



Université du Québec
à Rimouski

***WELLERODUS PRISCUS*, UN CHONDRICHTHYEN AVEC
AIGUILLONS PAIRS DU DÉVONIEN MOYEN (GIVÉTIEN)
DE L'ÉTAT DE NEW YORK, ÉTATS-UNIS**

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RÉSUMÉ

Récemment, plusieurs découvertes ont mené à la réorganisation des hypothèses classiques concernant la phylogénie des gnathostomes basaux. Dans le cas des chondrichthyens, le scénario, imprécis, pourrait être appelé à changer avec les récurrentes unions des acanthodiens aux chondrichthyens et le nombre grandissant de taxons identifiés comme chondrichthyens putatifs. Un nouveau *Konzentrat-Lagerstätte* du Dévonien moyen découvert à Cairo, N.Y., É.-U., a révélé plusieurs gnathostomes articulés, dont des spécimens du chondrichthyen *Wellerodus priscus*. Trois spécimens décomposés partiellement articulés ont été préparés et ont révélé une combinaison de traits anatomiques, dont des familles dentaires et suffisamment de spécimens pour caractériser une variation dans la morphologie dentaire qui confirme la correspondance du genre avec *Antarctilamna*. *Wellerodus priscus* présente de façon non ambiguë des aiguillons dorsaux et pectoraux, ainsi que de possibles aiguillons pré-pelviens. Les aiguillons sont caractérisés par une insertion superficielle et des crêtes composées d'une succession de nodosités, elles-mêmes ornementées de crêtes longitudinales. Les aiguillons pectoraux sont plus courbés et présentent une rangée distale de denticules postérieurs. Les aiguillons pré-pelviens putatifs sont plus trapus et leur ornementation plus simple. L'écaillure est composée d'écaillures de type cténacanthé présentant des odontodes sub-parallèles. La diversité de l'écaillure couvre une variation dans l'organisation des odontodes au sein des écaillures du corps et des écaillures plates et arrondies, possiblement céphaliques, présentant un motif "étoilé". La régionalisation dans l'écaillure implique un couvert d'écaillures réduit au niveau de la tête, un corps couvert (flancs et dos) par des écaillures de type cténacanthé et une transition au niveau pelvien vers des écaillures plus plates avec crêtes. La taille relativement petite des spécimens (ca. 50 à 70 cm en longueur totale), l'état de décomposition dans la préservation des fossiles et l'environnement estuarien interprété pour Cairo suggèrent que les spécimens de *Wellerodus* pourraient être des juvéniles. La combinaison d'aiguillons pairs avec des caractères chondrichthyens distinctifs tels que des familles de dents et des écaillures avec croissance aréale argumentent en faveur d'un lien entre les chondrichthyens et les chondrichthyens putatifs en plus de démontrer une distribution phylogénétique plus large de caractères "acanthodiens". Ces caractères pourraient de plus définir le Baüplan du requin basal.

Mots clés : Chondrichthyes, Elasmobranchii, Antarctilamnidae, Dévonien, gnathostome, taxonomie, phylogénie, aiguillons, dents, écaillures

