotrichia that form a stiff shaft.

Burrow & Turner 2010 (54)

753. Pectoral leading edge denticles rows (iniopterygian), number of

1 (0)

2 (1)

≥ 3 (2)

Grogan *et al.*, 2012 (94)

754. Paired fin spines, base, scales, type of

Unmodified (0)

Enlarged (1)

UBERON 4500009 Paired fin spine: Fin spine that is part of a paired fin.

Burrow & Turner 2010 (31)

755. Fin webs, longitudinal scale alignment

Present (0)

Absent (1)

UBERON 4300031 Fin web: Membrane that connects the lepidotrichia or ceratotrichia of a fin

Giles *et al.*, 2015 (13), Lu *et al.*, 2016 (13), King *et al.*, 2017 (468)

756. Ridge scales, scute-like (basal fulcrum)

Absent (0)

Present (1)

UBERON 2002082 Basal fulcrum: Fulcrum that is large, laterally expanded, paired or unpaired, scale-like, and that precedes the base of a fin.

Zhu *et al.*, 2009 (144), Giles *et al.*, 2015 (27), Lu *et al.*, 2016 (27), Qiao *et al.*, 2016 (264), King *et al.*, 2017 (471)

757. Fulcral scales

Absent (0)

Present (1)

Brazeau 2009 (14)

758. (N) Basipterygium element

Absent (0)

Present (1)

UBERON 2100623 Basipterygium element: Endochondral element that is paired and supports the pelvic fin. The basipterygium has a posteromedial process called the ischiac process

759. Basipterygium element, shape of

Elongate (0)

Triangular (1)

UBERON 2100623 Basipterygium element: Endochondral element that is paired and supports the pelvic fin. The basipterygium has a posteromedial process called the ischiac process

Geogan & Lund 2000 (55), 2004 (77), 2008 (83), Grogan *et al.*, 2012 (97)

760. Pelvic girdle skeleton

Unfused across midline (0)

Fused across midline (1)

UBERON 0007832 Pelvic girdle skeleton: Skeletal subdivision consisting of a set of bones linking the axial series to the hindlimb zeugopodium and offering anchoring areas for hindlimb and caudal musculature

Grogan & Lund 2000 (53)

761. Pelvic girdle skeleton, mineralization of

Bone tissue (0)

Prismatic cartilage (1)

UBERON 0007832 Pelvic girdle skeleton: Skeletal subdivision consisting of a set of bones linking the axial series to the hindlimb zeugopodium and offering anchoring areas for hindlimb and caudal musculature

UBERON 0002481 Bone tissue: Skeletal tissue with a collagen-rich extracellular matrix vascularized, mineralized with hydroxyapatite and typically including osteocytes located in lacunae that communicate with one another by cell processes (in canaliculi). Bone is deposited by osteoblasts.

UBERON 0018352 Prismatic cartilage: Cartilage arranged into tesserae, blocks of calcified cartilage that fit together as tiles on a floor form a mosaic. Found only in chondrichthyans.

Grogan & Lund 2004 (75), Grogan & Lund 2008 (81), Grogan *et al.*, 2012 (95)

762. Pelvic girdle skeleton, fused puboischiadic

Absent (0)

Present (1)

UBERON 0007832 Pelvic girdle skeleton: Skeletal subdivision consisting of a set of bones linking the axial series to the hindlimb zeugopodium and offering anchoring areas for hindlimb and caudal musculature

Coates *et al.*, 2017 (131)

763. Pelvic girdle skeleton, substantial dermal component

Present (0)

Absent (1)

UBERON 0007832 Pelvic girdle skeleton: Skeletal subdivision consisting of a set of bones linking the axial series to the hindlimb zeugopodium and offering anchoring areas for hindlimb and caudal musculature

Zhu *et al.*, 2013 (252), Long *et al.*, 2014 (252), Dupret *et al.*, 2014 (252), Qiao *et al.*, 2016 (239), Chevrinais *et al.*, 2017 (252), King *et al.*, 2017 (433)

764. Pelvic fin

Absent (0)

Present (1)

UBERON 0000152 Pelvic fin: Paired fin located in the abdominal position of the body.

Brazeau 2009 (117), Davis *et al.*, 2012 (121), Zhu *et al.*, 2013 (121), Long *et al.*, 2014 (121), Dupret *et al.*, 2014 (121), Giles *et al.*, 2015 (208), Lu *et al.*, 2016 (208), Qiao *et al.*, 2016 (117), Chevrinais *et al.*, 2017 (121), King *et al.*, 2017 (394)

765. Pelvic fin, insertion of

As broad or broader than fin height (0)

Shorter than fin height (1)

UBERON 0000152 Pelvic fin: Paired fin located in the abdominal position of the body.

Zhu *et al.*, 2009 (134)

766. (N) Pelvic, dorsal process

Absent (0)

Present (1)

767. Posterior dorsal fin, calcified base plate

Absent (0)

Present (1)

UBERON 0000152 Pelvic fin: Paired fin located in the abdominal position of the body.

Coates *et al.*, 2017 (141)

768. Pelvic radials, position of

Majority on girdle (0)

~ 50 % on basipterygium (1)

Majority on basipterygium (2)

UBERON 2100623 Basipterygium element: Endochondral element that is paired and supports the pelvic fin. The basipterygium has a posteromedial process called the ischiac process

Grogan & Lund 2000 (56), 2004 (78), 2008 (85), Grogan *et al.*, 2012 (98)

769. Prepelvic fin spine

Absent (0)

Present (1)

UBERON 4200111 Prepelvic fin spine: Spine located anterior to the pelvic fin and posterior to the pectoral fin.

Chevrainais *et al.*, 2017 (130)

770. Pelvic fin spine

Absent (0)

Present (1)

Zhu *et al.*, 2013 (253), Long *et al.*, 2014 (253), Dupret *et al.*, 2014 (253), Qiao *et al.*, 2016 (240), Chevrinais *et al.*, 2017 (253), King *et al.*, 2017 (434)

771. (N) Pelvic fin spine, curvature of

Curved for most of its length (0)

Straight (1)

Plate-like (2)

772. (N) Pelvic fin spine, ornamentation of

Striated (0)

Ribbed (1)

Tuberculated ribs (2)

Smooth (3)

773. (N) Pelvic fin spine, ribs/stries, orientation of

Converged on leading edge for most of the fin spine length (0)

Parallel the leading edge to near the distal tip (1)

774. (N) Pelvic fin spine, ribs/stries per side, number of

1 to 5 (0)

6 to 10 (1)

>10 (2)

775. (N) Pelvic fin spine, ribs/stries, organisation of

Subparallel with divergences (0)

Parallel without divergences (1)

776. (N) Pelvic fin spine, ribs/stries divergences, position of

Restricted to leading edge (0)

Not restricted to leading edge (1)

777. (N) Pelvic fin spine, insertion, relative length of

<25% of spine length (0)

>25% of spine length (1)

778. (N) Pelvic fin spine, smooth apex

Absent (0)

Present (1)

779. (N) Pelvic fin spine, cavity

Open for less than half spine length (0)

Open for more than half spine length (1)

780. (N) Prepelvic spine, series of

Absent (0)

Present (1)

UBERON 4200111 Prepelvic fin spine: Spine located anterior to the pelvic fin and posterior to the pectoral fin.

781. Prepelvic spine series, shape of

Conical, sub-oval cross section (0)

Compressed and blade-like (1)

UBERON 4200111 Prepelvic fin spine: Spine located anterior to the pelvic fin and posterior to the pectoral fin.

Burrow & Turner 2010 (55)

782. Intermediate spine

Absent (0)

Present (1)

UBERON 4200097 Intermediate spine: Spine ventrally located on the body and not part of the pectoral, pelvic or anal fins.

Brazeau 2009 (127), Davis *et al.*, 2012 (130), Zhu *et al.*, 2013 (130), Long *et al.*, 2014 (130), Dupret *et al.*, 2014 (130), Giles *et al.*, 2015 (217), Lu *et al.*, 2016 (217), Qiao *et al.*, 2016 (126), King *et al.*, 2017 (460)

783. Intermediate spine, number of

One pair (0)

Multiple pairs (1)

UBERON 4200097 Intermediate spine: Spine ventrally located on the body and not part of the pectoral, pelvic or anal fins.

Giles *et al.*, 2015 (219), Lu *et al.*, 2016 (219), Qiao *et al.*, 2016 (316), King *et al.*, 2017 (473)

784. Intromittent organ and pelvic fins, association of

Present (0)

Absent (1)

UBERON 0008811 Intromittent organ: An external organ of a male organism that is specialized to deliver sperm during copulation. Intromittent organs are found most often in terrestrial species, as most aquatic species fertilize their eggs externally, although there are exceptions

UBERON 0000152 Pelvic fin: Paired fin located in the abdominal position of the body

Long *et al.*, 2014 (122), King *et al.*, 2017 (395)

785. Intromittent organ, one large J-shaped element

Absent (0)

Present (1)

UBERON 0008811 Intromittent organ: An external organ of a male organism that is specialized to deliver sperm during copulation. Intromittent organs are found most often in terrestrial species, as most aquatic species fertilize their eggs externally, although there are exceptions

Long *et al.*, 2014 (258), Qiao *et al.*, 2016 (250), King *et al.*, 2017 (396)

786. Distal part of pelvic fin, intromittent organ

Absent (0)

Present (1)

UBERON 0008811 Intromittent organ: An external organ of a male organism that is specialized to deliver sperm during copulation. Intromittent organs are found most often in terrestrial species, as most aquatic species fertilize their eggs externally, although there are exceptions

UBERON 0000152 Pelvic fin: Paired fin located in the abdominal position of the body

Long *et al.*, 2014 (259), Qiao *et al.*, 2016 (251), King *et al.*, 2017 (397)

787. Prepelvic clasper

Absent (0)

Present (1)

UBERON 0017623 Prepelvic clasper: A supplemental clasper in Holocephali, in front of the pelvic fin.

Grogan & Lund 2004 (79), 2008 (87), Grogan *et al.*, 2012 (100)

788. Prepelvic clasper, position of

Adjacent to fin (0)

Anterior to fin (1)

UBERON 0017623 Prepelvic clasper: A supplemental clasper in Holocephali, in front of the pelvic fin.

Grogan & Lund 2004 (79), 2008 (87), Grogan *et al.*, 2012 (100)

789. (N) Clasper

Absent (0)

Present (1)

UBERON 0010516 Clasper: male anatomical structure found some groups of animals, used in mating. Male cartilaginous fish have claspers formed from the posterior portion of their pelvic fin which serve as intromittent organs used to channel semen into the female's cloaca during mating. The act of mating in some fish including sharks usually includes one of the claspers raised to allow water into the siphon through a specific orifice. The clasper is then inserted into the vagina, where it opens like an umbrella to anchor its position. The siphon then begins to contract expelling water and sperm. Male chimaeras have cephalic claspers on their heads, which are thought to aid in holding the female during mating

790. Clasper, pair of

Single (0)

Multiple (1)

UBERON 0010516 Clasper: male anatomical structure found some groups of animals, used in mating. Male cartilaginous fish have claspers formed from the posterior portion of their pelvic fin which serve as intromittent organs used to channel semen into the female's cloaca during mating. The act of mating in some fish including sharks usually includes one of the claspers raised to allow water into the siphon through a specific orifice. The clasper is then inserted into the vagina, where it opens like an umbrella to anchor its position. The siphon then begins to contract expelling water and sperm. Male chimaeras have cephalic claspers on their heads, which are thought to aid in holding the female during mating

Grogan & Lund 2004 (3), 2008 (1), 2009 (1)

791. Pelvic fin clasper

Absent (0)

Present (1)

UBERON 0010518 Pelvic fin clasper: The rod-like extension of the medial portion of the pelvic fin in male Elasmobranchii and Holocephali. Claspers are used as intromittent organs (not in clasping), the grooves on their facing surfaces together forming a tube for the transmission of sperm when the claspers are held together. The anterior proximal opening is called the apophysis, the posterior distal opening the rhipidion.

Brazeau 2009 (119), Davis *et al.*, 2012 (122), Zhu *et al.*, 2013 (122), Long *et al.*, 2014 (122), Dupret *et al.*, 2014 (122), Giles *et al.*, 2015 (209), Lu *et al.*, 2016 (209), Qiao *et al.*, 2016 (118), Chevrin *et al.*, 2017 (122)

792. Pelvic fin clasper, ossification of

Absent (0)

Present (1)

UBERON 0010518 Pelvic fin clasper: The rod-like extension of the medial portion of the pelvic fin in male Elasmobranchii and Holocephali. Claspers are used as intromittent organs (not in clasping), the grooves on their facing surfaces together forming a tube for the transmission of sperm when the claspers are held together. The anterior proximal opening is called the apophysis, the posterior distal opening the rhipidion.

Brazeau 2009 (118), Davis *et al.*, 2012 (123), Zhu *et al.*, 2013 (123), Long *et al.*, 2014 (123), Dupret *et al.*, 2014 (123), Giles *et al.*, 2015 (210), Lu *et al.*, 2016 (210), Qiao *et al.*, 2016 (119), Chevrinais *et al.*, 2017 (123)

793. Clasper, distal end

Simple (0)

Complex (1)

UBERON 0010516 Clasper: male anatomical structure found some groups of animals, used in mating. Male cartilaginous fish have claspers formed from the posterior portion of their pelvic fin which serve as intromittent organs used to channel semen into the female's cloaca during mating. The act of mating in some fish including sharks usually includes one of the claspers raised to allow water into the siphon through a specific orifice. The clasper is then inserted into the vagina, where it opens like an umbrella to anchor its position. The siphon then begins to contract expelling water and sperm. Male chimaeras have cephalic claspers on their heads, which are thought to aid in holding the female during mating

Grogan & Lund 2000 (57)

794. Fringing fulcrum

Absent (0)

Present (1)

UBERON 2002083 Fringing fulcrum: Fulcrum that is a small, paired dermal structure associated with the marginal, leading rays of paired and/or unpaired fins.

Zhu *et al.*, 2009 (143), Zhu *et al.*, 2013 (145), Long *et al.*, 2014 (145), Dupret *et al.*, 2014 (145), Qiao *et al.*, 2016 (252), Chevrinais *et al.*, 2017 (145), King *et al.*, 2017 (467)

795. Lepidotrichium

Absent (0)

Present (1)

UBERON 4000172 Lepidotrichium: Dermal bone that is rod-like, formed and usually contained in a fin membrane, and jointed to or adjacent to distal radials. Lepidotrichia are formed from paired hemitrichia surrounding actinotrichia. There are usually two more lepidotrichia than distal radials.

Zhu *et al.*, 2009 (141), Chevrinais *et al.*, 2017 (7)

796. Lepidotrichium, barbed

Absent (0)

Present (1)

UBERON 4000172 Lepidotrichium : Dermal bone that is rod-like, formed and usually contained in a fin membrane, and jointed to or adjacent to distal radials. Lepidotrichia are formed from paired hemitrichia surrounding actinotrichia. There are usually two more lepidotrichia than distal radials.

Lu *et al.*, 2016 (268)

797. Fin webs, lepidotrichium

Absent (0)

Present (1)

UBERON 4000172 Lepidotrichium: Dermal bone that is rod-like, formed and usually contained in a fin membrane, and jointed to or adjacent to distal radials. Lepidotrichia are formed from paired hemitrichia surrounding actinotrichia. There are usually two more lepidotrichia than distal radials.

Brazeau 2009 (7)

798. Lepidotrichium, differentiation of

Absent (0)

Present (1)

UBERON 4000172 Lepidotrichium: Dermal bone that is rod-like, formed and usually contained in a fin membrane, and jointed to or adjacent to distal radials. Lepidotrichia are formed from paired hemitrichia surrounding actinotrichia. There are usually two more lepidotrichia than distal radials.

Giles *et al.*, 2015 (14), Lu *et al.*, 2016 (14), Qiao *et al.*, 2016 (261), King *et al.*, 2017 (469)

799. Lepidotrichium or lepidotrichium-like scale, alignment

Present (0)

Absent (1)

UBERON 4000172 Lepidotrichium: Dermal bone that is rod-like, formed and usually contained in a fin membrane, and jointed to or adjacent to distal radials. Lepidotrichia are formed from paired hemitrichia surrounding actinotrichia. There are usually two more lepidotrichia than distal radials.

Davis *et al.*, 2012 (7), Zhu *et al.*, 2013 (7), Long *et al.*, 2014 (7), Dupret *et al.*, 2014 (7), Qiao *et al.*, 2016 (6), Chevrinais *et al.*, 2017 (262), Coates *et al.*, 2017 (8)

800. Median ventral prepectoral spine

Absent (0)

Present (1)

UBERON 4200110 Prepectoral spine: Spine located anterior to the pectoral fin.

King *et al.*, 2017 (482)

801. Median fin spines

Absent (0)

Present (1)

UBERON 4200070 Median fin spine: Fin spine that is part of a median fin.

Zhu *et al.*, 2009 (133)

802. (N) Dorsal fin

Absent (0)

Present (1)

UBERON 0003097 Dorsal fin: Median fin located on the dorsal surface of the organism.

803. Dorsal fins, number of

1 (0)

2 (1)

3 (2)

UBERON 0003097 Dorsal fin: Median fin located on the dorsal surface of the organism.

Grogan & Lund 2000 (59), 2004 (81), 2008 (90), Wilson & Märss 2009 (47), Brazeau 2009 (133), Burrow & Turner 2010 (38), Grogan *et al.*, 2012 (103), Davis *et al.*, 2012 (136), Zhu *et al.*, 2013 (136), Long *et al.*, 2014 (136), Dupret *et al.*, 2014 (136), Giles *et al.*, 2015 (228), Lu *et al.*, 2016 (228), Qiao *et al.*, 2016 (132), Chevrinais *et al.*, 2017 (136), Coates *et al.*, 2017 (140), King *et al.*, 2017 (450)

804. Anterior dorsal fin

Absent (0)

Present (1)

UBERON 4200023 Anterior dorsal fin: A dorsal fin located anterior to posterior dorsal fin.

Grogan & Lund 2000 (61), 2004 (83), 2008 (92)

805. (N) Anterior dorsal fin, base, composition of

All radials (0)

Basal plate and radials (1)

Basal plate (2)

UBERON 4200023 Anterior dorsal fin: A dorsal fin located anterior to posterior dorsal fin.

806. (N) Posterior dorsal fin

Absent (0)

Present (1)

UBERON 4100014 Posterior dorsal fin: Dorsal fin located posterior to the anterior dorsal fin.

807. (N) Posterior dorsal fin, relative size of

Shorter than anterior (0)

Longer than anterior (1)

Same as anterior (2)

UBERON 4100014 Posterior dorsal fin: Dorsal fin located posterior to the anterior dorsal fin.

808. Posterior dorsal fin, shape of

Base approximately as broad as tall not broader than all of other median fins (0)

Base longer than height of the fin substantially longer than any other dorsal fins (1)

UBERON 4100014 Posterior dorsal fin: Dorsal fin located posterior to the anterior dorsal fin.

Giles *et al.*, 2015 (229), Lu *et al.*, 2016 (229), Qiao *et al.*, 2016 (320), King *et al.*, 2017 (476)

809. Posterior dorsal fin, base, composition of

All radials (0)

Basal plate and radials (1)

Basal plate (2)

UBERON 4100014 Posterior dorsal fin: Dorsal fin located posterior to the anterior dorsal fin.

Grogan & Lund 2000 (68), 2004 (91), 2008 (100), Grogan *et al.*, 2012 (113)

810. Posterior dorsal fin, delta-shaped cartilage

Absent (0)

Present (1)

Coates *et al.*, 2017 (142)

811. Dorsal fin basal plate and branching radial structure, articulation of

Absent (0)

Present (1)

UBERON 0003097 Dorsal fin: Median fin located on the dorsal surface of the organism.

Giles *et al.*, 2015 (231), Lu *et al.*, 2016 (231), Qiao *et al.*, 2016 (322), King *et al.*, 2017 (456)

812. Series of median hexagonal scutes anterior to first dorsal fin

Absent (0)

Present (1)

UBERON 0003097 Dorsal fin: Median fin located on the dorsal surface of the organism.

King *et al.*, 2017 (480)

813. Dorsal fin, basal plate

Absent (0)

Present (1)

UBERON 0003097 Dorsal fin: Median fin located on the dorsal surface of the organism.

Giles *et al.*, 2015 (230), Lu *et al.*, 2016 (230), Qiao *et al.*, 2016 (321), King *et al.*, 2017 (477)

814. (N) Dorsal fin, squamation of

Absent (0)

Present (1)

UBERON 0003097 Dorsal fin: Median fin located on the dorsal surface of the organism.

815. Dorsal fin, squamation, cover of

Complete covering (0)

Crest of fin only (1)

Upon radials (2)

UBERON 0003097 Dorsal fin: Median fin located on the dorsal surface of the organism.

Grogan & Lund 2000 (42), 2004 (65), 2008 (70), Grogan *et al.*, 2012 (83)

816. Dorsal fin spine

Absent (0)

Present (1)

Grogan & Lund 2000 (60), 2004 (82), 2008 (91), Brazeau 2009 (123), Grogan *et al.*, 2012 (104), Davis *et al.*, 2012 (126), Zhu *et al.*, 2013 (126), Long *et al.*, 2014 (126), Dupret *et al.*, 2014 (126), Giles *et al.*, 2015 (213), Lu *et al.*, 2016 (213), Qiao *et al.*, 2016 (122), Chevrinais *et al.*, 2017 (126), Coates *et al.*, 2017 (134), King *et al.*, 2017 (457)

817. Dorsal fin spine, number of

One (0)

Two (1)

Grogan & Lund 2000 (60), 2004 (82), 2008 (91), Grogan *et al.*, 2012 (104)

818. (N) Dorsal fin spine, denticles

Absent (0)

Present (1)

819. (N) Dorsal fin spine, denticle rows, number of

Double row along trailing edge (0)

Single row along trailing edge (1)

820. (N) Anterior and posterior dorsal fin spine, different shape between

Absent (0)

Present (1)

821. (N) Dorsal fin spine, shape of

Straight (0)

Curved (1)

822. (N) Dorsal fin spine, insertion, relative size of

<25% of spine length (0)

>25% of spine length (1)

823. (N) Anterior and posterior dorsal fin spine, different ornamentation between

Absent (0)

Present (1)

824. (N) Dorsal fin spine, ornamentation of

Striated (0)

Ribbed (1)

Tuberculated ribs (2)

Smooth (3)

825. (N) Dorsal fin spine, ribs/stries, orientation of

Converged on leading edge for most of the fin spine length (0)

Parallel the leading edge to near the distal tip (1)

826. (N) Dorsal fin spine, ribs/stries, organisation of

Subparallel with divergences (0)

Parallel without divergences (1)

827. (N) Dorsal fin spine, ribs/stries divergences, position of

Restricted to the leading edge (0)

Not restricted to the leading edge (1)

828. (N) Dorsal fin spine, stries/ribs per side, number of

1 to 5 (0)

6 to 10 (1)

>10 (2)

829. (N) Dorsal fin spine, cavity, opening of

Open for less than half spine length (0)

Open for more than half spine length (1)

830. (N) Anterior dorsal fin spine, direction of

Anteriorly directed (0)

Posteriorly directed (1)

831. (N) Posterior dorsal fin spine, direction of

Anteriorly directed (0)

Posteriorly directed (1)

832. (N) Anterior dorsal fin spine, insertion of

Fixed (0)

Mobile (1)

833. Anterior dorsal fin spine, relative length of

Shorter than posterior dorsal fin spine (0)

Longer than posterior dorsal fin spine (1)

Same as posterior dorsal fin spine (2)

Burrow & Turner 2010 (39)

834. Anterior dorsal fin/spine, support, type of

Basal plate/radials (0)

Synarcuum (1)

On head (2)

Shoulder girdle (3)

Grogan & Lund 2004 (84), 2008 (93), Grogan *et al.*, 2012 (106)

835. Dorsal fin spine, basals, ossification of

Absent (0)

Present (1)

Burrow & Turner 2010 (40)

836. Anal fin

Absent (0)

Present (1)

UBERON 4000163 Anal fin: Median fin that is located posterior to the anus.

Grogan & Lund 2000 (58), 2004 (80), 2008 (79), Wilson & Märss 2009 (48), Brazeau 2009 (134), Grogan *et al.*, 2012 (102), Davis *et al.*, 2012 (137), Zhu *et al.*, 2013 (137), Long *et al.*, 2014 (137), Dupret *et al.*, 2014 (137), Giles *et al.*, 2015 (232), Lu *et al.*, 2016 (232), Qiao *et al.*, 2016 (133), Chevrinais *et al.*, 2017 (137), Coates *et al.*, 2017 (143), King *et al.*, 2017 (466)

837. Anal fin spine

Absent (0)

Present (1)

Brazeau 2009 (124), Davis *et al.*, 2012 (127), Zhu *et al.*, 2013 (127), Long *et al.*, 2014 (127), Dupret *et al.*, 2014 (127), Giles *et al.*, 2015 (214), Lu *et al.*, 2016 (214), Qiao *et al.*, 2016 (123), Chevrinais *et al.*, 2017 (127), Coates *et al.*, 2017 (137), King *et al.*, 2017 (458)

838. (N) Anal fin spine, ornamentation of

Striated (0)

Ribbed (1)

Tuberculated ribs (2)

Smooth (3)

839. (N) Anal fin spine, ribs/stries, orientation of

Converged on leading edge for most of the fin spine length (0)

Parallel the leading edge to near the distal tip (1)

840. (N) Anal fin spine, ribs/stries per side, number of

1 to 5 (0)

6 to 10 (1)

>10 (2)

841. (N) Anal fin spine, ribs/stries, organisation of

Subparallel with divergences (0)

Parallel without divergences (1)

842. (N) Anal fin spine, ribs/stries divergences, position of

Restricted to the leading edge (0)

Not restricted to the leading edge (1)

843. (N) Anal fin spine, insertion, size of

<25% of its length (0)

>25% of its length (1)

844. (N) Anal fin spine, smooth apex

Absent (0)

Present (1)

845. (N) Anal fin spine, cavity, opening of

Open for less than half spine length (0)

Open for more than half spine length (1)

846. Anal fin, base, length of

Base as broad as fin depth (0)

Base broader than fin depth (1)

Base not broader than fin depth (2)

UBERON 4000163 Anal fin: Median fin that is located posterior to the anus.

Burrow & Turner 2010 (58)

847. Anal fin, basal plate

Absent (0)

Present (1)

UBERON 4000163 Anal fin: Median fin that is located posterior to the anus.

Giles *et al.*, 2015 (233), Lu *et al.*, 2016 (233), Qiao *et al.*, 2016 (323), King *et al.*, 2017 (478)

848. Anal fin, notch

Absent (0)

Present (1)

UBERON 4000163 Anal fin: Median fin that is located posterior to the anus.

Wilson & Märss 2009 (34)

849. (N) Admedian spines

Absent (0)

Present (1)

850. Admedian spines, support of

Attached to plates (0)

Not attached to plates (1)

Burrow & Turner 2010 (48)

851. Intermediate spines, finlets

Absent (0)

Present (1)

UBERON 4200097 Intermediate spine: spine ventrally located on the body and not part of the pectoral, pelvic or anal fins.

King *et al.*, 2017 (481)

852. Median fin spines, bases, scales

Undifferentiated (0)

Enlarged (1)

UBERON 4200070 Median fin spine: Fin spine that is part of a median fin.

Burrow & Turner 2010 (32)

853. Fertilization

External (0)

Pelvic fin clasper in males (1)

UBERON 0010518 Pelvic fin clasper: The rod-like extension of the medial portion of the pelvic fin in male Elasmobranchii and Holocephali. Claspers are used as intromittent organs (not in clasping), the grooves on their facing surfaces together forming a tube for the transmission of sperm when the claspers are held together. The anterior proximal opening is called the apophyle, the posterior distal opening the rhipidion

Grogan & Lund 2008 (88), Grogan *et al.*, 2012 (101)

854. Sexual dimorphism

Absent (0)

Present (1)

Grogan & Lund 2000 (43), 2004 (66), 2008 (71), Grogan *et al.*, 2012 (84)

855. Chang's apparatus

Absent (0)

Present (1)

King *et al.*, 2017 (444)

856. Stomach' chamber

Funnel-shaped (0)

Barrel-shaped (1)

UBERON 0000945 Stomach: An expanded region of the vertebrate alimentary tract that serves as a food storage compartment and digestive organ. A stomach is lined, in whole or in part by a glandular epithelium

Wilson & Märss 2009 (42)

CAUDAL FIN

857. Caudal fin

Heterocercal (0)

Homocercal (1)

Diphycercal (2)

Triphycercal (3)

UBERON 4000164 Caudal fin: The caudal fin is the most posterior median fin. It is composed of a complex of modified centra and modified neural and hemal arches and spines.

