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PATRONS DE DÉVELOPPEMENT ET MODULARITÉ DES NAGEOIRES MÉDIANES CHEZ DES OSTÉICHTHYENS ACTUELS ET FOSSILES

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RÉSUMÉ

Un nombre croissant d'études visent à identifier des modules du développement. Ces modules sont moléculaires, soit des réseaux de gènes interagissant pour une fonction précise, ou morphologiques, soit une structure observable telle l'ébauche d'un organe chez un embryon. Les modules morphologiques sont généralement identifiés par de forts coefficients de corrélation entre différents traits, ce qui suggère des interactions développementales. Les modules sont aussi des unités pouvant subir des transformations au cours de l'évolution. Des patrons développementaux et phylogénétiques récurrents ont été documentés dans le développement des nageoires dorsale et anale des actinoptérygiens actuels. Entre autres, deux modules ont été reconnus: (1) le module de patron des nageoires dorsale et anale (MPNDA), où la différentiation des nageoires s'effectue toujours dans la même direction et (2) le module exosquelette-endosquelette (MEE), où la différentiation des radiaux et des lépidotriches procède toujours dans la même direction. Toutefois, ces deux modules n'ont pas été quantifiés et n'ont été inférés qu'à partir de l'observation de la direction de différentiation des structures. Pourtant, plusieurs autres évènements se produisent au cours du développement des nageoires (l'ossification des structures et la segmentation et la bifurcation des lépidotriches). De plus, l'absence de données concernant les taxons plus basaux ne permettait pas les inférences phylogénétiques pour les ostéichthyens. Cette étude propose: (1) de quantifier et valider les deux modules chez un actinoptérygien actuel, la truite arc-en-ciel (*Oncorhynchus mykiss*) en incluant une série d'évènements au cours du développement et (2) de décrire ces évènements à partir de séries de taille, ou séries ontogénétiques, de six taxons fossiles du Dévonien et du Carbonifère (un actinoptérygien, deux actinistiens, un porolépiforme, un dipneuste et un ostéolepiforme). Les résultats ont permis de décrire huit évènements consécutifs au cours du développement des nageoires chez la truite arc-en-ciel: (1) la différentiation des radiaux proximaux (RP), (2) la chondrification des RP, (3) la formation des lépidotriches, (4) la chondrification des radiaux distaux, (5) la segmentation des lépidotriches, (6) l'ossification des lépidotriches, (7) la bifurcation des lépidotriches, et (8) l'ossification des RP. Lorsque quantifiés, tous les évènements, sauf la bifurcation, sont congruents entre les deux nageoires, mais aussi entre les radiaux et les lépidotriches. Les observations chez les espèces fossiles ont permis de découvrir que: (1) les évènements observables suivent la même séquence générale que chez la truite, (2) la direction de développement des radiaux est similaire entre les nageoires dorsale et anale, (3) la direction d'ossification des radiaux et des lépidotriches est similaire chez les actinoptérygiens, (4) chez chaque espèce, le nombre de radiaux et de lépidotriches est similaire entre les nageoires dorsale et anale, sauf pour les dipneustes, (5) toutes les espèces ont le même patron de segmentation et de bifurcation, sauf lorsque la bifurcation est absente et (6) l'absence de bifurcation est homoplasique chez les ostéichthyens. Nos données suggèrent que le MEE est ancestral chez les actinoptérygiens et que le MPNDA est ancestral chez les ostéichthyens. Un patron de développement constant des lépidotriches a aussi permis de proposer la présence d'un troisième module, le module de patron des lépidotriches.

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CODE	**SIGNIFICATION**
A	Anal fin
Act.	Actinotrichia
AMNH	American Museum of Natural History, New York, USA
AQ	Achanarras Quarry, Scotland, UK
Bi	Bidirectional
Bif.	Bifurcation
BMNH	British Museum of Natural History, London, UK
b.pl.	Basal plate
D	Dorsal fin
DAFPM	Dorsal and anal fins patterning module
DR	Distal radial
EEM	Exoskeleton and endoskeleton module
FMNH	Field Museum of Natural History, Chicago, USA
L	Lepidotrichia
M	Miguasha, Québec, Canada
MC	Mazon Creek, Illinois, USA
MEE	Module exosquelette-endosquelette
MHNM	Musée d'Histoire Naturelle de Miguasha, Québec, Canada
mm	Millimetres
MPNDA	Module de patron des nageoires dorsale et anale
n	Sample size
PA	From posterior to anterior
PR	Proximal radials
r_s	Coefficient de corrélation de Spearman
SL	Standard length

SL50	Standard length at which 50% of the specimens have the state of interest
TL	Total length
ULQ	Université Laval, Québec, Canada
YPM	Yale Peabody Museum, New Haven, USA

INTRODUCTION

L'évolution des organismes vivants est aujourd'hui expliquée par la génétique des populations, mais aussi par la génétique du développement (Gilbert 2004; Müller 2007). La génétique des populations étudie les variations génétiques au sein des populations adultes. L'évolution serait causée par des changements dans la fréquence des gènes d'une génération à l'autre, la sélection naturelle permettant la survie des individus les mieux adaptés (Gilbert et al. 1996; Griffiths et al. 2002; Gilbert 2004). D'autre part, la génétique du développement est basée, entre autres, sur l'avancement des connaissances sur les gènes régulateurs du développement, tels les gènes Hox. Des modifications dans l'expression de ces gènes peuvent mener à des changements anatomiques importants (Raff 1996; Von Dassow et Munro 1999; Gilbert 2004; Müller 2007). L'évolution s'expliquerait alors par la transmission des modifications héréditaires et par la sélection de ces nouveautés anatomiques (Gilbert 2004). D'ailleurs, une discipline en plein essor, la biologie évolutive du développement, ou ÉvoDévo, étudie développement et évolution en parallèle. Ces études permettent de mieux comprendre les transformations au cours du développement, ou ontogénie, et de déterminer comment ces processus sont modifiés au cours de l'évolution (Mabee 2006). En fait, l'ontogénie faciliterait grandement l'évolution des organismes vivants car elle est modulaire (Raff 1996; Wagner 1996; Richardson 1999; Von Dassow et Munro 1999; Bolker 2000; Raff et Sly 2000; Winther 2001; Gilbert 2004).

L'embryon, tout comme l'adulte, est composé de modules. Les modules sont des unités structurelles hiérarchiques qui s'assemblent les unes avec les autres pour former des unités plus générales (Schlosser 2002; Gilbert 2004; Wagner et al. 2007). Ils peuvent être génétiques, par exemple des réseaux de gènes régulateurs codant pour une fonction précise, ou phénotypiques, soit des traits observables ou des structures morphologiques (Gilbert et Bolker 2001; Klingenberg 2002; Schlosser 2002; Gilbert 2004; Wagner et al. 2007). Dans ce dernier cas, les modules phénotypiques ou morphologiques sont, entres autres, les ébauches des organes chez l'embryon (Raff 1996; Raff et Sly 2000). Les modules sont généralement caractérisés par des interactions importantes au cours du développement entre les différentes unités constituant le module. De plus, bien que les interactions soient très fortes à l'intérieur des modules, ceux-ci sont semi-autonomes les uns par rapport aux autres (Raff 1996; Wagner 1996; Klingenberg 2002; Schlosser 2002; Klingenberg et al. 2003; Goswami 2007; Wagner et al. 2007). Cette autonomie facilite l'action des processus évolutifs internes tels, la dissociation, la duplication et la divergence, ainsi que la cooptation (Raff 1996). La modularité permet donc des modifications de certaines parties, ou fonctions de l'organisme, sans affecter les autres fonctions (Wagner 1996). Pour certains, les modules sont en fait les vraies «unités de l'évolution» (Wagner 1996; Schlosser 2002).

Les modules morphologiques sont aussi considérés comme des caractères homologues, identifiables en comparant l'ontogénie d'organismes apparentés (Raff 1996; Wagner 1996; Raff et Sly 2000; Winther 2001). Par conséquent, des inférences phylogénétiques peuvent être effectuées à partir de ces caractères. Un bon exemple concerne des modules bien connus en termes ontogénétiques et phylogénétiques, les membres des tétrapodes; ces derniers étant homologues des nageoires paires des poissons (Raff 1996; Coates et Cohn 1998; Richardson 1999; Kardong 2002; Mabee et al. 2002; Coates 2003; Gilbert 2004; Shubin et Davis 2004; Coates et Ruta 2007; Raff 2007; Tanaka et Tickle 2007).

Les exemples de modules bien décrits comme les membres des tétrapodes sont relativement rares. Cependant, Mabee et al. (2002) ont reconnu les nageoires impaires, ou médianes, des actinoptérygiens actuels comme un autre bon modèle d'évolution modulaire. En effet, ils ont identifié des patrons récurrents dans le développement des nageoires dorsale et anale de ces poissons. Les patrons de développement sont les séquences, soit l'ordre et la direction, dans lesquelles se développent des structures anatomiques. Entres autres, deux patrons ont été décrits: (1) la différentiation des éléments de l'exosquelette, soit les lépidotriches ou rayons, et de l'endosquelette, les radiaux, de toutes les nageoires se fait dans la même direction chez les actinoptérygiens et (2) la direction de différentiation est aussi la même pour les nageoires dorsale et anale. Ces directions concertées sous-entendent de possibles interactions développementales, entre l'exosquelette et l'endosquelette d'une même nageoire, mais aussi entre les nageoires dorsale et anale. Le lien lors du développement des lépidotriches et des radiaux a été désigné «Module exosquelette-endosquelette». Pour sa part, le développement concerté entre les nageoires dorsale et anale a été nommé «Module de patron des nageoires dorsale et anale». Ces modules seraient ancestraux, ou plésiomorphes, chez les actinoptérygiens (Mabee et al. 2002); les données disponibles ne permettant pas de conclure pour tous les ostéichthyens (actinoptérygiens et sarcoptérygiens). Toutefois, une étude récente a permis de mettre en évidence des indices de modularité lors du développement de l'endosquelette des nageoires dorsale et anale de l'ostéolepiforme *Eusthenopteron foordi* (Leblanc 2005), un poisson fossile du Dévonien supérieur (380 millions d'années) faisant partie du groupe des sarcoptérygiens, le deuxième sous-groupe au sein des ostéichthyens (Zhu et Schultze 2001). En effet, les radiaux des nageoires dorsale et anale de ce poisson fossile se développent dans la même direction (Leblanc 2005).

Globalement, les données déjà documentées sur la modularité des nageoires médianes ne fournissent que les patrons généraux de différentiation des structures (Mabee et al. 2002) ou ne font allusion qu'au développement de l'endosquelette (Leblanc 2005). Or, le développement des nageoires est plus complexe. D'abord, suite à leur différentiation sous la forme de précurseurs cartilagineux, pour les radiaux, et d'une matrice de collagène pour les lépidotriches (Akimenko et Smith 2007), ceux-ci s'ossifient. De plus, les lépidotriches ne sont pas que des baguettes continues supportant les nageoires; ils sont en fait constitués de plusieurs segments et parfois de ramifications, ou bifurcations, qui se forment tout au long du développement (Goodrich 1904; François 1958; Haas 1962; Géraudie et Landis 1982; Laforest et al. 1998; Marí-Beffa et al. 1999). Par conséquent, il y a d'autres processus importants dans le développement des nageoires qui n'ont pas encore été décrits dans une optique modulaire. Une description plus complète du développement des nageoires chez les poissons actuels est donc nécessaire pour favoriser les comparaisons avec des espèces fossiles, ce qui faciliterait grandement les inférences phylogénétiques.

Une description plus étoffée du développement des nageoires nécessite l'étude des patrons, ou des séquences, de développement à l'aide de séries ontogénétiques. De telles séries peuvent être constituées chez des espèces actuelles (e.g., Mabee 1993; Cubbage et Mabee 1996; Mabee et Trendler 1996; Bird et Mabee 2003; Mabee et Noordsy 2004; Grünbaum et al. 2003, 2007; Chu 2007), mais aussi chez des espèces fossiles (e.g., Schultze 1984; Schultze et Bardack 1987; Cloutier 1997; Carroll et al. 1999; Chipman et Tchernov 2002; Cote et al. 2002; Leblanc 2005; Schoch 2005; Charest et Cloutier 2006). Chez les espèces actuelles, les individus d'une même espèce sont échantillonnés à un moment connu de leur développement, soit un âge ou une taille donnés. La variable de temps ou de taille sert alors à ordonner des évènements se produisant au cours de l'ontogénie, soit des changements de forme ou de taille (e.g., Chu 2007; Grünbaum et al. 2007), ou des séquences de différentiation et d'ossification (e.g., Cubbage et Mabee 1996; Mabee et Trendler 1996; Mabee et al. 2000; Bird et Mabee 2003; Grünbaum et al. 2003; Cloutier et al. en prép.). Chez les espèces fossiles, des changements de forme et de taille (e.g., Thomson et Hahn 1968; Schultze 1984; Schultze et Bardack 1987; Chipman et Tchernov 2002), ainsi que des séquences d'ossification (e.g., Chipman et Tchernov 2002; Cote et al. 2002; Schoch 2004) peuvent aussi être étudiés, mais les séries ontogénétiques ne peuvent être constituées qu'à partir de la taille des spécimens; les individus de tailles différentes sont alors considérés d'âges différents (Schultze 1984; Cote et al. 2002).

Un nombre croissant d'études utilise des méthodes quantitatives pour tester des hypothèses de modularité et ainsi identifier de façon plus objective de nouveaux modules à l'aide des séquences de développement (e.g., Magwene 2001; Smith 2001; Klingenberg et al. 2003; Poe 2004; Goswami 2007). Les interactions lors du développement sont généralement identifiées par des séquences de développement fortement corrélées (Klingenberg 2002; Klingenberg et al. 2003; Poe 2004; Young 2004; Goswami 2007). Des coefficients de corrélation ou de concordance de Kendall sont couramment utilisés pour comparer des séquences de développement (Nunn et Smith 1998; Smith 2001; Grünbaum et al. 2003; Poe 2004; Goswami 2007). Une telle méthode doit être appliquée pour valider les modules de Mabee et al. (2002) chez les actinoptérygiens actuels.

Cette étude comporte deux objectifs principaux, soit (1) de décrire et quantifier le «module exosquelette-endosquelette» et le «module de patron des nageoires dorsale et anale» décrits par Mabee et al. (2002) chez un actinoptérygien actuel, la truite arc-en-ciel (*Oncorhynchus mykiss*) et (2) d'inférer l'évolution de ces deux modules chez les ostéichthyens en observant les patrons de développement des nageoires chez six taxons fossiles appartenant à cinq groupes d'ostéichthyens. Les espèces fossiles examinées proviennent de trois sites fossilifères reconnus pour la présence de poissons larvaires et juvéniles, permettant ainsi la constitution de séries ontogénétiques: (1) la carrière d'Achanarras (Dévonien moyen; Caithness, Écosse; Trewin 1986), (2) la Formation d'Escuminac (Dévonien supérieur; Miguasha, Québec, Canada; Thomson et Hahn 1968, Schultze 1984, Cloutier 1997, Cote et al. 2002, Leblanc 2005) et le site de Mazon Creek (Carbonifère supérieur; Illinois, États-Unis; Eastman 1902, 1903, Schultze 1972, 1985, Schultze et Bardack 1987, Charest et Cloutier 2006).

Deux prémisses sont proposées pour quantifier et valider les deux modules: (1) toutes les séquences correspondantes doivent être significativement congruentes entre l'exosquelette et l'endosquelette, et (2) toutes les séquences correspondantes doivent être significativement congruentes entre les nageoires dorsale et anale. Les séquences correspondantes pour le «module exosquelette-endosquelette» doivent être redéfinies en fonction de ces évènements: (1) la différentiation des radiaux (proximaux et distaux), (2) la différentiation des lépidotriches, (3) l'ossification des radiaux (proximaux et distaux) et (4) l'ossification des lépidotriches. Tandis que, les séquences correspondantes pour le «module de patron des nageoires dorsale et anale» doivent être redéfinies en fonction de ces évènements: (1) la différentiation des radiaux (proximaux et distaux), (2) la différentiation des lépidotriches, (3) la chondrification des radiaux (proximaux et distaux), (4) l'ossification des radiaux (proximaux et distaux), (5) l'ossification des lépidotriches, (6) la segmentation des lépidotriches et (7) la bifurcation des lépidotriches.

Bon nombre d'études s'intéressent à divers aspects du développement et de la régénération des nageoires chez les poissons actuels (e.g., Nabrit 1931; Birnie 1934; Prenant 1937; François et Blanc 1956; François 1958; Haas 1962; Géraudie et Landis 1982; Cubbage et Mabee 1996; Mabee et Trendler 1996; Laforest et al. 1998; Bemis et Grande 1999; Marí-Beffa et al. 1999; Borday et al. 2001; Grünbaum et al. 2003; Suzuki et al. 2003; Iovine 2007); la régénération des nageoires, après une blessure ou une amputation, étant reconnue comme une récapitulation du développement (Haas 1962; Laforest et al. 1998; Borday et al. 2001; Akimenko et Smith 2007; Iovine 2007). Bien que l'aspect modulaire ne figure pas explicitement dans ces études, un mécanisme d'induction ou d'interaction a été suggéré entre l'endosquelette et l'exosquelette lors du développement de la nageoire caudale (Nabrit 1931; Birnie 1934), de la nageoire pectorale (Bouvet 1974) et de la nageoire dorsale (Suzuki et al. 2003) d'actinoptérygiens actuels. Il y aurait donc une certaine contrainte sur l'ordre des évènements lors du développement d'une nageoire: le premier radial à se développer induirait le développement du premier lépidotriche, et ainsi de suite, d'où la similarité des séquences. Selon François (1958), les processus de différentiation des radiaux et des lépidotriches, ainsi que le processus d'ossification des lépidotriches auraient les mêmes séquences chez la truite arc-en-ciel. De plus, les séquences des nageoires dorsale et anale seraient identiques chez la truite arc-en-ciel (François 1958), le poisson zèbre (*Danio rerio*; Bird et Mabee 2003) et l'omble chevalier (*Salvelinus alpinus*; Cloutier et al. en prép.) Il est donc attendu que toutes les séquences correspondantes seront congruentes chez la truite arc-en-ciel.

Toutes les séquences observées chez la truite arc-en-ciel ne peuvent être observées chez les espèces fossiles car les structures cartilagineuses ne sont que rarement conservées à l'état fossile. Les séquences observées chez les poissons fossiles sont donc: (1) l'ossification des radiaux, (2) l'ossification des lépidotriches, (3) la segmentation des lépidotriches et (4) la bifurcation des lépidotriches.

Les données déjà disponibles pour *Eusthenopteron foordi* indiquent que le «module de patron des nageoires dorsale et anale» est présent chez cette espèce, ce qui suggère donc que ce module est ancestral chez les ostéichthyens (Leblanc 2005). Toutefois, plusieurs aspects de la morphologie des nageoires sont différents entre les différents groupes d'ostéichthyens et peuvent rendre difficile l'identification de modules. Par exemple, le nombre de lépidotriches pour chaque radial, qui est de un chez la plupart des actinoptérygiens actuels comme la truite, est plus élevé chez des actinoptérygiens possédant des caractères plus primitifs (Goodrich 1904; Lindsey 1955; Mabee et al. 2002) comme l'esturgeon (*Acipenser*), par exemple (Goodrich 1904; Lindsey 1955). Chez les sarcoptérygiens, les lépidotriches sont généralement articulés avec un nombre réduit de radiaux ou une unique plaque basale (Goodrich 1904, 1958), notamment chez les cœlacanthes (Cloutier 1990, 1991; Forey 1991). De plus, la divergence de taille entre les nageoires dorsale et anale, particulièrement chez les dipneustes (Eaton 1945; Cloutier et Ahlberg 1996; Arratia et al. 2001) est une autre différence pouvant rendre difficile l'identification des modules chez les taxons fossiles. Malgré tout, la présence des modules est attendue chez les espèces fossiles. En effet, il est plus parcimonieux de présumer que ces modules sont un héritage d'un ancêtre commun, plutôt que de supposer que le développement des nageoires a été réinventé au cours de l'évolution des ostéichthyens.

Les données récoltées favoriseront les comparaisons entre les espèces actuelles et fossiles, tout en permettant d'accroître les connaissances pour mieux décrire les modules de Mabee et al. (2002) et leur évolution. D'autres études concernant les séquences d'ossification chez des espèces fossiles (Cote et al. 2002) ou les mécanismes de formation des lépidotriches (Jeffery 2001; Johanson et al. 2005) mentionnent aussi le manque de données comparatives concernant les principaux groupes d'ostéichthyens. De plus, les comparaisons faites dans le cadre de cette études aideront à résoudre quelques problèmes liés à l'interprétation des séquences de développement chez des taxons fossiles (e.g., Johanson et al. 2005).

EVOLUTION OF MEDIAN FIN MODULARITY IN OSTEICHTHYANS

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1.1 SUMMARY

Morphological and developmental similarities as well as interactions among developing structures are usually interpreted as evidences of modularity. Such similarities have been documented between the dorsal and anal fins of living actinopterygians. Two distinct developmental modules were identified: (1) the dorsal and anal fin patterning module (DAFPM - where both fins differentiate in the same direction) and (2) the exoskeleton and endoskeleton module (EEM - where radials and lepidotrichia differentiate in the same direction). However, these modules were based on the observation of gross patterns of formation and data were lacking to make phylogenetic inferences. This study proposes to quantify and validate these two modules in a living actinopterygian while including all developmental events (differentiation/ossification of radials and lepidotrichia, and segmentation/bifurcation of lepidotrichia) and to examine the corresponding (preserved) events in six size (ontogenetic) series of Devonian and Carboniferous taxa from five osteichthyan groups (one actinopterygian, two actinistians, one porolepiform, one dipnoan and one osteolepiform species). Eight consecutive events are described during the development of the rainbow trout: (1) differentiation of proximal radials, (2) chondrification of proximal radials, (3) formation of lepidotrichia, (4) chondrification of distal radials, (5) segmentation of lepidotrichia, (6) ossification of lepidotrichia, (7) bifurcation of lepidotrichia and (8) ossification of radials. Except for the bifurcation, developmental patterns are significantly congruent between fins and between the exoskeleton and endoskeleton. Inferred phylogenetic patterns include: (1) the generalized developmental sequence is fairly conservative among osteichthyans, with homoplastic deletions of bifurcation, (2) within species, the number of radials and lepidotrichia is similar between dorsal and anal fins, with the exception of dipnoans, (3) similarity of radial ossification pattern between fins, (4) similarity of radial and lepidotrichia ossification in the actinopterygian and (5) same segmentation and bifurcation patterns found in all species (except for species with non-bifurcating lepidotrichia). Our data suggest that the EEM is plesiomorphic at least for actinopterygians and the DAFPM is plesiomorphic for osteichthyans, but decoupling occurs during phylogeny, causing the loss, or the alteration, of modules along phylogeny. Finally, recurrent patterns in the development of lepidotrichia have been suggested to indicate a third module, which was named the Fin Ray Patterning Module.