ABSTRACT

Recently many discoveries led to the reshuffling of well-accepted phylogenetic hypotheses regarding the relationships of early gnathostomes. We are still unable to establish a clear portrait of early chondrichthyans, a situation that might change with the recurrent relationships of acanthodians with chondrichthyans and the growing number of taxa identified as putative chondrichthyans. A new Middle Devonian *Konzentrat-Lagerstätte* found in Cairo, NY, USA, revealed many articulated gnathostomes, including specimens of the antarctilamid chondrichthyan *Wellerodus priscus*. Three almost complete, partially decayed specimens of *W. priscus* revealed a combination of features, including tooth families and enough specimens to characterize variation in tooth morphology that further suggests the generic synonymy with *Antarctilamna*. *Wellerodus priscus* possesses unambiguous dorsal and pectoral fin spines, as well as putative prepelvic spines. The fin spines are characterized by shallow insertion, ridges composed of a succession of nodes, themselves ornamented with longitudinal ridges. Pectoral fin spines are slightly curvier and present a single, distal row of posterior denticles. Possible prepelvic fin spines are stubbier and present a simpler ornamentation. The squamation is composed of ctenacanth-type scales, with subparallel odontodes. Variation in squamation encompasses variation in odontode organisation within body scales, and round, flat scales showing a radiating pattern interpreted as possible head scales. Regionalisation in squamation involves reduced scale covering at the level of the head, body covering (at least flanks and back side) with polyodontodes, ctenacanth-type scales and a transition at the pelvic level towards flatter, ridged scales. The relative small size of the animals (ca. 50 to 70 cm in total length), the decayed state of preservation of the fossils and the estuarine environment interpreted for Cairo suggest that the *Wellerodus* specimens represent either juveniles or subadults. The combination of paired fin spines with distinctive chondrichthyan characters such as tooth families and areally growing ctenacanth-type scales in *W. priscus* characterizes a morphological transition that argues in favour of a link between chondrichthyans and putative chondrichthyans and demonstrate a wider phylogenetic distribution of “acanthodian” characters. This further argues for a basal chondrichthyan or early shark Baüplan comprising paired fin spines, diplodont teeth and polyodontode, areal growing scales.

Keywords: Chondrichthyes, Elasmobranchii, Antarctilamnidae, Devonian, gnathostome, taxonomy, phylogeny, spines, teeth, scales

TABLE DES MATIÈRES

REMERCIEMENTS	ix
RÉSUMÉ.....	xiii
ABSTRACT	xv
TABLE DES MATIÈRES.....	xvii
LISTE DES FIGURES	xx
LISTE DES ACRONYMES.....	xxiii
INTRODUCTION GÉNÉRALE.....	1
CHAPITRE 1 : <i>WELLERODUS PRISCUS</i> , UN CHONDRICHTHYEN AVEC AIGUILLONS PAIRS DU DÉVONIEN MOYEN (GIVÉTIEN) DE L'ÉTAT DE NEW YORK, É.-U.	11
1.1 RESUME EN FRANÇAIS DU PREMIER ARTICLE	11
1.2 <i>WELLERODUS PRISCUS</i> , A CHONDRICHTHYAN WITH PAIRED FIN SPINES FROM THE MIDDLE DEVONIAN (GIVETIAN) OF THE NEW YORK STATE, USA	13
1.3 INTRODUCTION	13
1.4 GEOLOGICAL AND PALEOENVIRONMENTAL SETTINGS.....	19
1.5 MATERIAL AND METHODS.....	22
1.6 SYSTEMATIC PALEONTOLOGY	24
1.6.1 Description.....	28
1.7 DISCUSSION	51
1.7.1 Diplodont teeth in Devonian chondrichthyans	51
1.7.2 The case of <i>Ctenacanthus wrighti</i>	53

1.7.3	Comparison of fin spines within antarctilamnids	55
1.7.4	Fin spines in chondrichthyans, putative chondrichthyans and acanthodians	58
1.7.5	Taxonomic implications and the quest for the basal chondrichthyan	62
1.7.6	Phylogenetic implications	64
1.7.7	Speculations on chondrichthyan origin and distribution path	66
1.7.8	Paleobiological reflections based on taphonomical considerations	67
1.8	CONCLUDING REMARKS	72
1.9	FIGURES	75
	CONCLUSION GÉNÉRALE	94
	RÉFÉRENCES BIBLIOGRAPHIQUES	1000