Grogan & Lund 2000 (70), 2004 (93), 2008 (102), Zhu *et al.*, 2009 (135), Grogan *et al.*, 2012 (115)

858. Caudal lobe, horizontal

Absent (0)

Present (1)

King *et al.*, 2017 (451)

859. Caudal fin radial, element, position of

Extend beyond level of body wall and deep into hypochordal lobe (0)

Restricted to axial lobe (1)

UBERON 0018325 Caudal fin radial element: Radial element that is a part of the caudal fin

Davis *et al.*, 2012 (138), Zhu *et al.*, 2013 (138), Long *et al.*, 2014 (138), Dupret *et al.*, 2014 (138), Giles *et al.*, 2015 (234), Lu *et al.*, 2016 (234), Qiao *et al.*, 2016 (134), Chevrinais *et al.*, 2017 (138), King *et al.*, 2017 (453)

860. Caudal fin, axial lobe, supraneural bone

Absent (0)

Present (1)

UBERON 4000164 Caudal fin: The caudal fin is the most posterior median fin. It is composed of a complex of modified centra and modified neural and hemal arches and spines.

UBERON 2000442 Supraneural bone : endochondral bone that is median and located in the dorsal skeletogenous septum between the cranium and the dorsal fin.

Giles *et al.*, 2015 (235), Lu *et al.*, 2016 (235), Qiao *et al.*, 2016 (314), King *et al.*, 2017 (454)

861. Caudal fin, epichordal lepidotrichia

Absent (0)

Present (1)

UBERON 4000164 Caudal fin: The caudal fin is the most posterior median fin. It is composed of a complex of modified centra and modified neural and hemal arches and spines.

Zhu *et al.*, 2009 (142), Zhu *et al.*, 2013 (146), Long *et al.*, 2014 (146), Dupret *et al.*, 2014 (146), Giles *et al.*, 2015 (236), Lu *et al.*, 2016 (236), Qiao *et al.*, 2016 (140), Chevrinais *et al.*, 2017 (146), King *et al.*, 2017 (470)

862. Caudal axis upturned steeply supporting high aspect ratio (lunate) tail

Absent (0)

Present (1)

Coates *et al.*, 2017 (145)

863. Caudal peduncle and tail

Longer than high (0)

Higher than long (1)

Wilson & Märss 2009 (35)

864. Caudal fin, relative length of

Less than 30% of body (0)

More than 30 % of body (1)

UBERON 4000164 Caudal fin: The caudal fin is the most posterior median fin. It is composed of a complex of modified centra and modified neural and hemal arches and spines.

Wilson & Märss 2009 (49)

AXIAL SKELETON

865. Cervical neurals

Associated with next neurals (0)

Associated with occiput (1)

Grogan & Lund 2000 (74)

866. Spinal plates

Absent (0)

Present (1)

Chevrinais *et al.*, 2017 (267)

867. Synarcual region

Absent (0)

Present (1)

UBERON 4200129 Synarcual region: Axial subdivision that includes a series of fused cervical vertebrae or vertebral elements.

Brazeau 2009 (132), Davis *et al.*, 2012 (135), Zhu *et al.*, 2013 (135), Long *et al.*, 2014 (135), Dupret *et al.*, 2014 (135), Giles *et al.*, 2015 (226), Lu *et al.*, 2016 (226), Qiao *et al.*, 2016 (131), Chevrinains *et al.*, 2017 (135), Coates *et al.*, 2017 (126), King *et al.*, 2017 (465)

868. Thoracic supraneurals, series of

Absent (0)

Present (1)

Giles *et al.*, 2015 (227), Lu *et al.*, 2016 (227), Qiao *et al.*, 2016 (319), King *et al.*, 2017 (455)

869. Notochord, calcification of

Uncalcified (0)

Chordacentra (1)

Complete centra (2)

UBERON 0002328 Notochord: A flexible rod-shaped body found in embryos of all chordates. It is composed of cells derived from the mesoderm and defines the primitive axis of the embryo. In some chordates, it persists throughout life as the main axial support of the body, while in most vertebrates it becomes the nucleus pulposus of the intervertebral disc. The notochord is found ventral to the neural tube.

870. Keeled scutes, longitudinal rows, enlarged

Absent (0)

Present (1)

King *et al.*, 2017 (484)

871. Vertebral arcual, mineralization of

Uncalcified (0)

Regionalized (1)

Entire column (2)

Grogan & Lund 2000 (73), 2004 (96), 2008 (105), Grogan *et al.*, 2012 (118)

872. Vertebral central, calcification of

Absent (0)

Present (1)

Coates *et al.*, 2017 (123)

873. Chordacentra

Absent (0)

Present (1)

Coates *et al.*, 2017 (124)

874. Chordacentra, polyspondylous (narrow closely packed rings)

Absent (0)

Present (1)

Coates *et al.*, 2017 (125)

SCALES

875. Westoll-lines

Absent (0)

Present (1)

UBERON 4300197 Westoll-lines: More or less concentric lines of discontinuity in the cosmine of Dipnoi, probably due to cyclic resorption and redeposition during growth occurring on the bases of individual scales and also as large structures between headshield plates.

Lu *et al.*, 2016 (243), King *et al.*, 2017 (268)

876. Dermal scale, dentine

Absent (0)

Present (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

UBERON 0001751 Dentine: Collagen-rich odontogenic tissue characteristic of teeth and tooth-like skeletal elements (e.g., odontodes); mature dentine is mineralized and develops from predentine tissue; often (but not always) tubular and acellular.

King *et al.*, 2017 (10)

877. Dermal scale, dentine, kind of

Mesodentine (0)

Semidentine (1)

Orthodentine (2)

Metadentine (3)

Osteodentine (4)

Lamelline (5)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

UBERON 0001751 Dentine: Collagen-rich odontogenic tissue characteristic of teeth and tooth-like skeletal elements (e.g., odontodes); mature dentine is mineralized and develops from predentine tissue; often (but not always) tubular and acellular.

UBERON 4000097 Orthodentine: Odontoid tissue that typically contains tubules and is acellular.

Brazeau 2009 (5), Davis *et al.*, 2012 (5), Zhu *et al.*, 2013 (5), Long *et al.*, 2014 (5), Dupret *et al.*, 2014 (5), Giles *et al.*, 2015 (10), Lu *et al.*, 2016 (10), Qiao *et al.*, 2016 (5), Chevrinais *et al.*, 2017 (5), Coates *et al.*, 2017 (5), King *et al.*, 2017 (12)

878. Dermal scale, cosmine

Absent (0)

Present (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

Brazeau 2009 (6), Davis *et al.*, 2012 (6), Zhu *et al.*, 2013 (6), Long *et al.*, 2014 (6), Dupret *et al.*, 2014 (6), Chevrinais *et al.*, 2017 (6), Coates *et al.*, 2017 (6)

879. (N) Dermal scale, ganoine

Absent (0)

Present (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

UBERON 4000104 Ganoine: Odontogenic tissue that is hypermineralized acellular, noncollagenous, covered by an epidermis and often deposited in multiple layers.

880. (N) Dermal scale, elasmodin

Absent (0)

Present (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

881. (N) Dermal scale, enamel

Absent (0)

Present (1)

UBERON 0001752 Enamel: A dentine-like hypermineralized substance that covers the tooth tip. Enamel's primary mineral is hydroxylapatite, which is a crystalline calcium

phosphate. Unlike dentin and bone, enamel does not contain collagen. Instead, it has two unique classes of proteins called amelogenins and enamelin.

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

882. (N) Dermal scale, superficial hypermineralized layer, kind of

Enameloid (0)

Enamel (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

UBERON 0011692 Enameloid: Skeletal tissue that is hypermineralized and aprismatic and deposited by a combination of ameloblasts and odontoblasts that are excluded from the matrix. Enameloid develops from pre-enameloid tissue.

UBERON 0001752 Enamel: A dentine-like hypermineralized substance that covers the tooth tip. Enamel's primary mineral is hydroxylapatite, which is a crystalline calcium phosphate. Unlike dentin and bone, enamel does not contain collagen. Instead, it has two unique classes of proteins called amelogenins and enamelin

883. Dermal scale, hypermineralized layer, organisation of

Single-layered (0)

Multi-layered (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

UBERON 0001752 Enamel: A dentine-like hypermineralized substance that covers the tooth tip. Enamel's primary mineral is hydroxylapatite, which is a crystalline calcium phosphate. Unlike dentin and bone, enamel does not contain collagen. Instead, it has two unique classes of proteins called amelogenins and enamelin

Giles *et al.*, 2015 (6), Lu *et al.*, 2016 (6), Qiao *et al.*, 2016 (255), Chevrinais *et al.*, 2017 (266), King *et al.*, 2017 (16)

884. Scale, enamel layers, organisation of

Applied directly to one another (ganoine) (0)

Separated by layers of dentine (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

UBERON 0001752 Enamel: A dentine-like hypermineralized substance that covers the tooth tip. Enamel's primary mineral is hydroxylapatite, which is a crystalline calcium phosphate. Unlike dentin and bone, enamel does not contain collagen. Instead, it has two unique classes of proteins called amelogenins and enamelin

UBERON 0001751 Dentine: Collagen-rich odontogenic tissue characteristic of teeth and tooth-like skeletal elements (e.g., odontodes); mature dentine is mineralized and develops from predentine tissue; often (but not always) tubular and acellular.

Giles *et al.*, 2015 (7), Lu *et al.*, 2016 (7), Qiao *et al.*, 2016 (256), King *et al.*, 2017 (17)

885. Dermal scale, enameloid

Absent (0)

Present (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

UBERON 0011692 Enameloid: Skeletal tissue that is hypermineralized and aprismatic and deposited by a combination of ameloblasts and odontoblasts that are excluded from the matrix. Enameloid develops from pre-enameloid tissue.

Burrow & Turner 2010 (62)

886. Dermal scale, mid crown, dentine canals

Absent (0)

Present (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

UBERON 0001751 Dentine: Collagen-rich odontogenic tissue characteristic of teeth and tooth-like skeletal elements (e.g., odontodes); mature dentine is mineralized and develops from predentine tissue; often (but not always) tubular and acellular.

Wilson & Märss 2009 (30)

887. Dermal scale, mid crown, dentine tubules

Absent (0)

Present (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

UBERON 0001751 Dentine: Collagen-rich odontogenic tissue characteristic of teeth and tooth-like skeletal elements (e.g., odontodes); mature dentine is mineralized and develops from predentine tissue; often (but not always) tubular and acellular.

Wilson & Märss 2009 (31)

888. Dermal scale, crown, dentine, type of

With lacunae (0)

Without lacunae (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

UBERON 0001751 Dentine: Collagen-rich odontogenic tissue characteristic of teeth and tooth-like skeletal elements (e.g., odontodes); mature dentine is mineralized and develops from predentine tissue; often (but not always) tubular and acellular.

Burrow & Turner 2010 (63)

889. Dermal scale, pulp cavity

Absent (0)

Present (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

Wilson & Märss 2009 (26)

890. Dermal scale, pulp depression

Absent (0)

Present (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

Wilson & Märss 2009 (25)

891. Dermal scale, pulp cavity "pockets"

Absent (0)

Present (1)

Wilson & Märss 2009 (27)

892. (N) Dermal scale, pulp canals

Absent (0)

Present (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

893. Dermal scale, pulp canals, number of

Single (0)

Multiple (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

Wilson & Märss 2009 (28)

894. Dermal scale, main pulp canal, length of

<1/2 length of crown (0)

>1/2 length of crown (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

Wilson & Märss 2009 (29)

895. Dermal scale, sharpey fibre tubules

Absent (0)

Present (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

Wilson & Märss 2009 (32)

896. Dermal scale, type of

Micromeric (0)

Macromeric (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

Zhu *et al.*, 2009 (136)

897. Dermal scale, size of

Very small (0,1-0,5mm) (0)

Small (0,5-1,0mm) (1)

Medium (1-2mm) (2)

Large (>2mm) (3)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

Wilson & Märss 2009 (8)

898. Dermal scale, different size

Absent (0)

Present (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

Wilson & Märss 2009 (9)

899. Dermal scale, base, configuration of

Rounded (0)

Oval (1)

Quadrangular (2)

Rhombic (3)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

Wilson & Märss 2009 (21)

900. (N) Dermal scale, tesserae

Absent (0)

Present (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

901. (N) Dermal scale, different morphotype

Present (0)

Absent (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

902. (N) Dermal scale, morphotype, number of

2 (0)

3 (1)

4 (2)

>4 (3)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

903. (N) Dermal scale, base, relative depth of

Less than half crown length (0)

More than half crown length (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

904. (N) Dermal scale, base, width of

More than half length (0)

Less than half length (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

905. (N) Dermal scale, base, anterior process

Absent (0)

Present (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

906. Dermal scale, shape of

Rhomboid (0)

Round (1)

Kite (2)

Oval (3)

Flammate (4)

Water drop (5)

Rectangular (6)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

Wilson & Märss 2009 (21)

907. Dermal scale, type of

Placoid (0)

Zonal growth (1)

Fused placoid (2)

Ganoid (3)

Cosmoid (4)

Ctenoid (5)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

Grogan & Lund 2000 (38), 2004 (50), 2008 (56), Grogan *et al.*, 2012 (67)

908. Dermal scale, peg and socket connection

Absent (0)

Present (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

Zhu *et al.*, 2009 (138)

909. Dermal scale, anterodorsal process

Absent (0)

Present (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

Zhu *et al.*, 2009 (140), Zhu *et al.*, 2013 (144), Long *et al.*, 2014 (144), Dupret *et al.*, 2014 (144), Giles *et al.*, 2015 (20), Lu *et al.*, 2016 (20), Qiao *et al.*, 2016 (139), Chevrinais *et al.*, 2017 (144), King *et al.*, 2017 (493)

910. Dermal scale, neck, constriction of

Neck similar in width to crown (0)

Neck constricted resulting in anvil-like shape (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

Giles *et al.*, 2015 (22), Lu *et al.*, 2016 (22), Qiao *et al.*, 2016 (262)

911. Fin scale, alignment of

Aligned in rows (0)

Unaligned (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

Burrow & Turner 2010 (30)

912. (N) Basitrabecular rim scales

Absent (0)

Present (1)

913. Basitrabecular rim scales, type of

Generalized (0)

Denticles (1)

Plate (2)

Plate and spine (3)

Grogan & Lund 2004 (62), 2008 (67), Grogan *et al.*, 2012 (80)

914. Ethmorostral scales (cochlodont)

Absent (0)

Present (1)

Grogan & Lund 2004 (55), 2008 (61), Grogan *et al.*, 2012 (74)

915. Headshield, posterior, fused scale row

Absent (0)

Present (1)

UBERON 4300006 Scale row: A series of scales in alignment with each other along some axis of the body.

King *et al.*, 2017 (230)

916. (N) Head tesserae

Monodontode (0)

Polydontode, areal (1)

917. Otic scales

Absent (0)

Present (1)

Grogan & Lund 2004 (57), 2008 (63), Grogan *et al.*, 2012 (76)

918. Supraorbital scales

Absent (0)

Present (1)

Grogan & Lund 2004 (56), 2008 (62), Grogan *et al.*, 2012 (75)

919. (N) Orbit of skull, specialized scales

Absent (0)

Present (1)

UBERON 0001697 Orbit of skull: Subdivision of skeleton that is an anterolateral part of the cranium and structurally supports the eye. Includes bones formed and located in sclerotic layer of eyeball

920. Occipital scales

Absent (0)

Present (1)

Grogan & Lund 2004 (58), 2008 (64), Grogan *et al.*, 2012 (77)

921. Posterior mandibular scales

Absent (0)

Present (1)

Grogan & Lund 2004 (61), 2008 (66), Grogan *et al.*, 2012 (79)

922. Longitudinal rows of larger scales among smaller ones

Absent (0)

Present (1)

Wilson & Märss 2009 (3)

923. Dermal scale, neck

As narrow groove (0)

High and distinct (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

Wilson & Märss 2009 (20)

924. (N) Dermal scale, neck, canal

Absent (0)

Present (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

925. (N) Body scales

Absent (0)

Present (1)

926. Body scale, growth pattern, type of

Monodontode (0)

Polyodonte (1)

Brazeau 2009 (8), Davis *et al.*, 2012 (8), Zhu *et al.*, 2013 (8), Long *et al.*, 2014 (8), Dupret *et al.*, 2014 (8), Giles *et al.*, 2015 (15), lu *et al.*, 2016 (15), Qiao *et al.*, 2016 (7), Chevrinais *et al.*, 2017 (8), King *et al.*, 2017 (485)

927. (N) Dermal scale, polyodontode, superpostional growth

Absent (0)

Present (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

928. (N) Dermal scale, polyodontode, areal growth

Absent (0)

Present (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

929. (N) Dermal scale, polyodontode, appositionnal growth

Absent (0)

Present (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

930. (N) Dermal scale, polyodontode, concentric growth

Absent (0)

Present (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

931. (N) Dermal scale, crown, odontocomplex

Present (0)

Absent (1)

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

932. Body scales, relative size of

All of similar size (0)

Largest scales below second dorsal fin (1)

Scales decrease in size from pectoral to caudal region (2)

Burrow & Tuner 2010 (21)

933. Main sensory canal, anterior end, body scale, type of

Undifferentiated (0)

Enlarged, irregularly shaped (1)

Burrow & Turner 2010 (28)

934. Body scale, convex base

Absent (0)

Present (1)

Coates *et al.*, 2017 (12)

935. Body scale, flat base

Absent (0)

Present (1)

Coates *et al.*, 2017 (13)

936. Body scale, basal canal or open basal vascular cavity

Absent (0)

Present (1)

Coates *et al.*, 2017 (14)

937. Body scale, base, bone cell lacunae

Present (0)

Absent (1)

Burrow & turner 2010 (61), Giles *et al.*, 2015 (11), Lu *et al.*, 2016 (11), Qiao *et al.*, 2016 (259), King *et al.*, 2017 (11)

938. Body scale, profile of

Distinct crown and base demarcated by a constriction (neck) (0)

Flattened (1)

Brazeau 2009 (11), Davis *et al.*, 2012 (11), Zhu *et al.*, 2013 (11), Long *et al.*, 2014 (11), Dupret *et al.*, 2014 (11), Giles *et al.*, 2015 (21), Lu *et al.*, 2016 (21), Qiao *et al.*, 2016 (10), Chevrinais *et al.*, 2017 (11), King *et al.*, 2017 (488)

939. (N) Body scale, bulging ringed base

Absent (0)

Present (1)

940. (N) Body scale, base, bone tissue

Present (0)

Absent (1)

941. Scale transition from body to fins

Gradual (0)

Abrupt (1)

UBERON 0008897 Fin: An external projection of an aquatic animal as a fish used in propelling or guiding the body

Burrow & Turner 2010 (29)

942. (N) Fins, leading edge, different scales

Absent (0)

Present (1)

943. Flank scale, alignment of

Vertical rows (0)

Oblique rows or hexagonal/rhomboic packing (1)

Disorganised (2)

Brazeau 2009 (15), Davis *et al.*, 2012 (14), Zhu *et al.*, 2013 (14), Long *et al.*, 2014 (14), Dupret *et al.*, 2014 (14), Giles *et al.*, 2015 (26), Lu *et al.*, 2016 (26), Qiao *et al.*, 2016 (13), Chevrinais *et al.*, 2017 (14), King *et al.*, 2017 (491)

944. Scale, crown dentine, canal system opening out through pores

Absent (0)

Present (1)

UBERON 0001751 dentine: Collagen-rich odontogenic tissue characteristic of teeth and tooth-like skeletal elements (e.g., odontodes); mature dentine is mineralized and develops from predentine tissue; often (but not always) tubular and acellular. Dentine : dentin, dentin of tooth

Chevrinis *et al.*, 2017 (261)

945. Scale, pore canal, enamel lining

Absent (0)

Present (1)

UBERON 0008915 Pore: an anatomical space that is an opening, usually at the end of a canal or duct, on the surface of the integument or the lining of an internal anatomical space.

UBERON 0001752 Enamel: A dentine-like hypermineralized substance that covers the tooth tip. Enamel's primary mineral is hydroxylapatite, which is a crystalline calcium phosphate. Unlike dentin and bone, enamel does not contain collagen. Instead, it has two unique classes of proteins called amelogenins and amelins.

Zhu *et al.*, 2009 (147)

946. Scale, pore canal system, extensive

Absent (0)

Present (1)

UBERON 0008915 Pore: an anatomical space that is an opening, usually at the end of a canal or duct, on the surface of the integument or the lining of an internal anatomical space.

Long *et al.*, 2014 (5), Giles *et al.*, 2015 (8), Qiao *et al.*, 2016 (257), King *et al.*, 2017 (5)

947. Scale, base, pores

Absent (0)

Present (1)

UBERON 0008915 Pore: an anatomical space that is an opening, usually at the end of a canal or duct, on the surface of the integument or the lining of an internal anatomical space.

Giles *et al.*, 2015 (25), Lu *et al.*, 2016 (25), Qiao *et al.*, 2016 (263), King *et al.*, 2017 (495)

948. (N) Body scale, ascending canals

Absent (0)

Present (1)

Canals that are located at the boundary between crown and basal plate. Analogue to pulp cavity.

949. Body scale, ascending canals, relative size of

Larger than dentine tubule (0)

Equal or smaller than dentine tubule (1)

Canals that are located at the boundary between crown and basal plate. Analogue to pulp cavity.

Burrow & Turner 2010 (23)

950. Scale, crown, pore canal system

Absent (0)

Present (1)

Burrow & Turner 2010 (65)

951. Scale, ganoine surface, pores

Absent (0)

Present (1)

UBERON 4000104 Ganoine: Odontogenic tissue that is hypermineralized acellular, noncollagenous, covered by an epidermis and often deposited in multiple layers.

King *et al.*, 2017 (497)

952. Scale, resorption and redeposition of odontodes

Lacking (0)

Developed (1)

UBERON 2001622 Odontode: Multi-tissue structure composed of enameloid and dentine surrounding a pulp cavity, and found either attached to dermal bone or freely in the skin

Zhu *et al.*, 2009 (148), Zhu *et al.*, 2013 (139), Long *et al.*, 2014 (139), Dupret *et al.*, 2014 (139), Qiao *et al.*, 2016 (157), Chevrinais *et al.*, 2017 (139), King *et al.*, 2017 (14)

953. Scale, generations of odontodes, type of

Buried (0)

Areally growing (1)

Resorbed (2)

UBERON 2001622 Odontode: Multi-tissue structure composed of enameloid and dentine surrounding a pulp cavity, and found either attached to dermal bone or freely in the skin

Giles *et al.*, 2015 (17), Lu *et al.*, 2016 (17)

954. Scale, crown, strangewebe

Absent (0)

Present (1)

Burrow & Turner 2010 (64)

955. (N) Scale, crown surface, inclination of

Flattened (0)

Moderately raised (<45 deg.) (1)

Strongly raised (>45 deg.) (2)

956. Scale, crown, ventro-posterior structures, type of

One point (0)

Three or more points (1)

Fine serration (2)

None (3)

Wilson & Märss 2009 (12)

957. (N) Scale, crown, anterior, ornamentation of

Smooth (0)

Tuberculates (1)

Spikes (2)

Ridges (3)

Stries (4)

958. (N) Scale, crown, anterior, ridges, type of

Straight (0)

Convergent (1)

Divergent (2)

Vermiformes (3)

Tuberculated (4)

Spiked (5)

959. (N) Scale, crown, posterior, ornamentation of

Smooth (0)

Tuberculates (1)

Spikes (2)

Ridges (3)

Stries (4)

960. (N) Scale, crown, posterior, ridges, type of

Straight (0)

Convergent (1)

Divergent (2)

Vermiformes (3)

Tuberculated (4)

Spiked (5)

961. (N) Scale, crown, straight/divergent ridges, maximum of

1 to 5 (0)

6 to 10 (1)

>10 (2)

962. (N) Scale, crown, posterior margin, type of

Angular (0)

Serrated (1)

Rounded (2)

Straight (3)

963. Scale, crown, postero-lateral spines

Absent (0)

Present (1)

Wilson & Märss 2009 (13)

964. Scale, crown, postero-lateral spines, orientation of

Horizontally (0)

Vertically (1)

Wilson & Märss 2009 (14)

965. Body scale, high crest

Absent (0)

Present (1)

Crest present in the middle of the crown froming a more pronounced ridge continuing forward posterior portion of the crown

Wilson & Märss 2009 (15)

966. (N) Scale, crown, overlaps

Absent (0)

Present (1)

967. Scale, crown, overlaps, length of

Slightly or moderately ($<1/2$ of crown length) (0)

Greatly ($>1/2$ of crown length) (1)

Wilson & Märss 2009 (16)

SPINE HISTOLOGY

968. (N) Spine, tissue surrounding central pulp cavity, type of

Bone (0)

Mesodentine (1)

Semidentine (2)

Osteodentine / Trabecular dentine (3)

Orthodentine (4)

Lamellar dentine / Lamellar bone (5)

969. (N) Spine, middle layer, tissue, type of

Bone (0)

Mesodentine (1)

Semidentine (2)

Osteodentine / Trabecular dentine (3)

Orthodentine (4)

970. (N) Spine, external layer, tissue, type of

Dentine (0)

Hypermineralized layer (Enameloid) (1)

971. (N) Spine, tissue, cellular bone

Absent (0)

Present (1)

972. (N) Spine, tissue, acellular bone

Absent (0)

Present (1)

973. (N) Spine, tissue, lamellar bone

Absent (0)

Present (1)

974. (N) Spine, pore opening

Absent (0)

Present (1)

975. (N) Spine, proximal section, shape of

Rounded (0)

Triangular (1)

Horseshoe (2)

Oval (3)

Round with lateral wings (4)

976. (N) Spine, distal section, shape of

Rounded (0)

Triangular (1)

Horseshoe (2)

Oval (3)

Round with lateral wings (4)

Biconcave sides (5)

977. Cephalic spines

Absent (0)

Present (1)

UBERON 0017621 Cephalic spine: One of the spines, probably denticle derivatives, occurring singly or in pairs just behind the orbit on the cheek area in some fossil sharks.

Coates *et al.*, 2017 (139)

Annex 3: ontology list

This section lists the various ontology code used in the description of the morphological character. They come from the UBERON vocabulary (Mungall *et al.*, 2012), the most suitable set of ontology for the early vertebrate morpho-anatomy descriptions.

UBERON 0000033 Head: The head is the anterior-most division of the body

UBERON 0000041 Odontode scale: Multi-tissue structure composed of enameloid, dentine surrounding a pulp cavity, and bone of attachment anchoring the element into the dermis

UBERON 0000151 Pectoral fin: Paired fin that is located in the thoracic region of the body.

UBERON 0000152 Pelvic fin: Paired fin located in the abdominal position of the body.

UBERON 0000165 Mouth: The proximal portion of the digestive tract, containing the oral cavity and bounded by the oral opening. In vertebrates, this extends to the pharynx and includes gums, lips, tongue and parts of the palate. Typically also includes the teeth, except where these occur elsewhere

UBERON 0000167 Oral cavity teeth: Anatomical cavity at the start of the digestive tract that is enclosed by the mouth. The boundaries and contents vary depending on the species. In vertebrates, the boundaries are the oral opening, the cheeks, the palate and (if present) the palatoglossal arch

UBERON 0000941 Cranial nerve II: Cranial nerve fiber tract which is comprised of retinal ganglion cell axons running posterior medially towards the optic chiasm, at which some of the axons cross the midline and after which the structure is termed the optic tract. Transmits visual information from the retina to the brain

UBERON 0000945 Stomach: An expanded region of the vertebrate alimentary tract that serves as a food storage compartment and digestive organ. A stomach is lined, in whole or in part by a glandular epithelium

UBERON 0001105 Clavicle bone: A paired dermal or endochondral bone that is part of the pectoral girdle. The clavicle may be in contact with the interclavicle or coracoid and forms an attachment site for pectoral musculature

UBERON 0001532 Internal carotid artery : A terminal branch of the left or right common carotid artery which supplies oxygenated blood to the brain and eyes Internal carotid artery

UBERON 0001567 Cheek : A fleshy subdivision of one side of the face bounded by an eye, ear and the nose.

UBERON 0001645 Trigeminal nerve: Cranial nerve that has three branches - the ophthalmic (supplying the skin of the nose and upper jaw), the maxillary and the mandibular (supplying the lower jaw).

UBERON 0001647 Facial nerve: Cranial nerve that branches into the supraorbital (supplying the skin of the eye region and the lateral line organs here), the palatine (to the roof of the buccal cavity), and the hyomandibular (dividing into the jugular and mental branches).

UBERON 0001649 Glossopharyngeal nerve: Cranial nerve that branches into the ramus communicans (to the skin), the pretrematic (to the walls of the pharynx and mouth, viscerosensory fibers), and the larval post-trematic branch (lost in the adult).

UBERON 0001677 Sphenoid bone: An unpaired bone situated at the base of the skull in front of the temporal bone and basilar part of the occipital bone. The sphenoid bone is one of the seven bones that articulate to form the orbit. Its shape somewhat resembles that of a butterfly or bat with its wings extended

UBERON 0001679 Ethmoid bone : A bone in the skull that separates the nasal cavity from the brain. As such, it is located at the roof of the nose, between the two orbits. The cubical

bone is lightweight due to a spongy construction. The ethmoid bone is one of the bones that makes up the orbit of the eye

UBERON 0001681 Nasal bone: One of two small oblong bones, varying in size and form in different individuals; they are placed side by side at the middle and upper part of the face, and form, by their junction, 'the bridge' of the nose[WP]. Paired dermal bones, likened to a bone tube, positioned lateral to the supraethmoid. Nasal bones are transversed by the anterior most part of the supraorbital canals and bear one neuromast foramen in zebrafish[ZFA].