1.2 INTRODUCTION

Modularity is a crucial property of development that favors the evolution of living organisms (Raff 1996; Von Dassow and Munro 1999; Raff and Sly 2000). Developmental modularity concerns organismal organization from gene regulatory networks to morphological structures (Gilbert and Bolker 2001; Klingenberg 2002; Schlosser 2002; Wagner et al. 2007). In the later case, a morphological (phenotypic) developmental module may represent a localized process such as an incipient structure (e.g., organ rudiments) (Raff 1996; Raff and Sly 2000). Such modules can be recognized by high correlations among morphological traits owing to important developmental interactions (Klingenberg 2002; Klingenberg et al. 2003; Poe 2004; Young 2004; Goswami 2007; Wagner et al. 2007). While strong interactions exist among intra-modular events and structures, each modular unit is quite autonomous with respect to other modules (Raff 1996; Wagner 1996; Schlosser 2002; Klingenberg et al. 2003; Goswami 2007; Wagner et al. 2007). This autonomy among modules allows dissociation, duplication/divergence and co-option - the three internal evolutionary processes (Raff 1996).

Morphological developmental modules can also be interpreted as characters or homologies that are recognizable in the development of comparable organisms (Raff 1996; Wagner 1996; Raff and Sly 2000; Winther 2001), thus allowing the reconstruction of their phylogenetic history. For example, the tetrapod limbs and the homologous paired fins of piscine sarcopterygians are modules for which their ontogenetic and phylogenetic changes are well documented (Raff 1996; Coates and Cohn 1998; Richardson 1999; Coates 2003; Shubin and Davis 2004; Coates and Ruta 2007; Raff 2007; Tanaka and Tickle 2007). Very few examples of modular evolution are as well-documented as that of paired appendages. Mabee et al. (2002) consider the median fins of fishes as another good case of modular evolution. Recurrent developmental patterns found in living actinopterygians were interpreted as evidences of modularity. Among others, two modules were identified in the patterning (i.e., sequences and direction of development) of dorsal and anal fins (Mabee et al. 2002): (1) the Dorsal and Anal Fin Patterning Module (DAFPM), where the skeletal elements of both fins differentiate in the same direction in all actinopterygians and (2) the Exoskeleton and Endoskeleton Module (EEM), where the direction of development of the exoskeleton (the lepidotrichia or fin rays) and the endoskeleton (the radials or fin rays supports) are similar in all actinopterygians. These similarities in the direction of development might be due to some developmental interactions between the exoskeleton and the endoskeleton of a given fin, and between the dorsal and anal fins.

The DAFPM and the EEM are considered to be maintained during actinopterygian phylogeny (Mabee et al. 2002) but have not been reported in other living and extinct osteichthyans. Recently, the study of a size series of the extinct sarcopterygian *Eusthenopteron foordi* revealed that endoskeletal elements of the dorsal and anal fins have a shared direction of development (Leblanc 2005). Since the DAFPM is found both in living actinopterygians and at least in one extinct sarcopterygian, thus, it could have been inherited from a common osteichthyan ancestor (Leblanc 2005). Except for *E. foordi*, data are absent for basal sarcopterygians (Mabee et al. 2002), basal actinopterygians and more specifically, for fossil taxa. A broad phylogenetic sampling of median fin development in actinopterygians and sarcopterygians is necessary to understand the extent of related modules in osteichthyan phylogeny.

Additionally, previous studies mentioned only general patterns of differentiation (Mabee et al. 2002) and the ossification sequences of the endoskeleton (Leblanc 2005), whereas important developmental events have not been considered. The ossified skeleton is generally the only fossilized part of an extinct organism, so every patterns of the skeleton related to some developmental events such as segmentation and bifurcation of lepidotrichia (Fig. 1) should be considered in living actinopterygians to facilitate comparisons with fossil taxa.

Moreover, beyond the observation of patterns, quantitative approaches to test for modularity were developed in the last few years (e.g., Magwene 2001; Smith 2001; Klingenberg et al. 2003; Poe 2004; Young 2004; Goswami 2007). Developmental (modular) interactions are generally identified from developmental sequences that are highly correlated (Klingenberg 2002; Klingenberg et al. 2003; Poe 2004; Young 2004; Goswami 2007; Wagner et al. 2007). Non-parametric correlations or Kendall concordance coefficients are used to compare such sequences (Nunn and Smith 1998; Smith 2001; Grünbaum et al. 2003; Poe 2004; Goswami 2007). This method should be applied to hypothesis of modularity for median fins of actinopterygians in order to validate the patterns that are reported in Mabee et al. (2002).

Thus the main objectives of this study are (1) to describe and to quantify the DAFPM and the EEM in a living actinopterygian, the rainbow trout (*Oncorhynchus mykiss*), and (2) to infer the evolution of these two modules during osteichthyan phylogeny based on developmental patterns described in six fossil taxa from five osteichthyan groups.

Our premises in quantifying median fin modules in living actinopterygians are: (1) all corresponding sequences should be significantly congruent between dorsal and anal fins, and (2) all corresponding sequences should be significantly congruent between the exoskeleton and endoskeleton. The corresponding sequences for the DAFPM must be described in function of these events: (1) differentiation of radials, (2) differentiation of lepidotrichia, (3) chondrification of radial, (4) ossification of radial, (5) ossification of lepidotrichia, (6) segmentation of lepidotrichia, and (7) bifurcation of lepidotrichia. The corresponding sequences for the EEM must be described in function of these events: (1) differentiation of radials, (2) differentiation of lepidotrichia, (3) ossification of radials and (4) ossification of lepidotrichia. While Mabee et al. (2002) used the term differentiation as a synonym of development, in our study this term represents the formation of the primordia of studied structures: mesenchymal cell condensations for radials and collagenous matrix for lepidotrichia (Suzuki et al. 2003).

Many studies are describing diverse aspects of development and regeneration of fins (e.g., Nabrit 1931; Birnie 1934; Prenant 1937; François and Blanc 1956; François 1958; Haas 1962; Géraudie and Landis 1982; Cubbage and Mabee 1996; Mabee and Trendler 1996; Laforest et al. 1998; Bemis and Grande 1999; Marí-Beffa et al. 1999; Borday et al. 2001; Grünbaum et al. 2003; Suzuki et al. 2003; Akimenko and Smith 2007; Iovine 2007); regeneration being considered as a recapitulation of development (Haas 1962; Laforest et al. 1998; Borday et al. 2001; Akimenko and Smith 2007; Iovine 2007). Even if modularity is rarely mentioned in these studies, an induction or interaction mechanism between radials and lepidotrichia is suggested during the development of the caudal fin (e.g., Nabrit 1931; Birnie 1934), the pectoral fin (e.g., Bouvet 1974) and the dorsal fin (e.g., Suzuki et al. 2003) of some actinopterygian species. Consequently, this interaction may affect the developmental sequence; the first radial to develop induces the formation of the first lepidotrichium and so on. Also, according to François (1958), the sequences of differentiation of radials and lepidotrichia as well as the sequence of ossification of lepidotrichia are congruent in the rainbow trout. Moreover, the development of the dorsal and anal fins is recognized to be similar in terms of sequence and timing in the rainbow trout (François 1958) and the Artic charr (*Salvelinus alpinus*; Cloutier et al. in prep.). Similar sequences, but different timing, were also observed in the zebrafish (*Danio rerio*; Bird and Mabee 2003). Therefore, congruence is expected among all corresponding sequences in the rainbow trout.

Because the cartilaginous structures are rarely preserved in fossils, the observed sequences for fossil fishes are: (1) ossification of radials, (2) ossification of lepidotrichia, (3) segmentation of lepidotrichia, and (4) bifurcation of lepidotrichia.

Leblanc (2005) has mentioned the presence of the DAFPM in *Eusthenopteron foordi*. However, many morphological differences in the median fins of different osteichthyan groups can make comparisons difficult. For example, the ratio of lepidotrichia per radial is 1:1 in many actinopterygians, including the rainbow trout, but this ratio is recognized as a derived character in actinopterygians (Goodrich 1904; Lindsey 1955; Mabee et al. 2002). Also, sarcopterygians present generally a small number of radials or a unique basal plate to support fin rays in the dorsal and anal fins (Goodrich 1904, 1958; Eaton 1945; Cloutier 1990, 1991; Forey 1991). Finally, the important size divergence between the dorsal and anal fins in the evolution of dipnoans (Eaton 1945; Cloutier and Ahlberg 1996; Arratia et al. 2001) is another important morphological difference which makes the identification of modules not as simple as in living actinopterygians. Nevertheless, the parsimony principle allows to expect that most median fin developmental patterns are ancestral for osteichthyans.

While bringing new data to describe the DAFPM and the EEM and to infer their evolution, this study will also contribute to fill the lack of comparative data in the study of sequences of ossification among different osteichthyan groups (e.g., Cote et al. 2002; Johanson et al. 2005).

1.3 MATERIAL AND METHODS

1.3.1 Living actinopterygian

Dorsal and anal fins (Fig.1) developmental sequences were obtained from embryo-juvenile rainbow trout (*Oncorhynchus mykiss*). Examined specimens range from 8 days pre-hatching to 100 days post hatching (dph). Larva-juvenile were reared in a swimming channel (see Grünbaum et al. 2008 for detail on rearing system) under constant water velocity (0.4 cm/s) in 2005 (see Chu 2007 for rearing conditions). Specimens were sampled every day from 8 days pre-hatching to 34 dph, every other day from 34 to 80 dph, and every four days up to 100 dph. Samples were fixed in neutral buffered formalin for 48h, and then preserved in 70% ethanol. Two series of cleared-and-double stained (Alizarin red S for bones and Alcian blue for cartilages: Dingerkus and Uhler 1977; Potthoff 1984) specimens have been used in this study. Pre-hatching specimens were removed from their egg capsule prior to be cleared and stained solely with Alcian blue. Digital photographs were taken before staining and 5-10 days after staining to avoid interpretive errors owing to destaining. The first series includes one specimen for each sampling day. The second series was used to cope with staining problems (Redfern et al. 2007); additional specimens from 0 to 24 dph were stained. A total of 86 specimens have been examined to reconstruct developmental sequences.

All observations were made under a Leica MZ16A stereodissecting microscope equipped with a digital camera. Standard length (SL) was measured prior to staining with Northern Eclipse Software (Version 6.0, Empix Imaging Inc., Ontario, Canada). Since SL and dph are highly correlated ($r^2 = 0.952$; $p < 0.001$) and SL is recognized as a better proxy for morphological development in fishes (Fuiman et al. 1998; Faustino and Power 1999), SL was used for all statistical analyses.

Coding was based on color uptake (i.e., cartilages are blue and bones are red) and color intensity (i.e., first structures to take color are darker). Developmental states for radials are: (1) present (cell condensation without stain uptake), (2) cartilaginous (blue), and (3) ossified (red). Developmental states for lepidotrichia are: (1) present, (2) ossified (red), (3) segmented (number of segments per lepidotrichium), and (4) bifurcated (position of the bifurcation). Because the number of serial elements (i.e., radials and lepidotrichia) varies among individuals, positional homologies and numbering of elements (e.g., dorsal radials 1-14, dorsal lepidotrichia 1-17, anal radials 1-14, anal lepidotrichia 1-16) were inferred *a posteriori* by lining up all specimens with the third radial (variability being more important in peripheral areas) and by comparing similarities between sequences of similar sized-specimens. Furthermore, myomere counts (from head to tail) were used in the earliest larval stages as a topographical criterion to identify the first proximal radials to differentiate. The dorsal fin is positioned at the level of myomeres 21-32, whereas the anal fin is positioned at the level of myomeres 40-50. The skeletal elements were numbered following their order from anterior (1) to posterior (up to 17).

Logistical regressions were used to estimate the standard length (SL) at which 50% (SL_{50}) of the specimens have reached the developmental state of interest (i.e., cartilaginous, ossified, segmented and bifurcated) for each element. Values of SL_{50} were subsequently used to order and reconstruct developmental sequences among serial elements within a fin. Significance of the logistical regressions was tested using the G^2 statistic (Quinn and Keough 2002). The significance level used to interpret a regression for a given element was calculated using the Bonferroni correction: the collective significance level of 0.05 was divided by the number of elements to get the nominal significance level for each regression. Statistical analyses were performed using SYSTAT (Version 11.00.01, SYSTAT Software Inc., 2004, Richmond, California).

In order to validate the DAFPM and the EEM, Spearman rank correlation coefficients were used to describe the relation between corresponding sequences in the dorsal and anal fins, and in the exoskeleton and endoskeleton. Only the elements for which the logistical model was significant were considered for Spearman correlations. The significance level used was 0.05.

1.3.2 Fossil osteichthyans

Size series of fossil taxa are considered equivalent to ontogenetic, or growth, series for living specimens (Schultze 1984). Data were collected on six taxa from five osteichthyan clades (Table 1, Fig. 2).

Fossil specimens were examined under a stereodissecting Leica MZ9.5 binocular equipped with a drawing tube, and were photographed with an Olympus Camedia C5060 digital camera mounted on a photographic stand. Ammonium chloride and water immersion were used to enhance some anatomical details. Coding was done according to sequences previously mentioned for living actinopterygians. For each species, the skeletal elements of the fins were numbered following their order from anterior to posterior.

When available, SL was measured on digital photographs using Northern Eclipse. When specimens were incomplete, a proxy was used to estimate SL with a regression equation. Standard length of *Elonichthys peltigerus* was estimated from the distance between the posterior part of head to the anal fin insertion (HA): $SL = 2.961 + 2.470\ HA$ (Schultze and Bardack 1987). Standard length of *Rhabdoderma exiguum* was estimated based on the distance between the insertion of the first and second dorsal fins (D1D2) ($r = 0.894$; $p < 0.001$): $SL = 3.604 + 8.376\ D1D2$. Total length was used for *Miguashaia bureaui* specimens. Specimens of *Quebecius quebecensis* are too scarce to estimate length from a regression equation. Standard length and the distance between the insertion of the anal fin and the caudal fin (An-C) were measured on two complete specimens (MHNM 06-1148, MHNM 06-1474a). The standard length for the third, incomplete, specimen (MHNM 06-1244) was estimated from the mean of the ratio An-C/SL obtained from the complete specimens, assuming isometric growth. The distance between the operculum and the caudal fin insertion of *Dipterus valenciennesi* was used rather than SL. Standard length of *E. foordi* was estimated based on the relation with the distance between the first and second dorsal fins insertions and with the distance between the second dorsal and caudal fins insertions (Leblanc 2005). Size ranges for each species are indicated in Table 1.

1.4 RESULTS

1.4.1 Living actinopterygian

The 86 specimens of *O. mykiss* examined have a SL that ranges from 10.1 to 32.7 mm.

The number of proximal radials is variable in the dorsal and anal fins among individuals, ranging from 6 to 15 radials in the dorsal fin and from 3 to 14 radials in the anal fin. Linear regressions were used to verify the cause of this variability by estimating the relation between the number of elements (radial and lepidotrichia) and SL. This variability is mostly due to ontogenetic changes; there is a significant positive correlation between SL and the number of radials in the dorsal ($r_s = 0.682$; $p < 0.001$) and the anal ($r_s = 0.635$; $p < 0.001$) fins. The unexplained portion of the variability is probably due to differences among individuals. Each proximal radial is usually associated with one distal radial. The only exception concerns the anteriormost proximal radial where the distal radial is frequently missing; lepidotrichia are thus articulated directly with the proximal radial.

Ontogenetic changes are also good explanations for the variability in the number of lepidotrichia in the dorsal ($r_s = 0.817$; $p < 0.001$) and anal ($r_s = 0.857$; $p < 0.001$) fins. There are up to 18 lepidotrichia in the dorsal fin and up to 16 in the anal fin. There is a 1:1 relationship between the number of radials and lepidotrichia except for the first and last radials: three to four lepidotrichia are associated with the first radial and two lepidotrichia are associated with the last radial (Fig. 1).

Eight events were studied in the development of the dorsal and anal fins (Table 2). Their order of initiation is: (1) differentiation of proximal radials, (2) chondrification of proximal radials, (3) differentiation of lepidotrichia, (4) chondrification of distal radials, (5) segmentation of lepidotrichia, (6) ossification of lepidotrichia, (7) bifurcation of lepidotrichia, and (8) ossification of proximal radials. After initiation, these developmental events proceed simultaneously.

The differentiation of proximal radials begins 5 days before hatching in specimens reaching 10 mm in SL. The first proximal radials to differentiate are radials 4-9 in the dorsal fin and radials 4-10 in the anal fin. Radial differentiation is quickly followed by chondrification. In fact, only three specimens (pre-hatched and 0 dph) show cell condensations in one or both fins prior to the beginning of chondrification. Consequently, the differentiation of proximal radials was not analysed statistically owing to the lack of specimens showing this state. The first cartilaginous proximal radials for both fins form in a 12 mm long specimen. The first proximal radials to chondrify are radials 4-9 in the dorsal fin and radials 6-8 in the anal fin. The sequences of chondrification of the proximal radials are highly congruent between both fins ($r_s = 0.919$; $p < 0.001$; Table 3), but a slight timing divergence occurs posterior to radial 8 (Fig. 3A).

The formation of actinotrichia precedes the formation of lepidotrichia, which differentiate proximo-distally. The differentiation of lepidotrichia begins with only a slight delay after the differentiation of the first proximal radial in a 14 mm long specimen (Table 3). The first lepidotrichia to form are lepidotrichia 7-11 in the dorsal fin and lepidotrichia 6-9 in the anal fin (Table 2). The pattern of differentiation of the lepidotrichia is highly congruent between both fins ($r_s = 0.860$; $p < 0.001$; Table 3, Fig. 3B), but a timing divergence is shown posteriorly to lepidotrichia 11 (Fig. 3B). The pattern of differentiation is congruent between the endoskeleton and the exoskeleton; the first lepidotrichia to form are supported by the first proximal radials to appear.

Sequences of chondrification for distal radials were observed but not quantified, owing to some ambiguities due to staining problems. Nevertheless, the observations, based on color intensity, suggest that first distal radials to chondrify are radials 3-7 in both fins. Thus, the location of the initiation of chondrification is congruent between proximal and distal radials as well as between fins (Table 2). Unfortunately, the available data do not allow to confirm a directional pattern for the chondrification of distal radials. In addition, there is no sequence of ossification for these radials because their ossification occurs after 100 dph.

Lepidotrichia get longer by the addition of new segments proximo-distally. First segmentations of lepidotrichia of both fins occur in specimens reaching ca. 17 mm in SL (Table 2). The first lepidotrichia to display segmentations are lepidotrichium 12 in the dorsal fin and lepidotrichia 7-10 in the anal fin (Table 2). New segments are first added to lepidotrichia 10-12 in the dorsal fin and lepidotrichia 8-10 in the anal fin (Table 2). From these first lepidotrichia, segmentation proceeds bidirectionally. The sequences of first segmentation are significantly correlated between fins ($r_s = 0.669$; $p < 0.05$, Table 3) and the timing is similar (Fig. 3C). The second ($r_s = 0.573$; $p < 0.05$) and third segmentations ($r_s = 0.511$; $p < 0.05$) are also, but less, correlated between fins whereas subsequent segmentations are not (Table 3). The specimens examined have a maximum of seven segments per lepidotrichium, indicating six segmentation events. The 7^{th} segment is only seen in the dorsal fin of three specimens at the end of the size series, between 28 and 32 mm in SL. The first two lepidotrichia are never segmented in both fins, whereas the third one is occasionally segmented.

The exoskeletal elements of the dorsal and anal fins ossify before the endoskeletal elements (Table 2). The ossification of lepidotrichia in both fins begins in specimens reaching ca. 19 mm. The first lepidotrichia to ossify are lepidotrichia 6-8 in the dorsal fin and lepidotrichia 5-6 in the anal fin (Table 2; Fig. 3D). Thus, the origin of ossification is located anterior to the original point of differentiation and segmentation. The ossification proceeds proximo-distally (Fig. 5). The direction of ossification of the dorsal and anal lepidotrichia is bidirectional. There is a highly significant positive correlation between the ossification sequences of the lepidotrichia in both fins ($r_s = 0.958$; $p < 0.001$; Table 3). The timing is similar between fins (Fig. 3D).

The first bifurcations occur earlier in the dorsal fin (ca. 24 mm long specimen in SL) than in the anal fin (ca. 25 mm in SL) (Table 2). The first bifurcation appears distally on lepidotrichium 14 in the dorsal fin and lepidotrichium 10 in the anal fin (Table 2). The first bifurcations are located posterior to the first differentiation, first segmentation and the origin of ossification. In the dorsal fin, from the first lepidotrichium to show a bifurcation, bifurcations are gradually located more distally on the subsequent lepidotrichia to show bifurcation. The subsequent lepidotrichia are located on both side of the first lepidotrichia (Fig. 3E), thus the directional pattern seems bidirectional from a posterior center of induction, but the sequences obtained from the logistical regressions do not support any pattern. Also, sequences are not significantly congruent between fins (Table 3, Fig. 3E). In fact, this apparently bidirectional pattern was not as clear in the anal fin. Only one bifurcation order (i.e., the number of consecutive bifurcations on the proximo-distal axis of a given lepidotrichia) was observed in the specimens examined.

The ossification of the dorsal proximal radials (ca. 25 mm long specimen in SL) precedes that of the anal radials (ca. 28 mm) (Table 2). This timing difference between fins is persistent all along the ossification of the radials (Fig. 3F). Radial 4 is the first endoskeletal element to ossify in both fins and ossification proceeds bidirectionally (Table 2). The sequences of ossification of the radials are highly congruent between fins (r_s = 0.927; $p < 0.001$; Table 3, Fig. 3F). Moreover, the sequences of ossification of the radials are correlated positively with the sequences of ossification of the lepidotrichia within the dorsal ($r_s = 0.854$; $p < 0.001$; Table 3, Fig. 4A) and anal ($r_s = 0.839$; $p < 0.01$; Table 3, Fig. 4B) fins.