LISTE DES FIGURES

Figure 1 : Information géographique et stratigraphique de la carrière de Cairo, New York, É.-U.	75
Figure 2 : Section sélectionnée de la carte du <i>Konzentrat-Lagerstätte</i> de la carrière de Cairo présentant la position des spécimens partiellement articulés étudiés	76
Figure 3 : Spécimen partiellement articulé NYSM 19051a du requin antarctilamnide <i>Wellerodus priscus</i> ; région céphalique.....	77
Figure 4 : Spécimen partiellement articulé NYSM 19051b du requin antarctilamnide <i>Wellerodus priscus</i> ; aiguillon médian dorsal.....	78
Figure 5 : Spécimen partiellement articulé NYSM 19051c du requin antarctilamnide <i>Wellerodus priscus</i> ; région pelvienne.	79
Figure 6 : Spécimen partiellement articulé NYSM 19052 du requin antarctilamnide <i>Wellerodus priscus</i> (photographie).....	80
Figure 7 : Spécimen partiellement articulé NYSM 19052 du requin antarctilamnide <i>Wellerodus priscus</i> (illustration)	82
Figure 8 : Spécimen partiellement articulé NYSM 19053 du requin antarctilamnide <i>Wellerodus priscus</i> (photographie)	83
Figure 9 : Spécimen partiellement articulé NYSM 19053 du requin antarctilamnide <i>Wellerodus priscus</i> (illustration)	84
Figure 10 : Morphologie et variations des dents du requin antarctilamnide <i>Wellerodus priscus</i>	85
Figure 11 : Organisation des dents <i>in situ</i> au sein du requin antarctilamnide <i>Wellerodus priscus</i> ; détail du spécimen NYSM 19051a.....	87

Figure 12 : Aiguillons pectoraux pairs du spécimen de requin antarctilamnide <i>Wellerodus priscus</i> ; organisation <i>in situ</i> et détail.....	88
Figure 13 : Détails de l'ornementation des aiguillons du requin antarctilamnide <i>Wellerodus priscus</i>	90
Figure 14 : Aiguillons prépelviens du requin antarctilamnide <i>Wellerodus priscus</i> ; détail du spécimen NYSM 19051c.....	91
Figure 15 : Morphotypes des écailles composant l'écaillure du requin antarctilamnide <i>Wellerodus priscus</i>	92
Figure 16 : Comparaison de l'organisation des éléments radiaux de la nageoire pectorale de <i>Centroscyllium fabrici</i> (juvénile) et <i>Wellerodus priscus</i>	93

LISTE DES ABRÉVIATIONS, DES SIGLES ET DES ACRONYMES

AMNH American Museum of Natural History

NYSM New York State Museum

UQAR Université du Québec à Rimouski

INTRODUCTION GÉNÉRALE

Les processus de fossilisation nécessitant des conditions particulières, il est impossible de s'attendre à trouver tous les spécimens permettant d'obtenir un portrait complet de l'évolution des espèces - ou, du moins, à ce que ce dernier soit facile à dresser. En fonction des spécimens disponibles et de l'interprétation qu'il est possible d'en faire, un parcours hypothétique est construit sur la base des scénarios relationnels les plus parcimonieux, et ce afin de représenter les relations entre chaque espèce. L'une des conséquences de la relative rareté de certains spécimens est que le portrait obtenu peut facilement n'être qu'au mieux couvert par les scénarios les plus fragiles. Ainsi, on retrouvera parmi les spécimens les plus anciens d'une lignée des organismes pour lesquels il est impossible d'associer avec certitude une forme plus basale. Incidemment, l'une des conséquences de cette situation est que la découverte d'un simple spécimen peut suffire à réorganiser, parfois de manière considérable, ces hypothèses relationnelles. Cette situation est très bien illustrée par le cas des gnathostomes.