UBERON 0001682 Palatine bone: a paired dermal bone situated in the mid-palate that helps form the hard palate

UBERON 0001683 Jugal bone: The quadrilateral bone that forms the prominence of the cheek.

UBERON 0001684 Mandible: A dentary bone that is the only bone in one of the lateral halves of the lower jaw skeleton

UBERON 0001697 Orbit of Skull: subdivision of skeleton that is an anterolateral part of the cranium and structurally supports the eye. Includes bones formed and located in sclerotic layer of eyeball

UBERON 0001703 Neurocranium: subdivision of skeletal system that surrounds and protects the brain. Includes the skull base, sensory capsules and the central part of the skull roof.

UBERON 0001708 Jaw skeleton: Subdivision of skeleton which includes upper and lower jaw skeletons.

UBERON 0001751 Dentine: Collagen-rich odontogenic tissue characteristic of teeth and tooth-like skeletal elements (e.g., odontodes); mature dentine is mineralized and develops from predentine tissue; often (but not always) tubular and acellular. Dentine is a *bona fide*

vertebrate novelty, and dentine-secreting odontoblasts represent a cell type that is exclusively derived from the neural crest.

UBERON 0001752 Enamel: A dentine-like hypermineralized substance that covers the tooth tip. Enamel's primary mineral is hydroxylapatite, which is a crystalline calcium phosphate. Unlike dentin and bone, enamel does not contain collagen. Instead, it has two unique classes of proteins called amelogenins and amelins.

UBERON 0001840 Semicircular canal: One of three half-circular, interconnected tubes located inside each ear.

UBERON 0001860 Endolymphatic duct: The small membranous canal, connecting with both saccule and utricle of the membranous labyrinth, passing through the aqueduct of vestibule, and terminating in the endolymphatic sac

UBERON 0001891 Midbrain: The midbrain is the middle division of the three primary divisions of the developing chordate brain or the corresponding part of the adult brain (in vertebrates, includes a ventral part containing the cerebral peduncles and a dorsal tectum containing the corpora quadrigemina and that surrounds the aqueduct of Sylvius connecting the third and fourth ventricles)

UBERON 0001893 Telencephalon: Part of the forebrain consisting of paired olfactory bulbs and cerebral hemispheres.

UBERON 0002028 Hindbrain: The most posterior of the three principal regions of the brain

UBERON 0002037 Cerebellum: Part of the metencephalon that lies in the posterior cranial fossa behind the brain stem

UBERON 0002216 Symphysis: Cartilaginous joint in which the articulating bones or cartilages are connected by fibrocartilage

UBERON 0002221 Fontanelle: Anatomical structure that is a membranous gap between bones of the skull

UBERON 0002229 Interparietal bone : The bone of the cranium that lies above and anterior to the occipital bone.

UBERON 0002244 Premaxilla: one of the bones of the upper jaw situated between and in front of the maxillae

UBERON 0002265 Olfactory tract: White matter tract that contains projections from the olfactory bulb to other parts of the brain.

UBERON 0002328 Notochord: A flexible rod-shaped body found in embryos of all chordates. It is composed of cells derived from the mesoderm and defines the primitive axis of the embryo. In some chordates, it persists throughout life as the main axial support of the body, while in most vertebrates it becomes the nucleus pulposus of the intervertebral disc. The notochord is found ventral to the neural tube

UBERON 0002396 Vomer : The triangular flat bone of the nasal septum.

UBERON 0002397 Maxilla: The bone which normally forms the lateral upper jaw in osteichthyans, including tetrapods.

UBERON 0002481 Bone tissue: Skeletal tissue with a collagen-rich extracellular matrix vascularized, mineralized with hydroxyapatite and typically including osteocytes located in lacunae that communicate with one another by cell processes (in canaliculi). Bone is deposited by osteoblasts.

UBERON 0002513 Endochondral bone: Replacement bone that forms within cartilage.

UBERON 0002517 Basicranium: the base of skull is the most inferior area of the skull, composed of the endocranium and lower parts of the skull roof.

UBERON 0002540 Lateral line system: a line of sensory organs and associated structures along the sides of fish and amphibia that detect vibrations and pressure changes.

UBERON 0003097 Dorsal fin: Median fin located on the dorsal surface of the organism.

UBERON 0003107 Meckel's cartilage: Meckel's cartilage is the bilaterally paired, rod-like, cartilaginous ventral component of the lower jaw, or ventral mandibular arch. It is typically resorbed in adults.

UBERON 0003108 Suspensorium: (1) the arrangement of bones which supports the jaw from the braincase; (2) in teleost fish, a large, usually triangular, bone which supports the jaw. The teleost suspensorium is formed by fusion of various elements which vary among different taxa.

UBERON 0003110 Otic region: Anatomical cluster that is a posterolateral part of the cranium and structurally supports the vestibuloauditory system.

UBERON 0003111 Sphenoid region : Anatomical cluster that forms the floor and sidewalls of the middle part of the cranium

UBERON 0003113 Dermatocranium: Subdivision of skeleton that includes all dermal bones in the cranial skeleton

UBERON 0003129 Skull: Anatomical structure that is part of the head consisting entirely of cranium and mandible

UBERON 0003277 Skeleton of upper jaw: A subdivision of the skeleton that corresponds to the upper part of the mouth. The lower jaw skeleton includes the following elements, when present: upper jaw teeth, the maxilla and other upper jaw bones

UBERON 0003278 Skeleton of lower jaw: A subdivision of the skeleton that corresponds to the lower part of the mouth. The lower jaw skeleton includes the following elements, when present: lower jaw teeth, the mandible and other lower jaw bones, and Meckel's cartilage

UBERON 0003675 Crown: The portion of the tooth covered by enamel

UBERON 0003677 Root: The part of a tooth that is implanted in the gum; the root is normally located below the neck of the tooth, covered by cementum rather than enamel, and attached by the periodontal ligament to the alveolar bone

UBERON 0003687 Foramen magnum: In anatomy, in the occipital bone, the foramen magnum is one of the several oval or circular apertures in the base of the skull, through which the medulla oblongata (an extension of the spinal cord) enters and exits the skull vault. Apart from the transmission of the medulla oblongata and its membranes, the foramen magnum transmits the Spinal Accessory nerve, vertebral arteries, the anterior and posterior spinal arteries, the membrana tectoria and alar ligaments

UBERON 0004339 Vault of skull: upper part of skull, consisting of parietals, frontals, post-parietals, and in some species the squamosal and a portion of the alisphenoid.

UBERON 0004637 Otic capsule: The capsule surrounding the inner ear mechanism

UBERON 0004704 Bone fossa: A depression or hollow in a bone

UBERON 0004711 Jugular vein: The jugular veins are veins that bring deoxygenated blood from the head back to the heart via the superior vena cava.

UBERON 0004741 Cleithrum: Dermal bone on the margin of the scapula. The cleithrum is attached to the skull in fishes, but free from the latter in amphibians and disappears early in the evolution of reptiles.

UBERON 0004742 Dentary: the dentary is a dermal bone that forms the antero-lateral part of the lower jaw in fishes and amphibians, extending to the whole lower jaw in mammals

UBERON 0004743 Coracoid bone: endochondral bone that is paired and forms part of the socket for the humerus in tetrapods and acts as base of the pectoral fin in fish.

UBERON 0004745 Parasphenoid : A tooth- or denticle-covered plate which is attached to the sphenoid stem

UBERON 0004752 Palatoquadrate cartilage: The dorsal component of the mandibular arch

UBERON 0004753 Scapulocoracoid: Skeletal element that consists of the scapula and the coracoid

UBERON 0004767 Vomerine tooth: A tooth that is on the vomer.

UBERON 0004905 Articulation: Anatomical cluster that connects two or more adjacent skeletal elements or hardened body parts.

UBERON 0005412 Groove that is in the developing ventral optic cup and through which blood vessels pass to the enclosed mesenchyme

UBERON 0005600 Crus commune: A region formed by non-ampulated ends of posterior and superior semicircular canals of vestibular apparatus in inner ear.

UBERON 0005745 Optic foramen: An opening in the skull through which cranial nerve II passes

UBERON 0005805 Dorsal aorta: The dorsal aorta is a blood vessel in a single-pass circulatory system that carries oxygenated blood from the gills to the rest of the body. In a single-pass circulatory system blood passes once through the heart to supply the body once.

UBERON 0005902 Occipital region: Anatomical cluster that is located in the posterior region of the cranium and forms the margin of the foramen magnum and occipital condyles.

UBERON 0005928 External naris: A naris that provides one of the small external openings of the head that give passage to air for breathing

UBERON 0006321 Superior oblique extraocular muscle: The superior oblique muscle, or obliquus oculi superior, is a fusiform muscle in the upper, medial side of the orbit whose primary action is downward, lateral rotation of the eye. One of the extraocular muscles, the superior oblique is the only muscle innervated by the trochlear nerve (the fourth cranial nerve).

UBERON 0006332 Nasal capsule: An embryonic cartilaginous frame, the nasal capsule, an evolutionary-conserved structure composed of ventral and dorsal components: the mesethmoid and ectethmoid cartilages, respectively.

UBERON 0006333 Snout : Surface structure that is the region of the head in front of and between the orbits, and above the lower jaw. Nares are located on the snout

UBERON 0006428 Basisphenoid bone: Part of the base of the cranium between the basioccipital and the presphenoid, which usually ossifies separately in the embryo or in the young, and becomes a part of the sphenoid in the adult; in many animals it persists as a separate bone between the basioccipital bone and the presphenoidal bone.

UBERON 0006597 Quadrate bone: Ossified pars articularis of the palatoquadrate cartilage.

UBERON 0006605 Tectum synoticum: Unpaired thin dorsal sheet of cartilage that partially covers the posterior chondrocranium.

UBERON 0006606 Mandibular symphysis: A cartilaginous joint that connects left and right mandibles/dentary bones. Mandibular symphysis is unpaired.

UBERON 0006683 Posterior fontanelle: A gap between bones in the skull at the junction of the sagittal suture and lambdoidal suture.

UBERON 0006806 Entepicondyle of humerus: A bony projection on the distal epiphysis of the humerus that is the attachment site for the flexor muscles of the manus. This condyle faces posteriorly (for sprawling tetrapods) or medially (for erect tetrapods).

UBERON 0006844 Cusp of tooth: A raised area of the biting surface of a tooth

UBERON 0006849 Scapula: Endochondral bone that is dorsoventrally compressed and provides attachment site for muscles of the pectoral appendage

UBERON 0007380 Dermal scale: Dermal bone that is thin, flexible, and platelike, and that develops in overlapping skinfolds that cover the body and often the head of fish and the bases of the fins.

UBERON 0007804 Sclerotic ring: Sclerotic rings are rings of bone found in the eyes of several groups of vertebrate animals, except for mammals and crocodilians. They can be

made up of single bones or small bones together. They are believed to have a role in supporting the eye, especially in animals whose eyes are not spherical, or which live underwater. Fossil sclerotic rings are known for a variety of extinct animals, including ichthyosaurs, pterosaurs, and dinosaurs, but are often not preserved

UBERON 0007811 Craniocervical region: The anteriormost subdivision of the body that includes the head, jaws, pharyngeal region and the neck (if present). In vertebrates this is the subdivision that includes the cervical vertebrae

UBERON 0007831 Pectoral girdle skeleton: A subdivision of a limb or fin skeleton consisting of bones which connects the upper limb or fin to the axial skeleton on each side. It consists of the clavicle and scapula in humans and, in those species with three bones in the pectoral girdle, the coracoid. Some mammalian species (e.g. the dog and the horse) have only the scapula. In humans, the only joints between the shoulder girdle and axial skeleton are the sternoclavicular joints on each side. No joint exists between each scapula and the rib cage; instead the muscular connection between the two permits relatively great mobility of the shoulder girdle in relation to the pelvic girdle. In those species having only the scapula, no joint exists between the forelimb and the thorax, the only attachment being muscular.

UBERON 0007832 Pelvic girdle skeleton: Skeletal subdivision consisting of a set of bones linking the axial series to the hindlimb zeugopodium and offering anchoring areas for hindlimb and caudal musculature

UBERON 0008811 Intromittent organ: An external organ of a male organism that is specialized to deliver sperm during copulation. Intromittent organs are found most often in terrestrial species, as most aquatic species fertilize their eggs externally, although there are exceptions

UBERON 0008907 Dermal bone: Skeletal element that forms superficially in the organism, usually in association with the ectoderm.

UBERON 0008913 Perichondral bone: Bone element that is located on the surface of a cartilage element.

UBERON 0008915 Pore: anatomical space that is an opening, usually at the end of a canal or duct, on the surface of the integument or the lining of an internal anatomical space

UBERON 0008918 Ampulla of Lorenzini: The ampullae of Lorenzini are special sensing organs called electroreceptors, forming a network of jelly-filled pores. Each ampulla consists of a canal opening to the surface by a pore in the skin and ending blindly in a cluster of small pockets full of special jelly. The ampullae are mostly clustered into groups inside the body, each cluster having ampullae connecting with different parts of the skin, but preserving a left-right symmetry. The canal lengths vary from animal to animal, but the distribution of the pores is generally specific to each species. The ampullae pores are plainly visible as dark spots in the skin. They provide fish with a sixth sense capable of detecting electromagnetic fields as well as temperature gradients

UBERON 0009678 Tooth row: Anatomical cluster consisting of adjacent teeth constituting a row.

UBERON 0009979 Condyle: An articular prominence of a bone, typically present in pairs, resembling a pair of knuckles.

UBERON 0010019 Spiracle (sensu Vertebrata): A small hole behind each eye that opens to the mouth in some fish. In the primitive jawless fish the first gill opening immediately behind the mouth is essentially similar to the other gill openings.

UBERON 0010326 Optic pedicel: Permanent cartilage structure projecting from the site of origin of the recti muscles. Supports eyeball and aids rotation

UBERON 0010364 Dermal skeleton: Skeletal subdivision that undergoes direct development and includes elements that either develop in association with the basement membrane of the ectoderm or are homologous with such elements; includes dermatocranium,

components of the appendicular skeleton, teeth and tooth-like elements of the oropharynx, and integumentary elements.

UBERON 0010516 Clasper: male anatomical structure found some groups of animals, used in mating. Male cartilaginous fish have claspers formed from the posterior portion of their pelvic fin which serve as intromittent organs used to channel semen into the female's cloaca during mating. The act of mating in some fish including sharks usually includes one of the claspers raised to allow water into the siphon through a specific orifice. The clasper is then inserted into the vagina, where it opens like an umbrella to anchor its position. The siphon then begins to contract expelling water and sperm. Male chimaeras have cephalic claspers on their heads, which are thought to aid in holding the female during mating

UBERON 0010518 Pelvic fin clasper: The rod-like extension of the medial portion of the pelvic fin in male Elasmobranchii and Holocephali. Claspers are used as intromittent organs (not in clasping), the grooves on their facing surfaces together forming a tube for the transmission of sperm when the claspers are held together. The anterior proximal opening is called the apophyle, the posterior distal opening the rhipidion.

UBERON 0011169 Postorbital bone: The postorbital is one of the bones in vertebrate skulls which forms a portion of the dermal skull roof and, sometimes, a ring about the orbit. Generally, it is located behind the postfrontal and posteriorly to the orbital fenestra. In some vertebrates, the postorbital is fused with the postfrontal to create a postorbitofrontal.

UBERON 0011241 Ethmoid region: The most anterior region of the braincase. Provides structural support for peripheral olfactory organ

UBERON 0011248 Procoracoid element: Endochondral element of pectoral girdle, positioned posterior to the clavicle and anterior to the coracoid.

UBERON 0011287 Rostral organ: A putative electroreceptor organ located in the medial rostral cavity in the ethmoid portion of the chondrocranium of Coelacanth. It is surrounded by an insulating layer of adipose tissue and innervated by the superficial ophthalmic nerve.

UBERON 0011594 Dentary teeth: Tooth that is attached to a dentary/mandible.

UBERON 0011606 Hyomandibular bone : Replacement bone that is bilaterally paired and (in teleosts) articulates with the neurocranium dorsally and the opercle posteriorly.

UBERON 0011634 Ectopterygoid: A palatal bone which -- like many palatal bones -- may originally have developed as a dermal bone replacing part of the palatoquadrate, the primitive upper jaw. Like the palatine (also called dermopalatine), the ectopterygoid replaces the middle part of the autopalatine. It may be serially homologous with the palatine(s), but is somewhat specialized, being the last (most posterior in palatal view) of the series and bordering the fossa for the jaw muscles. In a typical tetrapod it abuts the palatine anteriorly, the maxilla laterally, the pterygoid or the fossa mandibularis medially, and the fossa posteriorly.

UBERON 0011635 Splenial bone: The splenial is a small bone in the lower jaw of reptiles, amphibians and birds, usually located on the lingual side (closest to the tongue) between the angular and surangular.

UBERON 0011636 Surangular bone: The surangular is a dermal bone of the lower jaw. It typically covers much of the dorsal and lateral surface of the posterior jaw and variably extends onto the medial (inside) surface. The surangular articulates with and supports the articular, which forms the jaw joint with the quadrate in most vertebrates and is in turn supported by the angular. More distally, the surangular bridges the mandibular fenestra, if one is present. It may also bear a raised dorsal coronoid process, an important attachment site for the mandibular adductors. At its distal (or rostral) end, the surangular meets the dentary, the main tooth-bearing bone of the lower jaw in most vertebrates.

UBERON 0011637 Prearticular bone: Osseous element of intramembranous origin that extends along the lingual margin of Meckel's cartilage

UBERON 0011655 Interclavicle: dermal bone of pectoral girdle that is median and ventral in position.

UBERON 0011692 Enameloid: Skeletal tissue that is hypermineralized and aprismatic and deposited by a combination of ameloblasts and odontoblasts that are excluded from the matrix. Enameloid develops from pre-enameloid tissue.

UBERON 0012079 Metapterygial axis: Proximodistal trajectory through a metapterygium

UBERON 0013411 Cranial cavity: Anatomical cavity that is the lumen of the skull and contains the brain.

UBERON 0013442 Postorbital process: The Postorbital Process marks the rear, upper edge of the eye socket and is a projection from the frontal bone.

UBERON 0013704 Notochordal canal: A tubular passage that extends from the primitive pit into the head process during the early stages of embryonic development in mammals. It perforates the splanchnopleure layer so that the yolk sac and the amnion are connected temporarily.

UBERON 0014682 Tooth whorl: A spirally arranged cluster of teeth.

UBERON 0017623 Prepelvic clasper: A supplemental clasper in Holocephali, in front of the pelvic fin.

UBERON 0018325 Caudal fin radial element: Radial element that is a part of the caudal fin

UBERON 0018339 Metotic fissure: An embryonic fissure between the otic capsule and the arches which develop into the occipital bones. The fissure may persist into adulthood. It is also referred to as the 'lateral otic fissure' The metotic fissure opens into the vestibular fontanelle, if the fontanelle is present.

UBERON 0018351 Precerebral fontanelle: The lack of chondrification of the anterior wall of the cranial cavity in front of the pineal foramen

UBERON 0018352 Prismatic cartilage: Cartilage arranged into tesserae, blocks of calcified cartilage that fit together as tiles on a floor form a mosaic. Found only in chondrichthyans.

UBERON 0034715 Pineal tract: a cranial nerve fiber tract that innervates the pineal body. This should be classified as an evaginated sensory afferents rather than cranial nerves, as they are part of the CNS

UBERON 0035884 Maxillary-premaxillary suture : A suture between the maxilla and premaxilla.

UBERON 1500000 Scapular blade: Enlarged and broad extension of the scapula distal to the glenoid region that conforms to the contour of the ribs. Origin for the major shoulder muscles including the deltoid group.

UBERON 2000240 Metapterygoid: Endochondral bone that forms the posteriormost element of the palatal complex. It overlies the quadrate and symplectic, posteriorly it articulates with the hyomandibula and anteriorly with the entopterygoid and ectopterygoid. It curves dorsally to form the posteroventral surface of the orbit. The metapterygoid is paired.

UBERON:2000250 Opercle: Dermal bone that forms the postero-dorsal part of the opercular series. The opercle articulates with the hyomandibula antero-dorsally and with the subopercle ventrally. The opercle is a paired bone. The opercle is usually a large, flat bone that may be partially covered by the posterior region of the preopercle.

UBERON 2000410 Postcleithrum: Dermal bone placed postero-medially to the supracleithrum and/or cleithrum

UBERON 2000442 Supraneural bone : endochondral bone that is median and located in the dorsal skeletogenous septum between the cranium and the dorsal fin.

UBERON 2000476 Branchiostegal ray: Dermal bone that is a flattened element that supports the branchiostegal membrane. Branchiostegal rays are generally present in a series articulating ventrally or ventro-medially with the anterior and posterior ceratobranchials

whereas the most posterior ray articulates with the subopercle. The branchiostegal ray is paired. Although the branchiostegals are articulated or attached to the hyoid arch, they belong to the opercular series. Branchiostegal rays are of variable shape and number and their homology is problematic. Usually they are numbered from anterior to posterior elements, instead from posterior to anteriorly considering that the last element of the series is consistently associated to the subopercle.

UBERON 2000452 Urohyal : Tendon bone that forms in the tendon of the sternohyoid muscles ventral to the anterior end of copula 1. The urohyal associates by ligaments to the ventral hypohyals or it articulates with the ventral hypohyals. The urohyal is an unpaired bone.

UBERON 2000620 Autopalatine: Endochondral bone that is part of the antero-lateral region of the palate. Commonly, it articulates with the maxilla anterolaterally and with the ethmoidal region medially. It may also articulate with the dermopalatine ventro-laterally and with the entopterygoid posteriorly. The autopalatine is paired.

UBERON 2000657 Entopterygoid: Dermal bone that forms the ventro-medial part of the palate and the antero-ventral and ventral wall of the orbit. The entopterygoid is a paired bone

UBERON 2000663 Extrascapula: dermal canal-bearing bone placed at the dorso-posterior region of the skull roof, lying on the posterior region of the pterotic and parietals, or the pterotic and epioccipital, or on the pterotic, epioccipital and occipital bones.

UBERON 2000691 Supraorbital bone: Dermal bone that is part of the dorsal or upper border or antero-dorsal border of the orbit. The supraorbital bone may contact the orbital margin of the frontal bone medially, the antorbital antero-ventrally and the dermosphenotic posteriorly. The supraorbital bone does not carry sensory canals. The supraorbital bone is paired

UBERON 2001607 Basipterygoid process of parasphenoid: Process that is the paired process of the parasphenoid that articulates with the suspensorium.

UBERON 2001612 Sensory canal: multi-tissue structure that is a fluid-filled canal in the integument and usually dermal bones and contains one or more neuromast organs. Sensory canals usually communicate with the environment via pores in the sensory canal or at the distal ends of tubules, which extend from canal where pores would otherwise be.

UBERON 2001629 Otic sensory canal: sensory canal between and in close proximity posteriorly with the post-otic and preoperculo-mandibular sensory canals, and anteriorly with the supraorbital and infraorbital sensory canals. The otic sensory canal is bilaterally paired.

UBERON 2001708 Dermosphenotic: Infraorbital that is the last bone of the infraorbital series, carrying the infraorbital canal, and sometimes also the supraorbital, temporal, and/or preopercular canals. The dermosphenotic is sometimes sutured or fused completely to the skull, e.g. to the autosphenotic.

UBERON 2001735 Scapular foramen: Foramen that is located in the scapula. The scapular foramen is paired and formed by a ring of bone

UBERON 2001753 Posttemporal fossae: Fossa where the exoccipital forms the medial portion and the epioccipital forms the lateral margin. The posttemporal fossa in most species has two openings separated by the epioccipital bridge. temporal groove

UBERON 2001787 Pectoral fin spine: Pectoral-fin lepidotrichium 1 with mostly co-ossified and unsegmented hemitrichia that form a stiff and usually thick shaft and enlarged basal processes that moveably articulate with the pectoral girdle. The pectoral fin spine may also result from the fusion of several lepidotrichia that form a stiff shaft.

UBERON 2001810 Supraorbital sensory canal: sensory canal anterior to and in close proximity to the otic and infraorbital sensory canals. The supraorbital sensory canal is bilaterally paired.

UBERON 2001811 Infraorbital sensory canal: Sensory canal lateral or ventral to and in close proximity to the otic and supraorbital sensory canals at their union. The infraorbital sensory canal is bilaterally paired and associated with the infraorbital bones.

UBERON 2001813 Preopercular sensory canal: sensory canal lateral or ventral to and in close proximity with the otic and post-otic sensory canals at their union, and anteroventrally with the mandibular sensory canal. The preopercular sensory canal is bilaterally paired and associated with the preopercle bone.

UBERON 2001814 Mandibular sensory canal: sensory canal anterior and ventral to and in close proximity with the preoperculo-mandibular sensory canal. The mandible sensory canal is bilaterally paired and associated with the angular and dentary bones.

UBERON 2001815 Nuchal plate: Dermal bone that is a bony expansion in the integument anterior to or flanking the dorsal fin that is part of and at the distal end of a supraneural or dorsal fin proximal radial.

UBERON 2001858 Suprapharyngobranchial: A pharyngobranchial bone that articulates with the neurocranium dorsally and epibranchial 1 and pharyngobranchial 2 ventrally; lies dorsal to other elements of the dorsal portions of the branchial arches. Articulates with the exoccipital or prootic depending on taxon.

UBERON 2001893 Hypobranchial element: Skeletal element that is bilaterally paired and articulates medially with a median skeletal element and laterally with a ceratobranchial element.

UBERON 2001909 Pharyngobranchial element : Skeletal element of the branchial arches located medial to the epibranchials.

UBERON 2001926 Posterior myodome: Fossa or chamber on posterior portion of orbital region of neurocranium that serves as attachment site for posterior extrinsic eye muscles.

UBERON 2001934 Rostral plate: dermal bone that is located on midline of snout in skin above mesethmoid and lateral ethmoid bones. Rostral plate bears type 1 odontodes and is unpaired

UBERON 2002053 Bony plates: Dermal bone that is located on or subjacent to the surface anywhere on the body and that is not part of the general complement of scales, dermal bone of the dermatocranium, postcranial axial skeleton or paired fin skeleton. Bony plate may exist singly, or as unpaired or paired clusters or series

UBERON 2002057 Gill opening: anatomical space that is the external opening of a gill slit connecting the pharyngeal cavity to the exterior. Gill opening is usually paired and located on the lateral or ventral surfaces of the head.

UBERON 2002082 Basal fulcrum: Fulcrum that is large, laterally expanded, paired or unpaired, scale-like, and that precedes the base of a fin.

UBERON 2002083 Fringing fulcrum : Fulcrum that is a small, paired dermal structure associated with the marginal, leading rays of paired and/or unpaired fins.

UBERON 2002089 Gular plate: Dermal bone located on the ventral surface of the skull and positioned between the two rami of the lower jaw. Anteriorly the gular attaches to the symphysis of the lower jaw through fibrous connective tissue. The gular is an unpaired median bone.

UBERON 2002101 Branchiostegal ray series: Anatomical cluster that consists of the branchiostegal rays within an individual.

UBERON 2005011 Pseudobranchial artery: A vascular loop attached to the efferent part of the mandibular arch that forms at 3.5 dpf

UBERON 2100623 Basipterygium element: Endochondral element that is paired and supports the pelvic fin. The basipterygium has a posteromedial process called the ischiac process

UBERON 3000036 Basal process of palatoquadrate: Process that extends medially from the ventromedial corner of the palatoquadrate cartilage and articulates or fuses to the anterior wall of the otic capsule via the basitrabecular process.

UBERON 3000037 Basicranial fenestra: Ventral opening of the neurocranium.

UBERON 3000166 Fenestra nasobasalis: Small opening at the anterior tip of the nasal capsule, on the floor of the cavum inferius. It is located medially to the base of the inferior prenasal cartilage and serves for the passage of the ramus medialis narium and arteria orbitonasalis.

UBERON 3000454 Postnasal wall: Paired, anteriorly concave structures that form the posterior limit of nasal capsule. It consists of two parts: a ventral piece, the lamina orbitonasalis, and a dorsal plate that is part of the tectum nasi

UBERON 3000543 Retroarticular process: Bony process that is part of the articular and is the point of insertion of the m. interhuoideus posterior

UBERON 3000547 Rostral process: Is a process of the nasal bone directed anteriorly towards the rostrum

UBERON 3000779 Pectoral fenestra: Ovoid space on the pectoral girdle limited anteriorly by the procoracoid, medially by the epicoracoid, and posteriorly by the coracoid

UBERON 3010092 Basitrabecular process: A process of the otic capsule that will bridge to the palatoquadrate basal process

UBERON 3010142 Occipital arch: Posterior chondrocranium forming ventral and lateral margins of foramen magnum, medial to otic capsules.