1.4.2 Fossil osteichthyans

1.4.2.1 Actinopterygii

Elonichthys peltigerus is one of the most common palaeonisciforms in the Carboniferous Mazon Creek fauna (Illinois, USA) where most specimens are small size. This species is known from many specimens of different sizes (Schultze and Bardack 1987), thus allowing the reconstruction of developmental sequences. In addition, this

Paleozoic actinopterygian species is exceptional for the preservation of radials in median fins.

There are two rows of radials in *E. peltigerus* with a 1:1 ratio between the proximal and distal radials. Proximal radials are only visible in six specimens because they are usually covered with scales. The dorsal fin is composed of 16-19 distal radials and 34-40 (mean = 36) lepidotrichia, whereas the anal fin has 19-23 radials and 39-47 (mean = 43) lepidotrichia; the anal fin is slightly longer than the dorsal fin. The general relationship between distal radials and lepidotrichia is 1:2, with some variation in anterior and posterior fin margins (i.e., 1:3 for the first radial).

The first distal radials to ossify are located in the anterior part of the dorsal and anal fins. Specimen FMNH PF 7493 (Fig. 6) shows clearly the sole presence of four complete distal radials and a small part of a fifth one at the anterior margin of the anal fin. The same is true for proximal radials; among the six specimens showing proximal radials, radials are always located in the anterior part of the fin (Fig. 7). The observation of specimens with many distal radials allows to infer a bidirectional pattern of ossification since anterior elements are better developed (Fig. 7) and radials 2-6 are more distinct and complete. Unfortunately, it is not possible to confirm the same pattern for proximal radials.

The dorsal and anal fins of specimen FMNH PF 7502 (Fig. 7) show well-developed lepidotrichia (14 and 19, respectively) in the anterior part of the fin, whereas the posterior lepidotrichia are shorter with only the outline of their distal extremities. This pattern suggests that the ossification begins from an anterior center in both fins. Thus, the ossification pattern for the lepidotrichia seems to be similar to the pattern seen for radials.

All specimens examined show segmentation of lepidotrichia. The smallest specimen (FMNH PF 7488; SL: 17.78 mm) shows one to three segments and the longest specimens show up to six or seven segments per lepidotrichium. The longest lepidotrichia are positioned in the anterior part of the dorsal and anal fins. In specimen FMNH PF 7502 the longest lepidotrichia are lepidotrichia 7-15 in the dorsal fin and lepidotrichia 10-13 in the anal fin (Fig. 7). This morphology suggests that segmentation starts at the level of the longest lepidotrichia, and then, proceeds bidirectionally. The longest lepidotrichia articulate with radials 5-6, which are among the first ones to ossify. It seems that in *E. peltigerus* there is a congruence between the ossification and the segmentation patterns. None of the specimens show bifurcated lepidotrichia.

1.4.2.2 Actinistia

Two actinistian species have been examined: (1) the Late Devonian *Miguashaia bureaui* and the Late Carboniferous *Rhabdoderma exiguum*. *M. bureaui* is considered as an actinistian basal taxon (Cloutier 1991, 1996a), whereas *R. exiguum* is a typical

Carboniferous actinistian. Both species where first described from juvenile specimens; but while *M. bureaui* is known from few specimens, with a great size range (Cloutier 1996a), *R. exiguum* (Eastman 1902, 1903) is essentially known from small juvenile specimens (Schultze 1972, 1985).

There are 27-28 lepidotrichia in the second dorsal fin and ca. 25 in the anal fin of *M. bureaui*. The longest lepidotrichia are in the anterior part of the fin at the level of lepidotrichia 4-6 in the dorsal fin and at the level of lepidotrichia 7-8 in the anal fin (MHNM 06-41; Fig. 9). This pattern is not seen in the juvenile specimen (ULQ 120b; Fig. 8) because the distal part of both median fins is not preserved.

In the juvenile specimen ULQ 120 (Total length (TL): 72 mm), the basal proximal segments are 2.8 mm long in the dorsal fin and 2.1 in the anal fin (Fig. 8). In specimen MHNM 06-41 (TL: 195 mm; Fig. 9), these proximal segments are longer; the basal segments reach 3.3 mm in the dorsal fin and 7.2 mm in the anal fin. Moreover, the length of the basal segments in both fins reach 9-10 mm in specimen MHNM 06-494 (TL: 375 mm). In specimen MHNM 06-41, the first segment distal to the basal element of lepidotrichium 11 seems to be half-merged with the basal element (Fig. 9). This observation is interpreted as a merging of proximal segments; thus explaining the length increase of the basal segment during growth. While the length of the basal elements increases, the size of the distal elements remains unchanged at 2 mm. However, while the total length of the distal segments does not increase, some important shape changes occur. In the juvenile specimen of *M. bureaui* (ULQ 120b; Fig. 8), lepidotrichial segments have a thin-rod shape with some segments showing small anteroproximal and posterodistal extensions. This characteristic interlocking pattern intensifies during growth and becomes more apparent in larger specimens [MHNM 06-41 (Fig. 9), MHNM 06-494 (Fig. 10)].

In the juvenile specimen ULQ 120 (Fig. 8), first bifurcations appear at the level of lepidotrichia 14-15, on segments 5 or 6 in both fins. The most proximal bifurcations in specimen MHNM 06-41 are also at the same level (Fig. 9). Bifurcations are gradually located distally on the following lepidotrichia, which are mainly anterior to the first lepidotrichium showing bifurcation. However, specimen ULQ 120 shows bifurcation on lepidotrichia that are on both side of the first lepidotrichium (Fig. 8B). Thus, a mainly postero-anterior direction is inferred for bifurcation events during development, but a bidirectional pattern is not excluded. There are up to three bifurcation orders in specimen MHNM 06-494.

The dorsal and anal fins of *R. exiguum* are similar in shape, size and maximum number of lepidotrichia (Fig. 11). The dorsal fin includes 12-21 lepidotrichia, whereas the anal fin has 9-21 lepidotrichia. This great variability is likely due to some taphonomic bias, coupled with ossification during growth; the maximum number of lepidotrichia is seen in specimens greater than 44.5 mm in SL. The longest lepidotrichia (i.e., the ones which have most segments) are the same in both fins: lepidotrichia 10-12. All the specimens, even the smallest (ca. 30 mm) show segmentation, but none of the specimens show bifurcation.

1.4.2.3 Porolepiformes

Porolepiforms are relatively rare in the fossil record, and thus size series are difficult to constitute. Only two porolepiforms are known from juvenile specimens, *Quebecius quebecensis* and *Holoptychius jarviki*, both from Miguasha (Quebec, Canada). Only 31 specimens of *Q. quebecensis* have been found; most of them are incomplete specimens. Two nearly complete juvenile specimens with well-preserved dorsal and anal fins (MHNM 06-1474a, SL: 46.6 mm; MHNM 06-1148, SL: 52.6 mm) and one adult specimen showing only the anal and caudal fins (MHNM 06-1244, estimated SL: 193.1 mm) were examined.

The number of lepidotrichia is variable among specimens. There are ca. 31 and 35 lepidotrichia, respectively, in the dorsal and anal fins of specimen MHNM 06-1474a and ca. 35 and 40 lepidotrichia, respectively, in the dorsal and anal fins of specimen MHNM 06-1148. Lepidotrichia of both juvenile specimens do not show clear segmentation or bifurcation. The adult specimen (MHNM 06-1244) shows 36 lepidotrichia in the anal fin. The pattern of bifurcation previously described in *M. bureaui* is present in the anal fin; the posterior lepidotrichia display more proximal bifurcations than the anterior lepidotrichia, thus suggesting a mainly postero-anterior developmental pattern. The more proximal bifurcations are seen on the first and second segments of lepidotrichia 30-34. Lepidotrichium 11 is the more anterior to show a bifurcation; this bifurcation is located on the fifth segment.

1.4.2.4 Dipnoiformes

Dipterus valenciennesi is recognized as a relatively basal dipnoan, owing to his generalized postcranial morphology with short-based and well-separated median fins (Cloutier and Ahlberg 1996). This species is known for its great quantity of specimens of different sizes (Trewin 1986).

The second dorsal and anal fins of *D. valenciennesi* differ considerably in terms of size and shape (Fig. 12). Based on the examined specimens, the dorsal fin has 42-48 lepidotrichia, whereas the anal fin has 21-28 lepidotrichia. The proximal third of all lepidotrichia of both fins is unsegmented. The bifurcated portion is restricted between lepidotrichia 15-18 to lepidotrichia 39-42 in the dorsal fin and between lepidotrichia 11-12 to 17-22 in the anal fin. In both fins, the posterior-most lepidotrichia showing bifurcation presents proximal bifurcations, whereas the anterior-most bifurcated lepidotrichia bear more distal bifurcations. There are up to three orders of bifurcation (BMNH P22187; Fig. 12B). In specimen BMNH P22187, the first order of bifurcation extends from lepidotrichia 15 to 42 in the second dorsal fin and from lepidotrichia 8 to 16 in the anal fin. The second order of bifurcation is found on lepidotrichia 28 to 35 in the dorsal fin and 9 to 14 in the anal fin. Finally, the third order is only visible in the anal fin on lepidotrichia 12-14; the posterior-most lepidotrichia that are branched. Thus, the inferred sequence of bifurcation is from posterior to anterior for both fins.

1.4.2.5 Osteolepiformes

Osteolepiforms are found from the Middle Devonian to the Lower Permian. Rare are the size series of osteolepiforms. *Eusthenopteron foordi* from the Upper Devonian is the best studied osteolepiform including extensive size series (e.g., Schultze 1984; Cote et al. 2002; Leblanc 2005).

The second dorsal and anal fins of *E. foordi* are similar in shape and size with up to 25 lepidotrichia and similar endoskeletal supports. The lepidotrichia are the first structures to ossify in the second dorsal and anal fins. Specimen MHNM 06-1754a (SL: 53.5 mm) has 25 lepidotrichia in the anal fin, which is comparable to the number of lepidotrichia found in the longest specimens. This small specimen shows segmentation on some lepidotrichia (Fig. 13) in contrast to Leblanc (2005) who reported the first evidence of segmentation only in a 102.3 mm long specimen. When lepidotrichia are well-preserved, segmentations are visible all along their length (Fig. 14) in contrast to Leblanc (2005) who reported them only from half length to a fifth of the length. The basal proximal segment is generally longer than the distal ones. For example, in the anal fin of specimen MHNM 06-1769 (Fig. 14), the basal element of lepidotrichia 14 is 2.95 mm long, whereas the second and third segments are ca. 1.24 mm long.

Bifurcations are present in the smallest specimens; MHNM 06-1754a shows nine lepidotrichia with bifurcation in the anal fin (Fig. 13). The most proximal bifurcation is on the first segment of lepidotrichia 18; which is the only one showing a second order of bifurcation. Lepidotrichia 17 and 19 show bifurcations located more distally than the one on lepidotrichia 18. The bifurcations anterior to lepidotrichia 17 are even more distal. The pattern seen in specimen MHNM 06-1754a can be generalized for all the specimens examined; the most proximal bifurcations and the greatest number of bifurcation orders are generally seen on lepidotrichia 17-19. For example, specimen MHNM 06-86 has a third order only on lepidotrichia 17. Generally, bifurcations are restricted between lepidotrichia 8-9 to lepidotrichia 21-25. Up to four orders of bifurcation are present in specimen MHNM 06-367 (SL: 204.2 mm), which is among the longest specimens examined. From these observations, the inferred direction for bifurcation is mainly postero-anterior for both fins.

The distal radials ossify before the basal plate. The ossification of radials occurs early during development; the proximal extremity of the third (posterior) radial is visible in the anal fin of a 43.6 mm long specimen (MHNM 06-528). In contrast to Leblanc (2005), the smallest specimen having the first (anterior) radial ossified is only 44.3 mm in SL (MHNM 06-535) instead of 54.2 mm (ULQ 121). In specimen (MHNM 06-535), the three radials are ossified in the dorsal fin whereas the second and third radials are present in the anal fin. However, specimen MHNM 06-1754a (SL: 53.5 mm; Fig.13) shows three ossified radials in both fins. Despite the early ossification, the ossification of radials proceeds from posterior (radial 3) to anterior (radial 1). The ossification of the basal plates quickly follows the ossification of the distal radials. The basal plate first occurs in the anal fin of a 69.6 mm long specimen (MHNM 06-213) and in the dorsal fin of a 88.9 mm long specimen (MHNM 06-111). These data suggest a timing difference between the ossification of the endoskeletal elements of the dorsal and anal fins; the anal fin is the first to ossify. These observations differ from that of Cote et al. (2002) and Leblanc (2005), who only reported the presence of an ossified basal plate in a 120 mm long specimen. The basal plate first appears as a rod-shaped element, while the distal anterior expansion develops in larger specimens. Thus, the general direction of ossification is from posterior to anterior (radial 3 to 1) and from distal to proximal (radial to basal plate) for both fins.

1.5 DISCUSSION

Recurrent patterns of differentiation in the median fins of living actinopterygians were interpreted as evidences of modularity by Mabee et al. (2002). Two modules were described: the DAFPM (where both fins differentiate in the same direction) and the EEM (where radials and lepidotrichia in the same fin differentiate in the same direction). However, a phylogenetic inference was not possible for osteichthyans other than living actinopterygians, owing to the absence of data concerning basal actinopterygians and sarcopterygians (Mabee et al. 2002). In order to address a better description of the osteichthyan condition, new data were needed concerning (1) median fin development in terms of distinct developmental events in living actinopterygians, (2) a quantification and recognition of modularity within the developmental sequences for each event in living actinopterygians, and (3) a comparison of these developmental events with fossil actinopterygians and sarcopterygians. Because fossilized ontogenetic sequences are rare and partial, only the comparison of developmental events allows the recognition of modularity in fossil taxa. Unfortunately, all the events can not be observed, because there are recurrent taphonomic bias for the ossified structures contra the cartilaginous structures.

The data collected in the rainbow trout revealed the presence of eight consecutive events during dorsal and anal fin development. The sequence of development includes: (1) the differentiation of proximal radials, (2) the chondrification of proximal radials, (3) the differentiation of lepidotrichia, (4) the chondrification of distal radials, (5) the segmentation of lepidotrichia, (6) the ossification of lepidotrichia, (7) the bifurcation of lepidotrichia, and (8) the ossification of proximal radials. In fact, this sequence of development was previously, but partially, described for various actinopterygian species (e.g., François 1958; Balart 1995; Faustino and Power 1999; Bird and Mabee 2003; Suzuki et al. 2003; Cloutier et al. in prep.) but these descriptions rarely mentioned the development of both skeletons (endo and exo) concurrently as well as the segmentation and bifurcation patterns of lepidotrichia. This study is the first one to quantify the sequences of development of the endoskeleton and exoskeleton, including the segmentation and bifurcation patterns, in the dorsal and anal fins of a living actinopterygian.

The observed sequence of development seems to be general for living actinopterygians (Faustino and Power 1999). Coupled with the observations of Mabee et al. (2002), the patterns of development are thus strongly conserved in actinopterygians. To look further in the osteichthyan phylogeny, data were collected on fossil taxa from five osteichthyan groups to infer the evolution of median fin modularity; these data will also allow verifying if the general sequence of development in living actinopterygians is in fact a general sequence for osteichthyans. In order to infer the phylogenetic patterns, all the events will be discussed in terms of ontogeny and phylogeny.

1.5.1 Differentiation and chondrification

It is generally recognized that the proximal radials are the first skeletal structures to form during fin development (François 1958; Faustino and Power 1999; Bird and Mabee 2003; Suzuki et al. 2003; Mabee and Noordsy 2004; Cloutier et al. in prep.). The proximal radials first appear as cell condensations, where chondrocytes differentiate subsequently (Suzuki et al. 2003). François (1958) and Bird and Mabee (2003) mentioned that the first endoskeletal structures form in the middle of the fin, with the subsequent radials forming bidirectionally, in the dorsal fin of the rainbow trout and the zebrafish (*Danio rerio*), respectively. Bird and Mabee (2003) mentioned the same pattern for the anal fin of the zebrafish. The sequences of chondrification for the dorsal and anal fins described in this study conform to the observation of François (1958) and Bird and Mabee (2003). The first stages of lepidotrichia formation appear next, following the bidirectional patterning of the proximal radials. This concerted bidirectional differentiation for the dorsal and anal fins *and* the proximal radials and lepidotrichia supports the DAFPM and EEM, as described by Mabee et al. (2002). The case of distal radials will be discussed later.

1.5.2 Segmentation of lepidotrichia

First segmentation of lepidotrichia appear prior to their ossification, and before the lepidotrichia have completely formed. Segmentations are essentially «gaps between the bony plates» (Haas 1962). New segments are added gradually at the distal end of the forming lepidotrichia (Goodrich 1904; Prenant 1937; François 1958; Haas 1962; Géraudie and Landis 1982; Laforest et al. 1998; Marí-Beffa et al. 1999; Iovine and Johnson 2000; Borday et al. 2001), whereas the ossification begins proximally (François 1958; Géraudie and Landis 1982). Haas (1962) observed that during the development of lepidotrichia, mesenchymal cells, which are the precursors of the bony segments, form a gap by changing their position prior to ossification. When ossification occurs before the gap is completely formed, this results in an incomplete segmentation.

Since first segmentations are formed prior to ossification in the rainbow trout, early segmentations were also expected in fossil osteichthyans because lepidotrichia are visible even in the smallest specimens examined. Early segmentation was observed in: *Elonichthys peltigerus* (Schultze and Bardack 1987), *Rhabdoderma exiguum* (Charest and Cloutier 2006; contra Arratia et al. 2001) and *Eusthenopteron foordi* (contra Eaton 1945, Cote et al. 2002 and Leblanc 2005).

Particularly elongated basal segments were observed in the lepidotrichia of three taxa in this study: *Miguashaia bureaui*, *Dipterus valenciennesi* and *Eusthenopteron foordi*. This particular morphology has been reported in the fins of some living actinopterygians (Prenant 1937; François 1958; Haas 1962; Bouvet 1974) as well as extinct actinopterygians (Goodrich 1904; Eaton 1945) and sarcopterygians [in osteolepiforms, porolepiforms, actinistians, dipnoans (Goodrich 1904; Eaton 1945); in rhizodontids (Cloutier and Ahlberg 1996; Jeffery 2001)]. Thus, this pattern seems to be highly preserved in the osteichthyan phylogeny.

Prenant (1937) explained the length of this basal element by a continuous proximo-distal growth taking place in the lepidotrichia, whereas some authors affirm that once formed, a segment does not increase in size (Haas 1962; Iovine and Johnson 2000). According to François (1958), the basal segment is primarily longer than the successive ones in juvenile specimens of trout. On the other hand, he observed pre-existing gaps filled by bony matrix on the basal segments of the lepidotrichia in the dorsal fin of a specimen of rainbow trout (7 cm long) and concluded that the size differences observed in longer specimens are secondarily due to the merging of pre-existing distal segments to the basal segment. However, what appears to be the same observation is interpreted differently by Haas (1962) who mentioned that incomplete gaps are formed by the ossification that occurs before segments are completely individualized.

Gradual elongation of basal segment was observed in *M. bureaui*; the merging of pre-existing segments is inferred to explain this increasing size during development. These observations suggest that this basal segment is simply part of a true lepidotrichium in contrast to Johanson et al. (2005) who proposed that this segment is not part of a lepidotrichium in sarcopterygians.

Segmentation pattern of the dorsal and anal fins are congruent in the rainbow trout as well as in fossil taxa. This congruence suggests that the DAFPM is not limited to differentiation patterns but includes as well the segmentation patterns.

Particular gene transcripts have been reported to be involved in the establishment of segments in lepidotrichia of all fins during fin development and regeneration in the zebrafish (Iovine and Johnson 2000; Borday et al. 2001). Moreover, the general patterns of segmentation were found to be similar between the rainbow trout and fossil osteichthyans. Thus, these molecular mechanisms of lepidotrichia growth appear general for osteichthyans.

1.5.3 Ossification of lepidotrichia and radials

The ossification patterns of the radials and lepidotrichia were found to be highly congruent between the dorsal and anal fins of the rainbow trout. The same observation was made by Bird and Mabee (2003) for the zebrafish. This ossification pattern is thus a part of the DAFPM.

Lepidotrichia ossify before radials in living (Géraudie and Landis 1982; Bemis and Grande 1999, Cote et al. 2002; Suzuki et al. 2003) and fossil osteichthyans (Cote et al. 2002; Leblanc 2005). This sequence was observed in the rainbow trout. Moreover, lepidotrichia and proximal radials ossify in the same direction and their respective sequences of ossification are significantly correlated, thus meeting the requirements to be included in the EEM. However, Mabee et al. (2002) described the EEM solely from these two consecutive steps: (1) differentiation/chondrification of radials and (2) differentiation of lepidotrichia that follows the patterning of the radials. Two more steps ought to be added to complete the description of this module: (3) ossification of lepidotrichia and (4) ossification of proximal radials that follows the patterning of lepidotrichia.

In fossil taxa, the cartilaginous skeleton is rarely preserved. Thus, fossil sequences should be interpreted based on the new steps 3 and 4. Consequently, when analysing the sequences obtained from *Elonichthys peltigerus* and *Eusthenopteron foordi*, the only two fossil species where radials were preserved, lepidotrichia are present (ossified) before radials. Based on the sequence in the rainbow trout and the new description of the EEM, this sequence observed in fossil fishes was expected. This view contrasts with Johanson et al. (2005), who questioned the presence of the EEM in fossil fishes because the formation of lepidotrichia precedes the formation of radials in juvenile specimens of sarcopterygians.

Data from *E. peltigerus* specimens are supporting the EEM; sequences of ossification of the distal radials and lepidotrichia seem congruent. However, the module identified in *E. peltigerus* is inferred from the sequences of ossification of distal radials, whereas in the rainbow trout, the EEM is described from the sequences of ossification of the proximal radials. Moreover, the absence of the EEM in *E. foordi* is inferred from the sequence of ossification of the three distal radials, which is from posterior to anterior in the dorsal and anal fins, whereas lepidotrichia show a morphological pattern that suggests an anterior center of induction for ossification. Besides, even if "proximal radials" are observable in *E. foordi*, comparisons with the sequence described in the rainbow are not possible because the proximal radials are in fact a sole basal plate for which the ossification is proximo-distal.