Les gnathostomes constituent un groupe de vertébrés défini par le fait d'avoir, en plus des mâchoires, des nageoires paires pelviennes, des ceintures internes de support pectorales et pelviennes, des organes d'intromission chez les mâles et un canal semicirculaire horizontal (Maisey, 1986; Janvier, 1996). Les gnathostomes se divisent en quatre groupes : deux toujours présents et deux autres exclusivement fossiles. On retrouve parmi les groupes extants les chondrichthyens (incluant requins, raies et chimères) et les ostéichthyens, qui comprennent quant à eux les poissons à nageoires rayonnées (les actinoptérygiens) et les poissons à nageoires charnues (les sarcoptérygiens et, incidemment, les tétrapodes). Les deux groupes exclusivement fossiles sont les placodermes et les acanthodiens. Les

placodermes ont la particularité d'être recouverts de plaques osseuses, tandis que pour les acanthodiens, la situation est moins définie, du fait que les délimitations du groupe deviennent de moins en moins évidentes ; cette situation sera abordée plus loin. Traditionnellement, les chondrichthyens et ostéichthyens sont positionnés comme les gnathostomes apicaux, avec les acanthodiens à la base des ostéichthyens et les placodermes à la base des autres gnathostomes (Janvier, 1996). De toutes les zones d'obscurité quant à leurs relations, l'une des plus intrigantes est celle portant sur les créatures se trouvant à la base de ces groupes, soit les gnathostomes basaux, d'où émergent les lignées connues.

Déterminer les relations entre les organismes situés à la base des lignées de gnathostomes est une problématique importante, d'actualité et encore éloignée d'une résolution claire (voir la revue de littérature de Brazeau & Friedman, 2015). De même, l'établissement clair des caractères définissant chacun de ces groupes (les synapomorphies) est en soi difficile et ces synapomorphies sont régulièrement remises en question (Brazeau & Friedman, 2014). Il n'est donc pas surprenant que toute information permettant d'en savoir plus sur la façon de polariser un caractère au sein d'un groupe de gnathostome (soit de déterminer s'il est plésiomorphe ou dérivé) permettra de gagner en plus de l'information sur les gnathostomes basaux. Cette quête s'est accompagnée de la recherche d'une lignée qui serait considérée comme la plus représentative de ces élusifs gnathostomes basaux.

Les chondrichthyens, compte tenu de leur présumée position basale dans l'organisation des relations entre gnathostomes, ont longtemps été considérés comme le possible groupe-clé présentant les caractères représentatifs de l'archétype du gnathostome basal (Maisey, 2012; Janvier & Pradel, 2015). Toutefois, cette supposée position basale ainsi que la structure de la phylogénie des gnathostomes ont été ébranlées par une série de découvertes récentes (Brazeau & Friedman, 2015; Janvier & Pradel, 2015). Un exemple de ces liens plus fragiles est la relation compliquée entre les chondrichthyens et les acanthodiens. Initialement considérés comme des "requins épineux" de par leur forme

générale, les acanthodiens étaient considérés jusqu'à tout récemment comme un groupe monophylétique (Denison, 1979; Long, 1986; Janvier, 1996; Hanke & Wilson, 2004). Tel qu'il l'a été mentionné précédemment, les acanthodiens étaient généralement considérés comme étant le groupe frère des ostéichthyens; cette conclusion était principalement basée sur l'interprétation du crâne d'*Acanthodes bronni* comme partageant plusieurs caractères avec les ostéichthyens (voir Davis *et al.*, 2012). Des études récentes sur les acanthodiens *Ptomacanthus anglicus* (Brazeau, 2009) et *Acanthodes bronni* (Davis *et al.*, 2012) ont résolu les acanthodiens comme un groupe paraphylétique, c'est-à-dire un groupe qui ne comprend pas tous les descendants d'un ancêtre commun. Selon les travaux de Brazeau (2009) et Davis *et al.* (2012), les acanthodiens étaient distribués à la base des chondrichthyens, à la base des ostéichthyens souche ou encore à la base des gnathostomes. La contribution du travail de Brazeau (2009) a été d'établir que le crâne de *P. anglicus* présentait des traits plésiomorphes aussi partagés par les placodermes et les chondrichthyens, tandis que d'autres se situaient entre les (situations) retrouvées chez les ostéichthyens et les chondrichthyens. Davis *et al.* (2012) ont établi en réétudiant le crâne d'*A. bronni* que celui-ci, contrairement à ce qui était proposé depuis des années, était beaucoup plus près d'une condition retrouvée chez les chondrichthyens que chez les ostéichthyens.