UBERON 3010146 Lacrimal: Investing bone in non-teleosts associated with nasolacrimal duct and lying between pars facialis of maxilla and prefrontal and sometimes nasal.

UBERON 3010720 Ramus hyomandibularis: the posttrematic branch of the facial nerve, both motor and sensory in function.

UBERON 4000097 Orthodentine: Odontoid tissue that typically contains tubules and is acellular.

UBERON 4000104 Ganoine: Odontogenic tissue that is hypermineralized acellular, noncollagenous, covered by an epidermis and often deposited in multiple layers.

UBERON 4000118 Cellular bone tissue: Mineralized bone tissue that always includes non-terminally differentiated osteoblasts and osteocytes

UBERON 4000122 Acellular bone tissue: Mineralized bone tissue that has terminally differentiated osteoblasts but lacks osteocytes.

UBERON 4000160 Anocleithrum: Dermal bone of pectoral girdle that is dorsal to and articulates with the cleithrum.

UBERON 4000163 Anal fin: Median fin that is located posterior to the anus.

UBERON 4000164 Caudal fin: The caudal fin is the most posterior median fin. It is composed of a complex of modified centra and modified neural and hemal arches and spines.

UBERON 4000182 Suprabranchial fin: Paired fin that is a bilaterally paired anterior outgrowth located high on the side of the animal, not far behind the orbit, with the posterior extremity corresponding with the expected posterior end of the branchial region.

UBERON 4100113 dermal intracranial joint: Hinge in the skull skeleton to allow for kinetic movement of different parts.

UBERON 4100119 Extratemporal bone: Skull bone in the posterior half of the cranium, bordering the squamosal and opercular.

UBERON 4100014 Posterior dorsal fin: Dorsal fin located posterior to the anterior dorsal fin.

UBERON 4200016 Postbranchial lamina: Medial facing projection or surface on the anterior (cranial) region of the cleithrum that is often textured or denticled. This process has two primary functions: 1) its shape enhances the vertical strength of the cleithrum and 2) it forms the edge of the gill chamber and helps to direct water after it has passed over the gills

UBERON 4200022 Extracleithrum: Narrow bone that lies ventral to the level of insertion of the pectoral fin and is sutured to the posterior edges of both the clavicle and cleithrum.

UBERON 4200023 Anterior dorsal fin: A dorsal fin located anterior to posterior dorsal fin.

UBERON 4200070 Median fin spine: Fin spine that is part of a median fin.

UBERON 4200097 Intermediate spine: spine ventrally located on the body and not part of the pectoral, pelvic or anal fins.

UBERON 4200102 Median dorsal plate: Dermal armour plate that is situated behind the head and constitute the dorsal most portion of the dermal shoulder girdle.

UBERON 4200110 Prepectoral spine: Spine located anterior to the pectoral fin.

UBERON 4200111 Prepelvic fin spine: Spine located anterior to the pelvic fin and posterior to the pectoral fin.

UBERON 4200115 Presupracleithrum: An skeletal element of the upper pectoral girdle overlapped by the opercular and posttemporal bones

UBERON 4200123 Scapular process: The dorsal extension of the scapulocoracoid above the level of the glenoid region in basal gnathostomes.

UBERON 4200129 Synarcual region: Axial subdivision that includes a series of fused cervical vertebrae or vertebral elements.

UBERON 4000172 Lepidotrichium : Dermal bone that is rod-like, formed and usually contained in a fin membrane, and jointed to or adjacent to distal radials. Lepidotrichia are formed from paired hemitrichia surrounding actinotrichia. There are usually two more lepidotrichia than distal radials.

UBERON 4200215 Suture: Line of junction between two parts immovably connected

UBERON 4200245 Parasymphysial plate: Bone, often with tooth attachments, on the lingual side of the anterior of the lower jaw

UBERON 4200250 Meckelian bone: The ossification of the Meckel's cartilage."

UBERON 4300015 Ventral cleithrum & UBERON 4300014 Dorsal cleithrum: In "placoderms" there are large overlapping plates which completely encircle the body and superficially may be matched with those in osteichthyans (Stensio, 1959; Forey, 1980; Jarvik, 1980). Thus, the anterior median ventral, anteroventral and anterior lateral of "placoderms" lie in the same positions as the interclavicle, clavicle (ventral cleithrum) and cleithrum (dorsal cleithrum) of osteichthyans.

UBERON 4300023 Interolateral plate: Dermal bone that is part of the scapular complex in placoderms and located anterior to the anterior ventrolateral (AVL) plate

UBERON 4300025 Posterior dorsolateral plate: Dermal bone that is part of the scapular complex in "placoderms", located posterior to the main components of the complex

UBERON 4300029 Dermal neck joint: Dermal articulation between skull and shoulder girdle localized to paired dermal neck-joint between anterior dorsolateral plate (ADL) and paranuchal (PNu) plates in "placoderms"

UBERON 4300031 Fin web: Membrane that connects the lepidotrichia or ceratotrichia of a fin

UBERON 4300127 Nuchal crest: Bony protuberance on the external surface of the occipital bone

UBERON 4300134 Lateral commissure: Region of the braincase which bears the facets for the hyomandibula in fishes. This region disappears in the origin of tetrapods and the space it occupied comes to contribute to the fenestra vestibulii.

UBERON 4300195 rostral tubule: Consists of a set of tubuli occupying the space between the external dermal bones above the dorsal and anterior wall of the nasal capsule below.

UBERON 4300197 Westoll-lines: More or less concentric lines of discontinuity in the cosmine of Dipnoi, probably due to cyclic resorption and redeposition during growth occurring on the bases of individual scales and also as large structures between headshield plates.

UBERON 4300199 Postsplenial: Dermal bone of the lower jaw.

UBERON 4300202 Endoskeletal cranial joint: The braincase of most plesiomorphic sarcopterygians is divided by the intracranial point into ethmosphenoid and otic-occipital portions each covered by dermal bones. The function of the joint is presumably to increase the gape of the mouth rapidly during opening phases.

UBERON 4300203 Tectum orbital: The dorsal portion of the endocranium that covers the orbital region

UBERON 4300212 Acrodin: odontoid tissue forming a cap on teeth found in teeth of actinopterygian fishes.

UBERON 4300241 Ethmoid commissure: Sensory canal that traverses the rostral bone. ethmoid lateral line commissure

UBERON 4500009 Paired fin spine: Fin spine that is part of a paired fin.

UBERON 7500071 Rostrum: An anatomical structure that protrudes from the head region. In vertebrates, this includes the part of the cranium (skull) in front of the zygomatic arches that also holds the teeth, palat, and nasal cavity. In invertebrates it is the forward extension of the carapace and/or the piercing mouthparts.

Annex 4: Taxa list

This section presents all of the taxa used in this thesis. They are classified by clade or recognized groups and information about the geological formation, the age used for the calibration and the associated bibliography can be found in the following table.

Taxon	Formation	Age	Bibliography
CHONDRICHTHYANS (include putative chondrichthyans)			
<i>Ageleodus pectinatus</i>	Catskill	361.1	Downs & Daeschler 2001
<i>Altholepis composita</i>	Loy Poyales, Freshwater West	411.6	Burrow & Turner 2018, Martínez-Pérez <i>et al.</i> , 2010
<i>Altholepis salopensis</i>	Freswater West	416.4	Burrow & Turner 2018
<i>Anareodus statei</i>	Aztec Siltstone	385.2	Long & Young 1995
<i>Antarctilamna prisca</i>	Aztec Siltstone	385.2	Long <i>et al.</i> , 1995
<i>Apedolepis tomlinsonae</i>	Stokes	459.8	Young 1997
<i>Areyonga oervigi</i>	Stokes	459.8	Young 1997
<i>Aztecodus harmsenae</i>	Aztec Siltstone	385.2	Long <i>et al.</i> , 1995
<i>Canyonlepis smithae</i>	Harding Sandstone	455.7	Andreev <i>et al.</i> , 2015
<i>Chenolepis asketa</i>	Ymogantau	435.9	Sansom <i>et al.</i> , 1999
<i>Cladodoides wildungensis</i>	Emyaksin	361.2	Hairapetian & Ginter 2009
<i>Cladolepis gunnelli</i>	Boyle	385.2	Wells 1944
<i>Ctenacanthus compressus</i>	Bedford	361.3	Newberry 1889
<i>Ctenacanthus randalli</i>	Bedford	361.3	Newberry 1889

<i>Dalmehodus turnerae</i>	Dalmeh	363.3	Hairapetian & Ginter 2009
<i>Deihim mansureae</i>	Dalmeh	363.3	Hairapetian & Ginter 2009
<i>Deltalepis magna</i>	Chargat	433.7	Andreev <i>et al.</i> , 2017
<i>Deltalepis parva</i>	Chargat	433.7	Andreev <i>et al.</i> , 2017
<i>Diademodus dominicus</i>	Virgin Hills	377.4	Roelofs <i>et al.</i> , 2015
<i>Diademodus hydei</i>	Cleveland Shale	361.3	Harris 1951
<i>Diademodus utahensis</i>	Pilot Shale	361.3	Ginter 2008
<i>Doliodus latispinosus</i>	Campbellton	409	Burrow <i>et al.</i> , 2017
<i>Elegestolepis grossi</i>	Baital	428.2	Andreev <i>et al.</i> , 2017
<i>Emerikodus ekstrapelus</i>	Gneudna	377.4	Trinajstić & George 2009
<i>Ferromirum oukherbouchi</i>	Ibâouane	365.5	Frey <i>et al.</i> , 2020
<i>Gladbachus adentatus</i>	Torrington	383.5	Heidtke & Krätschmer 2001
<i>Gogoselachus lynbeazleyae</i>	Gogo	377.4	Long <i>et al.</i> , 2015
<i>Jalodus australiensis</i>	Dalmeh	363.3	Long 1990
<i>Kannathalepis milleri</i>	Cape Phillips	428.9	Märss & Gagnier 2001
<i>Karksilepis parva</i>	Burtneki	386.8	Märss <i>et al.</i> , 2008
<i>Karksiodus mirus</i>	Burtneki	386.8	Ivanov <i>et al.</i> , 2011, Ivanov & Märss 2014, Ivanov & Plax 2018
<i>Knerialepis mashkovae</i>	Nogueras	411.6	Martínez-Pérez <i>et al.</i> , 2010
<i>Manberodus fortis</i>	Chariseh	383.4	Hairapetian <i>et al.</i> , 2008a
<i>Mcmurdodus whitei</i>	Cravens Peak	394.7	Turner & Young 1987
<i>Melanodus loonesi</i>	Blacourt	383.5	Darras <i>et al.</i> , 2008

<i>Mongolepis rozmanae</i>	Chargat	433.7	Karatajūtė-Talimaa 1995
<i>Neosinacanthus planispinatus</i>	Guodingshan	430.4	Min & Min 1998
<i>Omalodus bryanti</i>	Alchedat	383.5	Ginter & Ivanov 1992
<i>Omalodus grabaui</i>	Renanué Bed 27	385.2	Ginter <i>et al.</i> , 2008
<i>Orodus aramisi</i>	Magunao	361.1	Lelièvre & Derycke 1998
<i>Phoebodus australiensis</i>	Mae Sam Lap	363.3	Long 1990
<i>Phoebodus bifurcatus</i>	Lyaioi', Gneuda, Virgin Hills	361.1	Ginter & Ivanov 1992, Ivanov 2003
<i>Phoebodus curvatus</i>	Yaya	380	Ivanov 2021
<i>Phoebodus depressus</i>	Gour Bedda	365.5	Hairapetian & Ginter 2009
<i>Phoebodus fastigatus</i>	Virgin Hills	377.4	Ginter & Ivanov 1992, Ginter <i>et al.</i> , 2008
<i>Phoebodus gothicus</i>	Dalmeh	363.3	Ginter & Ivanov 1992
<i>Phoebodus latus</i>	Virgin Hills	377.4	Ginter & Ivanov 2000
<i>Phoebodus limpidus</i>	Dalmeh, Mighan	361.1	Ginter & Ivanov 2000
<i>Phoebodus politus</i>	Anti-Atlas, Cleveland Shale	361.1	Turner 1982a
<i>Phoebodus rayi</i>	Parry Islands	363.3	Ginter & Turner 1999
<i>Phoebodus sophiae</i>	Shishtu	383.4	Ginter & Ivanov 2000
<i>Phoebodus turnerae</i>	Holy Cross Mountain	369.9	Ginter & Ivanov 1992
<i>Phoebodus typicus</i>	Dalmeh, Pokayama	363.3	Ginter & Ivanov 2000
<i>Pilolepis margaritifera</i>	Cape Phillips	427.9	Qu <i>et al.</i> , 2010
<i>Plesioselachus macracanthus</i>	Witpoort	365.7	Gess & Coates 2015
<i>Polymerolepis whitei</i>	Freshwater West	417.8	Hanke <i>et al.</i> , 2013
<i>Portalodus bradshawae</i>	Aztec Siltstone	385.2	Long <i>et al.</i> , 1995

<i>Portalodus mannoliniae</i>	Platekill	386.8	Potvin-Leduc <i>et al.</i> , 2015
<i>Protacrodus aequalis</i>	Burlya, Kushelga, Popovskiy Ryauzyak, Sholokh-Sai, Sikaza, Termyantash, Usuli	361.1	Ivanov & Plax 2018, Ivanov 1996
<i>Protacrodus orientalis</i>	Meggongago	361.1	Lelièvre & Derycke 1998
<i>Protacrodus vetustus</i>	Holy Cross Mountain	373.9	Ginter 2002
<i>Protodus jexi</i>	Campbellton	405.2	Turner & Miller 2008
<i>Pucapampella rodrigae</i>	Sica Sica	388	Janvier & Suarez- Riglos 1986
<i>Rongolepis cosmetica</i>	Ymogantau	435.9	Sansom <i>et al.</i> , 1999, Andreev <i>et al.</i> , 2020
<i>Roongodus phijani</i>	Chariseh	361.1	Hairapetian & Ginter 2009
<i>Seretolepis elegans</i>	Nogueras	411.6	Martínez-Pérez <i>et al.</i> , 2010
<i>Shiqianolepis hollandi</i>	Ymogantau	435.9	Sansom <i>et al.</i> , 1999
<i>Siamodus janvieri</i>	Mae Sam Lap	361.1	Long 1990
<i>Siberiodus mirabilis</i>	Chariseh, Cheybekkiol	377.2	Ivanov & Rodina 2004
<i>Sinacanthus micracanthus</i>	Silverband	421.1	Burrow <i>et al.</i> , 2010, Burrow 2003
<i>Sinacanthus triangulatus</i>	Guodingshan	430.4	Min & Min 1998
<i>Sinacanthus wuchangensis</i>	Guodingshan	430.4	Min & Min 1998
<i>Solinalepis levis</i>	Harding Sandstone	455.7	Andreev <i>et al.</i> , 2016
<i>Sphenacanthus serrulatus</i>		360	Dick 1998
<i>Squatinactis glabrum</i>	Shishtu	363.3	Hairapetian & Ginter 2009
<i>Stethacanthus resistens</i>	Holy Cross Mountain	373.9	Ginter 2002
<i>Stethacanthus thomasii</i>	Tafilalet	361.1	Derycke 1992

<i>Taklamakanolepis asiaticus</i>	Ymogantau	435.9	Andreev <i>et al.</i> , 2020
<i>Tamiobatis vestutus</i>	Cleveland Shale	370.8	Williams 1998
<i>Tantalepis gatehousei</i>	Stairway Sandstone	464.2	Sansom <i>et al.</i> , 2012
<i>Tarimacanthus bachuensis</i>	Qingshui, Fentou	435.9	Min & Min 1998
<i>Tassilodus lessardi</i>	Guezzam, Oued Felaou, Anou Izileg	400.45	Derycke & Goujet 2011
<i>Teslepis jucunda</i>	Chargat	433.7	Andreev <i>et al.</i> , 2016
<i>Tezakia hardingensis</i>	Harding Sandstone, Winnipeg	455.7	Andreev <i>et al.</i> , 2015
<i>Thrinacodus tranquillus</i>	Dalmeh	363.3	Hairapetian & Ginter 2009
<i>Tielikewatielepis sinensis</i>	Ymogantau, Tataertag	436.8	Andreev <i>et al.</i> , 2020
<i>Tuvalepis schultzei</i>	Khondergei	419.7	Zigaite & Karatajute-Talimaa 2008
<i>Wellerodus priscus</i>	Platekill	386.8	Potvin-Leduc <i>et al.</i> , 2015
<i>Xiaohaizilepis liui</i>	Ymogantau, Tataertag	436.8	Andreev <i>et al.</i> , 2020
<i>Xinjiangichthys pluridentatus</i>	Yimugantawu	435.9	Andreev <i>et al.</i> , 2020
<i>Xinjiangichthys tarimensis</i>	Yimugantawu	435.95	Nanzhong <i>et al.</i> , 1998
<i>Yuanolepis bachunensis</i>	Ymogantau	435.9	Andreev <i>et al.</i> , 2020
« ACANTHODIANS »			
<i>Acanthacanthus ornatus</i>	Severnaya Zemlya	417.7	Valiukevicius 2003a
<i>Acanthopora transitans</i>	Severnaya Zemlya	417.7	Valiukevicius 2003a
<i>Acanthospina irregulare</i>	Severnaya Zemlya	417.7	Valiukevicius 2003a
<i>Acritolepis urvantsevi</i>	Severnaya Zemlya	417.7	Valiukevicius 2003a
<i>Acritolepis ushakovi</i>	Severnaya Zemlya	417.7	Valiukevicius 2003a

<i>Ankylacanthus convexus</i>	Campbellton, Wahnbachschichten, Taunusquarzit, Rimmert, York River, Jauf, Manacapuru	406.2	Burrow <i>et al.</i> , 2008
<i>Ankylacanthus incurvus</i>	Campbellton	405.2	Burrow <i>et al.</i> , 2008
<i>Arcticacanthus bicostatus</i>	Pod'emaya, Spokojnaya, Rusanov	406.8	Valiukevicius 2003a
<i>Arenaceacanthus arcuatacanalis</i>	Vievis, Dubysa, Lapès, Neris, Nevezis, Dukstyna, Birstonas	427.5	Valiukevicius 2004a
<i>Atopacanthus dentatus</i>	Genese, West Falls	377.4	Burrow 2004
<i>Atopacanthus juvai</i>	Bahram	369.9	Hairapetian & Burrow 2019
<i>Brachyacanthus scutiger</i>	Dundee	413.4	Denison 1979, Newman & Davidson 2010
<i>Bracteatacanthus assiduus</i>	Jura	421.1	Valiukevicius 2004a
<i>Brochoadmones milesi</i>	Road River	415	Hanke & Wilson 2006
<i>Bryantonchus peracutus</i>	Water Canyon	400.4	Burrow 2007
<i>Byssacanthoides debenhami</i>	Aztec Siltstone	385.2	Young & Burrow 2004
<i>Cacheacanthus utahensis</i>	Water Canyon	400.4	Burrow 2007
<i>Cambaracanthus goodhopensis</i>	Cavan Bluff Limestone	405.2	Lindley 2000
<i>Canadalepis linguiformis</i>	Minija, Girdziai, Kelmé, Rietavas	421.1	Valiukevicius 1998, Märss 1997
<i>Cassidiceps vermiculatus</i>	Road River	415	Gagnier & Wilson 1996
<i>Cavanacanthus warrooensis</i>	Cavan Bluff Limestone	405.2	Lindley 2000
<i>Cheiracanthoides mosolovicus</i>	Lekeiyaga	390.5	Valiukevicius 2003b
<i>Cheiracanthoides pinskensis</i>	Lopushany	390.5	Plax 2019
<i>Cheiracanthus flabellcostatus</i>		385,2	Pinakhina 2018
<i>Cheiracanthus grandispinus</i>	Flagstone	390.5	Burrow <i>et al.</i> , 2020

<i>Cheiracanthus latus</i>	Narva	388	Burrow <i>et al.</i> , 2020
<i>Cheiracanthus murchisoni</i>	Flagstone	390.5	Burrow <i>et al.</i> , 2020
<i>Cheiracanthus peachi</i>	Flagstone	390.5	Burrow <i>et al.</i> , 2020
<i>Climatius reticulatus</i>	Turin hill	415	Burrow <i>et al.</i> , 2015
<i>Climatius ornatus</i>	Ohesaare	415	Burrow 2017
<i>Culmacanthus antarctica</i>	Aztec Siltstone	385.2	Young & Burrow 2004
<i>Culmacanthus stewarti</i>	Mt Howitt	377.4	Long 1983
<i>Devononchus concinnus</i>	Gauja, Podsnetogor	380.9	Gross 1930
<i>Diplacanthus crassisimus</i>	Flagstone, Mey, Rousay	390.5	Pinakhina & Märss 2018
<i>Diplacanthus ellsi</i>	Escuminac	377.4	Cloutier & Schultze 1996
<i>Diplacanthus gravis</i>	Polotsk	385.2	Valiukevicius 2003a
<i>Diplacanthus horridus</i>	Escuminac	377.4	Cloutier & Schultze 1996
<i>Diplacanthus pechorensis</i>	Naul'	409.2	Valiukevicius 2003b
<i>Diplacanthus tenuistriatus</i>	Flagstone, Mey, Rousay	390.5	Burrow <i>et al.</i> , 2016
<i>Diplacanthus poltnigi</i>	Pod'emaya	411.9	Valiukevicius 2003a
<i>Diplacanthus solidus</i>	Vstrechnaya	390.5	Valiukevicius 2003a
<i>Drygantacanthus semirotonda</i>	Ivanie	411.6	Voichyshyn & Szaniawski 2018
<i>Erriwacanthus falcatus</i>	Czortkow	411.6	Ørvig 1967, Voichyshyn & Szaniawski 2012
<i>Erriwacanthus manbrookensis</i>	Moor Cliff	418.4	Schultze 1979
<i>Erymnacanthus clivus</i>	Road River	418	Blais <i>et al.</i> , 2015
<i>Euryacanthus rugosus</i>	Road River	415	Blais <i>et al.</i> , 2015

<i>Euthacanthus gracilis</i>	Arbuthnott	415	Powrie 1870, Newman <i>et al.</i> , 2011
<i>Euthacanthus macnicoli</i>	Arbuthnott	415	Newman <i>et al.</i> , 2014
<i>Fecundosquama basiglobosa</i>	Jura, Vievis, Minija	420.4	Valiukevicius 2004a
<i>Florestacanthus morenoi</i>	Cuche	373.9	Burrow <i>et al.</i> , 2003
<i>Ginkgolepis tenericostatus</i>	Šventoji	379.9	Pinakhina & Märss 2018
<i>Gladiobranthus probaton</i>	Road River	415	Hanke & Davis 2008
<i>Gomphonchoporus hoppei</i>	Krasnaya Bukhta	421.1	Burrow 2003b, Vergoossen 1999
<i>Gomphonchus abruptus</i>	Eptarma	421.1	Valiukevicius 2003b
<i>Gomphonchus boekschoteni</i>	Oosterhaule	421.1	Vergoossen 1999
<i>Gomphonchus mediocostatus</i>	Oosterhaule	421.1	Vergoossen 1999
<i>Gomphonchus minicostatus</i>	Eptarma	421.1	Valiukevicius 2003b
<i>Gomphonchus minutus</i>	Minija	421.1	Valiukevicius 2004b
<i>Gomphonchus nordicus</i>	Krasnaya Bukhta	421.1	Valiukevicius 2003a
<i>Gomphonchus sandelensis</i>	Krasnaya Bukhta, Severnaya Zemlya, Pod'Emaya, Spokojnaya, Rusanov, Al'banov, Vievis, Dubysa, Lapès, Neris, Nevezis, Dukstyna, Birstonas, Lapès	410.5	Burrow 2003b
<i>Granulacanthus joenelsoni</i>	Road River	429.5	Hanke <i>et al.</i> , 2001
<i>Grenfellacanthus zerinae</i>	Hunter	361.1	Long <i>et al.</i> , 2004
<i>Gyracanthides warreni</i>	Aztec Siltstone	385.2	Warren <i>et al.</i> , 2000
<i>Haplacanthus marginalis</i>	Polotsk	385.2	Newman <i>et al.</i> , 2019
<i>Helolepis bellarugosus</i>	Delaware	388	Bentley 1988

<i>Helolepis venustiloides</i>	Delaware	388	Bentley 1988
<i>Homalacanthus concinnus</i>	Escuminac	377.4	Cloutier & Schultze 1996
<i>Howittacanthus kentoni</i>	Avon River	377.4	Long 1986a
<i>Iranolepis ginteri</i>		380.9	Hairapetian <i>et al.</i> , 2006
<i>Ischnacanthus gracilis</i>	Arbuthnott	415	Schultze 1979
<i>Ischnacanthus wickhami</i>	ORS	415	Burrow 2017
<i>Kasperacanthus serratus</i>	Chortvik, Ivanie	413.0	Voichyshyn & Szaniawski 2018
<i>Kathemacanthus rosulentus</i>	Road River	417.7	Hanke & Wilson 2010, Gagnier & Wilson 1996
<i>Laliacanthus ligeriensis</i>	La Grange, Jawf	400.4	Vidal <i>et al.</i> , 1994, Burrow <i>et al.</i> , 2006
<i>Laliacanthus singularis</i>	Vitebsk	394.7	Plax 2015
<i>Latviacanthus ventispilensis</i>	Kemeri	400.4	Schultze & Zidek 1982
<i>Lenacanthus priscus</i>	Moyerocan, Khaastyr, Agidy	438.6	Karatajūtė-Talimaa & Smith 2002
<i>Lodeacanthus gaujicus</i>	Lode	380.9	Upeniece & Beznosov 2002
<i>Lupopsyroides macracanthus</i>	Road River	417.7	Hanke & Wilson 2004
<i>Lupopsyrus pygmaeus</i>	Road River	417.7	Hanke & Davis 2012
<i>Machaeracanthus goujeti</i>	Nogueras	411.6	Botella <i>et al.</i> , 2012
<i>Machaeracanthus hunsrueckianum</i>	Kaub	405.2	Südkamp & Burrow 2007
<i>Machaeracanthus major</i>	Corniferous	415	Burrow <i>et al.</i> , 2010b
<i>Machaeracanthus pectinatus</i>	Cravens Peak	394.7	Burrow & Young 2005
<i>Machaeracanthus polonicus</i>	Winna, Barcza	405.7	Burrow & Szrek 2018

<i>Melanoacanthus minutus</i>	Bear Rock	400.4	Cumbaa & Schultze 2002
<i>Mesacanthus grandis</i>	Wood Bay	412.2	Gagnier & Goujet 1997
<i>Mesacanthus mitchelli</i>	Turin hill	415	Schultze 1979
<i>Milesacanthus ancestralis</i>	Jawf	405.2	Burrow <i>et al.</i> , 2006
<i>Milesacanthus antarctica</i>	Aztec Siltstone	385.2	Young & Burrow 2004
<i>Monopleuroodus ohhesaarensis</i>	Ohesaare	421.1	Schultze 1979
<i>Monospina erecta</i>	Greben	421.1	Valiukevicius 2003b, Valiukevicius 2005
<i>Nerepisacanthus denisoni</i>	Cunningham Creek, Bertie	421.1	Burrow 2011
<i>Nodocosta denisoni</i>	Water Canyon	400.4	Burrow 2007
<i>Nodocosta pauli</i>	Sietni, Gauja	381.7	Burrow 2007
<i>Nostolepis adzvensis</i>	Khatayakha	415	Valiukevicius 2003b
<i>Nostolepis alifera</i>	Targale	415	Valiukevicius 2004b
<i>Nostolepis alta</i>	Jura	421.1	Valiukevicius 2005, Märss 1986
<i>Nostolepis amplifica</i>	Jura, Miniija	421.1	Valiukevicius 2003c
<i>Nostolepis consueta</i>	Vievis, Dubysa, Lapès, Neris, Nevezis, Dukstyna, Birstonas, Lapès	426.3	Valiukevicius 2003c
<i>Nostolepis costata</i>	Jawf, Saint-Cénéré	406.8	Burrow & Murphy 2016, Burrow <i>et al.</i> , 2006
<i>Nostolepis decora</i>	Severnaya Zemlya	417.7	Valiukevicius 2003a
<i>Nostovicina elegans</i>	Jura, Robert Mount	419.1	Plax 2015
<i>Nostolepis fragilis</i>	Severnaya Zemlya	417.7	Valiukevicius 2003a
<i>Nostolepis gaujensis</i>	Sietni, Gauja, Sventoji	380.9	Pinakhina & Märss 2018