The few data concerning chondrification of distal radials in the rainbow trout limits comparisons between living and fossil taxa. On the other hand, it was observed that the first distal radials to chondrify are congruent with the first proximal radials to chondrify in the rainbow trout. In addition, according to Bird and Mabee (2003), ossification generally follows the same direction as chondrification and distal radials ossify in the same direction as proximal radials in the zebrafish. Thus, it is likely that the sequences of chondrification and ossification are similar between proximal and distal radials in the rainbow trout. In this case, comparisons would be possible between proximal radials of living actinopterygians and distal radials of fossil taxa such as *E. peltigerus*. In contrast, in their description of the sequences of chondrification and ossification in the dorsal and anal fins of the Arctic charr (*Salvelinus alpinus*), Cloutier et al. (in prep.) mentioned an antero-posterior formation of distal radials. Thus, a greater consideration must be given to the sequences of development of the distal radials in future investigations.

The sequences obtained from *E. foordi* do not allow to identify the EEM in sarcopterygians, whereas the data from *E. peltigerus* confirm its presence in a Carboniferous actinopterygian. Thus, the EEM is at least plesiomorphic for actinopterygians, for which it is easier to identify congruent sequences between radials and lepidotrichia. On the other hand, ossification patterns were found to be congruent between the dorsal and anal fins of different fossil taxa, thus suggesting that the DAFPM is plesiomorphic for osteichthyans.

1.5.4 Bifurcation of lepidotrichia

Bifurcations are resulting from the subdivision of the growing distal end of lepidotrichia (Goodrich 1904), prior to the ossification of the distal end. In fact, as it was the case for segmentation, bifurcations are formed distally whereas ossification begins proximally. Thus, each bifurcation is formed before the ossification process fixes it in a bone matrix. This fact suggests the possibility that early bifurcations could be observed in fossil fishes. Leblanc (2005) mentioned the first evidence of bifurcation in the pectoral fin of a 41.8 mm long specimen of *Eusthenopteron foordi* (MHNM 06-90). A similar observation was made in the anal fin of a 53.5 mm long specimen of *E. foordi* (MHNM 06-1754). Early bifurcation was also observed in *M. bureaui* (ULQ 120, TL: 76 mm).

From the pattern quantified in the dorsal fin of the rainbow trout, the first bifurcation is forming posteriorly to: (1) the first differentiation (radials and lepidotrichia), (2) the first ossification (radials and lepidotrichia), and (3) the first segmentation (lepidotrichia). In the anal fin, this pattern is not as evident; the origin of bifurcation is not different from the origin of the others events. Following these results, sequences of bifurcation of the dorsal and anal fins are not congruent. However, sample size was quite small; only 20 specimens showed bifurcation in the anal fin, and 28 specimens in the dorsal fin. Also, important intraspecific variability was observed in the database for the bifurcation of the anal fin. This could explain the absence of congruence for bifurcation in the fins of the rainbow trout. Despite the difference between the dorsal and anal fins, the morphology is similar; the most proximal bifurcations are located on the posterior lepidotrichia, whereas the most distal bifurcations are located on the anterior lepidotrichia. In the future, attention must be given to the study of bifurcation in a growth series where specimens would be sampled every day because similar morphologies suggest strongly similar developments.

The data from *M. bureaui, Q. quebecensis, D. valenciennesi* and *E. foordi* suggest that the first bifurcation is the most proximal one, located on the posterior lepidotrichia, and that the direction of bifurcation for the following lepidotrichia is mainly from posterior to anterior. A bidirectional pattern was not excluded in *M. bureaui* because a bifurcated lepidotrichium was observed posterior to the inferred first bifurcation. In fact, bidirectional patterns observed in the rainbow trout and *M. bureaui* are quite asymmetrical and are considered similar to the "mainly antero-posterior" patterns seen in *Q. quebecensis, D. valenciennesi* and *E. foordi*. The state of preservation of fins in some specimens could make the identification of posterior bifurcations difficult because lepidotrichia are very small. However, more attention must be given to this.

Therefore, the bifurcation pattern described in the rainbow trout seems to be general in osteichthyans. In fact, it is documented that particular genes are expressed prior to the formation of a bifurcation in fin rays (Laforest et al. 1998; Quint et al. 2002; Akimenko et al. 2003). Among others, the signalling molecule *sonic hedgehog,* which is expressed were new bone is forming during fin ray growth, appears generally in a group of cells centered in the fin ray, but in two groups of cells positioned laterally, prior to the formation of a bifurcation (Laforest et al. 1998; Quint et al. 2002). Thus, molecular mechanisms for bifurcation seem preserved among groups because morphology are similar.

However, the absence of bifurcation is homoplastic during the osteichthyan phylogeny. *M. bureaui* was considered the only actinistian showing bifurcation (Cloutier 1991; Forey 1991; Forey 1998), but bifurcations are visible in the pectoral fin of *Shoshonia arctopteryx* (Fig. 2 in Friedman et al. 2007). The absence of bifurcation is also observed among living (François 1958; Witten and Huysseune 2007) and fossil actinopterygians (e.g., *E. peltigerus*; Schultze and Bardack 1987). In contrasts to other events during median fin development, bifurcation is initiated in the posterior part of the dorsal and anal fins. According to Lindsey (1955), the posterior part of median fins is the last formed in modern fishes and thus is more alterable experimentally. Moreover, the bifurcation is the last event during fin ray formation; epigenetic phenomenons are thus more susceptible to operate and suppress the bifurcation of fin rays.

1.5.5 Median fin modules

Among others, modules are characterized by a hierarchical organization (Raff 1996). The DAFPM is the larger module considered in this study. Mabee et al. (2002) described the DAFPM from the sole observation of a similar direction of differentiation for the dorsal and anal fins (1). The observations made on the rainbow trout allow to complete the description of the DAFPM: (2) the direction of ossification (radials and lepidotrichia) are similar between fins, (3) the direction of segmentation (lepidotrichia) are similar between fins and (4) the morphology of both fins suggests a similar direction of bifurcation. Also, an additional developmental pattern was observed in *M. bureaui*, the simultaneous and gradual development of the interlocking pattern in the dorsal and anal fins. This pattern, described only in few early actinistians (Cloutier 1996a; Friedman et al. 2007) could be a part of the DAFPM as well. Unfortunately, there is no living taxon allowing to study this pattern.

The DAFPM was found to be conserved in fossil taxa: (1) patterns of ossification of radials are congruent between fins (*E. peltigerus* and *E. foordi*), (2) morphological patterns of ossification of lepidotrichia are congruent between fins, (3) morphological patterns of segmentation are similar between fins (*E. peltigerus*, *M. bureaui*, *R. exiguum* and *E. foordi*) and (4) patterns of bifurcation are similar between fins (*M. bureaui* and *E. foordi*).

Dipterus valenciennesi is the only examined taxa for which dorsal and anal fins present an important size difference, thus limiting comparisons between fins. Nevertheless, the general patterns of development seem similar (e.g., antero-posterior direction of bifurcation). This size difference, recognized by many authors (Eaton 1945; Cloutier 1996b; Cloutier and Ahlberg 1996; Arratia et al. 2001), is even greater in other Devonian dipnoans as *Scaumenacia curta* and *Fleurantia denticulata* (Cloutier 1996b). Furthermore, while Devonian dipnoans have independent median fins (second dorsal, anal and caudal fins), Late Paleozoic to living species have lost the three independent median fins (Arratia et al. 2001). A process of dissociation is inferred between the dorsal and anal fins of dipnoans, which would explain this divergence during phylogeny. Additionally, some characters of dipnoans are considered evidences of pedomorphosis. One of these characters is the gradual fusion of the dorsal, anal and caudal fins during the dipnoan evolution (Bemis 1984; Arratia et al. 2001).

The DAFPM include a smaller unit, the EEM. Mabee et al. (2002) suggested that the exoskeleton and the endoskeleton of all fins form a module, because their directions of development are similar. Data collected in this study allow to describe the EEM from four steps, which were mentioned previously. This module was found to be plesiomorphic at least for actinopterygians. Unfortunately, data obtained from fossil sarcopterygians do not allow to infer this module. When possible, additional investigations should be made in the study of the developmental patterns of the fin skeletons of sarcopterygian fishes, living or extinct.

The EEM is composed of two units. Fins contain two different skeletons, or modules, formed by distinct developmental processes: (1) the dermal (exo) skeleton and (2) the endochondral skeleton (Shubin and Davis 2004). Differences among the major osteichthyan clades would be due to relative size, shape and position of the exo and endoskeleton in their fins, and in a particular group, tetrapods, the lost of the exoskeleton module in paired fins, for example (Shubin and Davis 2004).

The exoskeleton was found to be the location of many developmental interactions among its constituents. Such interactions were found during the regeneration of the caudal fin and contribute to elucidate the coordinated patterning (bifurcation and segmentation) among fin rays (Marí-Beffa et al. 1999; Murciano et al. 2002, 2007). The position of segmentations and bifurcations are dependant of the position of the ray within the fin (Murciano et al. 2002, 2007). As a limb bud can be grafted to a new location and grows normally, a fin ray can be grafted to a new location and grows quite normally by the addition of new segments (Birnie 1947; Murciano et al. 2002, 2007). On the other hand, rays regenerating without contact with other rays do not bifurcate; interactions with adjacent tissues are thus necessary to achieve the original morphology (Murciano et al. 2002). These observations corroborate the exoskeleton as a module and allow recognizing a smaller modular unit within fins, lepidotrichia or fin rays.

Data obtained from the rainbow trout allow to describe a developmental sequence for lepidotrichia: (1) differentiation, (2) segmentation, (3) ossification and (4) bifurcation. Data from fossil taxa are quite in agreement with this sequence, which seems preserved in osteichthyans. Moreover, lepidotrichia are formed by two symmetrical parallel hemirays (Géraudie and Landis 1982) which have simultaneous congruent differentiation patterns (Géraudie and Landis 1982; Marí-Beffa et al. 1999; Murciano et al. 2007; Witten and Huysseune 2007). This "Fin Ray Patterning Module" is surely generalized in all fins of all osteichthyans.

Moreover, developmental interactions are recognized to control coordination of segmentation and bifurcation between hemirays (Murciano et al. 2007). However, a single hemiray may autonomously regenerate and segmentate in a new location (Murciano et al. 2007). Thus, the hemiray could be the smallest unit of regeneration (and development) in the hierarchical (modular) organization of fins (Akimenko and Smith 2007).

1.6 CONCLUSIONS

The sequence of eight consecutive developmental events studied in the rainbow trout as a model for living actinopterygians facilitate the interpretation of the developmental sequences found in fossil fishes. In fact, data suggest that this sequence is conservative during osteichthyan phylogeny. Modularity is supposed to imply such constraint on the order of the events. The two modules described by Mabee et al. (2002) are not restricted to the differentiation pattern. The quantification and correlation of corresponding sequences of development in the dorsal and anal fins of rainbow trout as well as in the exoskeleton and endoskeleton support the DAFPM and EEM, in all events, except for the bifurcation of lepidotrichia. The ossification sequences of the exoskeleton and the endoskeleton were found congruent in the fossil actinopterygian species examined, but not in the sarcopterygian species, suggesting that the EEM is plesiomorphic for actinopterygians. However, the ossification, segmentation and bifurcation patterns were fairly congruent between fins, except for the taxa where the bifurcation was absent. The DAFPM is thus plesiomorphic for osteichthyans. The recurrent sequence of development of lepidotrichia observed in living and fossil osteichthyans (i.e., (1) segmentation, (2) ossification and (3) bifurcation) as well as the developmental interactions documented for lepidotrichia suggest the presence of an additional developmental module within fins, the Fin Ray Patterning Module, where the constitutive units, the hemirays, have a synchronous and similar development. The dorsal and anal fins of osteichthyans are thus a good example of hierarchical organization of modularity and preservation of modules during phylogeny.

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1.8 REFERENCES

Akimenko, M.-A., M. Marí-Beffa, J. Becerra and J. Géraudie, 2003. Old questions, new tools, and some answers to the mystery of fin regeneration. *Developmental Dynamics* 226: 190-201

Akimenko, M.-A. and A. Smith, 2007. Paired fin repair and regeneration. In Hall, B. K. (ed.) *Fins into limbs – Evolution, Development and Transformation.* The University of Chicago Press, Chicago (USA). p. 152-162

Arratia, G., H.-P. Schultze and J. Casciotta, 2001. Vertebral column and associated elements in dipnoans and comparison with other fishes: development and homology. *Journal of Morphology* 250: 101-172

Balart, E.F., 1995. Development of the vertebral column, fins and fin supports in the japonese anchovy, *Engraulis japonicus* (Clupeiformes: Engraulididae). *Bulletin of Marine Science* 56(2): 495-522

Bemis, W.E., 1984. Paedomorphosis and the evolution of the Dipnoi. *Paleobiology* 10: 293-307

Bemis, W. E. and L. Grande, 1999. Development of the median fins of the North American paddlefish (*Polyodon spathula*), and a re-evaluation of the lateral fin-fold hypothesis. In Arratia, G. and H.-P. Schultze (eds.), *Mesozoic Fishes 2— Systematics and Fossil Record.* Verlag Dr. Friedrich Pfeil, München, Germany. p. 41-68

Bird, N.C. and P.M. Mabee, 2003. Developmental morphology of the axial skeleton of the zebrafish, *Danio rerio* (Ostariophysi: Cyprinidae). *Developmental Dynamics* 228: 337-357

Birnie, J.H., 1934. Regeneration of the tail-fins of *Fundulus* embryos. *Biological Bulletin* 66: 316-325

Birnie, J.H., 1947. Regeneration and transplantation of fin rays in the Goldfish. *The Anatomical Record* 99: 648

Borday, V., C. Thaëron, F. Avaron, A. Brulfert, D. Casane, P. Laurenti and J. Géraudie, 2001. *evx1* transcription in bony fin rays segment boundaries leads to a reiterated pattern during zebrafish fin development and regeneration. *Developmental Dynamics* 220: 91-98

Bouvet, J., 1974. Différentiation et ultrastructure du squelette distal de la nageoire pectorale chez la truite indigène (*Salmo trutta fario L.*) II: Différentiation et ultrastructure des lépidotriches. *Archives d'Anatomie Microscopique* 63(4): 323-335

Charest, F. and R. Cloutier, 2006. Developmental patterns of the juvenile Carboniferous coelacanth *Rhabdoderma exiguum. Journal of Vertebrate Paleontology* 26, Supplement to 3: 49A

Chu, K.P., 2007. Effet de la vélocité du courant sur la plasticité morphologique des premiers stades de développement de la truite arc-en-ciel (*Oncorhynchus mykiss*). MSc thesis. Université du Québec à Rimouski, Rimouski.

Cloutier, R., 1990. Phylogenetic interrelationships of the actinistians (Osteichthyes: Sarcopterygii): patterns, trends, and rates of evolution. PhD Thesis. University of Kansas, Lawrence (USA)

Cloutier, R., 1991. Patterns, trends, and rates of evolution within the Actinistia. *Environmental Biology of Fishes* 32: 23-58

Cloutier, R., 1996a. The primitive actinistian *Miguashaia bureaui* Schultze (Sarcopterygii). In Schultze, H.–P. and R. Cloutier (eds.) *Devonian Fishes and Plants of Miguasha, Quebec, Canada*. Verlag Dr. Friedrich Pfeil, München, Germany. p. 227-247

Cloutier, R., 1996b. Dipnoi (Akinetia: Sarcopterygii). In Schultze, H.–P. and R. Cloutier (eds.) *Devonian Fishes and Plants of Miguasha, Quebec, Canada*. Verlag Dr. Friedrich Pfeil, München, Germany. p. 198-226

Cloutier, R. and P.E. Ahlberg, 1996. Morphology, characters, and the interrelationships of basal sarcopterygians. In Stiassny, M.L.J., L.R. Parenti and G.D. Johnson (eds.) *Interrelationship of fishes*. Academic Press, New-York, p. 445-479

Cloutier, R., A. Caron, T. Grünbaum, V. Canevet and N.R. Le François, in prep. Influence of water velocity on the sequence of chondrification and ossification of the median fins of larval Arctic charr *Salvelinus alpinus*.

Coates, M.I., 2003. The evolution of paired fins. *Theory in Biosciences* 122: 266-287

Coates, M.I. and M.J. Cohn, 1998. Fins, limbs, and tails: outgrowths and axial patterning in vertebrate evolution. *BioEssays* 20: 371-381

Coates, M.I. and M. Ruta, 2007. Skeletal changes in the transition from fins to limbs. In Hall, B. K. (ed.) *Fins into limbs – Evolution, Development and Transformation.* The University of Chicago Press, Chicago, United States. p.15-38

Cote, S., R.L. Carroll, R. Cloutier and L. Bar-Sagi, 2002. Vertebral development in the Devonian sarcopterygian fish *Eusthenopteron foordi* and the polarity of vertebral evolution in non-amniote tetrapods. *Journal of Vertebrate Paleontology* 22: 497-502

Cubbage, C.C. and P.M. Mabee, 1996. Development of the cranium and paired fins in the zebrafish *Danio rerio* (Ostariophysi, Cyprinidae). *Journal of Morphology* 229: 212-160

Dingerkus, G. and L.D. Uhler, 1977. Enzyme clearing of Alcian blue stained whole small vertebrates for demonstration of cartilage. *Biotechnic and Histochemistry* 52(4): 229-232

Eaton, T.H., 1945. Skeletal supports of the median fins of fishes. *Journal of Morphology* 76(3): 193-212

Faustino, M. and D.M. Power, 1999. Development of the pectoral, pelvic, dorsal and anal fins in cultured sea bream. *Journal of Fish Biology* 54: 1094-1110

Forey, P.L., 1991. *Latimeria chalumnae* and its pedigree. *Environmental Biology of Fishes* 32: 75-97

Forey, P.L., 1998. *History of the Coelacanth Fishes*. Chapman and Hall, London.

François, Y., 1958. Recherches sur l'anatomie et le développement de la nageoire dorsale des téléostéens. *Archives de Zoologie Expérimentale et Générale* 97: 1-108

François, Y. and M. Blanc, 1956. Sur la croissance en longueur des rayons de nageoires chez les poissons téléostéens. *Bulletin de la Société Zoologique de France* 81: 26-33

Friedman, M., M.I. Coates and P. Anderson, 2007. First discovery of a primitive coelacanth fin fills a major gap in the evolution of lobed fins and limbs. *Evolution & Development* 9(4): 329-337

Fuiman, L.A., K.R. Poling and D.M. Higgs, 1998. Quantifying developmental progress for comparative studies of larval fishes. *Copeia* 1998(3): 602-611

Géraudie, J. and W.J. Landis, 1982. The fine structure of the developing pelvic fin skeleton in the trout, *Salmo gairdneri. American Journal of Anatomy* 163: 141-156

Gilbert, S.F. and J.A. Bolker, 2001. Homologies of process and modular elements of embryonic construction. *Journal of Experimental Zoology (Mol Dev Evol)* 291: 1-12

Goodrich, E.S., 1904. On the dermal fin-rays of fishes – living and extinct. *Quarterly Journal of the Microscopical Society* 47: 465-522

Goodrich, E.S., 1958. *Studies on the structure and development of the vertebrates*. Dover Publications, New-York.

Goswami, A. 2007. Cranial modularity and sequence heterochrony in mammals. *Evolution & Development* 9(3): 290-298

Grünbaum, T., R. Cloutier and P. Dumont, 2003. Congruence between chondrification and ossification sequences during caudal skeleton development: a Moxostomatini case study. In Browman, H.I. and Skiftesvik A.B. (eds.), *The Big Fish Bang*, Proceedings of the 26th Annual Larval Fish Conference, Bergen, Norway. p. 161-176

Grünbaum, T., R. Cloutier and N.R. Le François, 2008. Positive effects of exposure to increased water velocity on growth of newly hatched Arctic charr, *Salvelinus alpinus* L. *Aquaculture Research* 39(1): 106-110

Haas, H.J., 1962. Studies on mechanisms of joint and bone formation in skeleton rays of fish fins. *Developmental Biology* 5: 1-34

Iovine, M.K., 2007. Conserved mechanisms regulate outgrowth in zebrafish fins. *Nature Chemical Biology* 3(10): 613-618

Iovine, M.K. and S.L. Johnson, 2000. Genetic analysis of isometric growth control mechanisms in the zebrafish caudal fin. *Genetics* 155: 1321-1329

Jeffery, J.E., 2001. Pectoral fins of rhizodontids and the evolution of pectoral appendages in the tetrapod stem-group. *Biological Journal of the Linnean Society* 74: 217-239

Johanson, Z., C. Burrow, A. Warren and J. Garvey, 2005. Homology of fin lepidotrichia in osteichthyan fishes. *Lethaia* 38: 27-36

Klingenberg, C.P., 2002. Morphometrics and the role of the phenotype in studies of the evolution of developmental mechanisms. *Gene* 287: 3-10

Klingenberg, C.P., K. Mebus and J.-C. Auffray, 2003. Developmental integration in a complex morphological structure: how distinct are the modules in the mouse mandible? *Evolution & Development* 5(5): 522-531

Laforest, L., C.W. Brown, G. Poleo, J. Géraudie, M. Tada, M. Ekker and M.-A. Akimenko, 1998. Involvement of the *Sonic Hedgehog*, *patched 1* and *bmp2* genes in patterning of the zebrafish dermal fin rays. *Development* 125: 4175-4184

Leblanc, J., 2005. Précisions sur l'anatomie de l'ostéolépiforme *Eusthenopteron foordi* du Dévonien supérieur de Miguasha, Québec. MSc thesis. Université du Québec à Rimouski, Rimouski.