Un pas vers la résolution de ces relations problématiques a été fait avec la découverte d'*Entelognathus primordialis*, un placoderme présentant des os de mâchoire de type ostéichthyen. L'étude associée a permis de nouvelles analyses phylogénétiques qui ont regroupé les chondrichthyens avec les acanthodiens. Ces derniers se retrouvaient maintenant à la base des chondrichthyens (Zhu *et al.*, 2013). Cette relation a aussi été récupérée lors d'analyses ultérieures par Dupret *et al.* (2014), Brazeau & de Winter (2015), Giles *et al.* (2015), Long *et al.* (2015b), King *et al.* (2016) et Qiao *et al.* (2016). Les analyses phylogénétiques de Burrow *et al.* (2016), aussi basées sur la matrice de Zhu *et al.*

(2013), supportent un groupe composé des acanthodiens et des chondrichthyens, avec un sous-groupe d'acanthodiens retrouvé à la base des chondrichthyens "traditionnels".

Puisqu'on semble devoir retrouver acanthodiens et chondrichthyens si fréquemment associés, il pourrait être pertinent de s'attarder aux synapomorphies qui définissent ces deux groupes, afin de mieux voir où et en quoi ils peuvent être apparentés. Les chondrichthyens sont bien établis en tant que groupe monophylétique sur la base de critères morphologiques et moléculaires (Maisey, 1984a; Heinicke *et al.*, 2009, voir aussi références dans Grogan *et al.*, 2012). Deux synapomorphies leur sont propres : une méthode de minéralisation endosquelettique particulière, le cartilage prismatique calcifié, et la présence de ptérygopodes, des organes copulatoires propres aux individus mâles (Grogan *et al.*, 2012). Les ptérygopodes fossilisent plus difficilement et ne sont pas connus au-delà de spécimens datant de la fin du Dévonien (*i.e.* *Diademodus hydei* (Harris, 1951)). La minéralisation par cartilage prismatique calcifiée, cependant, a été identifiée chez les plus anciens spécimens articulés, soit *Doliodus problematicus* (Miller *et al.*, 2003; Maisey, 2013), *Pucapampella* sp. (Maisey, 2001; Maisey & Anderson, 2001; Maisey, 2013) et *Antarctilamna prisca* (Young, 1982; Maisey, 2013).

La situation est moins claire pour les acanthodiens. Ils étaient initialement caractérisés par la présence d'aiguillons aux nageoires paires (Denison, 1979; Janvier, 1996) et un mode de croissance particulier des écailles nommé « box-in-box » dans lequel une couche subséquente de tissu recouvre la précédente à la manière de pelures d'oignons (Janvier, 1996). Le premier caractère a été invalidé en tant que synapomorphie des acanthodiens par la présence chez *D. problematicus* d'aiguillons aux nageoires pectorales (Miller *et al.*, 2003). Des aiguillons pairs sont aussi connus chez d'autres gnathostomes, notamment chez l'ostéichthyen *Psarolepis* (Zhu *et al.*, 1999). Le caractère apomorphe du type de croissance des écailles a aussi été remis en question. Par exemple, la découverte d'acanthodiens présentant des écailles plus typiquement associées aux chondrichthyens

(Hanke & Wilson, 2010; Hanke *et al.*, 2013) en a fragilisé la spécificité. Il est probable que le type de croissance en oignon caractérise un groupe monophylétique au sein des acanthodiens mais ne soit pas suffisant pour tous les rassembler (Brazeau & Friedman, 2014). Le seul caractère encore passible de rassembler les acanthodiens est la présence d'un aiguillon sur la nageoire anale (Brazeau & Friedman, 2014), un caractère qui s'invaliderait si *Polymerolepis* s'avère être un chondrichthyen basal (Hanke *et al.*, 2013).