<i>Nostolepis gracilis</i>	Krasnaya Bukhta, Severnaya Zemlya, Pod'Emaya, Spokojnaya, Rusanov, Al'banov	410.5	Valiukevicius 2003a, Plax 2015
<i>Nostolepis kozhymica</i>	Ovinparma	415	Valiukevicius 2003b, Plax 2015
<i>Nostovicina lacrima</i>	Cookeys Plains	419.9	Burrow 2003b
<i>Nostovicina laticristata</i>	Pod'emaya, Spokojnaya, Rusanov	404.4	Valiukevicius 2003a
<i>Nostolepis latvica</i>	Targale	415	Valiukevicius 2004b
<i>Nostolepis linleyensis</i>	Castle Sandstone	422.3	Miller & Märss 1999
<i>Nostolepis longipostera</i>	Khatayakha	415	Valiukevicius 2003b
<i>Nostolepis minilonga</i>	Toravey	415	Valiukevicius 2003b
<i>Nostolepis minima</i>	Severnaya Zemlya, Pod'emaya	415	Valiukevicius 2003a, Plax 2015
<i>Nostolepis musca</i>	Jura, Minija	421.1	Valiukevicius 2003c
<i>Nostolepis parathleta</i>	Toravey	415	Valiukevicius 2003b
<i>Nostovicina paravolborthi</i>	Khatayakha	419.9	Valiukevicius 2003b
<i>Nostovicina platycrista</i>	Toravey	415	Valiukevicius 2003b
<i>Jolepis robusta</i>	Freshwater West	417.8	Valiukevicius 2003a, Plax 2015
<i>Nostolepis scotica</i>	Dundee	413.4	Burrow & Turner 2010
<i>Nostolepis striata</i>	Krasnaya Bukhta, Severnaya Zemlya, Pod'Emaya, Spokojnaya, Rusanov, Al'banov	410.5	Vergoossen 1999, Burrow <i>et al.</i> , 2013a, Schultze 1979
<i>Nostolepis taimyrica</i>	Rusanov, Al'banov	402.8	Valiukevicius 1994, 2003a
<i>Nostovicina tareyensis</i>	Taimyr	411.6	Burrow 1995
<i>Nostolepis terraborea</i>	Toravey	415	Valiukevicius 2003b, Plax 2015
<i>Nostolepis tewonensis</i>	Miaogou	428.9	Plax 2015

<i>Nostovicina timanica</i>	Pod'emaya, Spokojnaya, Rusanov	406.8	Valiukevicius 2003a
<i>Nostolepis valentinae</i>	Toravey	415	Valiukevicius 2003b
<i>Nostolepis watsoni</i>	Rusanov, Al'banov	402.8	Valiukevicius 2003a
<i>Nostolepis zinaidae</i>	Ovinparma	415	Valiukevicius 2003b
<i>Nostovicina guangxiensis</i>	Point Hibbs	415.2	Burrow <i>et al.</i> , 1998
<i>Nostovicina multicostata</i>	Pod'emaya, Spokojnaya, Rusanov	406.8	Valiukevicius 2003a
<i>Obruchevacanthus ireneae</i>	Nogueras	412.2	Botella <i>et al.</i> , 2014
<i>Obtusacanthus corroconis</i>	Road River	417.7	Hanke & Wilson 2004
<i>Onchus major</i>	Downtown Castle Sandstone	421.3	Newman <i>et al.</i> , 2017
<i>Onchus murchisoni</i>	Downtown Castle Sandstone	421.3	Newman <i>et al.</i> , 2017
<i>Onchus tenuistriatus</i>	Downtown Castle Sandstone	421.3	Newman <i>et al.</i> , 2017
<i>Onchus wheathillensis</i>	Freshwater West	418.2	Newman <i>et al.</i> , 2017
<i>Parexus recurvus</i>	Freshwater West, Knoydart	418	Burrow <i>et al.</i> , 2013b
<i>Paucicanthus vanelsti</i>	Road River	417.8	Hanke 2002
<i>Pechoralepis juozasis</i>	Aztec Siltstone	385.2	Burrow <i>et al.</i> , 2009
<i>Persacanthus kermanensis</i>	Bidou	377.4	Schultze 1979
<i>Plectrodus mirabilis</i>	ORS	421.1	Schultze 1979
<i>Podoliacanthus zychi</i>	Chortvik, Ivanie	413.0	Voichyshyn & Szaniawski 2012
<i>Poracanthodes canadensis</i>	Cape Phillips	425.2	Burrow <i>et al.</i> , 1999
<i>Poracanthodes marssae</i>	Targale	415	Valiukevicius 2004b
<i>Poracanthodes punctatus</i>	Krasnaya Bukhta, Severnaya Zemlya, Pod'Emaya, Spokojnaya, Targale, Cape Philips	417.5	Burrow 2003c, Valiukevicius 2003a

<i>Poracanthodes sulcatus</i>	Targale	421.1	Valiukevicius 2004b
<i>Promesacanthus eppleri</i>	Road River	417.8	Hanke 2008
<i>Ptomacanthus anglicus</i>	Herbert Quarry	415	Brazeau 2012
<i>Ptychodictyon americanum</i>	Water Canyon, Beartooth Butte	400.4	Burrow 2007
<i>Ptychodictyon rimosum</i>	Narva	400.4	Pinakhina & Märss 2018
<i>Ptychodictyon sulcatum</i>	Narva	388	Pinakhina & Märss 2018
<i>Radioporacanthodes porosus</i>	Krasnaya Bukhta	421.1	Vergoossen 1999, Burrow 2003b
<i>Radioporacanthodes qujingensis</i>	Silverband	422.4	Nian-Zhong & Zhi-Zhong 1989
<i>Radioporacanthodes scheii</i>	Devon Islands	419.7	Burrow 2013
<i>Rhadinacanthus deltasquamosus</i>	Härma	385.2	Pinakhina & Märss 2018
<i>Rhadinacanthus longispinus</i>	Flagstone	385.2	Pinakhina & Märss 2018
<i>Rockycampacanthus milesi</i>	Rocky Camp	395.6	Long 1986b
<i>Rohonilepis breviornatus</i>	Ventspils, Minja	423.3	Valiukevicius 2004a
<i>Serradentus armstrongi</i>	Fiskeløfta	383.5	Newman <i>et al.</i> , 2019
<i>Sevyacanthus elliotti</i>	Water Canyon	400.4	Burrow 2007
<i>Striacanthus overathensis</i>	Holy Cross Mountain	373.9	Burrow & Szrek 2018
<i>Taemasacanthus cooradigbeensis</i>	Cavan Bluff Limestone	405.2	Lindley 2001
<i>Taemasacanthus erroli</i>	Cavan Bluff Limestone	405.2	Long 1986b, Blais <i>et al.</i> , 2015
<i>Taemasacanthus narrengullenensis</i>	Cavan Bluff Limestone	405.2	Lindley 2001
<i>Taemasacanthus porca</i>	Cavan Bluff Limestone	405.2	Lindley 2000
<i>Tchunacanthus obruchevi</i>	Balturino	435.6	Karatajute-Talimaa & Smith 2002

<i>Teneracanthus toombaensis</i>	Bracteata, Chinaman Creek	394.7	Burrow & Young 2005
<i>Tetanopsyrus breviacanthias</i>	Road River	417.8	Hank <i>et al.</i> , 2001b
<i>Tetanopsyrus lindoei</i>	Road River	417.8	Hank <i>et al.</i> , 2001b
<i>Triazeugacanthus affinis</i>	Escuminac	377.4	Cloutier & Schultze 1996
<i>Tricuspicanthus gannitus</i>	Road River	415	Blais <i>et al.</i> , 2015
<i>Tricuspicanthus pisciculus</i>	Road River	415	Blais <i>et al.</i> , 2015
<i>Trundlelepis cervicostulata</i>	Connemarra, Gleninga, Point Hibbs, Shield Creek	408.2	Burrow 1995
<i>Uraniacanthus curtus</i>	Arbuthnott, Dundee	415	Newman <i>et al.</i> , 2012
<i>Vernicomacanthus uncinatus</i>	Dundee, Flagstone	415	Schultze 1979
<i>Vesperalia perplexa</i>	Jura	419.8	Valiukevicius 2004a
<i>Watsonacanthus costatus</i>	Rusanov, Al'banov	402.8	Valiukevicius 2003a
<i>Watsonacanthus oervigi</i>	Al'banov, Grey Hoek, Wood Bay	400.4	Valiukevicius 1995
<i>Wetteldorfia triangula</i>	Jawf, Nogueras, Santa Cruz	405.2	Burrow <i>et al.</i> , 2006, Turner <i>et al.</i> , 2000
<i>Xylacanthus grandis</i>	ORS	415	Ørvig 1967
<i>Xylacanthus kenstewarti</i>	Road River	429.5	Hanke <i>et al.</i> , 2001a
<i>Xylacanthus minutus</i>	Wood Bay	412.2	Gagnier & Goujet 1997
<i>Yealepis douglasi</i>	Yea	425.2	Burrow & Young 1999
« PLACODERMS »			
<i>Bothriolepis canadensis</i>	Escuminac	377.4	Béchar <i>et al.</i> , 2014, Downs & Donoghue 2009
<i>Coccosteus cuspidatus</i>	Edderton	389.8	Miles & Westoll 1968
<i>Cowralepis mclachlani</i>	Merriganowry	381.7	Ritchie 2005

<i>Dicksonosteus arcticus</i>	Wood Bay	401.5	Goujet & Lehman 1975
<i>Entelognathus primordialis</i>	Kuanti	424.3	Zhu <i>et al.</i> , 2013
<i>Macropetalichthys rapheidolabis</i>	Onondaga	390.5	Stensiö & Farrington 1925
<i>Qilinyu rostrata</i>	Kuanti	424.3	Zhu <i>et al.</i> , 2016
<i>Romundina stellina</i>	Drake Bay	417.8	Dupret <i>et al.</i> , 2017
OSTEICHTHYANS			
<i>Cheirolepis canadensis</i>	Escuminac	377.4	Arratia & Cloutier 1996, Meunier <i>et al.</i> , 2018
<i>Eusthenopteron foordi</i>	Escuminac	377.4	Bjerring 1987, Cote <i>et al.</i> , 2002, Laurin <i>et al.</i> , 2007, Zylberberg <i>et al.</i> , 2010
<i>Gogonassus andrewsae</i>	Gogo	377.4	Long <i>et al.</i> , 2006, Holland 2013, 2014
<i>Howqualepis rostridens</i>	Avon River	377.4	Long 1988
<i>Kenichthys campbelli</i>	Chuandong	388.6	Meemann & Zhu 1993
<i>Meemannia eos</i>	Xitun	412.2	Zhu <i>et al.</i> , 2010
<i>Miguashaia bureaui</i>	Escuminac	377.4	Mondéjar-Fernández <i>et al.</i> , 2021, Cloutier 1996
<i>Mimipiscis toombsi</i>	Gogo	377.4	Choo 2012, Gardiner 1984
<i>Moythomasia durgaringa</i>	Gogo	377.4	Gardiner 1984
<i>Scaumenacia curta</i>	Escuminac	377.4	Cloutier 1997
<i>Styloichthys changae</i>	Xitun	415	Friedman 2007, Zhu & Yu 2002
<i>Tarachomyx multicostatus</i>	Chuandong	431.9	Qiao & Zhu 2008
OSTEOSTRACI			
<i>Ateleaspis tessellata</i>	Slot Burn, Fish Bed, Henshaw	431.95	Ritchie 1967

<i>Benneviaspis urvantsevi</i>	Spokoinaya	409.2	Mark-Kurik & Janvier 1995
<i>Cephalaspis lyelli</i>	Dundee	413.4	White 1958, Stensiö 1932
<i>Kalanaspis delectabilis</i>	Jõgeva	439.6	Tinn & Märss 2018
<i>Norselaspis glacialis</i>	Wood Bay	412.2	Janvier 1981,
<i>Procephalaspis oeselensis</i>	Himmiste	425.9	Robertson 1939
<i>Tremataspis mammillata</i>	Himmiste	425.9	Denison 1947, O'shea <i>et al.</i> , 2019
<i>Zenaspis salweyi</i>	St Maughans, Senni	412.2	Stensiö 1932
GALEASPIIDS			
<i>Tujiaaspis vividus</i>	Xishancun	417.8	Gai <i>et al.</i> , 2022
<i>Eugaleaspis changi</i>	Guodingshan	435.95	Liu <i>et al.</i> , 2018
<i>Hanyangaspis guodingshanensis</i>	Xishancun	417.8	Liu <i>et al.</i> , 2020
<i>Nochelaspis maeandrina</i>	Xishancun	418.1	Zhu 1992
<i>Polybranchiaspis liaojiaoshanensis</i>	Xikeng	435.95	Liu <i>et al.</i> , 2014
<i>Shuyu zhejiangensis</i>	Huixingshao, Maoshan, Tangijawu, Xikeng	435.95	Gai <i>et al.</i> , 2019
THELODONTS			
<i>Furcacauda fredholmae</i>	Road River	415	Wilson & Caldwell 1998
<i>Larolepis darbyi</i>	Gull River	423.3	Sansom & Elliott 2003
<i>Loganellia einari</i>	Tagavere	430.4	Märss 1996
<i>Nikolivia milesi</i>	Freshwater West	417.8	Turner 1982b
<i>Niurolepis susanae</i>	Niur	428.95	Hairapetian <i>et al.</i> , 2008b
<i>Paralogania klubovi</i>	Golomyannyj	439.65	Märss & Karatajute-Talimaa 2002
<i>Pezopallichthys ritchei</i>	Road River	430.4	Wilson & Caldwell 1998
<i>Shielia multispinata</i>	Samojlovich	425.2	Märss & Karatajute-Talimaa 2002

<i>Stroinolepis maenniki</i>	Strojnaya, Ozernaya	451.1	Märss & Karatajute- Talimaa 2002
<i>Thelodus calvus</i>	Samoijovich, Ust'Spokojnaya	428.2	Märss & Karatajute- Talimaa 2002

Annex 5: Resulting trees from Parsimony analyses

Resulting tree from parsimony analysis on the matrix with 84 taxa and 792 morphological characters. The trees are presented with branch length corresponding to evolutionary steps.

Ateleaspis tessellata as outgroup

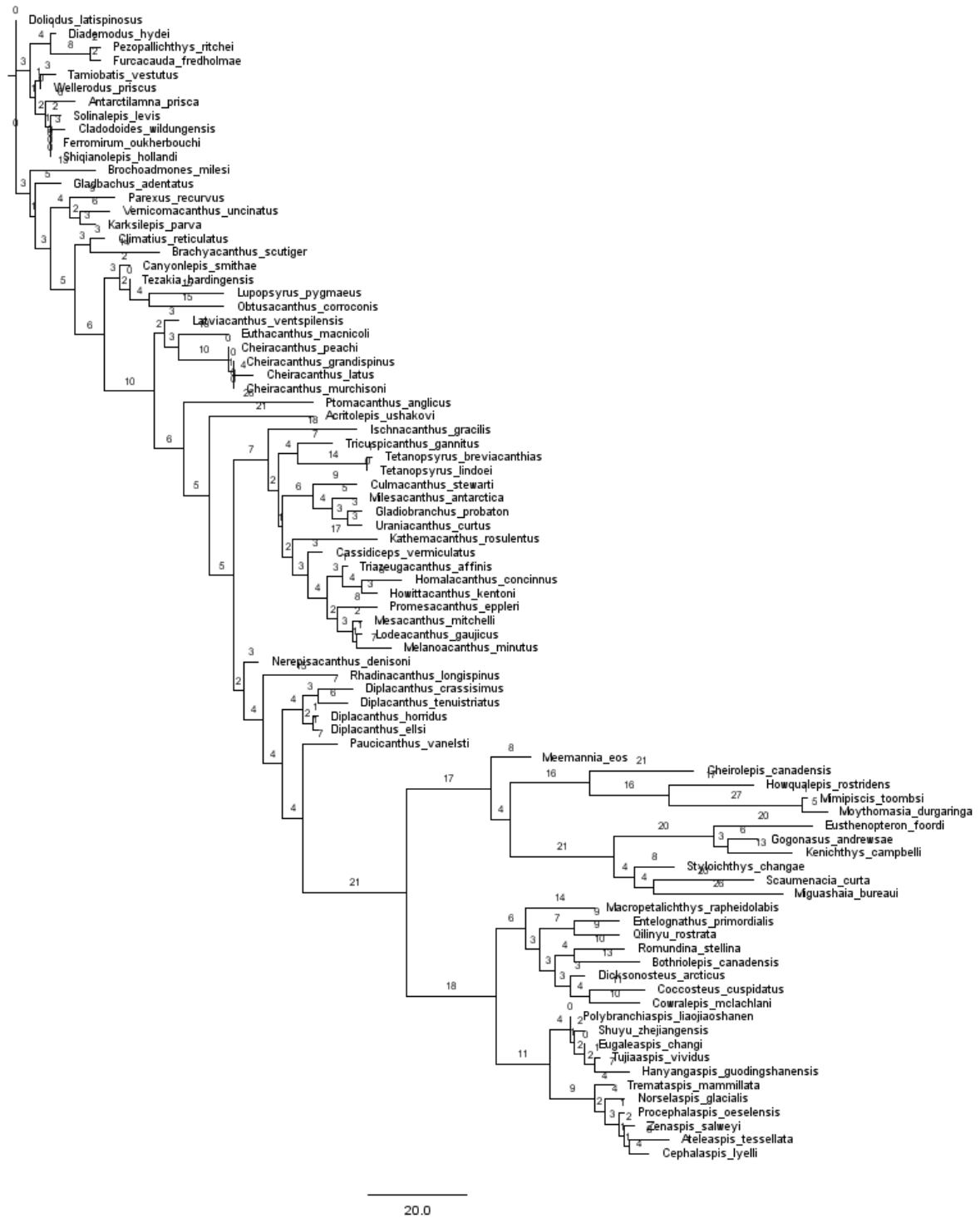


Dicksonosteus arcticus as outgroup



20.0

Doliodus latispinosus as outgroup



Furcacauda fredholmae as outgroup



20.0

Hanyangaspis guodingshanensis as outgroup



20.0

Solinalepis levis as outgroup



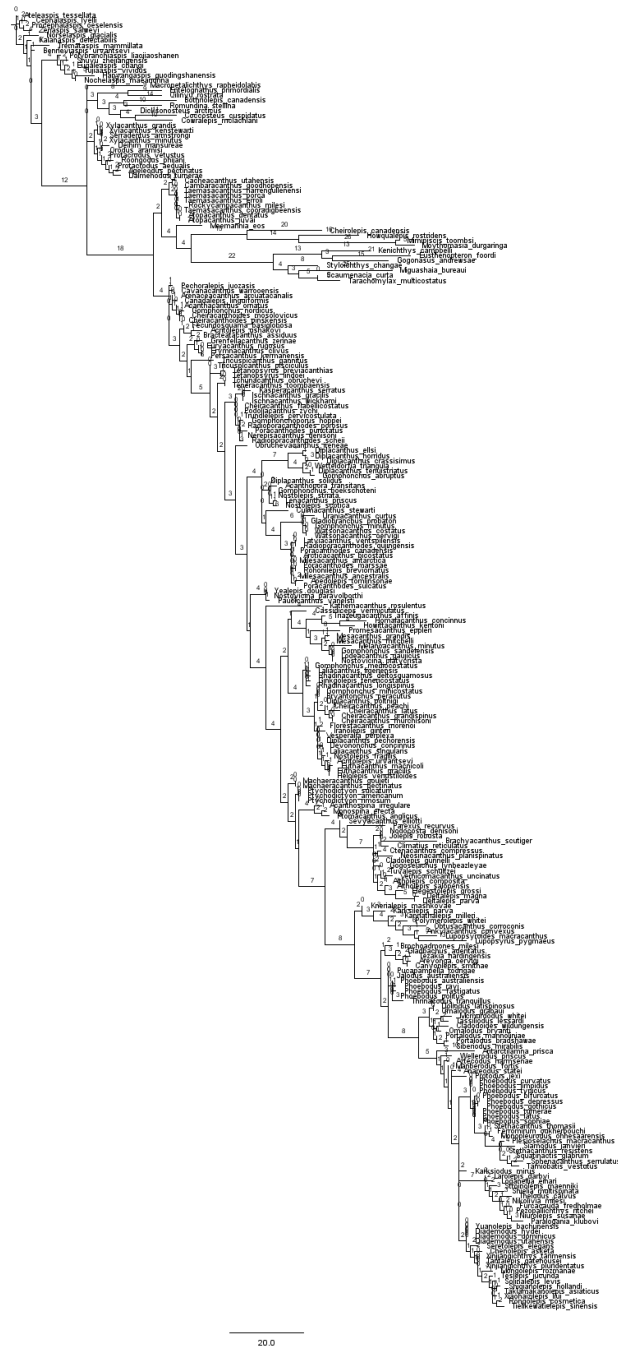
20.0

Styloichthys changae as outgroup

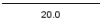


Resulting tree from parsimony analysis on the matrix with 259 taxa and 792 morphological characters. The trees are presented with branch length corresponding to evolutionary steps.

Ateleaspis tessellata as outgroup

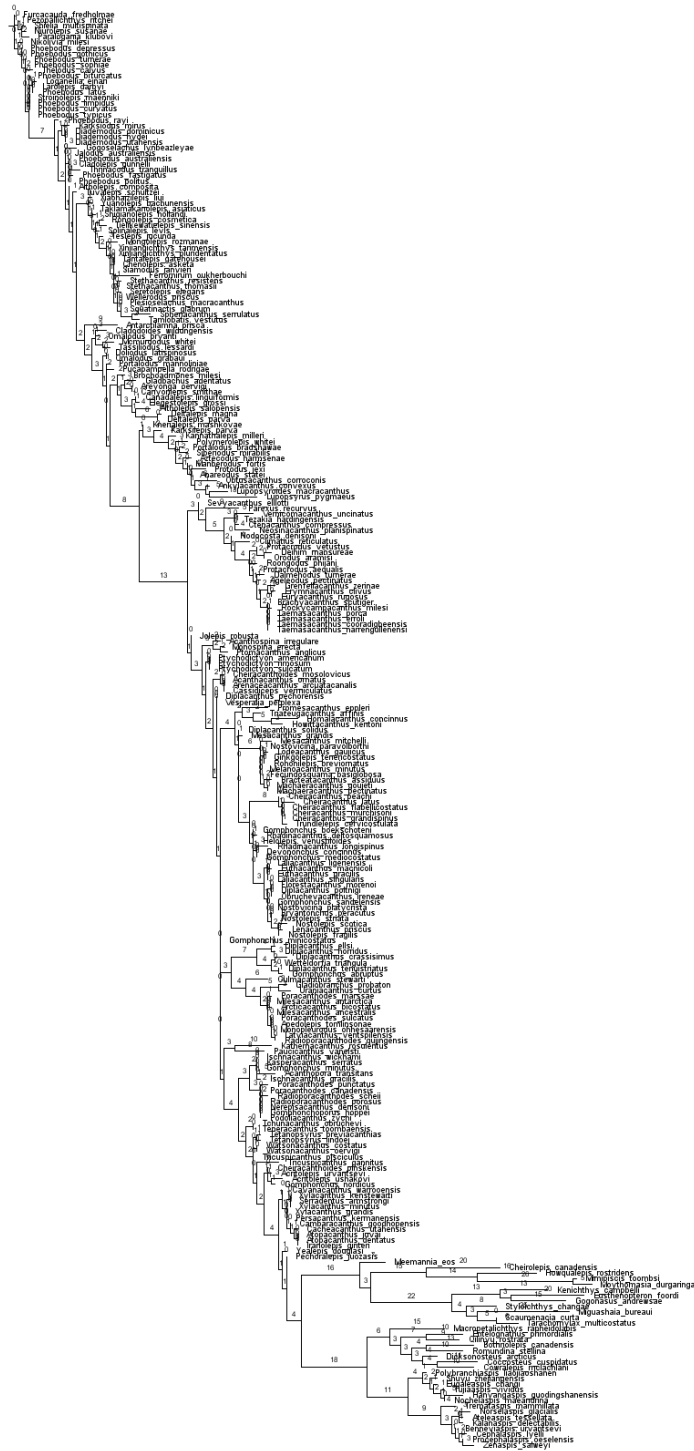


Dicksonosteus articus as outgroup



Doliodus latispinosus as outgroup

Furcacauda fredholmae as outgroup



Hanyangaspis guodingshanensis as outgroup



Solinalepis levis as outgroup

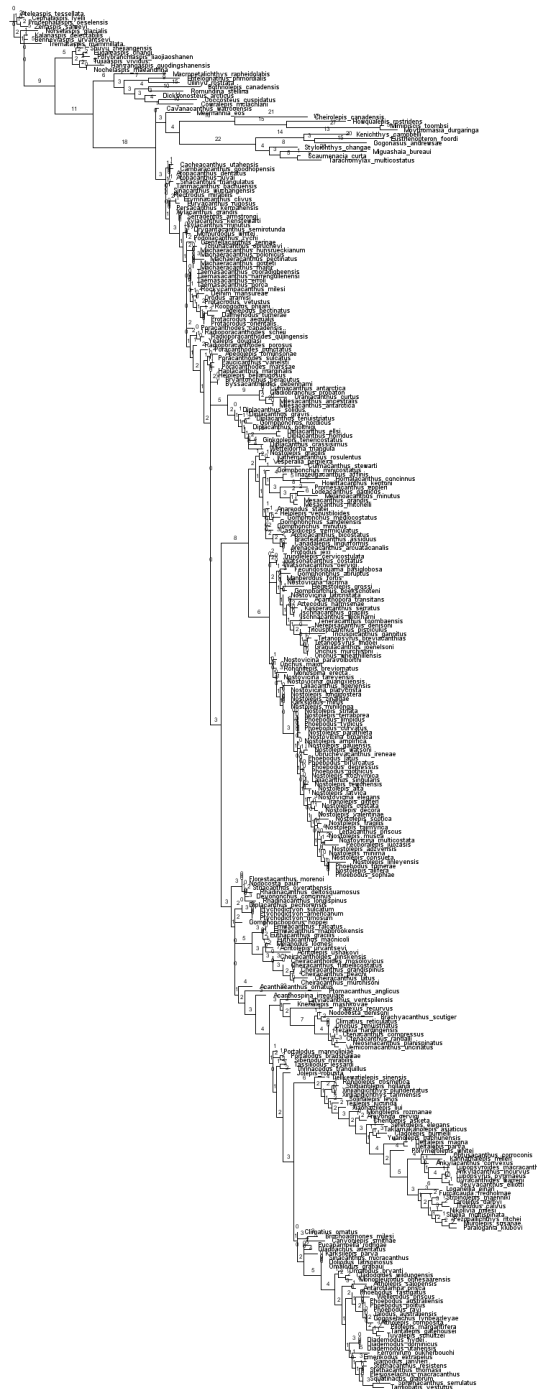


Styloichthys changae as outgroup



Resulting tree from parsimony analysis on the matrix with 320 taxa and 977 morphological characters. The trees are presented with branch length corresponding to evolutionary steps.

Ateleaspis tessellata as outgroup



Dicksonosteus articus as outgroup



Doliodus latispinosus as outgroup



Furcacauda fredholmae as outgroup



Phylogenetic tree of the genus *Phyllonoma* and related genera, showing relationships and bootstrap values. The tree is rooted at the top left and branches downwards. Bootstrap values are indicated at the nodes. The tree shows a large clade of *Phyllonoma* species, with several smaller clades of related genera like *Phyllonoma*, *Phyllonoma*, and *Phyllonoma*. The tree is highly detailed, with many species names listed at the tips of the branches.