Lindsey, C.C., 1955. Evolution of meristic relations in the dorsal and anal fins of teleosts fishes. *Transactions of the Royal Society of Canada* 49(series 3): 35-49

Mabee, P.M., P.L. Crotwell, N.C. Bird and A.C. Burke, 2002. Evolution of median fin modules in the axial skeleton of fishes. *Journal of Experimental Zoology (Mol Dev Evol)* 294: 77-90

Mabee, P.M. and M. Noordsy, 2004. Development of the paired fins in the Paddlefish, *Polyodon spathula*. *Journal of Morphology* 261: 334-344

Mabee, P.M. and T.A. Trendler, 1996. Development of the cranium and paired fins in *Betta splendens* (Teleostei: Percomorpha): intraspecific variation and interspecific comparisons. *Journal of Morphology* 227: 249-287

Magwene, P.M., 2001. New tools for studying integration and modularity. *Evolution* 55(9): 1734-1745

Marí-Beffa, M., P. Palmqvist, F. Marín-Girón, G.S. Montes and J. Becerra, 1999. Morphometric study of the regeneration of individual rays in teleost tail fins. *Journal of Anatomy* 195: 393-405

Murciano, C., T.D. Fernández, I. Durán, D. Maseda, J. Ruiz-Sánchez, J. Becerra, M.-A. Akimenko and M. Marí-Beffa, 2002. Ray-interray interactions during fin regeneration of *Danio rerio*. *Developmental Biology* 252: 214-224

Murciano, C., J. Pérez-Claros, A. Smith, F. Avaron, T.D. Fernández, I. Durán, J. Ruiz-Sánchez, F. García, J. Becerra, M.-A. Akimenko and M. Marí-Beffa, 2007. Position dependence of hemiray morphogenesis during tail fin regeneration in *Danio rerio*. *Developmental biology* 312: 272-283

Nabrit, S.M., 1931. The rôle of the basal plate of the tail in regeneration in the tail-fins of fishes (*Fundulus* and *Carassius*). *Biological Bulletin* 60: 60-63

Nunn, C.L. and K.K. Smith, 1998. Statistical analyses of developmental sequences: The craniofacial region in marsupial and placental mammals. *The American Naturalist* 152: 82-101

Poe, S., 2004. A test for patterns of modularity in sequences of developmental events. *Evolution* 58: 1852-1855

Potthoff, T., 1984. Clearing and staining techniques. In H.G. Moser, W.J. Richards, D.M. Cohen, M.P. Fahay, A.W. Kendall and S.L. Richardson (eds.), *Ontogeny and Systematics of Fishes*. American Society of Ichthyologists and Herpetologists, Special publication 1. Allen Press, Lawrence. p. 35-37

Prenant, M., 1937. Sur la croissance normale des lépidotriches articulés chez les téléostéen. *Bulletin de la Société Zoologique de France* 62: 190-195

Quinn, G.P. and M.J. Keough, 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge.

Quint, E., A. Smith, F. Avaron, L. Laforest, J. Miles, W. Gaffield and M.-A. Akimenko, 2002. Bone patterning is altered in the regenerating zebrafish caudal fin after ectopic expression of *sonic hedgehog* and *bmp2b* or exposure to cyclopamine. *PNAS* 99(13): 8713-8718

Raff, R.A., 1996. *The Shape of Life: Genes, development, and the evolution of animal form.* The University of Chicago Press, Chicago

Raff, R.A., 2007. Written in stone: fossils, genes and evo-devo. *Nature Reviews Genetics* 8: 911-920

Raff, R.A. and B.J. Sly, 2000. Modularity and dissociation in the evolution of gene expression territories in development. *Evolution & Development* 2(2): 102-113

Redfern, B.G., L.D. Wise and S. Spence, 2007. An alternative Alcian blue dye variant for the evaluation of fetal cartilage. *Birth Defects Research (Part B)* 80: 171-176

Richardson, M.K., 1999. Vertebrate evolution: the developmental origins of adult variation. *BioEssays* 21: 604-613

Schlosser, G., 2002. Modularity and the units of evolution. *Theory in Biosciences* 121: 1-80

Schultze, H.-P., 1972. Early growth stages in coelacanth fishes. *Nature New Biology* 236: 90-91

Schultze, H.-P., 1984. Juvenile specimens of *Eusthenopteron foordi* Whiteaves,1881 (osteolepiform rhipidistian, Pisces) from the Late Devonian of Miguasha, Québec, Canada. *Journal of Vertebrate Paleontology* 4(1): 1-16

Schultze, H.-P., 1985. Reproduction and spawning sites of *Rhabdoderma* (Pisces, Osteichthyes, Actinistia) in Pennsylvanian deposits of Illinois, USA. *Compte rendu Neuvième congr. Internat. Stratigr. Geol. Carbonifère (Washington & Champaign-Urbana)* 5: 326-330

Schultze, H.-P. and D. Bardack, 1987. Diversity and size changes in palaeonisciform fishes (Actinopterygii, Pisces) from the Pennsylvanian Mazon Creek fauna, Illinois, U.S.A. *Journal of Vertebrate Paleontology* 7(1): 1-23

Shubin, N.H. and M.C. Davis, 2004. Modularity in the evolution of vertebrate appendages. In Schlosser, G. and G.P. Wagner, (eds.), *Modularity in Development and Evolution*. University of Chicago Press, Chicago, p. 429-440

Smith, K.K., 2001. Heterochrony revisited: the evolution of developmental sequences. *Biological Journal of the Linnean Society* 73: 169-186

Suzuki, T., Y. Haga, T. Takeuchi, S. Uji, H. Hashimoto and T. Kurokawa, 2003. Differentiation of chondrocytes and scleroblasts during dorsal fin skeletogenesis in flounder larvae. *Development, Growth and Differentiation* 45: 435-448

Tanaka, M. and C. Tickle, 2007. The development of fins and limbs. In Hall, B.K. (ed.) *Fins into limbs – Evolution, Development and Transformation.* The University of Chicago Press, Chicago (USA). p. 65-78

Trewin, N.H., 1986. Palaecology and sedimentology of the Achanarras fish bed of the Middle Old Red Sandstone, Scotland. *Transactions of the Royal Society of Edinburgh* 77: 21-46

Von Dassow, G. and E. Munro, 1999. Modularity in animal development and evolution: elements of a conceptual framework for EvoDevo. *Journal of Experimental Zoology (Mol Dev Evol)* 285: 307-325

Wagner, G.P., 1996. Homologues, natural kinds and the evolution of modularity. *American Zoologist* 36: 36-43

Wagner, G.P., M. Pavlicev and J.M. Cheverud, 2007. The road to modularity. *Nature Reviews Genetics* 8: 921-931

Winther, R.G., 2001. Varieties of modules: Kinds, levels, origins, and behaviour. *Journal of Experimental Zoology (Mol Dev Evol)* 291: 116-129

Witten, P.E. and A. Huysseune, 2007. Mechanisms of chondrogenesis and osteogenesis in fins. In Hall, B. K. (ed.) *Fins into limbs – Evolution, Development and Transformation.* The University of Chicago Press, Chicago (USA). p. 79-92

Young, N., 2004. Modularity and integration in the hominoid scapula. *Journal of Experimental Zoology (Mol Dev Evol)* 302B: 226-240

Table 1: Six fossil taxa from five osteichthyan groups were examined in this study. Age, locality, sample size (n) and size ranges are given for each taxon. A list of specimens examined is given in Appendix 1.

Groups	Taxa	Age	Localities	n	Size range (mm)
Actinopterygii					
" Palaeonisciformes "	*Elonichthys peltigerus*	Upper Carboniferous (Pennsylvanian)	MC	17	17.2 - 49.5*
Sarcopterygii					
Actinistia	*Miguashaia bureaui*	Upper Devonian (Frasnian)	M	3	72 – 375**
	Rhabdoderma exiguum	Upper Carboniferous (Pennsylvanian)	MC	23	30.0-52.2*
Porolepiformes	*Quebecius quebecensis*	Upper Devonian (Frasnian)	M	3	46,6-193,1*
Dipnoi	*Dipterus valenciennesi*	Middle Devonian (Givetian)	AQ	5	69.6-158.8***
Osteolepiformes	*Eusthenopteron foordi*	Upper Devonian (Frasnian)	M	36	41.6-295.4*

MC: Mazon Creek, Illinois, USA; **M**: Miguasha, Québec, Canada; **AQ**: Achanarras Quarry, Scotland, UK
* Standard length
** Total length
*** Distance between the operculum and the insertion of the caudal fin.

Table 2: Origin, size and direction of the 13 events characterizing the development of the dorsal and anal fins of rainbow trout.

Events	First elements *		SL$_{50}$ (mm) **		Direction***	
	Dorsal	Anal	Dorsal	Anal	Dorsal	Anal
Proximal radial differentiation	4-9	4-10	na	na	na	na
Proximal radial chondrification	4-9	6-8	12.598	12.845	Bi	Bi
Distal radial chondrification	3-7	3-7	na	na	na	na
Lepidotrichia differentiation	7-11	6-9	13.287	12.884	Bi	Bi
Lepidotrichia segmentation: 1st	12	7-10	17.166	17.671	Bi	Bi
2nd	10	9-10	18.423	18.995	Bi	Bi
3rd	10	8	20.480	20.834	Bi	Bi
4th	11	8	22.217	23.456	Bi	Bi
5th	10	9	28.432	28.011	Bi	Bi
6th	10-12	ns	ns	ns	Bi	Bi
Lepidotrichia ossification	6-8	5-6	19.368	19.512	Bi	Bi
Lepidotrichia bifurcation	14	10	23.612	25.230	PA	PA
Radial ossification	4	4	25.524	28.258	Bi	Bi

* First elements to develop according to SL$_{50}$

** Respective size according to SL$_{50}$

*** Development proceeds either bidirectionally (Bi) or from posterior to anterior (PA)

na: Results for proximal radial differentiation are from observations on pre-hatching specimens (specimens where about 10 mm long). SL$_{50}$ were not calculated.

Results for distal radial chondrification are from observations; SL$_{50}$ were not calculated.

ns: Non significant results

Table 3: Spearman correlations between corresponding developmental sequences. Sample size (n) and Spearman coefficient (r_s) are given with significance levels in parenthesis.

Events	**n**	**r_s**
Radials chondrification (D and A)	13	0.919 ($p < 0.001$)
Lepidotrichia differentiation (D and A)	15	0.860 ($p < 0.001$)
Lepidotrichia 1st segmentation (D and A)	12	0.669 ($p < 0.05$)
2nd segmentation (D and A)	13	0.573 ($p < 0.05$)
3rd segmentation (D and A)	13	0.511 ($p < 0.05$)
4th segmentation (D and A)	11	0.282 ($p > 0.05$)
5th segmentation (D and A)	7	0.209 ($p > 0.05$)
Lepidotrichia ossification (D and A)	15	0.958 ($p < 0.001$)
Lepidotrichia bifurcation (D and A)	8	-0.405 ($p > 0.05$)
Radials ossification (D and A)	10	0.927 ($p < 0.001$)
Radials and lepidotrichia ossification (D)	11	0.854 ($p < 0.001$)
Radials and lepidotrichia ossification (A)	11	0.839 ($p < 0.01$)

D, Dorsal fin; A, anal fin

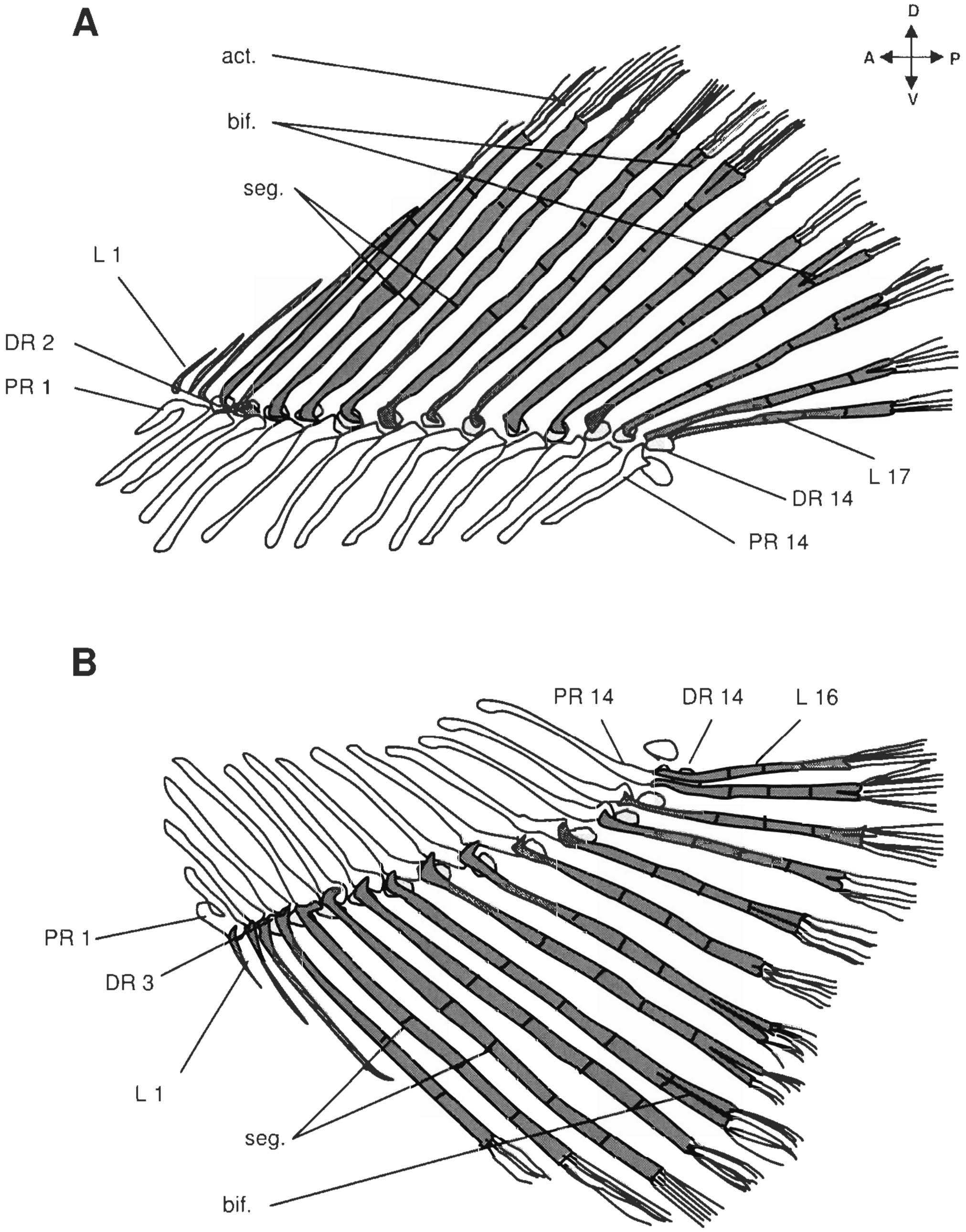

Figure 1: Dorsal fin (**A**) and anal fin (**B**) morphology of the rainbow trout (*Oncorhynchus mykiss*). **L**, lepidotrichia; **DR**, distal radial; **PR**, proximal radial; **act.**, Actinotrichia; **bif.**, Bifurcation; **seg.**, Segmentation

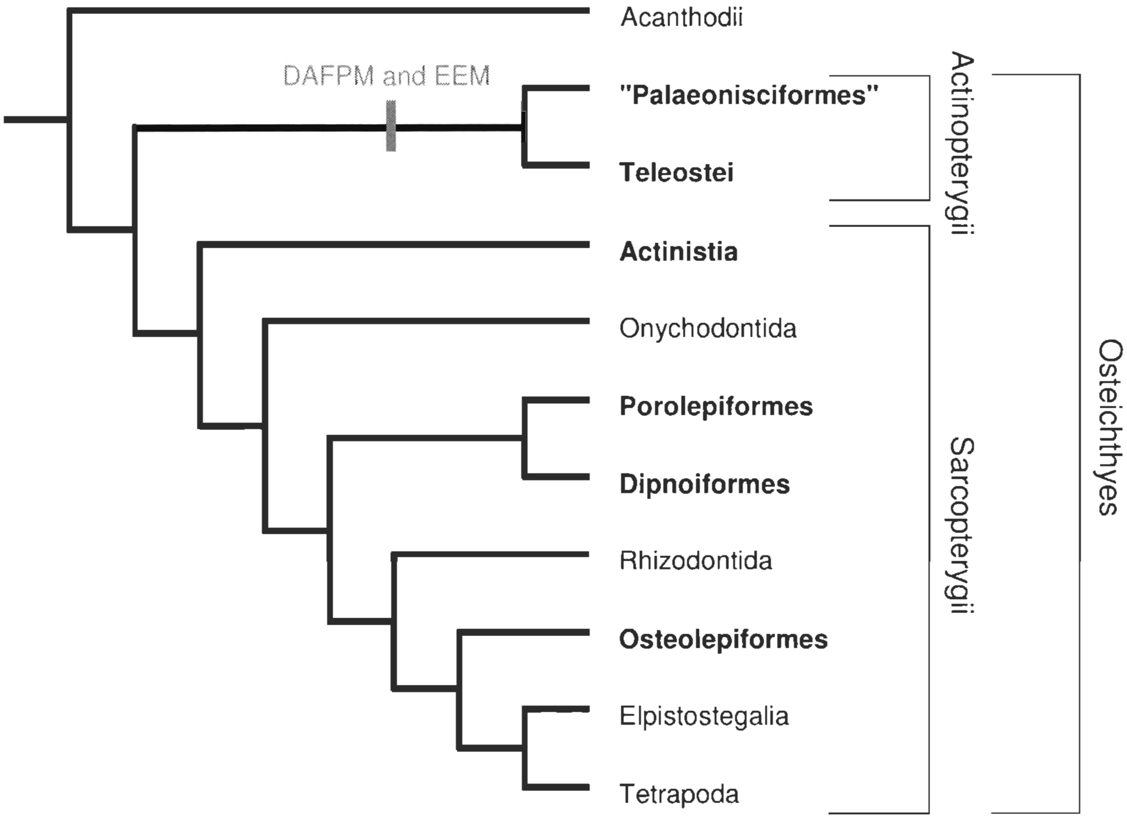

Figure 2: Osteichthyan phylogeny (based on Cloutier and Ahlberg, 1996) showing the phylogenetic position of studied taxa (in bold characters). The DAFPM and EEM are positioned according to the study of Mabee et al. (2002).

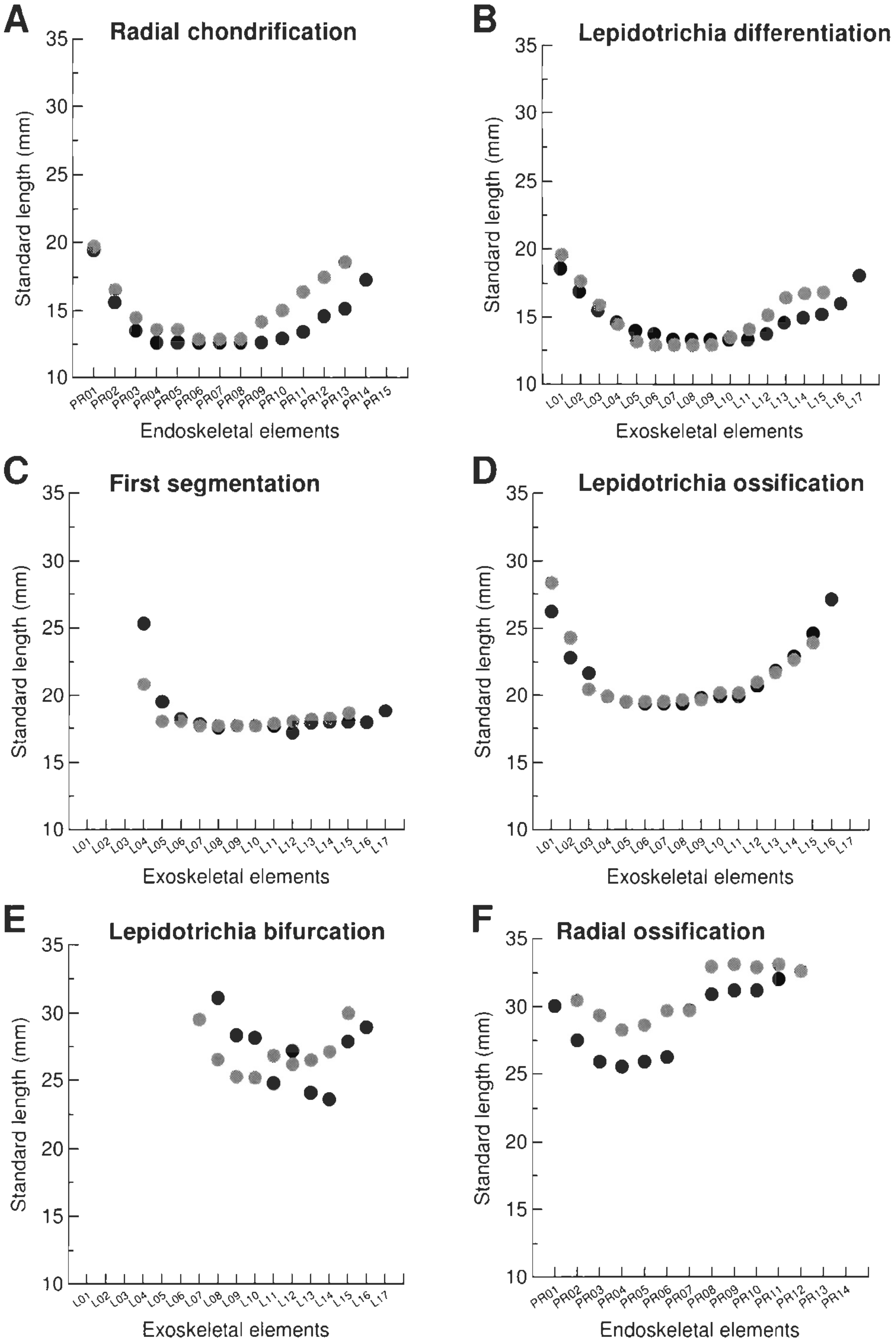

Figure 3: Relation between SL$_{50}$ (determined with logistical regressions) and the anatomical elements (from anterior to posterior) for six of the eight events during fin development (excluding the original radial differentiation). **PR01-14**, Proximal radials 01-14; **L01-17**, Lepidotrichia 01-17. ● **Dorsal fin** ● **Anal fin**

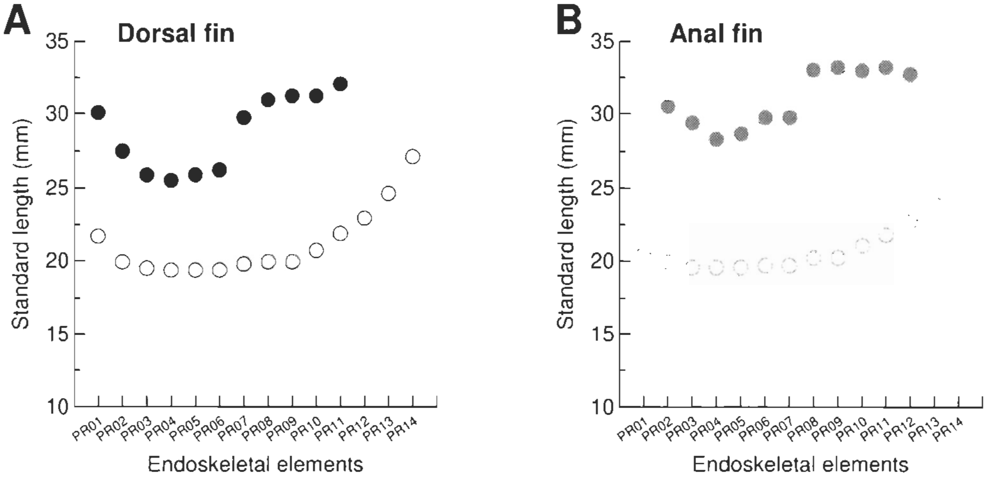

Figure 4: Relation between SL_{50} (determined with logistical regressions) and the anatomical elements (from anterior to posterior) for the ossification of the exoskeleton (**empty**) and the endoskeleton (**filled**). **PR01-14**, Proximal radials 01-14, each lined with their corresponding lepidotrichia.