Positionner les acanthodiens à la base des chondrichthyens soulève de nouvelles questions et comme il l'est systématiquement mentionné dans plusieurs publications récentes s'attaquant à ce problème, de nouveaux spécimens articulés sont essentiels si l'on cherche à mieux comprendre les chondrichthyens basaux ainsi que leur relation avec les acanthodiens. Cette tâche est compliquée par la rareté des spécimens articulés de chondrichthyens, qui existent pour peu de spécimens et encore moins d'espèces (Grogan *et al.*, 2012). Le plus ancien chondrichthyen basal articulé et presque complet est *Doliodus problematicus*, du Dévonien inférieur (Miller *et al.*, 2003). L'une des contributions surprenantes de cette découverte est la présence d'aiguillons pairs au niveau des nageoires pectorales. Les aiguillons pairs étaient jusqu'alors considérés comme une synapomorphie des acanthodiens (Denison, 1979; Janvier, 1996); leur présence chez *D. problematicus* a contribué à les réinterpréter en tant que caractère propre aux gnathostomes basaux (Miller *et al.*, 2003). *Doliodus problematicus* est indubitablement établi en tant que chondrichthyen par la présence de cartilage prismatique calcifié (Miller *et al.*, 2003; Maisey, 2013), mais il possède toutefois des spirales dentaires (Miller *et al.*, 2003; Turner, 2004; Maisey *et al.*, 2014), un caractère plus communément retrouvé chez les acanthodiens et les ostéichthyens basaux (Brazeau & Friedman, 2015). Le neurocrâne de *Doliodus* présente des caractères à la fois basaux et dérivés, mais cette combinaison est toutefois plus près d'un *Gestalt* de requin que celle observée au sein du neurocrâne de *Pucapampella*, le second plus ancien chondrichthyen connu à partir de matériel articulé, aussi du Dévonien inférieur (Maisey *et al.*, 2009).

Pucapampella est un genre initialement connu par diverses boîtes crâniennes datant de l'Emsien de l'Afrique du Sud (Maisey & Anderson, 2001) et de l'Emsien–Eifelien de la Bolivie (Maisey, 2001; Janvier & Maisey, 2010). D'autres spécimens incluent des éléments de la mâchoire, des parties du squelette viscéral, ainsi que, si *Zamponiopteron* s'avère être le même animal que *Pucapampella* (Janvier & Maisey, 2010), de possibles éléments pectoraux. La présence de caractères ostéichthyens dans la boîte crânienne de *Pucapampella*, tels qu'une fissure crânienne, une fontanelle dorsale postérieure et une articulation palatobasale, suggèrent que ceux-ci pourraient s'avérer être l'héritage évolutif d'une condition plésiomorphe (Maisey & Anderson, 2001). Cet état entre en conflit avec la présence de caractères crâniens différents chez *D. problematicus* (Maisey *et al.*, 2009), rendant difficile la réconciliation des deux taxons au sein d'une même lignée phylogénétique. Comme le concluaient Maisey *et al.* (2009), bien qu'autant *Doliodus* que *Pucapampella* puisse représenter la forme basale des chondrichthyens, les deux ne le peuvent pas simultanément puisqu'ils ne partagent pas un complément unique de plésiomorphies. *Pucapampella* est généralement récupéré comme basal à tous les autres chondrichthyens (Pradel *et al.*, 2011; Janvier & Pradel, 2015; Burrow *et al.*, 2016), mais cette position n'a pu que marginalement clarifier la trajectoire phylogénétique des chondrichthyens basaux.