Solinalepis levis as outgroup

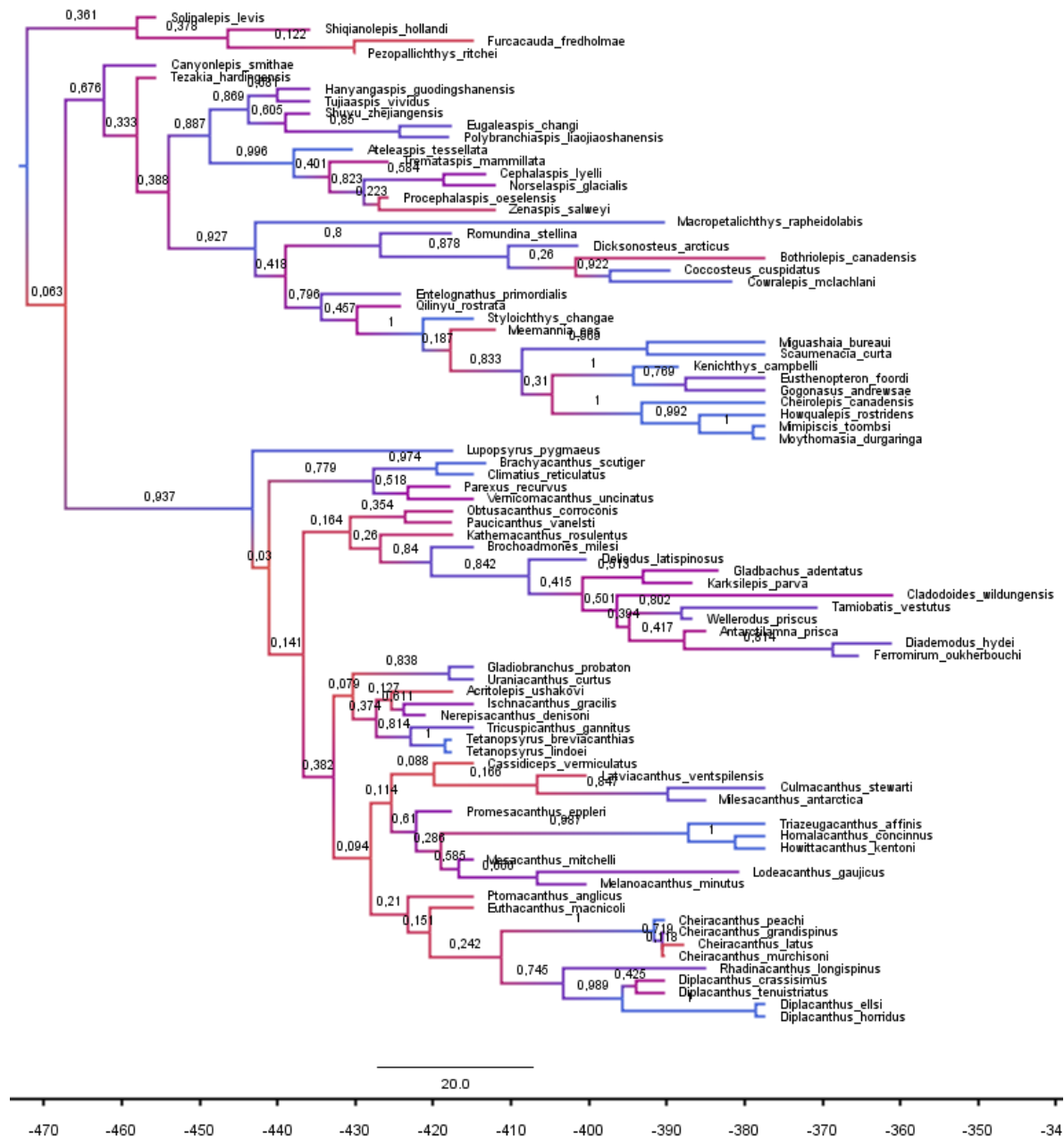


Styloichthys changae as outgroup

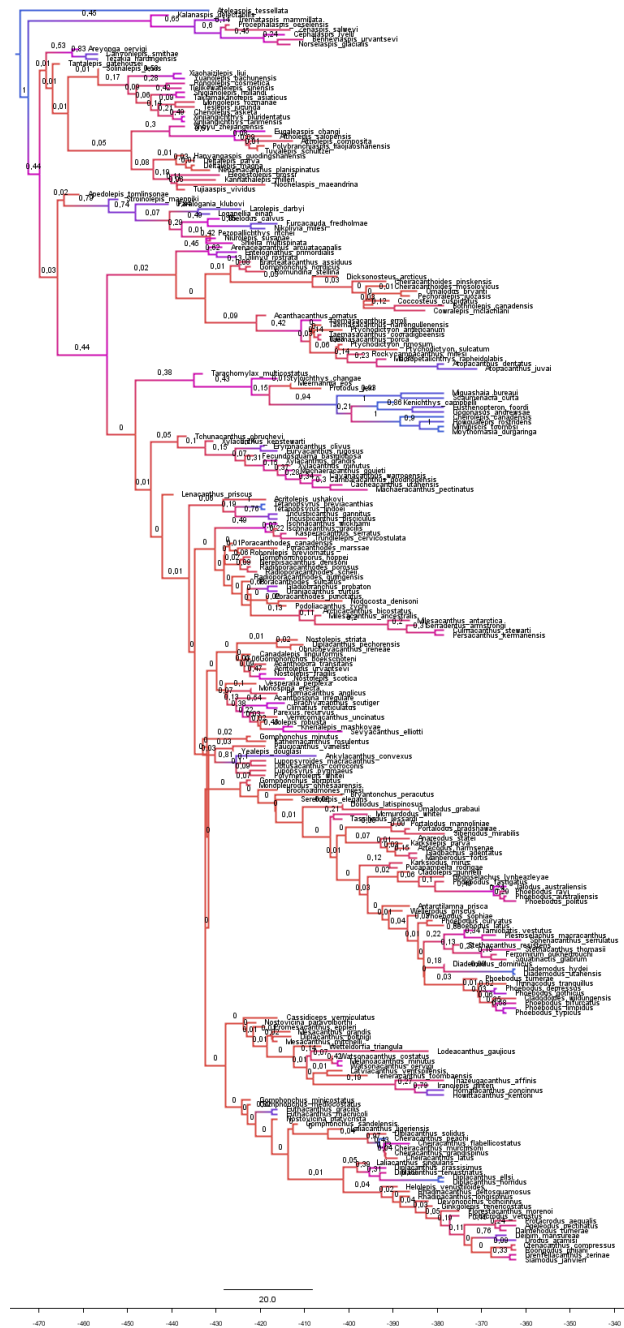


Annex 6: additional Bayesian calibrated trees from BEAST

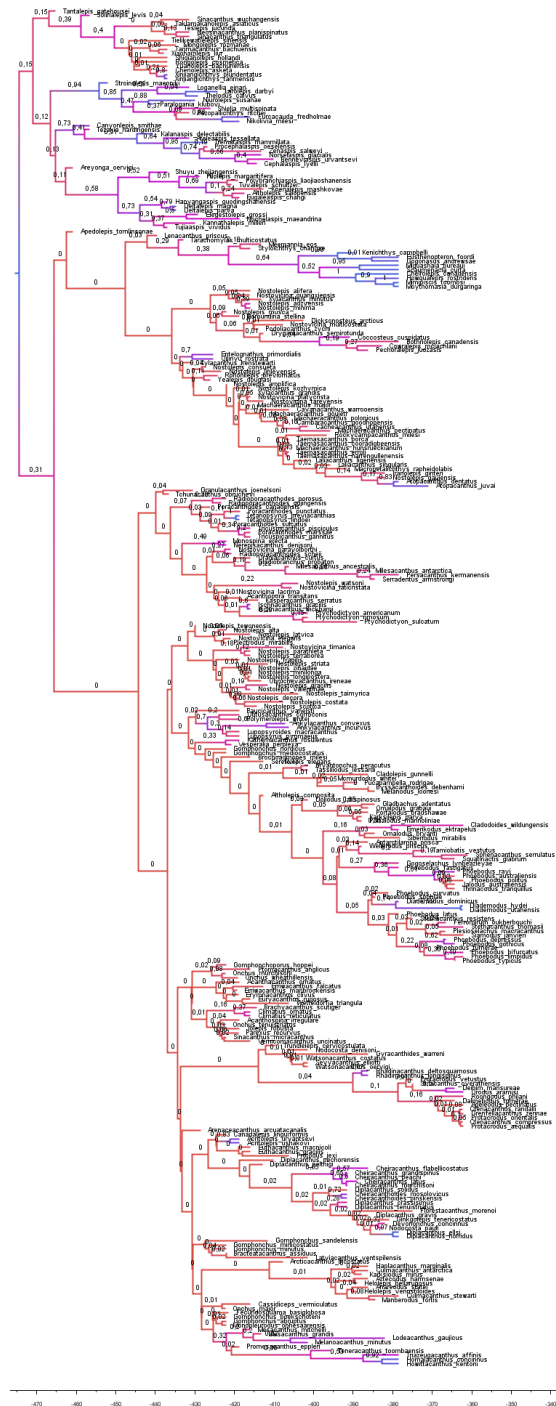
Resulting tree from matrix with 84 taxa and 792 morphological characters. Analyzed in BEAST with the FBD model, MCC tree reconstruction, no MRCA (unrooted tree) and branches colored with posterior support. Time scale in x axis.



Resulting tree from matrix with 259 taxa and 792 morphological characters. Analyzed in BEAST with the FBD model, MCC tree reconstruction, *Ateleaspis tessellata* as outgroup and branches colored with posterior support. Time scale in x axis.



Resulting tree from matrix with 320 taxa and 977 morphological characters. Analyzed in BEAST with the FBD model, MCC tree reconstruction, no MRCA (unrooted tree) and branches colored with posterior support. Time scale in x axis.



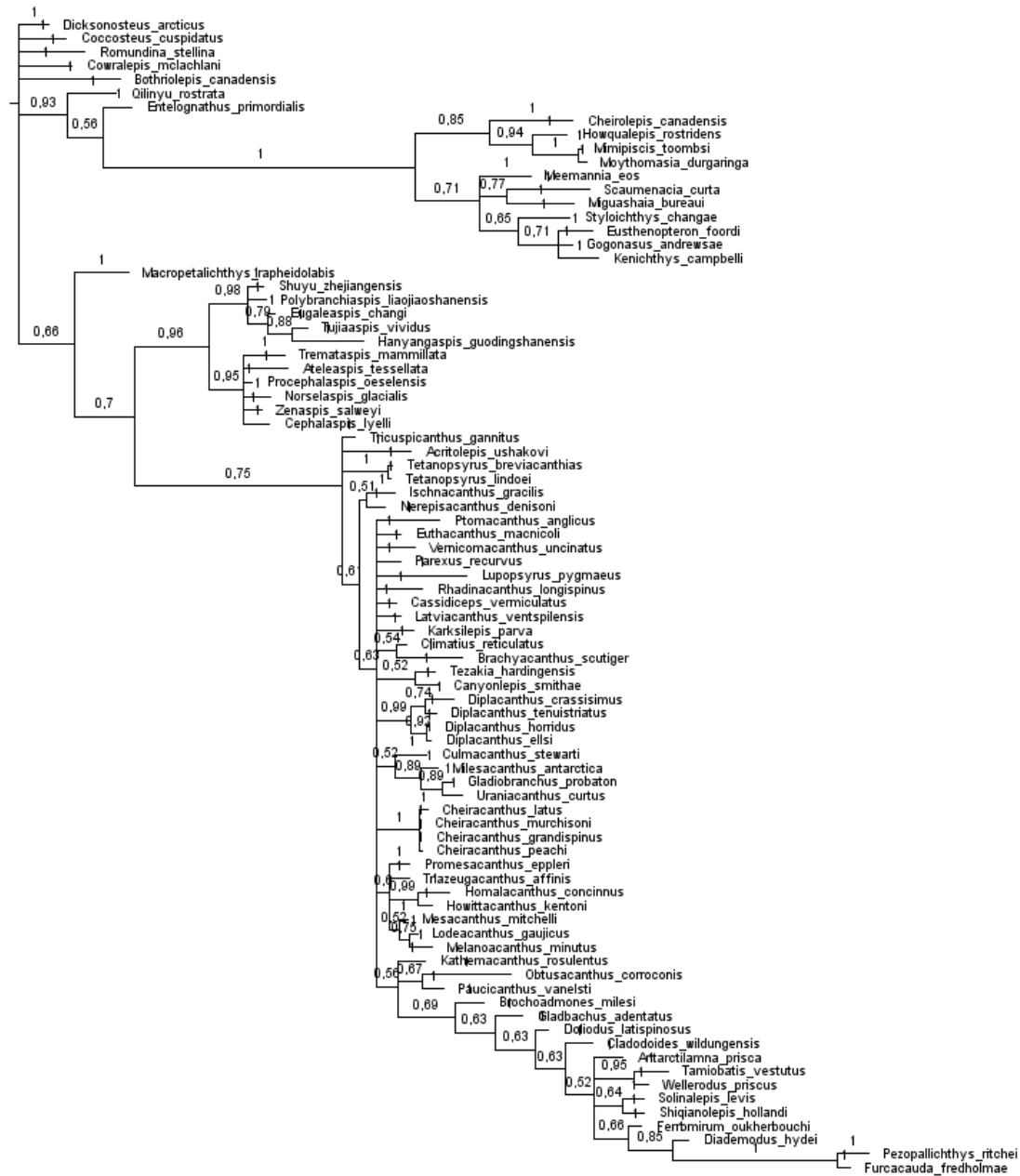
Annex 7: resulting trees from uncalibrated Bayesian analysis using MrBayes

Resulting trees from MrBayes, 50 majority rule consensus, for matrix with 84 taxa and 792 morphological characters. Branch labels represent posterior probability and the length of the branches the number of steps.

Ateleaspis tessellata as outgroup



Dicksonosteus articus as outgroup



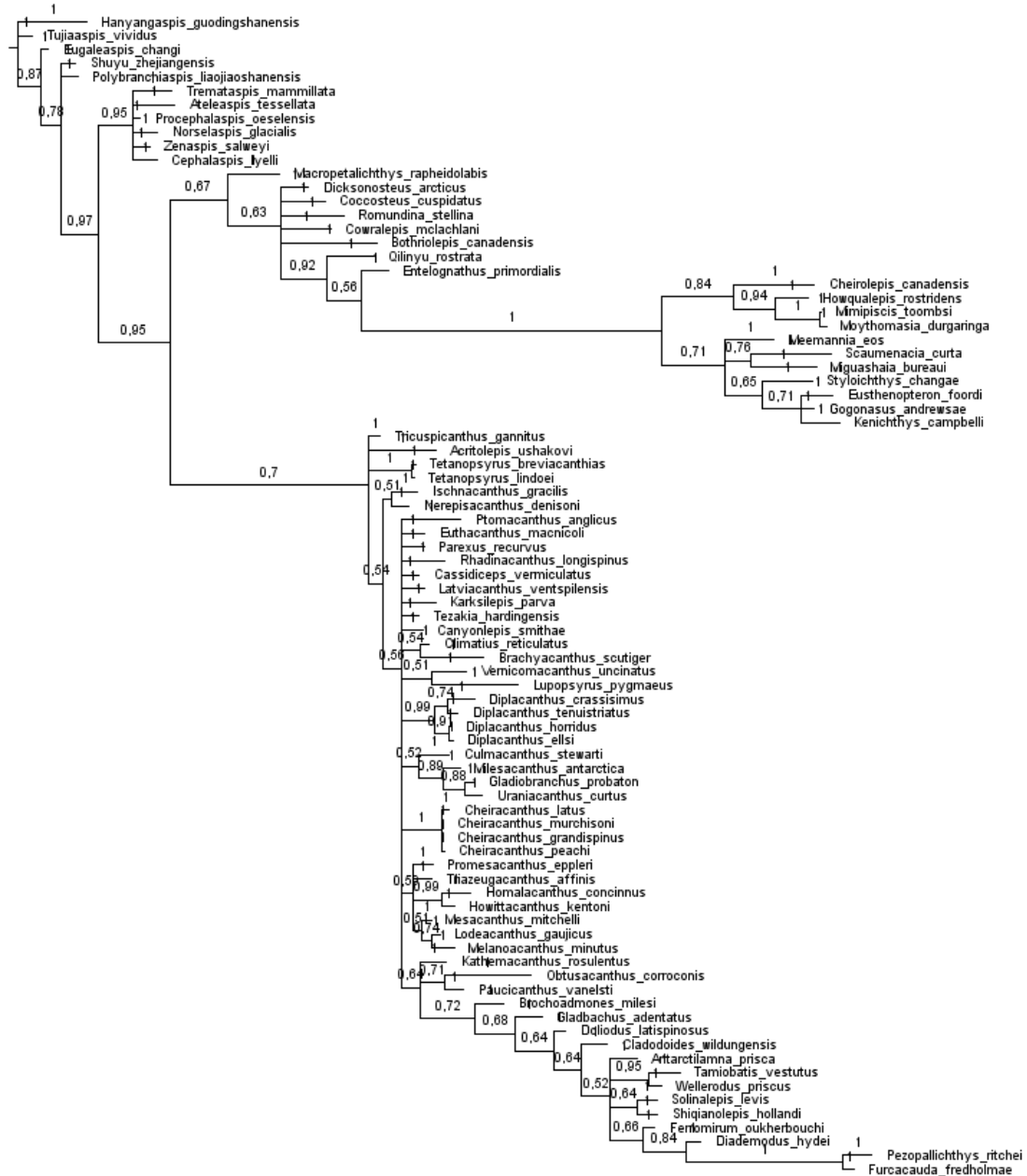
Doliodus latispinosus as outgroup



Furcacauda fredholmae as outgroup



Hanyangaspis guodingshanensis as outgroup



Solinalepis levis as outgroup

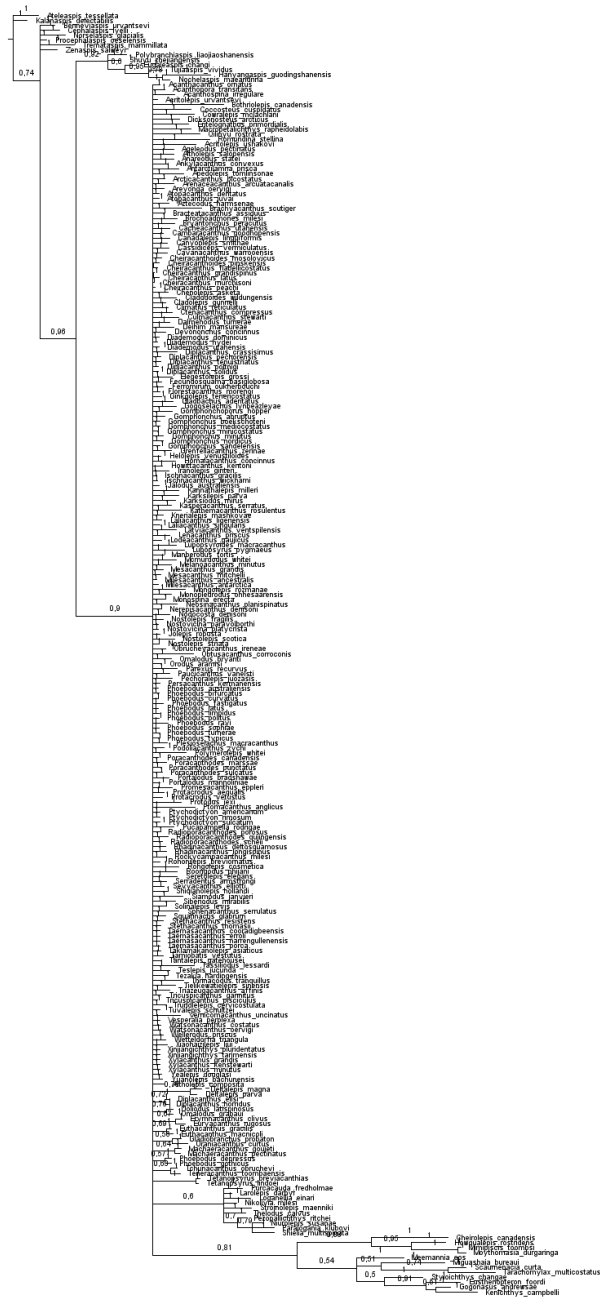


Styloichthys changae as outgroup

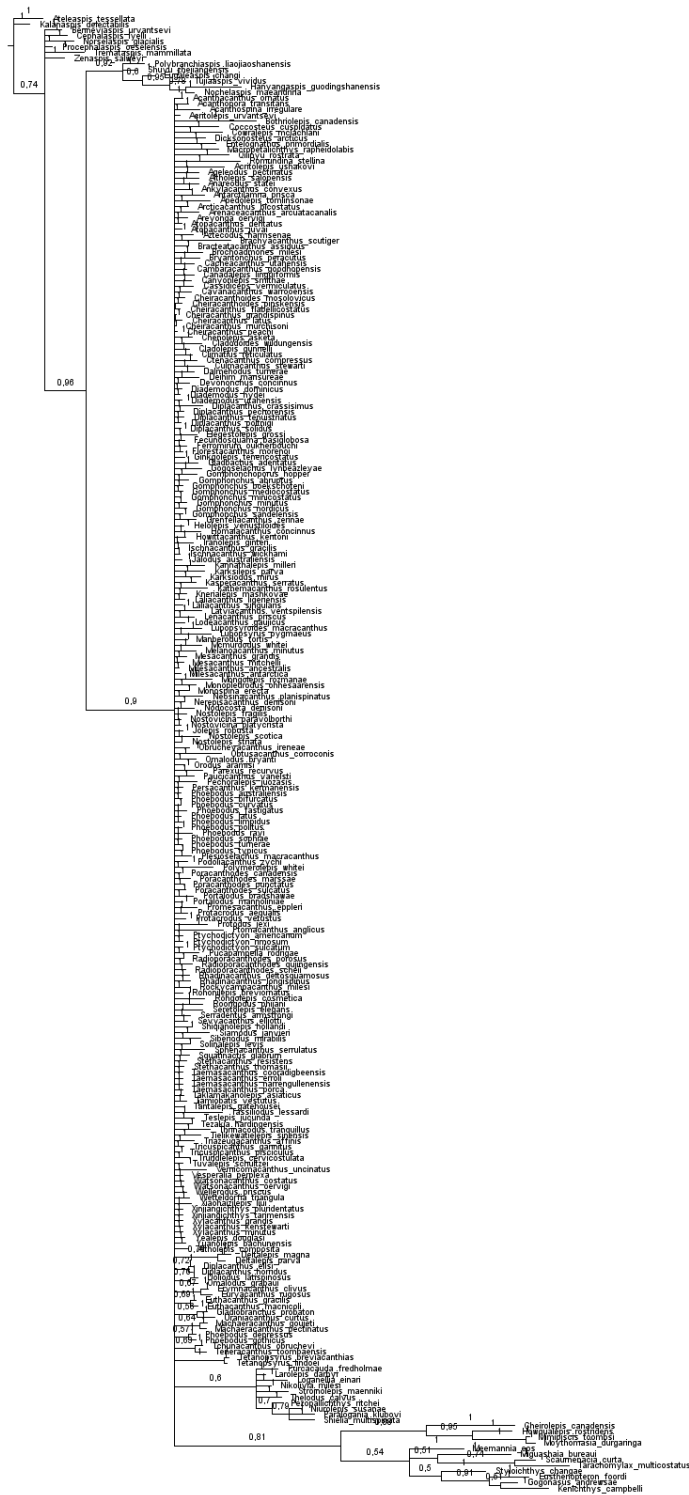


Resulting trees from MrBayes, 50 majority rule consensus, for matrix with 259 taxa and 792 morphological characters. Branch labels represent posterior probability and the length of the branches the number of steps.