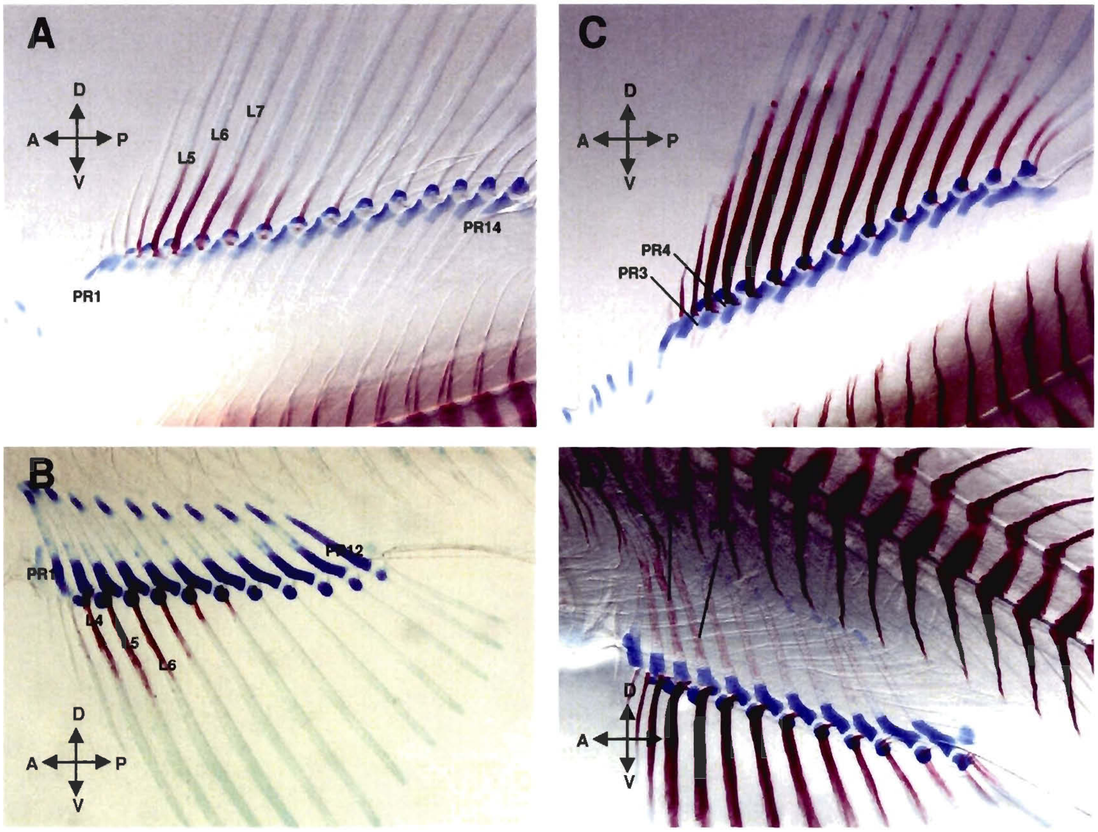

Figure 5: Cleared and stained specimens of rainbow trout showing bones red and cartilages blue. **A**) Dorsal fin showing the beginning of lepidotrichia ossification (specimen SL = 28.36 mm); **B**) Anal fin showing the beginning of lepidotrichia ossification (specimen SL = 19.80 mm); **C**) Dorsal fin showing the beginning of radial ossification (specimen SL = 24.90 mm); **D**) Anal fin showing the beginning of radial ossification (specimen SL = 24.90 mm). **L**, lepidotrichia; **PR**, proximal radial.

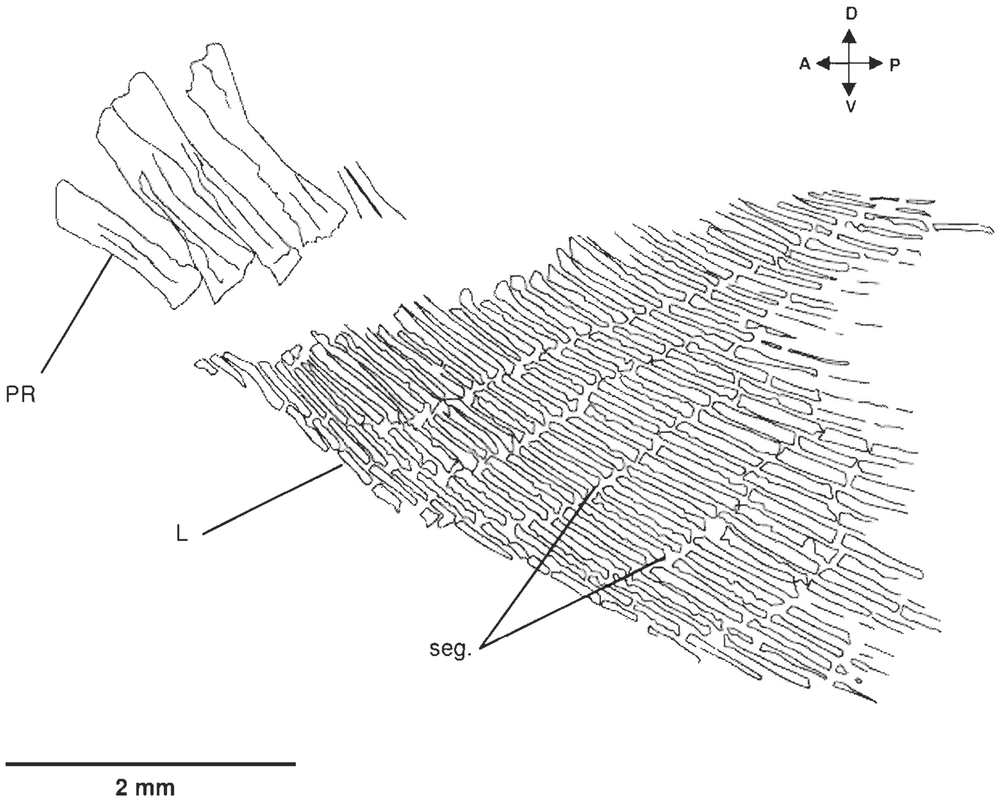

Figure 6: Juvenile Carboniferous actinopterygian *Elonichthys peltigerus* (FMNH PF 7493), SL = 28.9 mm. Anal fin in lateral view. Segmentations (**seg.**) are well defined, with up to 7 segments. **PR** , proximal radials; **L**, Lepidotrichia.

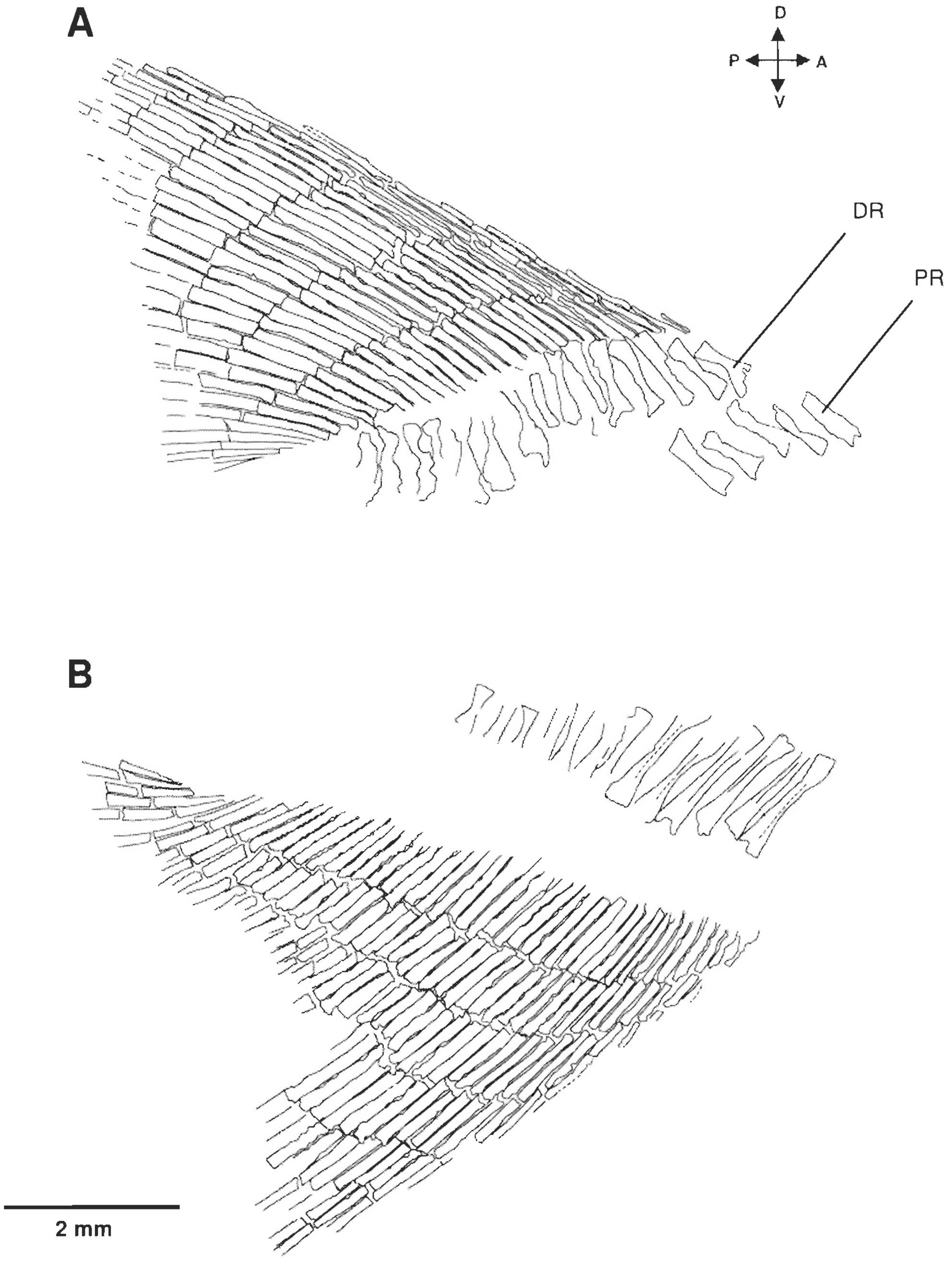

Figure 7: Carboniferous actinopterygian *Elonichthys peltigerus* (FMNH PF 7502), SL = 34.31 mm. **A)** Dorsal fin in lateral view. **B)** Anal fin in lateral view. **PR**, Proximal radial; **DR**, Distal radial.

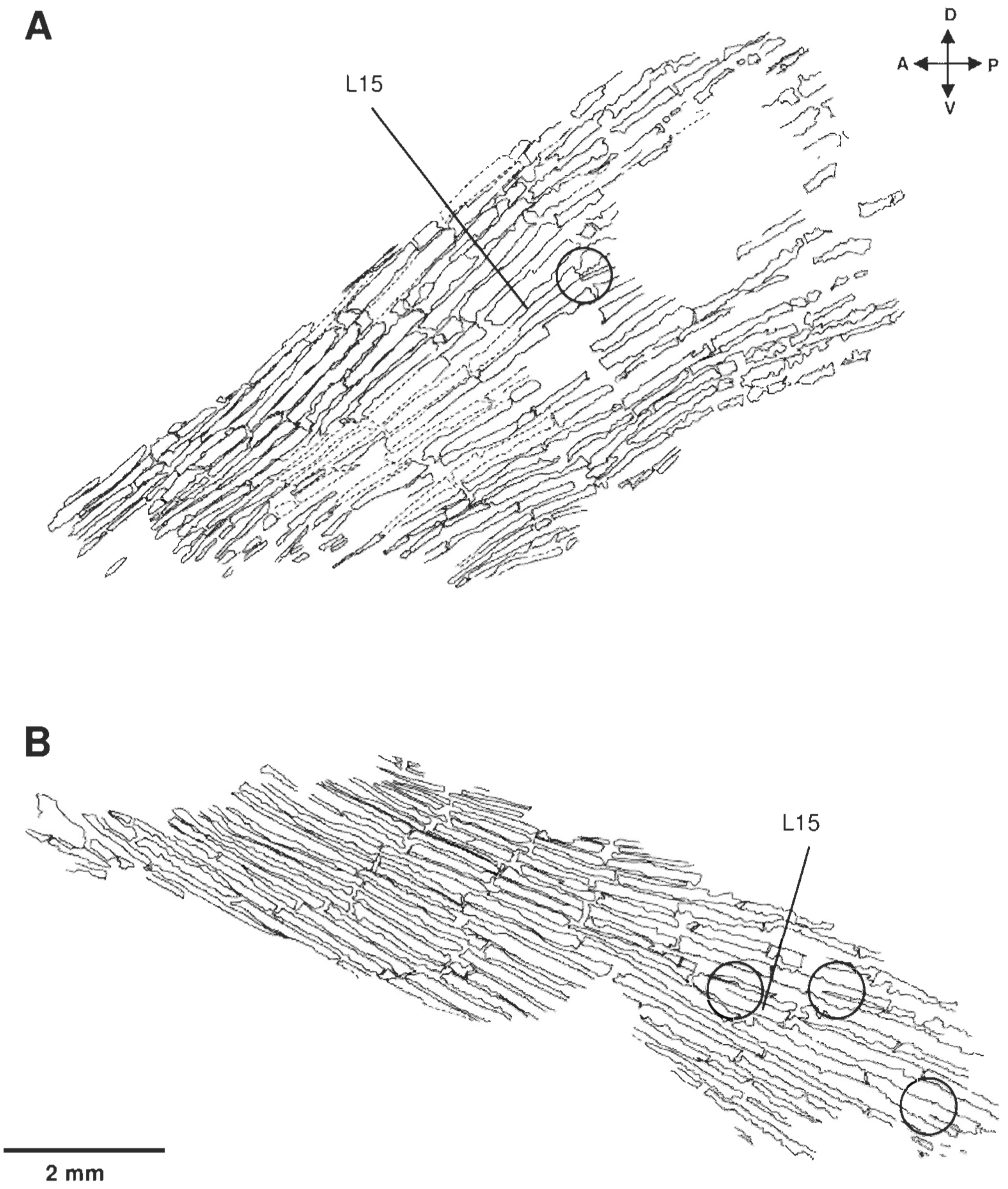

Figure 8: Juvenile Devonian actinistian *Miguashaia bureaui* (ULQ 120b), TL = 76 mm. **A)** Dorsal fin in lateral view. **B)** Anal fin in lateral view. The 15th lepidotrichia (**L15**) is the first to show bifurcation. All bifurcations are surrounded.

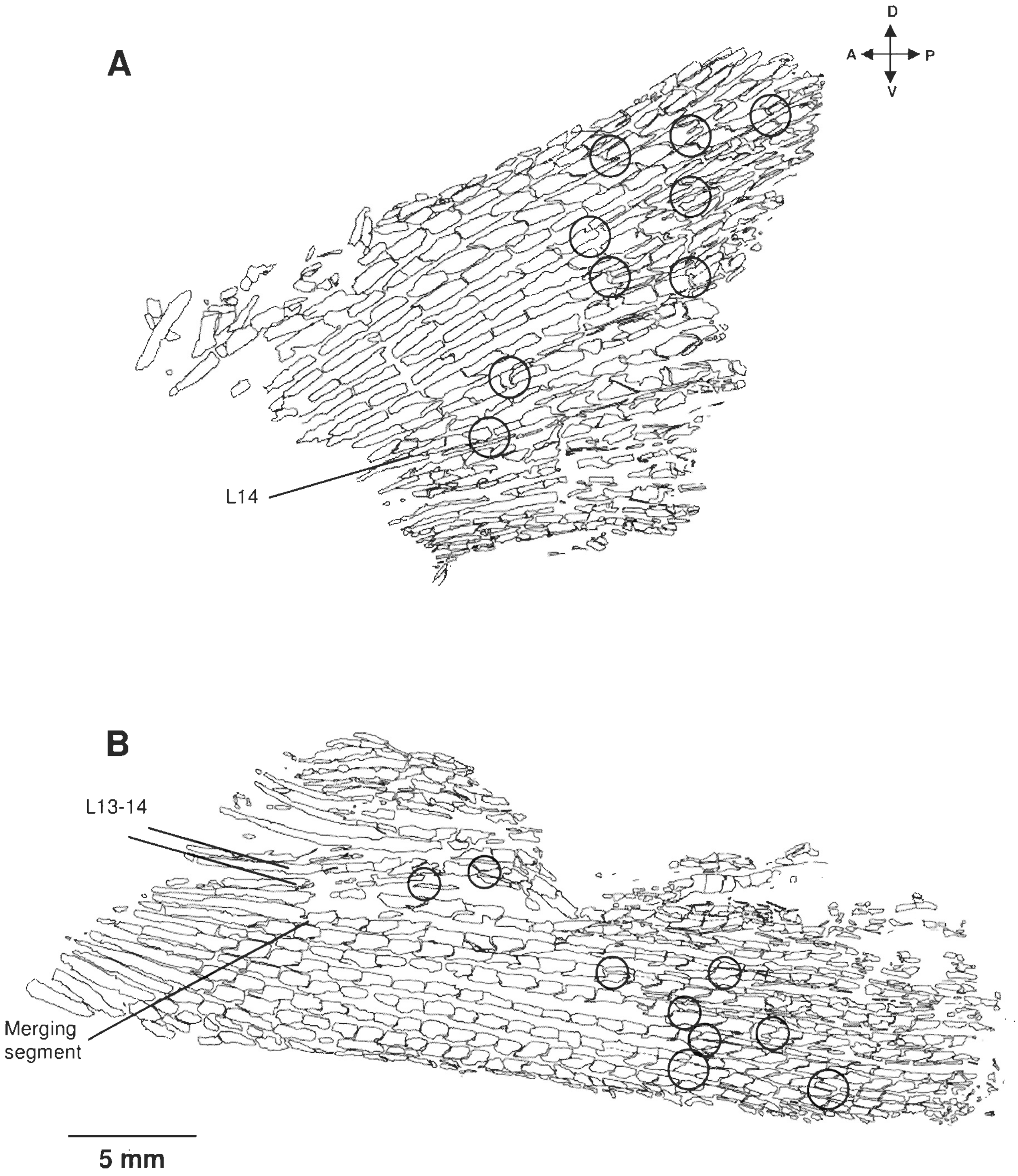

Figure 9: Devonian actinistian *Miguashaia bureaui* (MHNM 06-41), TL = 195 mm. **A)** Dorsal fin in lateral view. **B)** Anal fin in lateral view. Some bifurcations are surrounded. **L13-14**, the lepidotrichia 13 and 14

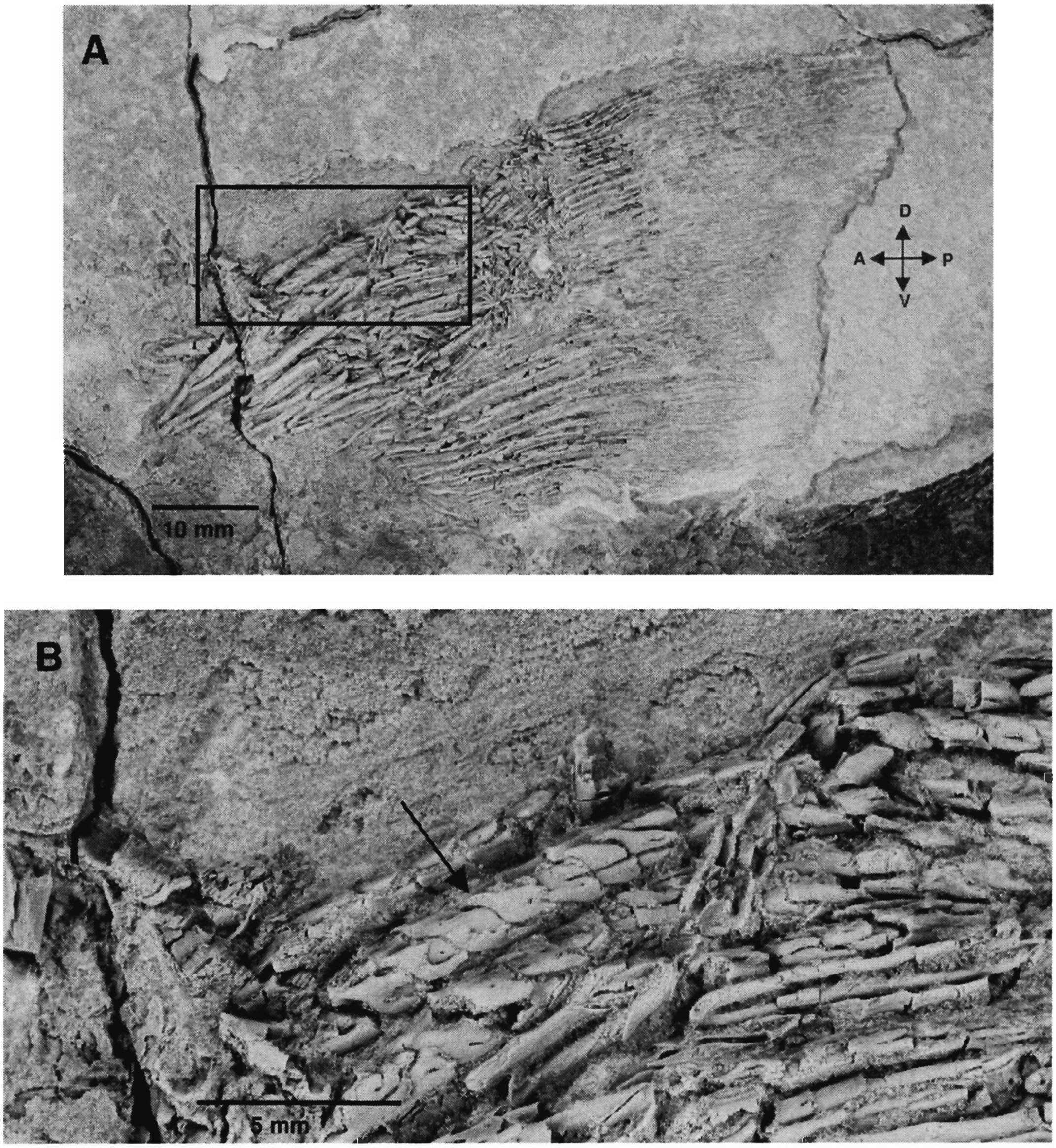

Figure 10: Devonian actinistian *Miguashaia bureaui* (MHNM 06-494), TL = 375 mm. **A)** Dorsal fin in lateral view. Area in a frame is shown in B). **B)** Lepidotrichia showing the interlocking pattern (black arrow).