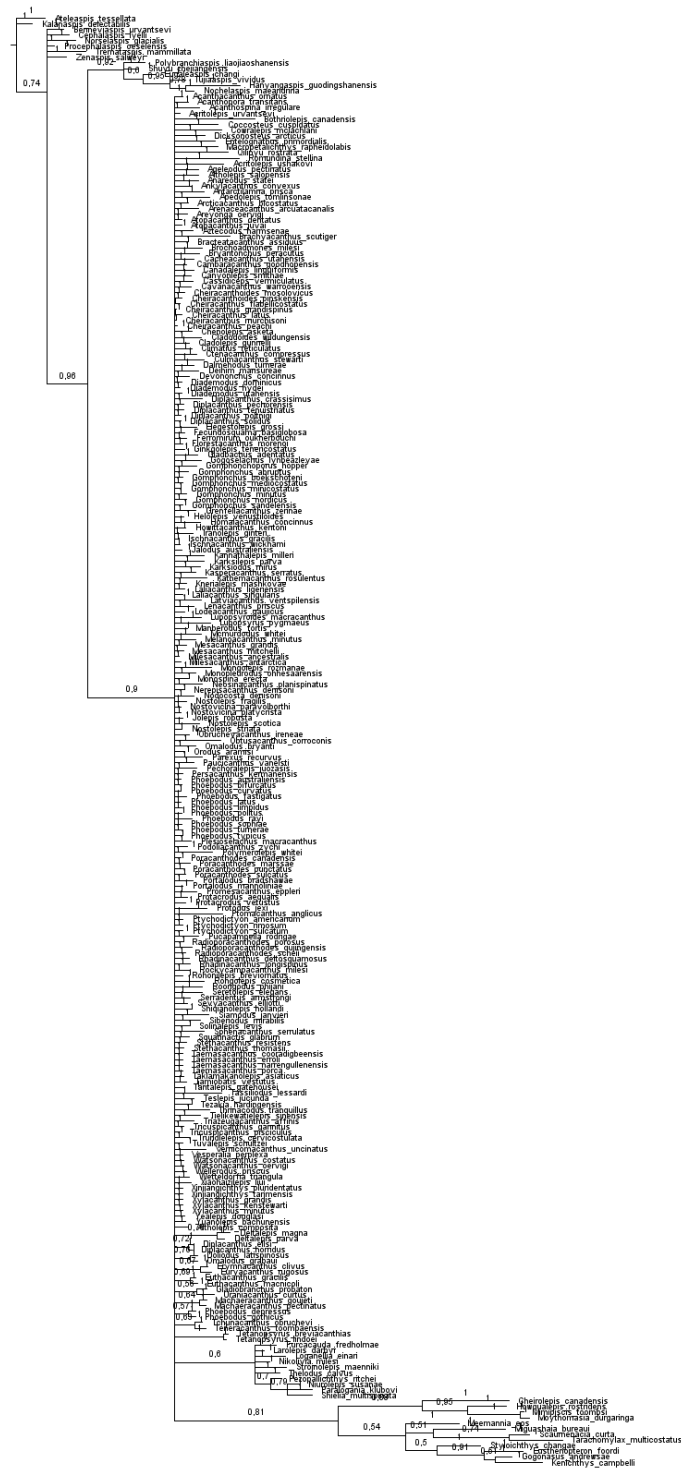
Ateleaspis tessellata as outgroup



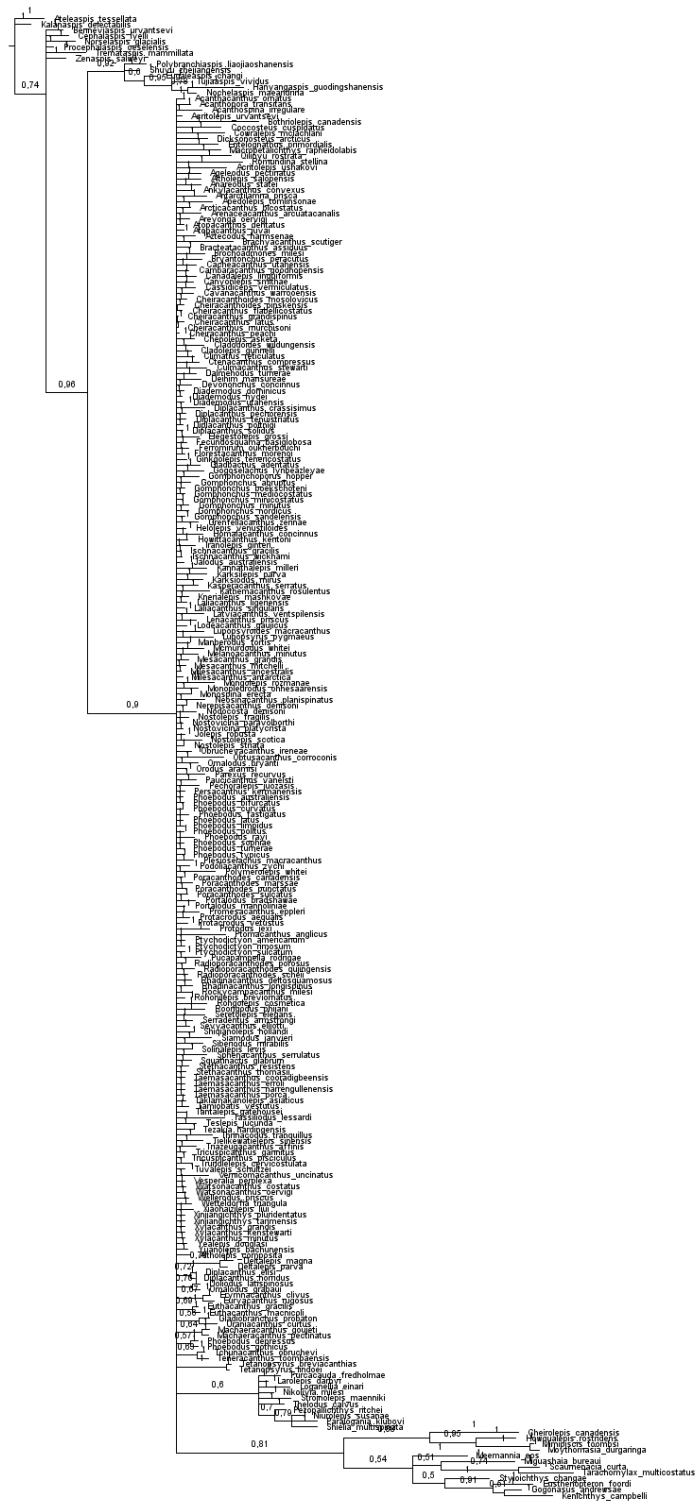
Dicksonosteus articus as outgroup



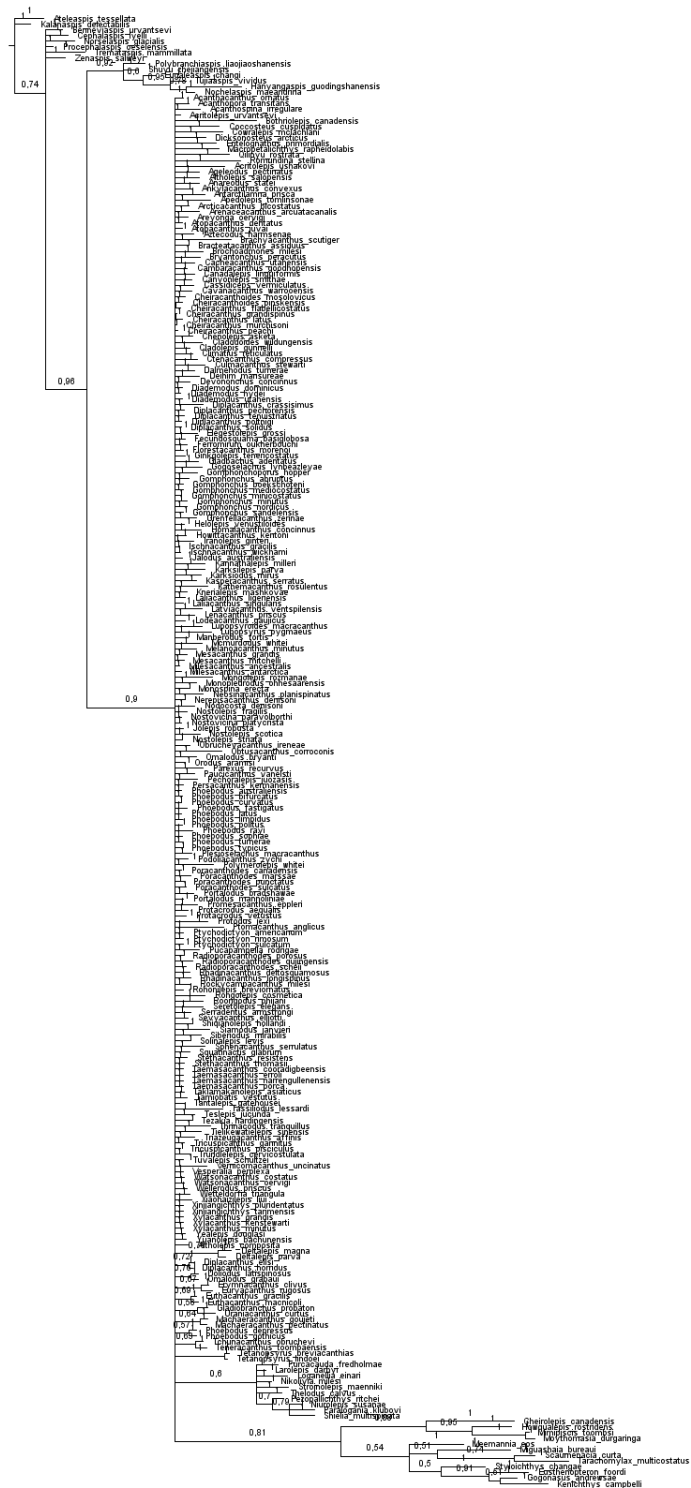
Doliodus latispinosus as outgroup



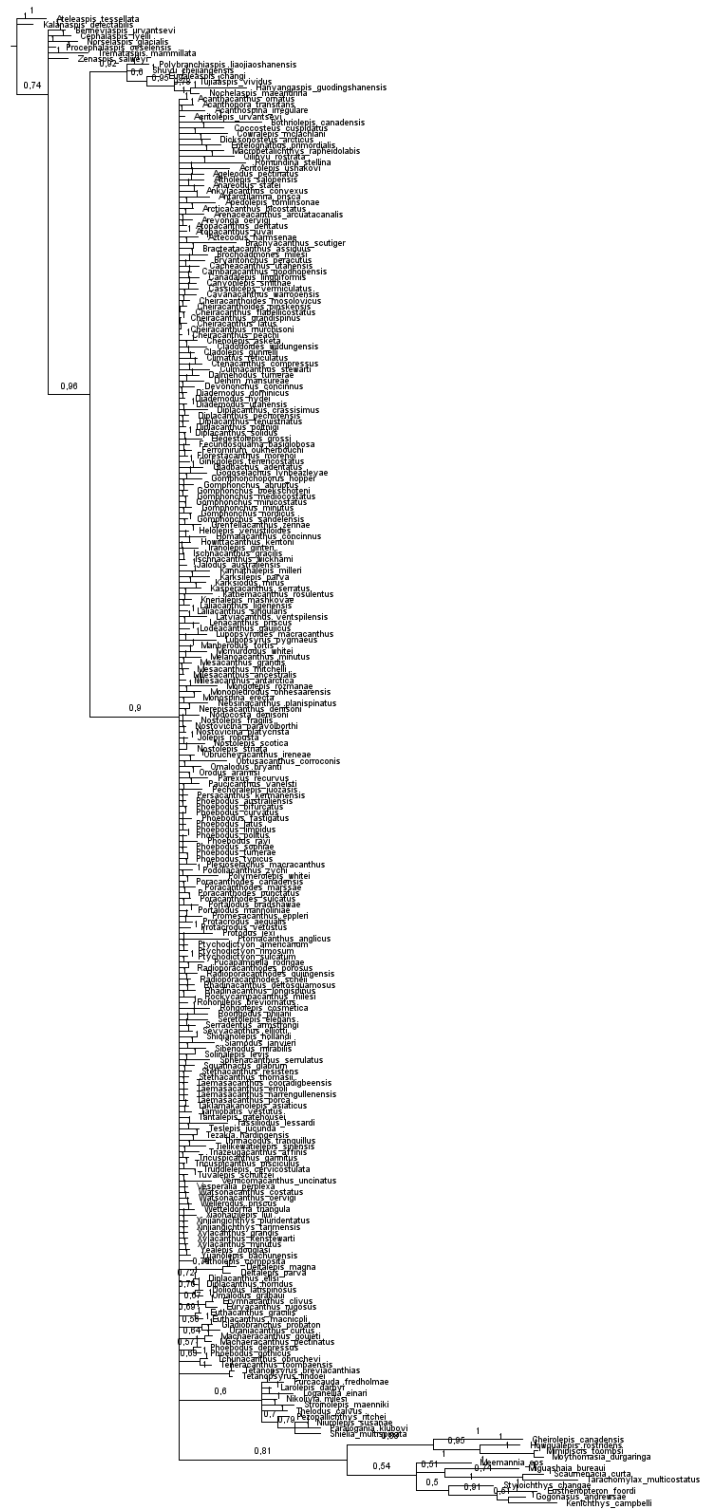
Furcacauda fredholmae as outgroup



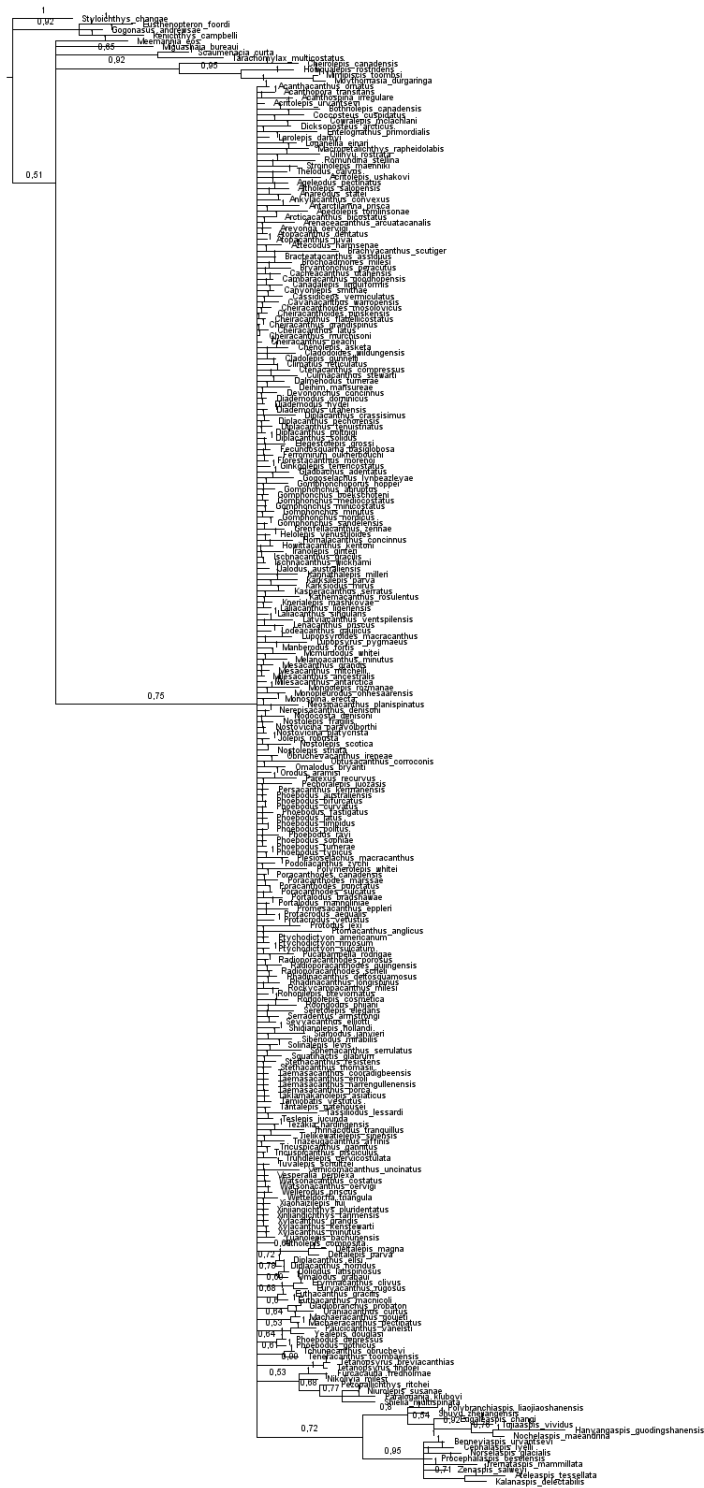
Hanyangaspis guodingshanensis as outgroup



Solinalepis levis as outgroup

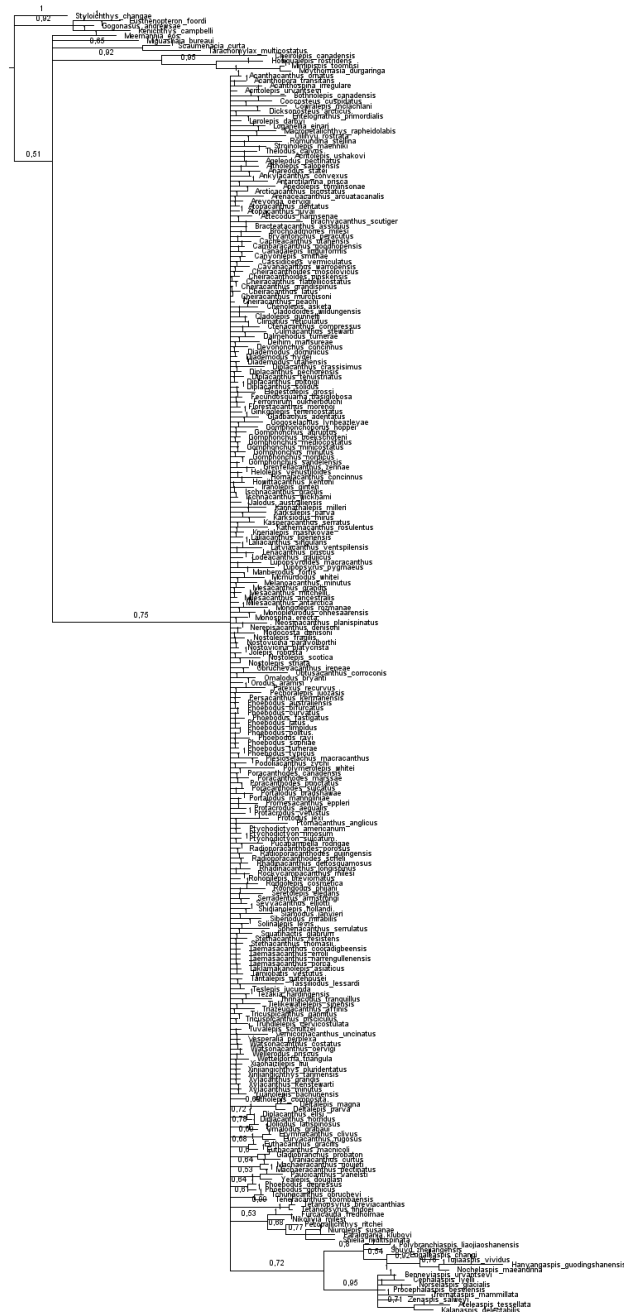


Styloichthys changae as outgroup

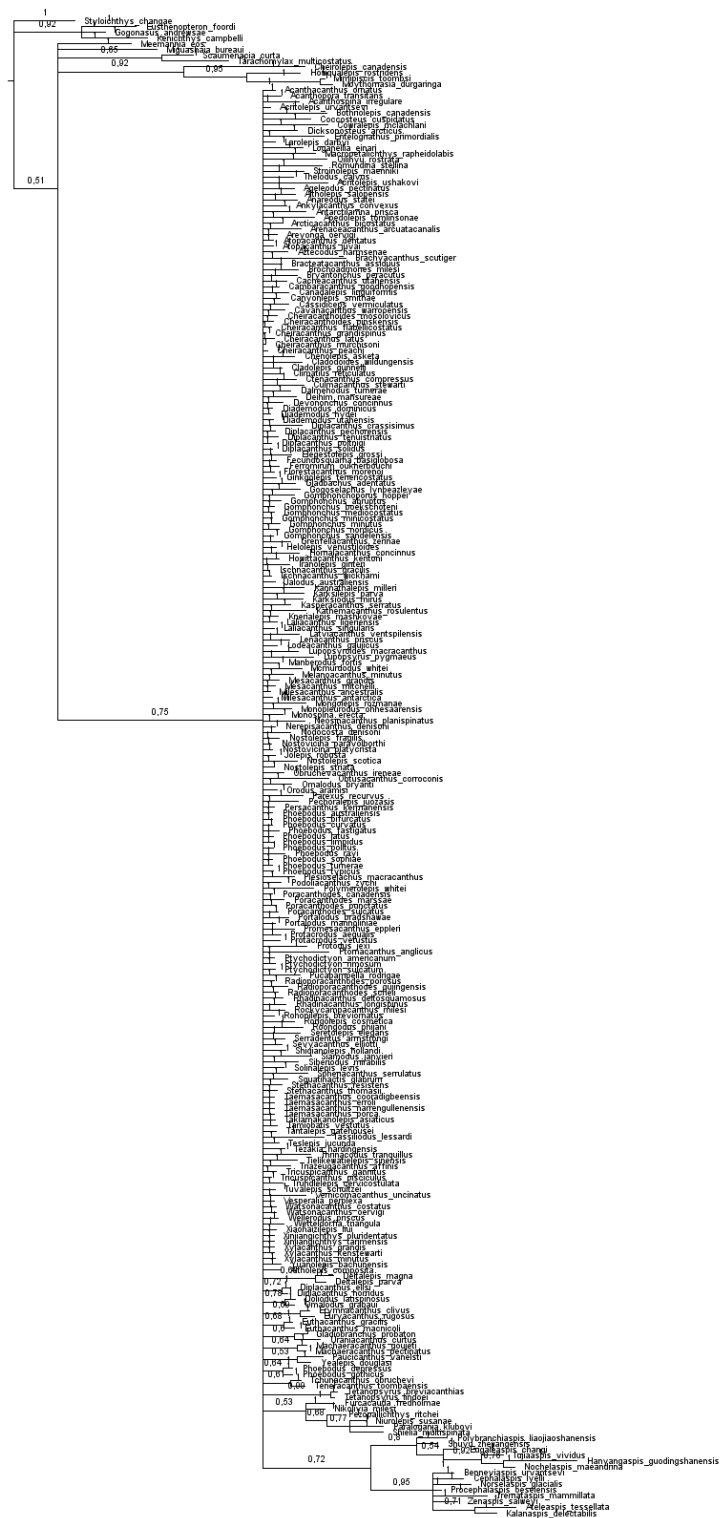


Resulting trees from MrBayes, 50 majority rule consensus, for matrix with 320 taxa and 977 morphological characters. Branch labels represent posterior probability and the length of the branches the number of steps.

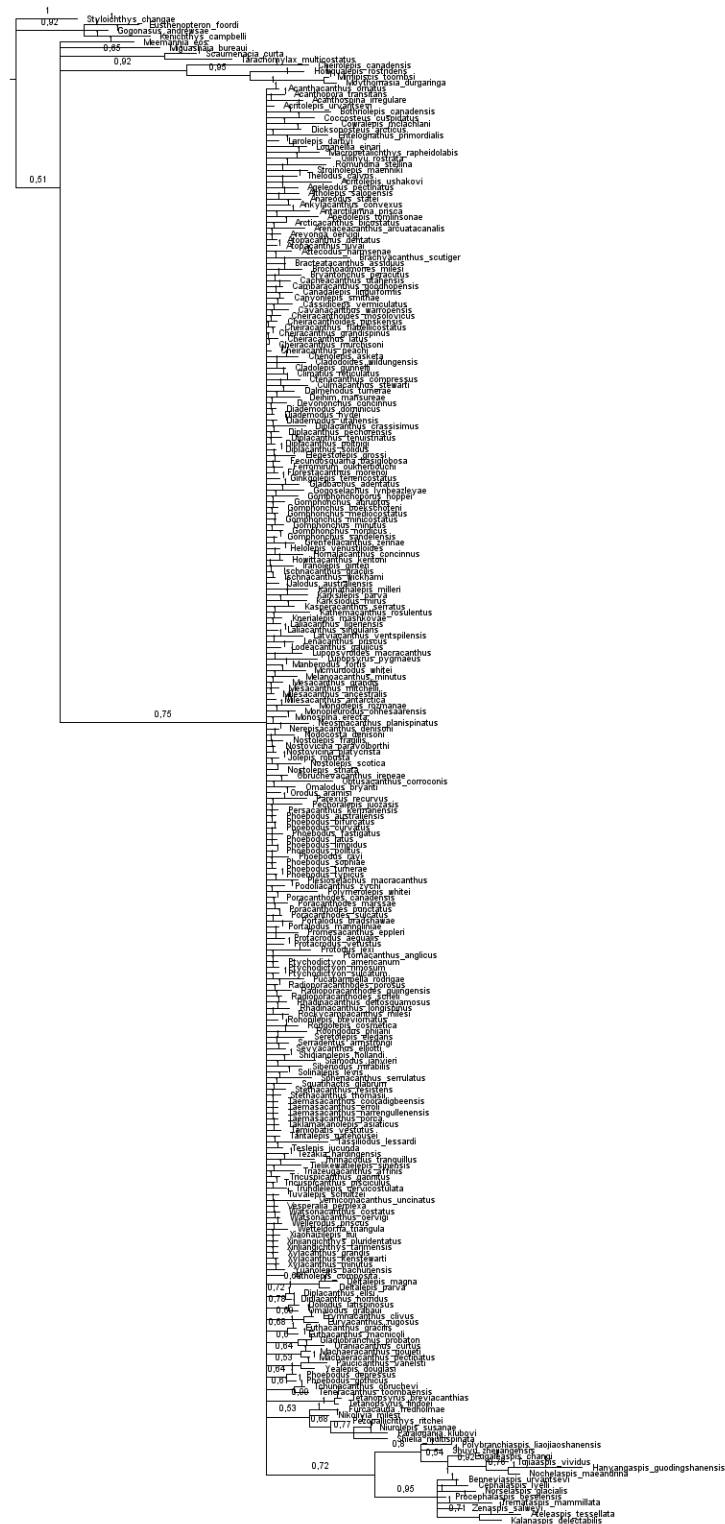
Ateleaspis tessellata as outgroup



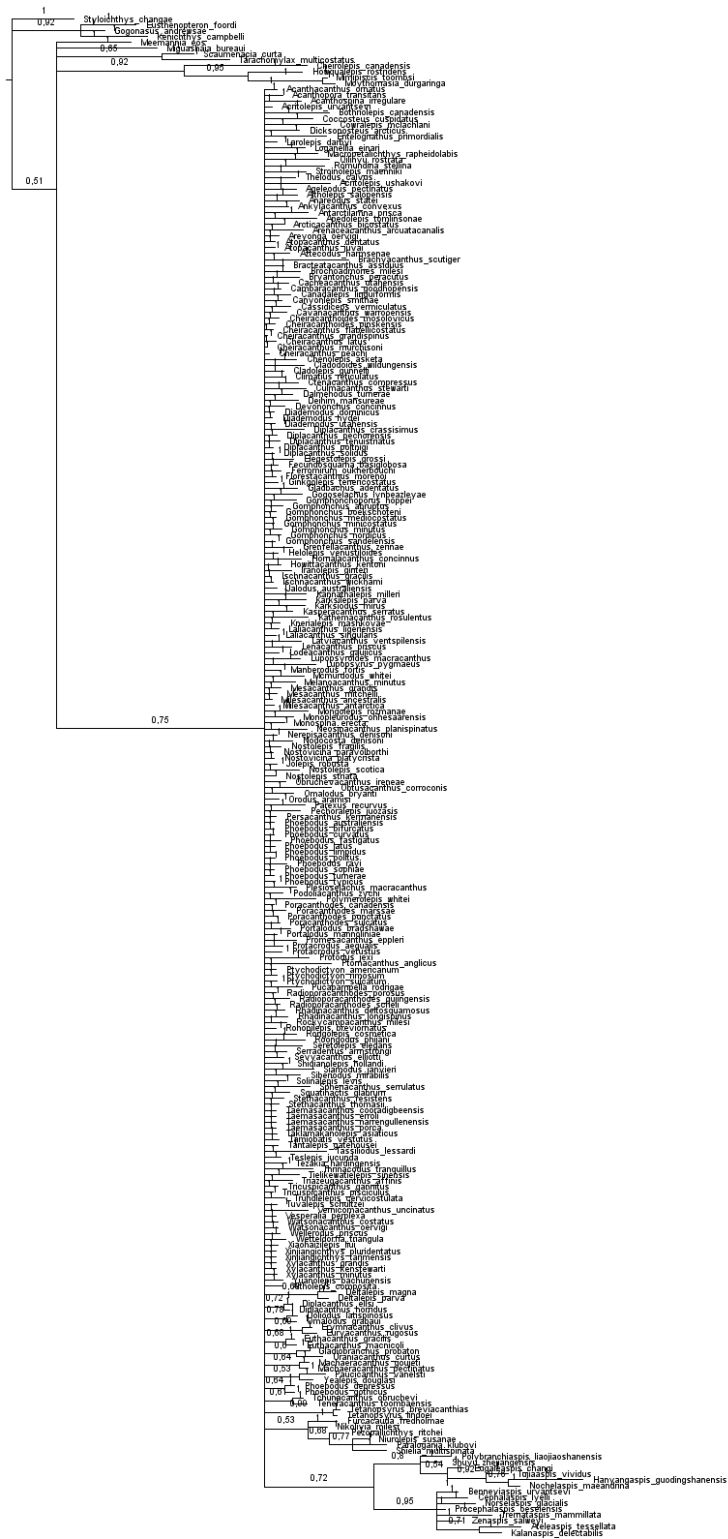
Dicksonosteus articus as outgroup



Doliodus latispinosus as outgroup



Furcacauda fredholmae as outgroup



Hanyangaspis guodingshanensis as outgroup



Solinalepis levis as outgroup

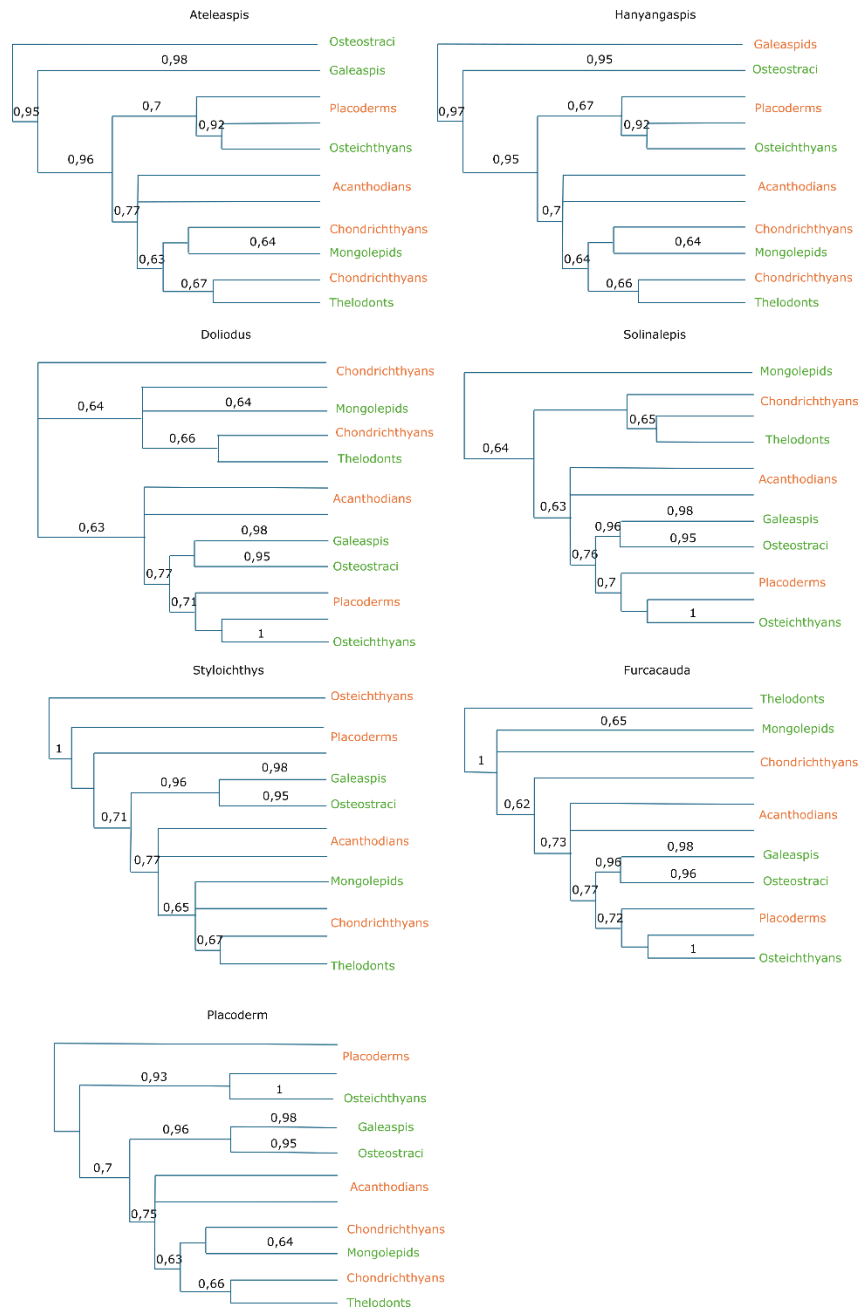


Styloichthys changae as outgroup

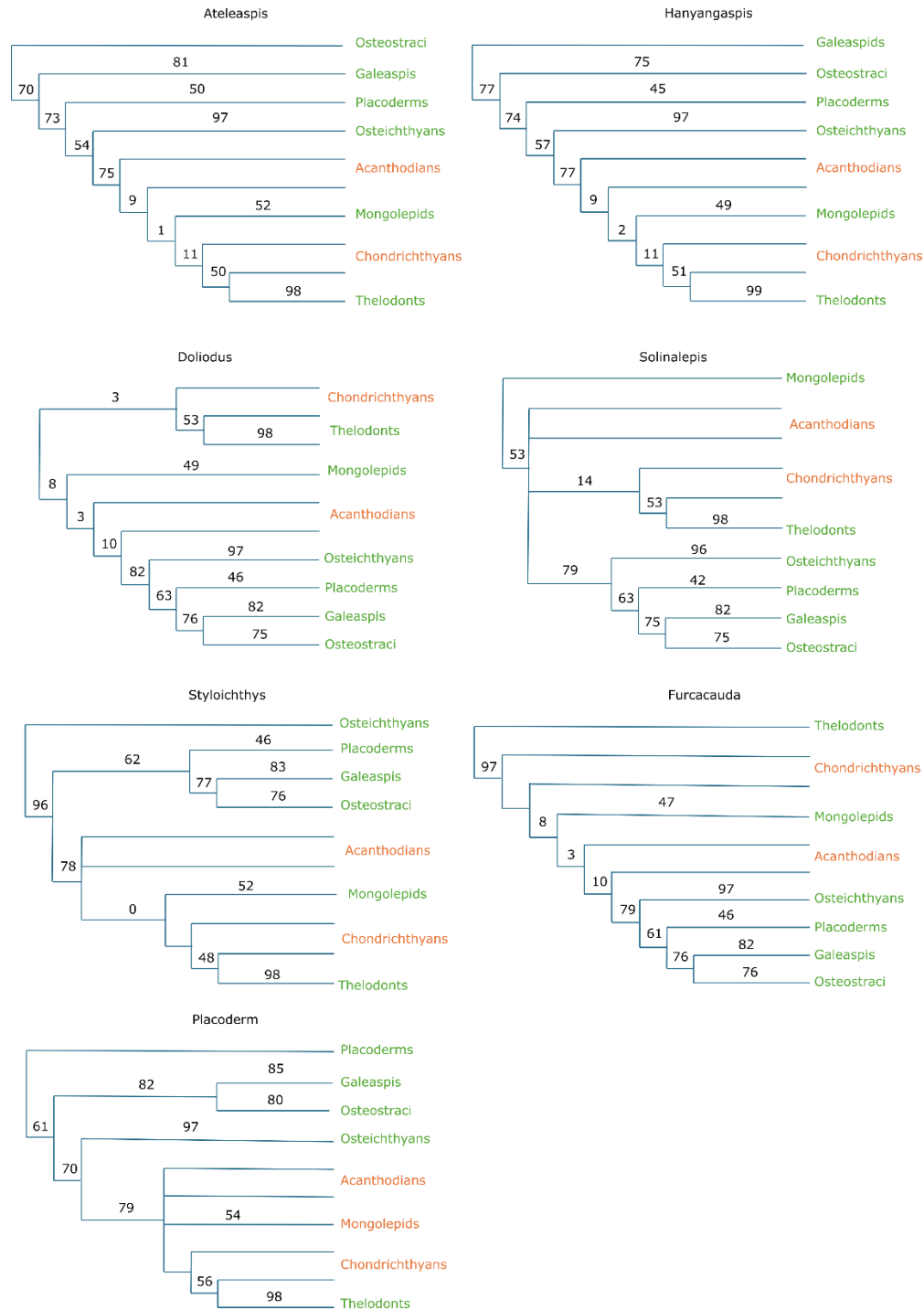


Annex 8: Resumed Trees for Network tree analysis

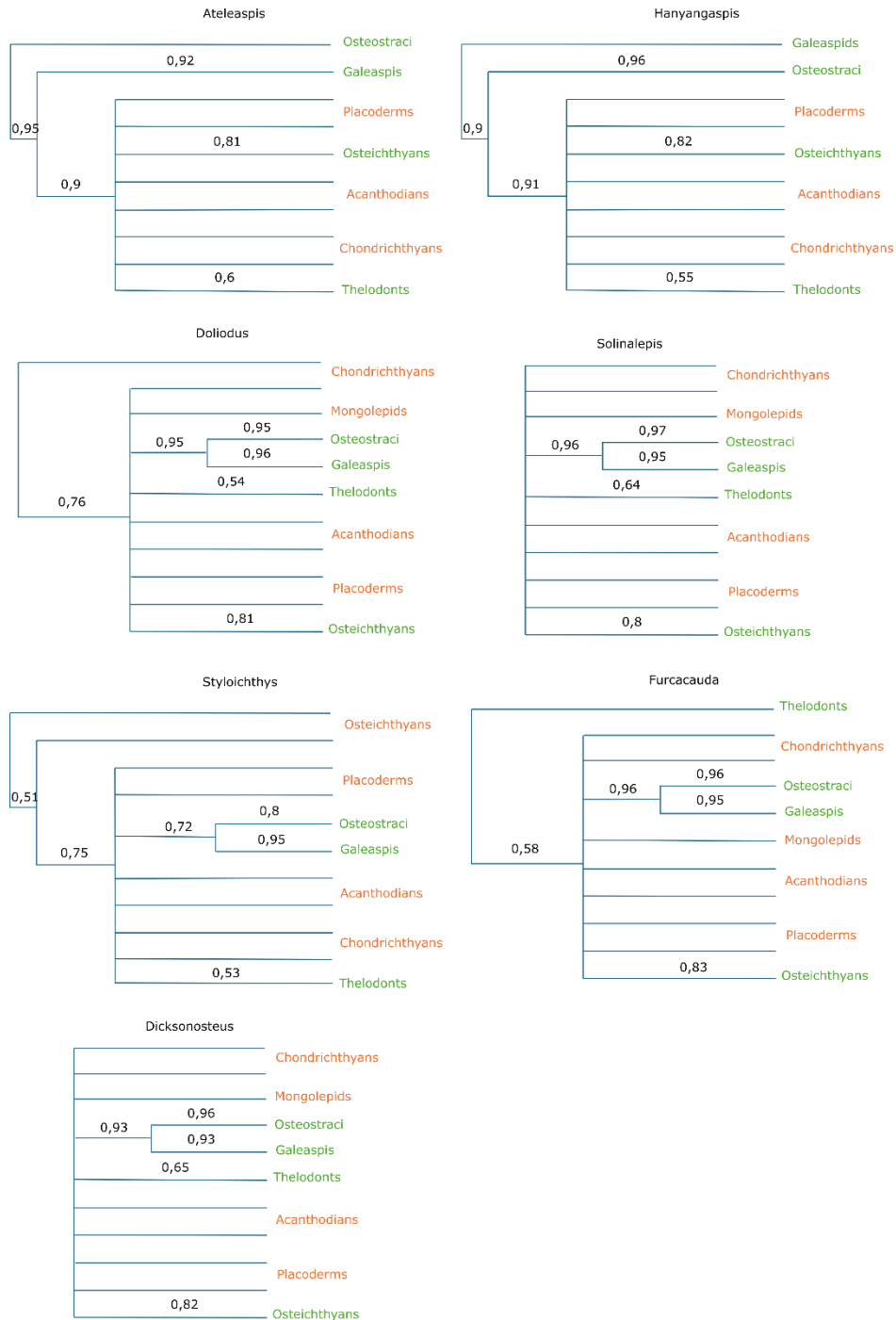
Simplified trees for the matrix with 84 taxa and 792 morphological characters in Bayesian uncalibrated method. Branch support is provided on branches. In green are represented the monophyletic group and in orange the paraphyletic or polyphyletic group.



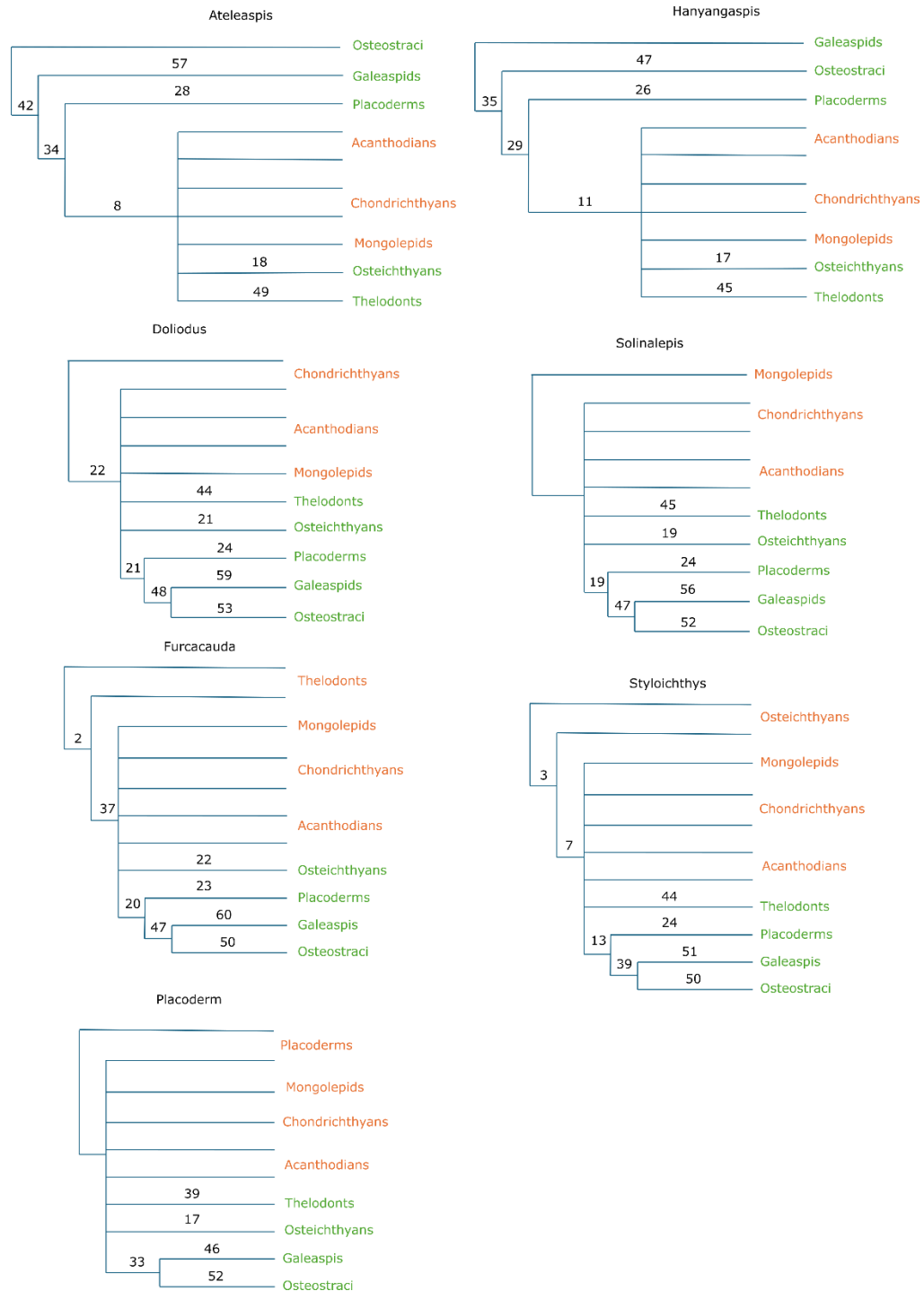
Simplified trees for the matrix with 84 taxa and 792 morphological characters in Maximum Parsimony method. Branch support is provided on branches. In green are represented the monophyletic group and in orange the paraphyletic or polyphyletic group.



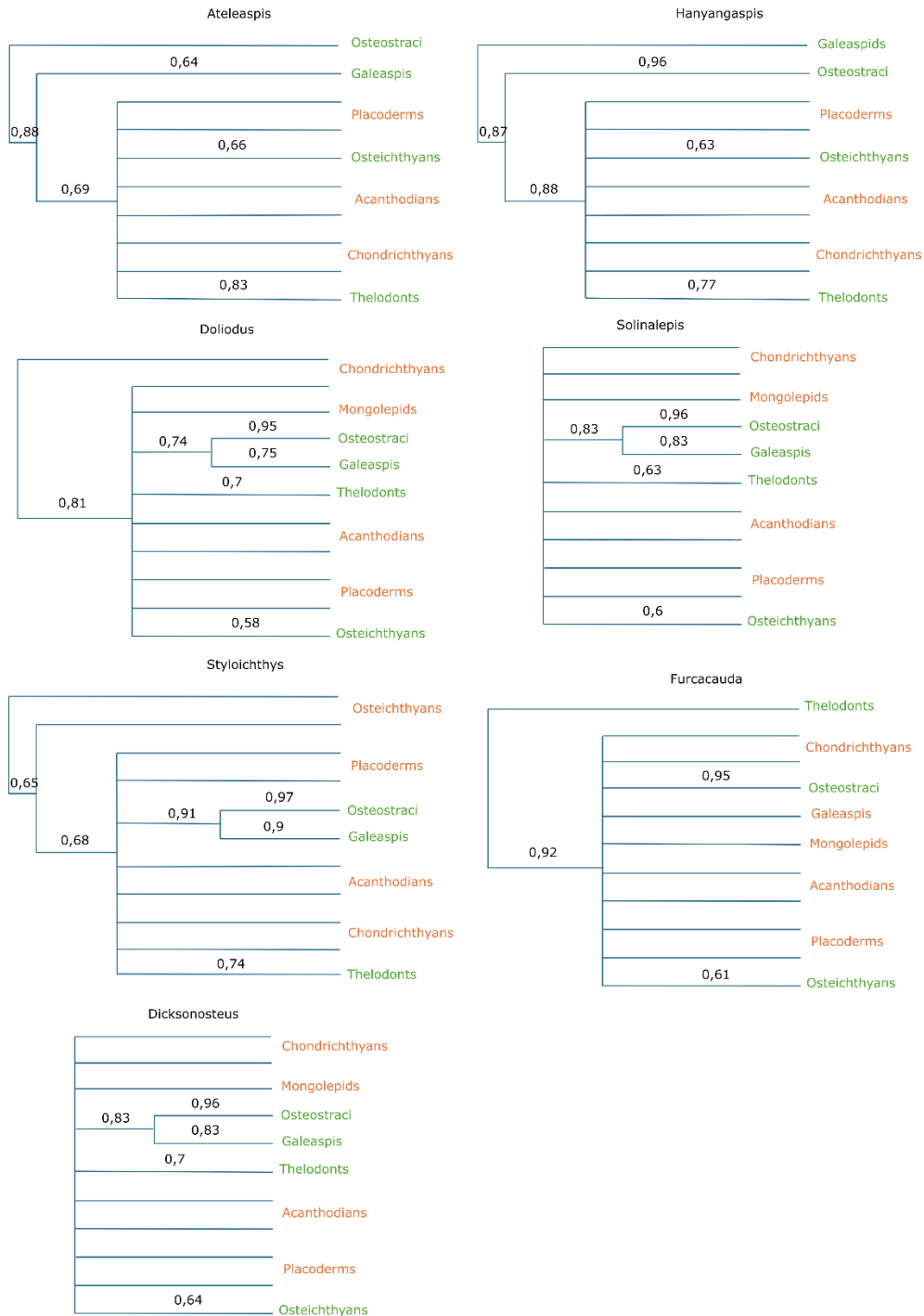
Simplified trees for the matrix with 259 taxa and 792 morphological characters in Bayesian uncalibrated method. Branch support is provided on branches. In green are represented the monophyletic group and in orange the paraphyletic or polyphyletic group.



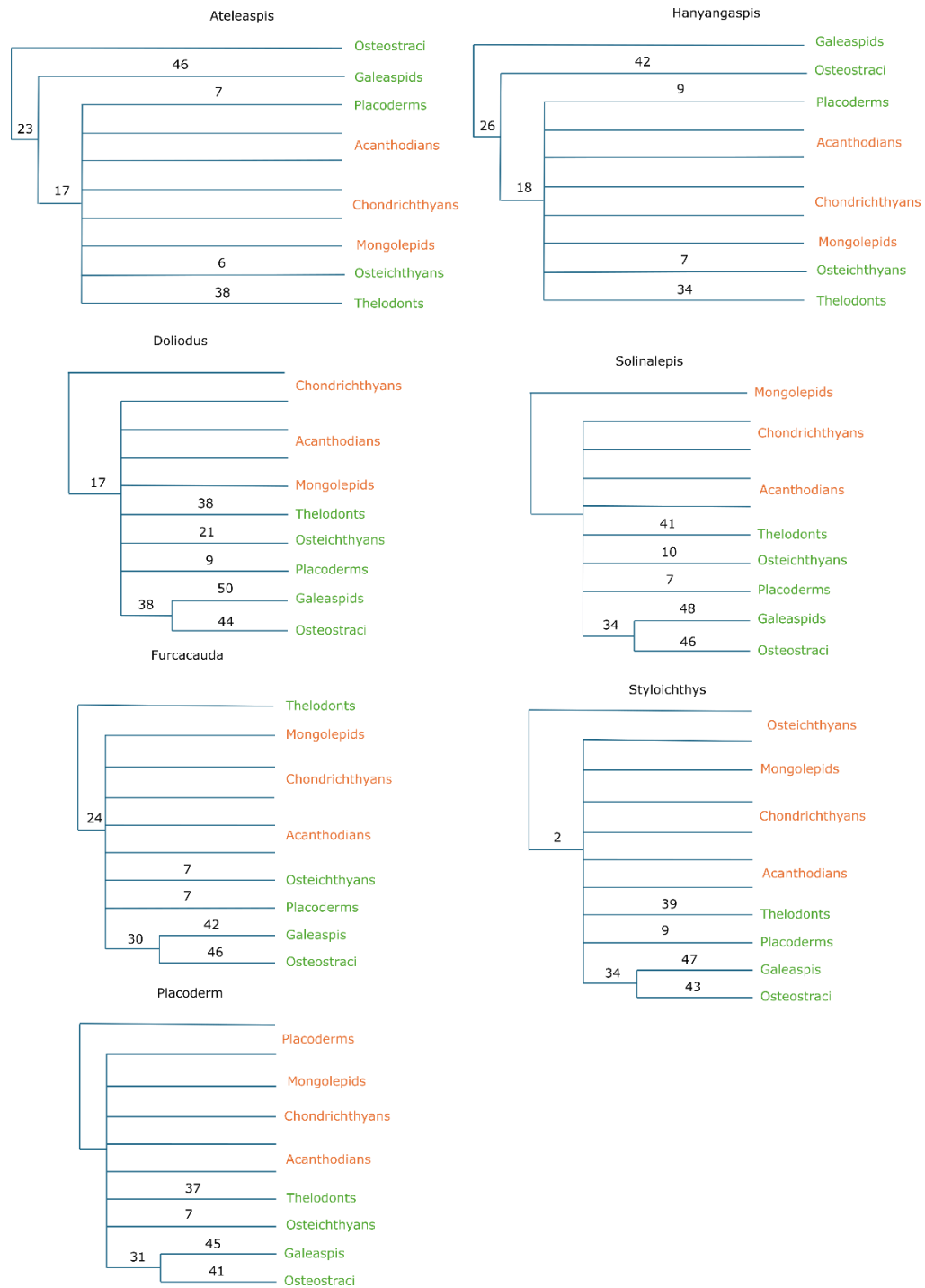
Simplified trees for the matrix with 259 taxa and 792 morphological characters in Maximum Parsimony method. Branch support is provided on branches. In green are represented the monophyletic group and in orange the paraphyletic or polyphyletic group.



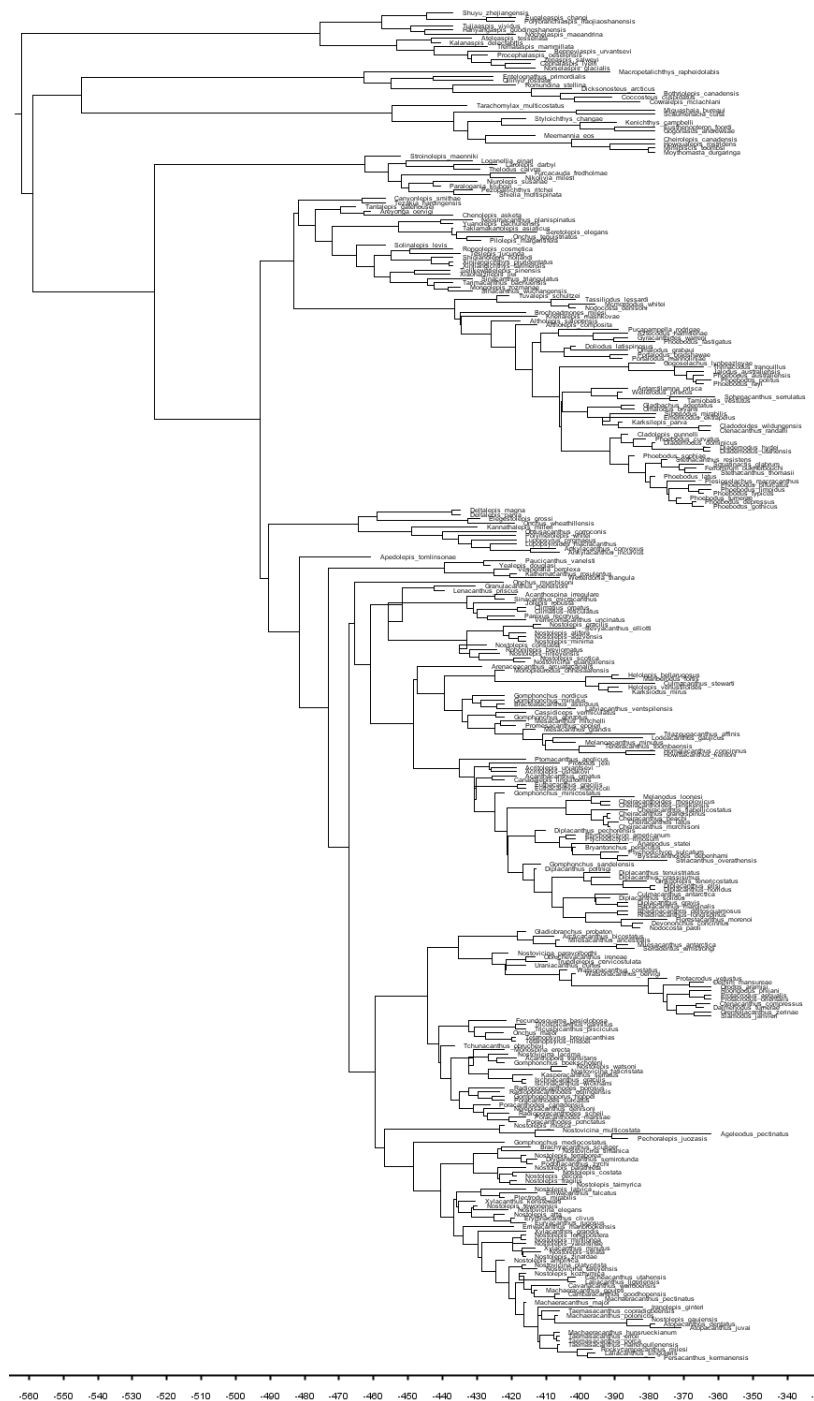
Simplified trees for the matrix with 320 taxa and 977 morphological characters in Bayesian uncalibrated method. Branch support is provided on branches. In green are represented the monophyletic group and in orange the paraphyletic or polyphyletic group.



Simplified trees for the matrix with 320 taxa and 977 morphological characters in Maximum Parsimony method. Branch support is provided on branches. In green are represented the monophyletic group and in orange the paraphyletic or polyphyletic group.



Annex 9: phylogeny from matrix composed of 320 taxa and 977 morphological characters. This phylogeny is the basis for the analysis of morphological evolutionary and diversification rates.



Annex 10: phylogeny from matrix composed of 277 taxa and 977 morphological characters. This phylogeny is the basis for the analysis of morphological disparity.



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'Benneviaspis urvantsevi'

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1??11101100111001000-0---1001???0?10110011---??00001110-0001-?10001---
110100?100111001210010110111000-10001110-----00---10-00-0--1--1---0-00021000--
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'Hanyangaspis guodingshanensis' 0-?????????000?-----
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'Howqualepis rostridens' ?-01?????????10????10?????0-
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'Kalanaspis delectabilis' ??????????????0?------
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'Kenichthys campbelli'

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'Larolepis darbyi'

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'Loganellia einari'

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'Macropetalichthys rapheidolabis' 0-

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'Meemannia eos'

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'Miguashaia bureaui'

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'Mimipiscis toombsi'

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'Moythomasia durgaringa'

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1001??10100100110010100-0---10010000?1?010001-----1001111100001-001-01---
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'Nikolivia milesi'

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'Niurolepis susanae'

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'Norselaspis glacialis' 0-0000????1?00?-----
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'Qilinyu rostrata' 0-0??00?????0?-----
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'Romundina stellina' 0-000000?10001111-000110100-
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'Scaumenacia curta' 0-01100000?0110--1001111?0-?-
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'Shielia multispinata'
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'Shuyu zhejiangensis' 0-??0?????000?-----
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'Stroinolepis maenniki'
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'Styloichthys changae'

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'Tarachomyx lax multicostatus'

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'Thelodus calvus'

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'Tremataspis mammillata'

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'Tujiaaspis vividus' 0-???????????0-----
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'Zenaspis salweyi' 0-0000?00?1000-----
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'Acritolepis ushakovi' 0-0???00011??1?????00111110-
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'Ageleodus pectinatus'
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'Ankylacanthus convexus'

'Ankylacanthus incurvus'

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'Antarctilamna prisca'

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121????10??????????????111????0???0???10??????????0????????3?????0-----
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'Apedolepis tomlinsonae'

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'Atopacanthus juvai'

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'Aztecodus harmsenae'

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'Brachyacanthus scutiger'

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'Bracteacanthus assiduus'

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'Brochodmones milesi'

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'Bryantonchus peracutus'

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'Byssacanthoides debenhami'

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'Cacheacanthus utahensis'

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'Cambaracanthus goodhopensis'

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'Canadalepis linguiformis'

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'Canyonlepis smithae'

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'Cassidiceps vermiculatus'

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'Cavanacanthus warrooensis' 0-0????????10???0???????-
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'Cheiracanthoides mosolovicus'
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'Cheiracanthus grandispinus' 0-0???000???-0-----

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'Cheiracanthus latus' 0-0???0000???0-----

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'Chenolepis asketa'

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'Cladodoides wildungensis'

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'Cladolepis gunnelli'

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'Climatius reticulatus'

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'Ctenacanthus compressus'

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'Climatius ornatus'

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'Ctenacanthus randalli'

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'Culmacanthus antarctica'

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'Culmacanthus stewarti'

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'Dalmehodus turnerae'

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'Deihim mansureae'

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'Devononchus concinnus'

[illegible]

'Diademodus dominicus'

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'Diademodus hydei'

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'*Diademodus utahensis*'

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'Diplacanthus crassissimus' 0-0?0???????0-----
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'Diplacanthus ellsii' 0-0?0???????0-----
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'Diplacanthus pechorensis'

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'Diplacanthus tenuistriatus'

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'Doliodus latispinosus'

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'Drygantacanthus semirotunda'

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'Erriwacanthus falcatus'

[illegible]

'*Erriwacanthus manbrookensis*'

[illegible]

'Erymnacanthus clivus' 0-??????????10????????????-
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'Euryacanthus rugosus' 0-??????????1?????????????-
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'Euthacanthus gracilis' 0-0?????????0-----
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'Euthacanthus macnicoli' 0-0?0?????????0-----
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'Gladbachus adentatus'

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'Gladiobranchus probaton'

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'Gogoselachus lynbeazleyae'

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'Gomphonchoporus hoppei'

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'Gomphonchus sandelensis'

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'*Helolepis venustiloides*'

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'*Homalacanthus concinnus*'

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'Howittacanthus kentoni'

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'Iranolepis ginteri'

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'Ichnacanthus gracilis' 0-000???????110--000011100--
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'Karksilepis parva'

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'Karksiodus mirus'

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'Knerialepis mashkovae'

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'Laliacanthus ligeriensis'

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'Laliacanthus singularis'

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'Latviacanthus ventspilensis'

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'Lenacanthus priscus'

'Lodeacanthus gaujicus'

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'Lupopsyroides macracanthus'

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'Lupopsyryus pygmaeus'

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'Machaeracanthus goujeti'

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'Machaeracanthus hunsrueckianum'

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'Machaeracanthus polonicus'

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'Manberodus fortis'

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'Mesacanthus mitchelli'

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'Milesacanthus ancestralis'

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'Milesacanthus antarctica' 0-0?????????0-----
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'Mongolepis rozmanae'
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'Neosinacanthus planispinatus'

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'Nerepisacanthus denisoni'

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'Nodocosta denisoni'

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'Nodocosta pauli'

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'Nostovicina lacrima'

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'Nostovicina laticristata'

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'Nostolepis longipostera'

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'Nostolepis scotica' 0-00?????????1?0--000101100-
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'Nostolepis striata'
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'Nostolepis taimyrica'

'Nostovicina tareyensis'

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'Obruchevacanthus ireneae' ?0?00000000120--000101100-

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'Omalodus bryanti'

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'Omalodus grabau'i'

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'Onchus major'

'Onchus murchisoni'

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'Orodus aramisi'

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'Parexus recurvus'

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'Paucicanthus vanelsti'

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'Pechoralepis juozasis'

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'Phoebodus rayi'

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'Phoebodus sophiae'

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'Plesioselachus macracanthus'

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'Podoliacanthus zychi'

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'Polymerolepis whitei'

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'Poracanthodes canadensis'

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'Protacrodus aequalis'

'Protacrodus orientalis'

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'Protacrodus vetustus'

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'Protodus jexi'

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'Ptomacanthus anglicus'

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'Ptychodictyon americanum'

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'Ptychodictyon rimosum'

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'Pucapampella rodrigae'

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'Radioporacanthodes porosus'

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'Rhadinacanthus deltosquamosus'

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'Rhadinacanthus longispinus'

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'Rohonilepis breviornatus'
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'Seretolepis elegans'

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'Serradentus armstrongi'

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'Sevyacanthus elliotti'

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'Shiqianolepis hollandi'

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'Siamodus janvieri'

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'Siberiodus mirabilis'

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'Sinacanthus micracanthus'

'Sinacanthus triangulatus'

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'Sphenacanthus serrulatus'

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'Squatinactis glabrum'

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'Tamiobatis vestutus'

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'Tantalepis gatehousei'

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'Tchunacanthus obrucheви'

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'Teneracanthus toombaensis'

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'Teslepis jucunda'

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'Tetanopsyrus breviacanthias'

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'Tetanopsyrus lindoei' 0-0??????????0-----
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'Tezakia hardingensis'
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'Triazeugacanthus affinis' 0-00?????????0-----
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'Tricuspicanthus gannitus' 0-0???????????11?????00?????---
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'Tricuspicanthus pisciculus'

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'Trundlelepis cervicostulata'

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'Vernicomacanthus uncinatus' 0-

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'Vesperalia perplexa'

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'Watsonacanthus costatus'

'Watsonacanthus oervigi'

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'Yealepis douglasi'

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'Yuanolepis bachunensis'

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[illegible]

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