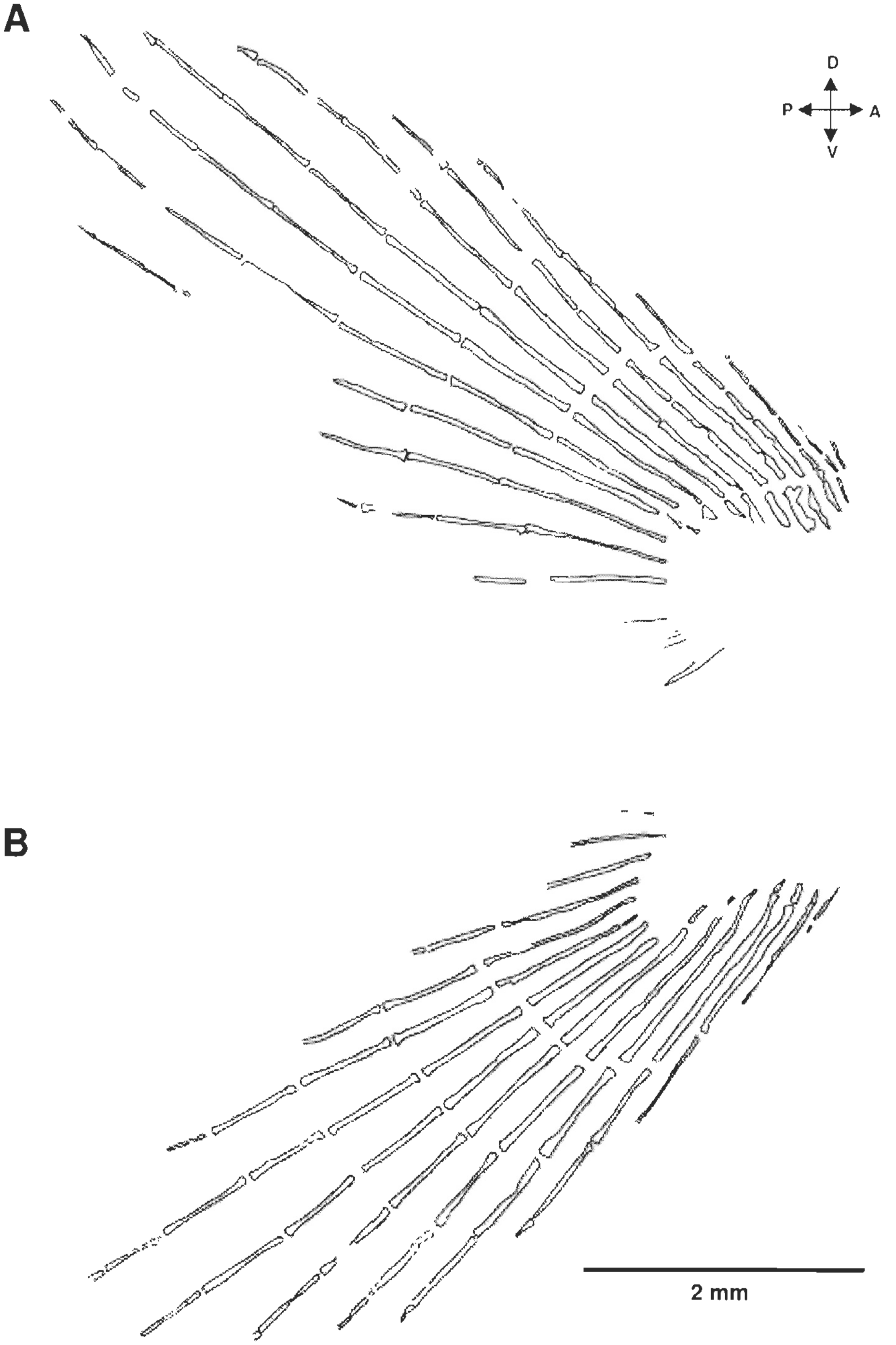

Figure 11: Larval Carboniferous actinistian *Rhabdoderma exiguum* (FMNH PF 9954), SL = 38.02 mm. **A)** Dorsal fin in lateral view. **B)** Anal fin in lateral view.

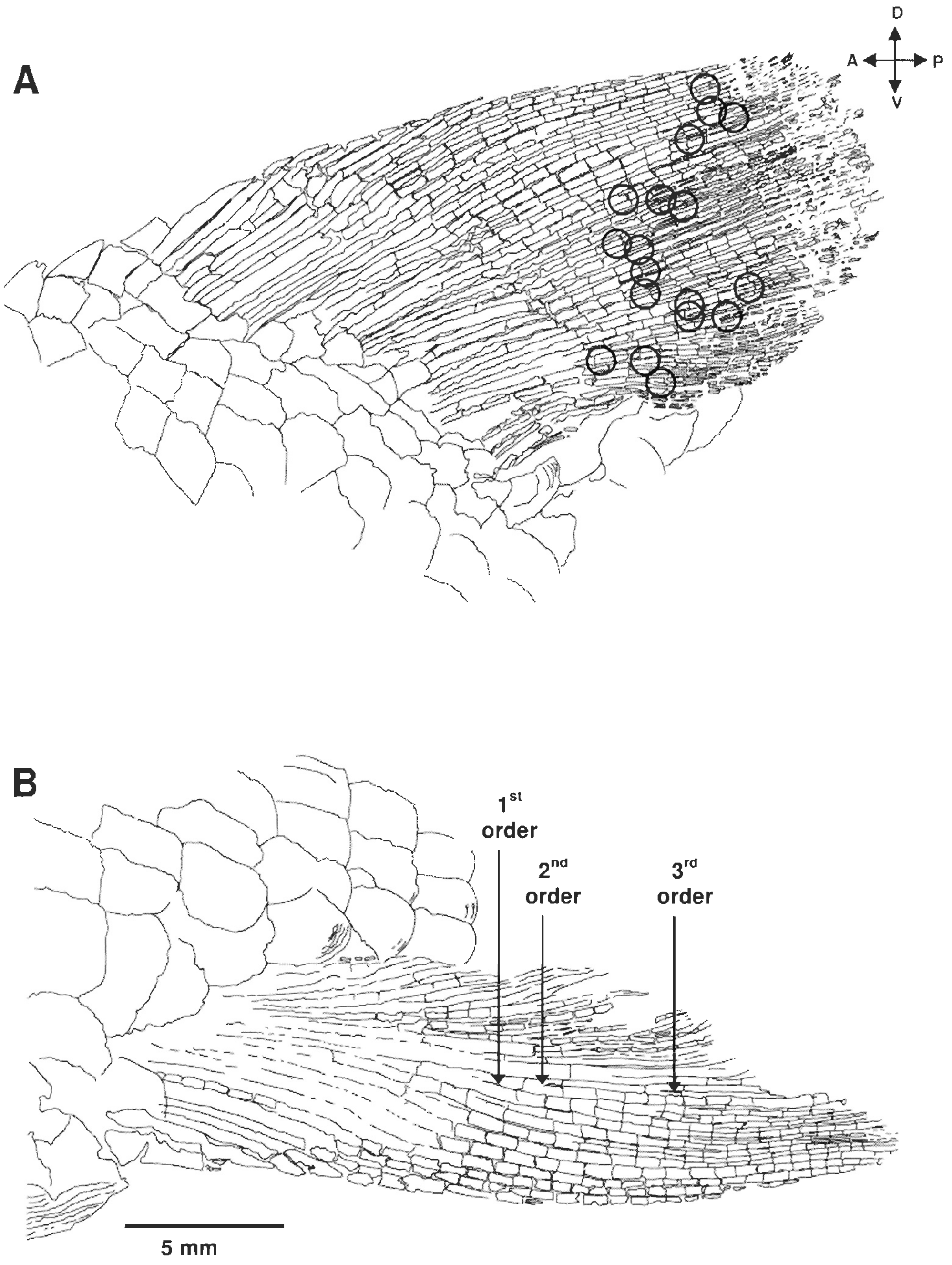

Figure 12: Devonian dipnoan *Dipterus valenciennesi* (BMNH P22187), SL = 149 mm (incomplete). **A)** Dorsal fin in lateral view. Some bifurcations are surrounded. **B)** Anal fin in lateral view showing three orders of bifurcation.

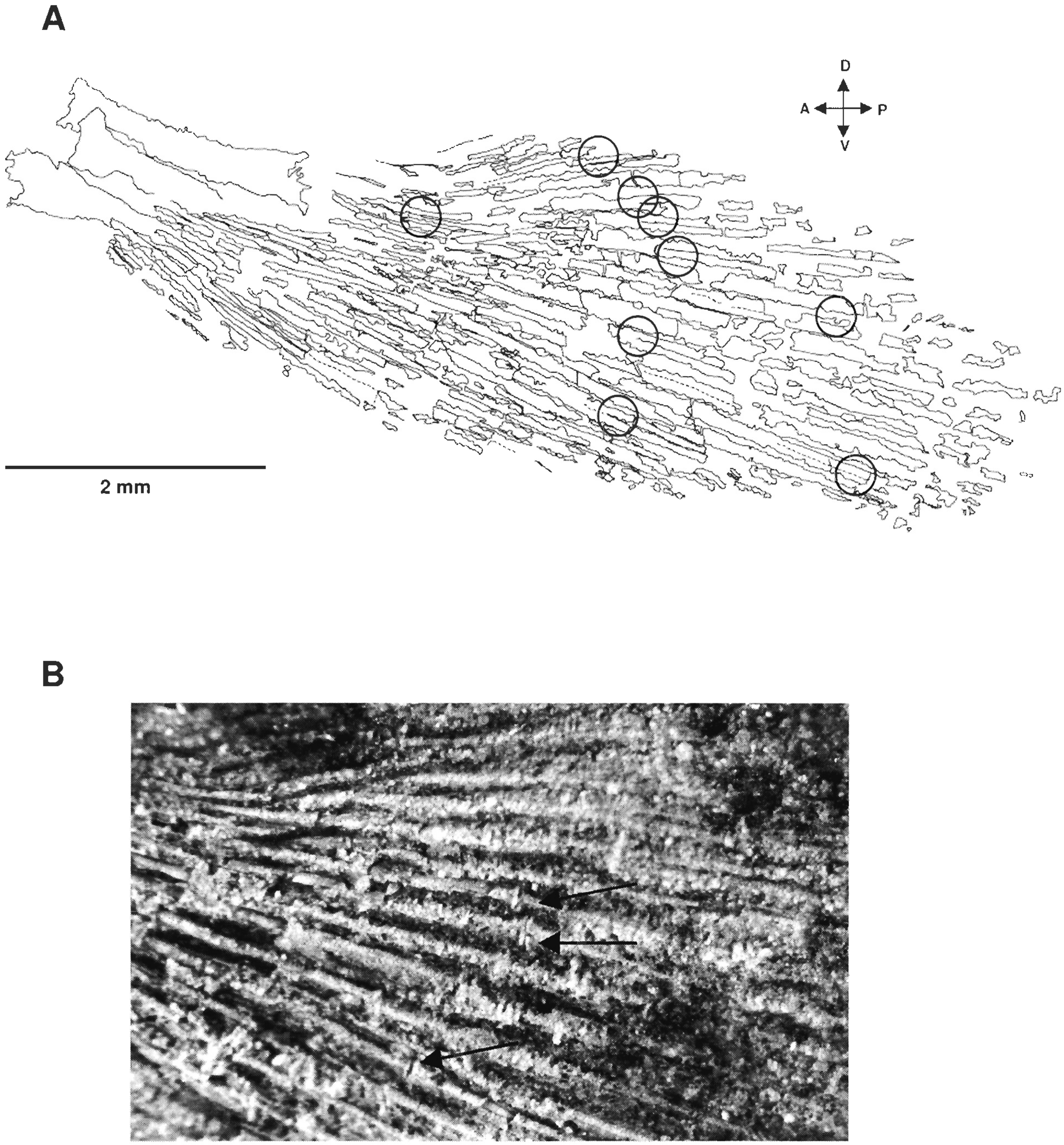

Figure 13: Juvenile Devonian osteolepiform *Eusthenopteron foordi* (MHNM 06-1754), SL = 53.5 mm. **A)** The anal fin in lateral view. **B)** Lepidotrichia showing segmentations (black arrows). Ammonium chloride is used to enhance details.

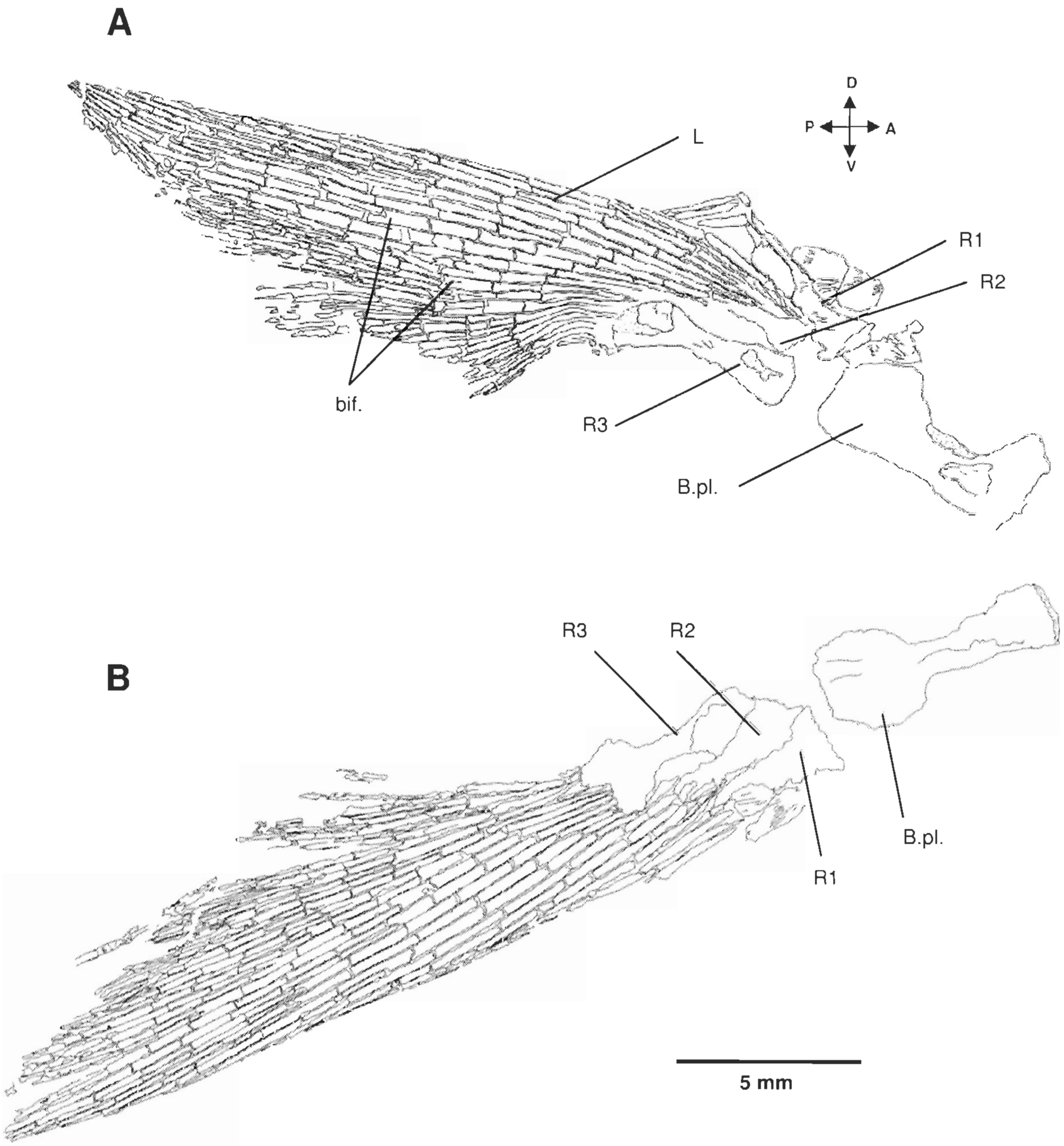

Figure 14: Devonian osteolepiform *Eusthenopteron foordi* (MHNM 06-1769), SL = 130.28 mm. **A)** Dorsal fin in lateral view. **B)** Anal fin in lateral view. **B.pl.**, Basal plate; **R1**, Anterior (first) radial; **R2,** Second (central) radial; **R3**, Third (posterior) radial; **L**, Lepidotrichia; **bif.**, Bifurcation

APPENDIX 1

List of fossil specimens examined

Elonichthys peltigerus – **FMNH** PF 3783; PF 7437; PF 7487; PF 7488; PF 7493; PF 7497; PF 7499; PF 7502; PF 7508; PF 7520; PF 7522; PF 7524; PF 8975; UF 524; UF 588; UF 589; UC 21715

Miguashaia bureaui – **MHNM** 06-41; 06- 494; **ULQ** 120a/b

Rhabdoderma exiguum – **FMNH** PF 3660; PF5494; PF5521; PF 5660; PF5760; PF 7338; PF7528; PF 7529; PF 8663; PF8666; PF 8667; PF8669; PF 8673; PF 8674; PF 8675; PF 8724; PF 8888; PF 9952; PF 9954; PF 12383; PF 12385; PF 12386; **YPM** 56748

Quebecius quebecensis – **MHNM** 06-1148; 06-1244; 06-1474a

Dipterus valenciennesi – **BMNH** P17638; P17640; P22187; P22189; P22195

Eusthenopteron foordi – **AMNH** 5895; 5900; 5903; 5906; 7535; 7650; 7687; 7842; 10187 20222; 20223; **MHNM** 06-36a; 06-47; 06-53a; 06-86; 06-111; 06-121; 06-128; 06-159; 06-213; 06-277; 06-288; 06-331a; 06-367; 06-428; 06-528; 06-535; 06-829; 06-850; 06-1336; 06-1526; 06-1635; 06-1649; 06-1754a; 06-1769; **ULQ** 574

CONCLUSION

Cette étude a permis d'explorer une thématique qui suscite de plus en plus d'intérêt en biologie évolutive du développement, la modularité. Par l'étude exhaustive d'une série de croissance chez un actinoptérygien actuel, il a été permis de compléter la description, amorcée par Mabee et al. (2002), de deux modules s'exprimant dans le développement des nageoires dorsale et anale : (1) le module exosquelette et endosquelette (MEE) et (2) le module de patron des nageoires dorsale et anale (MPNDA). L'utilisation de méthodes quantitatives a permis de valider et quantifier ces modules. De plus, l'étude de séries de croissance d'espèces fossiles a favorisé les inférences phylogénétiques pour ainsi mieux comprendre l'importance de ces modules dans l'évolution des poissons osseux (ostéichthyens), ce qui n'avait été abordé que partiellement chez une espèce fossile, *Eusthenopteron foordi*.

Les observations ont permis de décrire une série de huit évènements consécutifs lors du développement des nageoires dorsale et anale chez la truite arc-en-ciel: (1) la différentiation des radiaux proximaux, (2) la chondrification des radiaux proximaux, (3) la différentiation des lépidotriches, (4) la chondrification des radiaux distaux, (5) la segmentation des lépidotriches, (6) l'ossification des lépidotriches, (7) la bifurcation des lépidotriches et (6) l'ossification des radiaux. Quatre de ces évènements, 5 à 8, ont pu être observés chez les taxons fossiles. À la lumière des observations faites au cours de cette étude, l'ordre pour ces quatre évènements semble conservé entre les actinoptérygiens actuels et les taxons fossiles. La séquence générale de développement serait donc ancestrale chez les ostéichthyens.

Des séquences de développement ont été décrites pour six des huit évènements généraux à l'aide d'une approche quantitative qui visait à: (1) déterminer l'ordre d'apparition (ou d'ossification, de segmentation et de bifurcation) des structures et (2) d'évaluer la congruence entre les différentes séquences correspondantes pour chacun des modules étudiés. Les résultats ont permis de valider les deux modules de Mabee et al. (2002) chez la truite arc-en-ciel et même de compléter leur description. En effet, tels que décrits par Mabee et al. (2002), les modules ne concernaient que la différentiation des structures, alors que l'étude de tous les évènements démontre que les modules sont exprimés tout au cours du développement des nageoires; toutes les séquences correspondantes sont congruentes. La seule exception concerne les séquences de bifurcations, où les données disponibles n'ont pas permis de conclure de façon significative, malgré la morphologie similaire entre les deux nageoires.

Le MEE est maintenant décrit selon quatre évènements: (1) la différentiation/chondrification des radiaux, (2) la différentiation des lépidotriches en suivant la même direction que les radiaux, (3) l'ossification des lépidotriches et (4) l'ossification des radiaux en suivant la même direction que les lépidotriches. Pour sa part, le MPNDA concerne tous les évènements qui ont des patrons similaires entre les nageoires dorsale et anale: (1) différentiation/chondrification des radiaux proximaux et distaux, (2) ossification des radiaux proximaux, (3) différentiation des lépidotriches, (4) ossification des lépidotriches, (5) segmentation des lépidotriches et (6) bifurcation des lépidotriches.

Sur le plan phylogénétique, les patrons du développement des nageoires des taxons fossiles suggèrent la présence du MPNDA chez tous les taxons, avec toutefois une certaine incertitude pour le groupe des dipneustes, étant donné la tendance évolutive à la divergence de taille importante entre leurs nageoires dorsale et anale. Par conséquent, le MPNDA serait ancestral chez les ostéichthyens avec dissociation, ou perte, possible du module au cours de l'évolution des dipneustes. De plus, un évènement observé dans le développement des nageoires de la truite, la bifurcation des lépidotriches, s'est avéré absent chez certains taxons. Cet état est récurrent chez plusieurs groupes d'ostéichthyens tels les actinoptérygiens et les actinistiens. Dans le cas du MEE, les patrons de développement n'ont pu être observés que chez deux espèces chez lesquelles l'endosquelette est préservé, l'actinoptérygien *Elonichthys peltigerus* et le sarcoptérygien *Eusthenopteron foordi.* Les données disponibles n'ont pas permis de confirmer la présence du MEE chez les sarcoptérygiens alors que ce module s'avère ancestral chez les actinoptérygiens. Il n'est donc pas possible de démontrer que ce module est ancestral chez les ostéichthyens à partir des structures conservées chez les espèces étudiées.

Les données récoltées chez la truite et les espèces fossiles suggèrent la présence d'un module du développement supplémentaire. Ce module a été nommé «Module de patron des lépidotriches». En effet, les séquences de développement des lépidotriches observées dans le cadre de cette étude semblent congruentes entre les différents taxons étudiés: (1) différentiation (chez la truite seulement), (2) segmentation, (3) ossification, (4) bifurcation. De plus, des interactions sont documentées lors du développement des rayons; elles expliqueraient le développement concerté (différentiation, ossification, segmentation et bifurcation) des deux moitiés jumelles d'un même lépidotriche, les hémirayons.

Les nageoires dorsale et anale des ostéichthyens sont donc de bons exemples de l'organisation hiérarchique des modules et illustrent bien l'évolution et la conservation de modules du développement au cours de la phylogénie.

BIBLIOGRAPHIE

Akimenko, M.-A., M. Marí-Beffa, J. Becerra et J. Géraudie, 2003. Old questions, new tools, and some answers to the mystery of fin regeneration. *Developmental Dynamics* 226: 190-201

Akimenko, M.-A. et A. Smith, 2007. Paired fin repair and regeneration. In Hall, B. K. (ed.) *Fins into limbs – Evolution, Development and Transformation.* The University of Chicago Press, Chicago (USA). p. 152-162

Arratia, G., H-P. Schultze et J. Casciotta, 2001. Vertebral column and associated elements in dipnoans and comparison with other fishes: development and homology. *Journal of Morphology* 250: 101-172

Balart, E.F., 1995. Development of the vertebral column, fins and fin supports in the japonese anchovy, *Engraulis japonicus* (Clupeiformes: Engraulididae). *Bulletin of Marine Science* 56(2): 495-522

Bemis, W.E., 1984. Paedomorphosis and the evolution of the Dipnoi. *Paleobiology* 10: 293-307

Bemis, W. E. et L. Grande, 1999. Development of the median fins of the North American paddlefish (*Polyodon spathula*), and a re-evaluation of the lateral fin-fold hypothesis. Dans Arratia, G. et H.-P. Schultze (éds.), *Mesozoic Fishes 2— Systematics and Fossil Record.* Verlag Dr. Friedrich Pfeil, München, Germany. p. 41-68

Bird, N.C. et P.M. Mabee, 2003. Developmental morphology of the axial skeleton of the zebrafish, *Danio rerio* (Ostariophysi: Cyprinidae). *Developmental Dynamics* 228: 337-357

Birnie, J.H., 1934. Regeneration of the tail-fins of *Fundulus* embryos. *Biological Bulletin* 66: 316-325

Birnie, J.H., 1947. Regeneration and transplantation of fin rays in the Goldfish. *The Anatomical Record* 99: 648

Bolker, J.A., 2000. Modularity in development and why it matters to Evo-Devo. *American Zoologist* 40: 770-776

Borday, V., C. Thaëron, F. Avaron, A. Brulfert, D. Casane, P. Laurenti et J. Géraudie, 2001. *evx1* transcription in bony fin rays segment boundaries leads to a reiterated pattern during zebrafish fin development and regeneration. *Developmental Dynamics* 220: 91-98

Bouvet, J., 1974. Différentiation et ultrastructure du squelette distal de la nageoire pectorale chez la truite indigène (*Salmo trutta fario L.*) II: Différentiation et ultrastructure des lépidotriches. *Archives d'Anatomie Microscopique* 63(4): 323-335

Carroll, R.L., A. Kuntz et K. Albright, 1999. Vertebral development and amphibian evolution. *Evolution & Development* 1(1): 36-48

Charest, F. et R. Cloutier, 2006. Developmental patterns of the juvenile Carboniferous coelacanth *Rhabdoderma exiguum. Journal of Vertebrate Paleontology* 26, Supplement to 3: 49A

Chipman, A.D. et E. Tchernov, 2002. Ancient ontogenies: larval development of the Lower Cretaceous anuran *Shomronella jordanica* (Amphibia: Pipoidea). *Evolution & Development* 4(2): 86-95

Chu, K.P., 2007. Effet de la vélocité du courant sur la plasticité morphologique des premiers stades de développement de la truite arc-en-ciel (*Oncorhynchus mykiss*). Mémoire de maîtrise. Université du Québec à Rimouski, Rimouski.

Cloutier, R., 1990. Phylogenetic interrelationships of the actinistians (Osteichthyes: Sarcopterygii): patterns, trends, and rates of evolution. Thèse de doctorat. University of Kansas, Lawrence (États-Unis)

Cloutier, R., 1991. Patterns, trends, and rates of evolution within the Actinistia. *Environmental Biology of Fishes* 32: 23-58

Cloutier, R., 1996a. The primitive actinistian *Miguashaia bureaui* Schultze (Sarcopterygii). Dans Schultze, H.–P. et R. Cloutier (éds.) *Devonian Fishes and Plants of Miguasha, Quebec, Canada.* Verlag Dr. Friedrich Pfeil, München, Germany. p. 227-247

Cloutier, R., 1996b. Dipnoi (Akinetia: Sarcopterygii). Dans Schultze, H.–P. et R. Cloutier (éds.) *Devonian Fishes and Plants of Miguasha, Quebec, Canada.* Verlag Dr. Friedrich Pfeil, München, Allemagne. p. 198-226

Cloutier, R., 1997. Morphologie et variation du toit crânien du Dipneuste *Scaumenacia curta* (Whiteaves) (Sarcopterygii), du Dévonien supérieur du Québec. *Geodiversitas* 19(1): 61-105

Cloutier, R. et P.E. Ahlberg, 1996. Morphology, characters, and the interrelationships of basal sarcopterygians. Dans Stiassny, M.L.J., L.R. Parenti et G.D. Johnson (éds.) *Interrelationship of fishes*. Academic Press, New-York, p. 445-479

Cloutier, R., A. Caron, T. Grünbaum, V. Canevet et N.R. Le François, en prép. Influence of water velocity on the sequence of chondrification and ossification of the median fins of larval Arctic charr *Salvelinus alpinus*.

Coates, M.I., 2003. The evolution of paired fins. *Theory in Biosciences* 122: 266-287

Coates, M.I. et M.J. Cohn, 1998. Fins, limbs, and tails: outgrowths and axial patterning in vertebrate evolution. *BioEssays* 20: 371-381

Coates, M.I. et M. Ruta, 2007. Skeletal changes in the transition from fins to limbs. Dans Hall, B. K. (éd.) *Fins into limbs – Evolution, Development and Transformation.* The University of Chicago Press, Chicago, États-Unis. p.15-38

Cote, S., R.L. Carroll, R. Cloutier et L. Bar-Sagi, 2002. Vertebral development in the Devonian sarcopterygian fish *Eusthenopteron foordi* and the polarity of vertebral evolution in non-amniote tetrapods. *Journal of Vertebrate Paleontology* 22: 497-502

Cubbage, C.C. et P.M. Mabee, 1996. Development of the cranium and paired fins in the zebrafish *Danio rerio* (Ostariophysi, Cyprinidae). *Journal of Morphology* 229: 212-160

Dingerkus, G. et L.D. Uhler, 1977. Enzyme clearing of Alcian blue stained whole small vertebrates for demonstration of cartilage. *Biotechnic and Histochemistry* 52(4): 229-232

Eastman, C.R. 1902. The Carboniferous fish fauna of Mazon Creek, Illinois. *Journal of Geology* 10: 535-541

Eastman, C.R., 1903. Carboniferous fishes from the central western states. *Bulletin of the Museum of Comparative Zoology at Harvard College* 39:163-226

Eaton, T.H., 1945. Skeletal supports of the median fins of fishes. *Journal of Morphology* 76(3): 193-212

Faustino, M. et D.M. Power, 1999. Development of the pectoral, pelvic, dorsal and anal fins in cultured sea bream. *Journal of Fish Biology* 54: 1094-1110

Forey, P.L., 1991. *Latimeria chalumnae* and its pedigree. *Environmental Biology of Fishes* 32: 75-97

Forey, P.L., 1998. *History of the Coelacanth Fishes*. Chapman and Hall, London.

François, Y., 1958. Recherches sur l'anatomie et le développement de la nageoire dorsale des téléostéens. *Archives de Zoologie Expérimentale et Générale* 97: 1-108

François, Y. et M. Blanc, 1956. Sur la croissance en longueur des rayons de nageoires chez les poissons téléostéens. *Bulletin de la Société Zoologique de France* 81: 26-33

Friedman, M., M.I. Coates et P. Anderson, 2007. First discovery of a primitive coelacanth fin fills a major gap in the evolution of lobed fins and limbs. *Evolution & Development* 9(4): 329-337

Fuiman, L.A., K.R. Poling et D.M. Higgs, 1998. Quantifying developmental progress for comparative studies of larval fishes. *Copeia* 1998(3): 602-611

Géraudie, J. et W.J. Landis, 1982. The fine structure of the developing pelvic fin skeleton in the trout, *Salmo gairdneri. American Journal of Anatomy* 163: 141-156

Gilbert, S.F., 2004. *Biologie du Développement*. 2^e éd. De Boeck, Bruxelles.

Gilbert, S.F. et J.A. Bolker, 2001. Homologies of process and modular elements of embryonic construction. *Journal of Experimental Zoology (Mol Dev Evol)* 291: 1-12

Gilbert, S.F., J.M. Opitz et R.A. Raff, 1996. Resynthesizing evolutionary and developmental biology. *Developmental Biology* 173: 357-372

Goodrich, E.S., 1904. On the dermal fin-rays of fishes – living and extinct. *Quarterly Journal of the Microscopical Society* 47: 465-522

Goodrich, E.S., 1958. *Studies on the structure and development of the vertebrates.* Dover Publications, New-York.

Goswami, A. 2007. Cranial modularity and sequence heterochrony in mammals. *Evolution & Development* 9(3): 290-298

Griffiths, A.J.F., J.H. Miller, D.T. Suzuki, R.C. Lewontin et W.M. Gelbart, 2002. *Introduction à l'analyse génétique*, 3^e éd. De Boeck, Bruxelles

Grünbaum, T., R. Cloutier et P. Dumont, 2003. Congruence between chondrification and ossification sequences during caudal skeleton development: a Moxostomatini case study. Dans Browman, H.I. et Skiftesvik A.B. (éds.), *The Big Fish Bang*, Proceedings of the 26th Annual Larval Fish Conference, Bergen, Norway. p. 161-176

Grünbaum, T., R. Cloutier et N.R. Le François, 2008. Positive effects of exposure to increased water velocity on growth of newly hatched Arctic charr, *Salvelinus alpinus* L. *Aquaculture Research* 39(1): 106-110

Grünbaum, T., R. Cloutier, P.M. Mabee et N.R. Le François, 2007. Early developmental plasticity and integrative responses in arctic charr (*Salvelinus alpinus*): effects of water velocity on body size and shape. *Journal of Experimental Zoology (Mol Dev Evol)* 308B: 396-408

Haas, H.J., 1962. Studies on mechanisms of joint and bone formation in skeleton rays of fish fins. *Developmental Biology* 5: 1-34

Iovine, M.K., 2007. Conserved mechanisms regulate outgrowth in zebrafish fins. *Nature Chemical Biology* 3(10): 613-618

Iovine, M.K. et S.L. Johnson, 2000. Genetic analysis of isometric growth control mechanisms in the zebrafish caudal fin. *Genetics* 155: 1321-1329

Jeffery, J.E., 2001. Pectoral fins of rhizodontids and the evolution of pectoral appendages in the tetrapod stem-group. *Biological Journal of the Linnean Society* 74: 217-239

Johanson, Z., C. Burrow, A. Warren et J. Garvey, 2005. Homology of fin lepidotrichia in osteichthyan fishes. *Lethaia* 38: 27-36

Kardong, K.V., 2002. *Vertebrates – Comparative Anatomy, Function, Evolution*, 3rd ed. McGraw-Hill Higher Education, New-York.

Klingenberg, C.P., 2002. Morphometrics and the role of the phenotype in studies of the evolution of developmental mechanisms. *Gene* 287: 3-10

Klingenberg, C.P., K. Mebus et J.-C. Auffray, 2003. Developmental integration in a complex morphological structure: how distinct are the modules in the mouse mandible? *Evolution & Development* 5(5): 522-531

Laforest, L., C.W. Brown, G. Poleo, J. Géraudie, M. Tada, M. Ekker et M.-A. Akimenko, 1998. Involvement of the *Sonic Hedgehog*, *patched 1* and *bmp2* genes in patterning of the zebrafish dermal fin rays. *Development* 125: 4175-4184

Leblanc, J., 2005. Précisions sur l'anatomie de l'ostéolépiforme *Eusthenopteron foordi* du Dévonien supérieur de Miguasha, Québec. Mémoire de maîtrise. Université du Québec à Rimouski, Rimouski.

Lindsey, C.C., 1955. Evolution of meristic relations in the dorsal and anal fins of teleosts fishes. *Transactions of the Royal Society of Canada* 49(series 3): 35-49

Mabee, P.M., 1993. Phylogenetic interpretation of ontogenetic change: sorting out the actual and artefactual in an empirical case study of centrarchid fishes. *Zoological Journal of the Linnean Society* 107: 175-291

Mabee, P.M., 2006. Integrating Evolution and Development: The need for bioinformatics in Evo-Devo. *BioScience* 56(4): 310-309

Mabee, P.M. et M. Noordsy, 2004. Development of the paired fins in the Paddlefish, *Polyodon spathula. Journal of Morphology* 261: 334-344

Mabee, P.M. et T.A. Trendler, 1996. Development of the cranium and paired fins in *Betta splendens* (Teleostei: Percomorpha): intraspecific variation and interspecific comparisons. *Journal of Morphology* 227: 249-287

Mabee, P.M., P.L. Crotwell, N.C. Bird et A.C. Burke, 2002. Evolution of median fin modules in the axial skeleton of fishes. *Journal of Experimental Zoology (Mol Dev Evol)* 294: 77-90

Mabee, P.M., K.L. Olmstead et C.C. Cubbage, 2000. An experimental study of intraspecific variation, developmental timing, and heterochrony in fishes. *Evolution* 54(6): 2091-2106

Magwene, P.M., 2001. New tools for studying integration and modularity. *Evolution* 55(9): 1734-1745

Marí-Beffa, M., P. Palmqvist, F. Marín-Girón, G.S. Montes et J. Becerra, 1999. Morphometric study of the regeneration of individual rays in teleost tail fins. *Journal of Anatomy* 195: 393-405

Müller, G.B., 2007. Evo-devo: extending the evolutionary synthesis. *Nature Reviews Genetics* 8: 943-949

Murciano, C., T.D. Fernández, I. Durán, D. Maseda, J. Ruiz-Sánchez, J. Becerra, M.-A. Akimenko and M. Marí-Beffa, 2002. Ray-interray interactions during fin regeneration of *Danio rerio. Developmental Biology* 252: 214-224

Murciano, C., J. Pérez-Claros, A. Smith, F. Avaron, T.D. Fernández, I. Durán, J. Ruiz-Sánchez, F. García, J. Becerra, M.-A. Akimenko and M. Marí-Beffa, 2007. Position dependence of hemiray morphogenesis during tail fin regeneration in *Danio rerio. Developmental biology* 312: 272-283

Nabrit, S.M., 1931. The rôle of the basal plate of the tail in regeneration in the tail-fins of fishes (*Fundulus* and *Carassius*). *Biological Bulletin* 60: 60-63

Nunn, C.L. et K.K. Smith, 1998. Statistical analyses of developmental sequences: The craniofacial region in marsupial and placental mammals. *The American Naturalist* 152: 82-101

Poe, S., 2004. A test for patterns of modularity in sequences of developmental events. *Evolution* 58: 1852-1855

Potthoff, T., 1984. Clearing and staining techniques. Dans H.G. Moser, W.J. Richards, D.M. Cohen, M.P. Fahay, A.W. Kendall et S.L. Richardson (éds.), *Ontogeny and Systematics of Fishes*. American Society of Ichthyologists and Herpetologists, Special publication 1. Allen Press, Lawrence. p. 35-37

Prenant, M., 1937. Sur la croissance normale des lépidotriches articulés chez les téléostéen. *Bulletin de la Société Zoologique de France* 62: 190-195

Quinn, G.P. et M.J. Keough, 2002. *Experimental design and data analysis for biologists.* Cambridge University Press, Cambridge.

Quint, E., A. Smith, F. Avaron, L. Laforest, J. Miles, W. Gaffield et M.-A. Akimenko, 2002. Bone patterning is altered in the regenerating zebrafish caudal fin after ectopic expression of *sonic hedgehog* and *bmp2b* or exposure to cyclopamine. *PNAS* 99(13): 8713-8718

Raff, R.A., 1996. *The Shape of Life: Genes, development, and the evolution of animal form.* The University of Chicago Press, Chicago.

Raff, R.A., 2007. Written in stone: fossils, genes and evo-devo. *Nature Reviews Genetics* 8: 911-920

Raff, R.A. et B.J. Sly, 2000. Modularity and dissociation in the evolution of gene expression territories in development. *Evolution & Development* 2(2): 102-113

Redfern, B.G., L.D. Wise et S. Spence, 2007. An alternative Alcian blue dye variant for the evaluation of fetal cartilage. *Birth Defects Research (Part B)* 80: 171-176

Richardson, M.K., 1999. Vertebrate evolution: the developmental origins of adult variation. *BioEssays* 21: 604-613

Schlosser, G., 2002. Modularity and the units of evolution. *Theory in Biosciences* 121: 1-80

Schoch, R.R., 2004. Skeletal formation in the Branchiosauridae: a case study in comparing ontogenetic trajectories. *Journal of Vertebrate Paleontology* 24(2): 309-319

Schultze, H.-P., 1972. Early growth stages in coelacanth fishes. *Nature New Biology* 236: 90-91

Schultze, H.-P., 1984. Juvenile specimens of *Eusthenopteron foordi* Whiteaves,1881 (osteolepiform rhipidistian, Pisces) from the Late Devonian of Miguasha, Québec, Canada. *Journal of Vertebrate Paleontology* 4(1): 1-16

Schultze, H.-P., 1985. Reproduction and spawning sites of *Rhabdoderma* (Pisces, Osteichthyes, Actinistia) in Pennsylvanian deposits of Illinois, USA. *Compte rendu Neuvième congr. Internat. Stratigr. Geol. Carbonifère (Washington & Champaign-Urbana)* 5: 326-330

Schultze, H.-P. et D. Bardack, 1987. Diversity and size changes in palaeonisciform fishes (Actinopterygii, Pisces) from the Pennsylvanian Mazon Creek fauna, Illinois, U.S.A. *Journal of Vertebrate Paleontology* 7(1): 1-23

Shubin, N.H. et M.C. Davis, 2004. Modularity in the evolution of vertebrate appendages. Dans Schlosser, G. et G.P. Wagner, (éds.), *Modularity in Development and Evolution*. University of Chicago Press, Chicago, p. 429-440

Smith, K.K., 2001. Heterochrony revisited: the evolution of developmental sequences. *Biological Journal of the Linnean Society* 73: 169-186

Suzuki, T., Y. Haga, T. Takeuchi, S. Uji, H. Hashimoto et T. Kurokawa, 2003. Differentiation of chondrocytes and scleroblasts during dorsal fin skeletogenesis in flounder larvae. *Development, Growth and Differentiation* 45: 435-448

Tanaka, M. et C. Tickle, 2007. The development of fins and limbs. Dans Hall, B.K. (éd.) *Fins into limbs – Evolution, Development and Transformation.* The University of Chicago Press, Chicago (États-Unis). p. 65-78

Thomson K.S. et K.V. Hahn, 1968. Growth and form in fossil rhipidistian fishes (Crossopterygii). *Journal of Zoology (London)* 156: 199-223

Trewin, N.H., 1986. Palaecology and sedimentology of the Achanarras fish bed of the Middle Old Red Sandstone, Scotland. *Transactions of the Royal Society of Edinburgh* 77: 21-46

Von Dassow, G. et E. Munro, 1999. Modularity in animal development and evolution: elements of a conceptual framework for EvoDevo. *Journal of Experimental Zoology (Mol Dev Evol)* 285: 307-325

Wagner, G.P., 1996. Homologues, natural kinds and the evolution of modularity. *American Zoologist* 36: 36-43

Wagner, G.P., M. Pavlicev et J.M. Cheverud, 2007. The road to modularity. *Nature Reviews Genetics* 8: 921-931

Winther, R.G., 2001. Varieties of modules: Kinds, levels, origins, and behaviour. *Journal of Experimental Zoology (Mol Dev Evol)* 291: 116-129

Witten, P.E. et A. Huysseune, 2007. Mechanisms of chondrogenesis and osteogenesis in fins. Dans Hall, B. K. (éd.) *Fins into limbs – Evolution, Development and Transformation.* The University of Chicago Press, Chicago (USA). p. 79-92

Young, N., 2004. Modularity and integration in the hominoid scapula. *Journal of Experimental Zoology (Mol Dev Evol)* 302B: 226-240

Zhu, M. et H.-P. Schultze, 2001. Interrelationships of basal osteichthyans. Dans Ahlberg, P.E. (éd), *Major Events in Early Vertebrate Evolution.* Taylor and Francis, New-York, p. 289-314