Les autres chondrichthyens du Paléozoïque connus par des spécimens articulés ont fourni des informations ambiguës. Certaines de ces espèces dressent une trajectoire phylogénétique vers un *Gestalt* de type « requin » déjà bien établi. Des espèces comme *Tamiobatis vetustus* (Schaeffer, 1981; Williams, 1998), *Cladoselache* sp. (Dean, 1909; Bendix-Almgren, 1975; Tomita, 2015) ou des taxons du Carbonifère tels qu'*Akmonistion zangerli* (Coates & Sequeira, 2001), *Kawichthys moodiei* (Pradel *et al.*, 2011), *Onychoselache traquairi* (Coates & Gess, 2007) ou l'ichthyofaune de Bear Gulch (*i.e.* *Thrinacosleache gracia* (Grogan & Lund, 2008); voir aussi les revues de littérature de Lund, 1990, et Grogan *et al.*, 2012), bien que permettant de polariser certains caractères,

demeurent cependant trop dérivées pour qu'il soit possible d'en extraire l'organisation des chondrichthyens basaux. Il est vrai que certaines formes du Dévonien pourraient démontrer des caractères plésiomorphes, telles qu'*Antarctilamna prisca* (Young, 1982), pour laquelle a été évoquée la possible présence d'aiguillons pairs (Miller *et al.*, 2003; Wilson *et al.*, 2007; Hanke & Wilson, 2010), ou *Gogoselache lynbeazleyae* (Long *et al.*, 2015a), un spécimen démontrant une possible transition évolutive vers le cartilage prismatique calcifié. D'un autre côté, d'autres spécimens de chondrichthyens sont encore trop mal compris pour que soient clarifiées les hypothèses, comme c'est le cas pour *Gladbachus adentatus* (Heidtke & Krätschmer, 2001), chez lequel certains caractères rendent problématique l'association avec les chondrichthyens (par exemple, son écaillage, comme l'expliquent Burrow & Turner, 2013). Au-delà de ces formes, le plus ancien chondrichthyen reconnu est *Leonodus carlsi*, du Dévonien inférieur. Ce taxon est principalement connu par des dents isolées (Mader, 1986; Botella, 2006; Botella *et al.*, 2009a, b). Il est toutefois difficile d'élaborer sur les formes basales des chondrichthyens à partir des plus anciens taxons connus.

Doliodus semble déjà s'approcher d'une apparence de type « requin », tandis que *Leonodus* est maintenant connu par des écailles et des aiguillons qui présentent des similarités avec *Antarctilamna prisca* (Soler-Gijón & Hampe, 2003; Botella *et al.*, 2005). Ces espèces présentent des traits qui suggèrent un Baüplan de requin (tels que des dents typiques par leur forme et leur organisation et des écailles de type cténacanthé) déjà bien établi et assez éloigné de *Pucapampella*, sans forme de transition évidente et sans suggérer directement une hypothétique forme basale. Conséquemment, les taxons qui permettraient de combler les lacunes entre les gnathostomes basaux, les chondrichthyens et les acanthodiens sont difficiles à identifier. Bien qu'il ait été suggéré que les caractères basaux puissent être identifiés à partir des inioptérygiens, un clade issu du Mississippien (Grogan & Lund, 2009; Grogan *et al.*, 2012) dont toutefois plusieurs autres caractères sont dérivés,

une alternative pourrait impliquer les formes considérées comme des chondrichthyens putatifs.

Plusieurs des taxons associés aux chondrichthyens putatifs ont été basés sur des traits se rapportant aux écailles. La reconnaissance et l'établissement de ces taxons doit beaucoup aux efforts de Karatajūtė-Talimaa (voir, par exemple, Karatajūtė-Talimaa, 1992; 1998). L'état des connaissances concernant les écaillures basales et leur relation avec les chondrichthyens putatifs a été efficacement résumé par Hanke & Wilson (2010). Plusieurs de ces taxons ne sont établis qu'à partir d'écailles isolées; certains sont retrouvés durant l'Ordovicien (Sansom *et al.*, 2012; Andreev *et al.*, 2015), soulignant l'ancienneté de ce type d'écaille. D'autres formes sont toutefois connues par des spécimens au moins partiellement articulés mais, malgré les informations importantes qu'ils apportent, ces spécimens soulèvent tout de même leur lot d'interrogations. Des taxons comme *Frigorilepis caldwelli* et *Wellingtonella gagnieri*, du Silurien inférieur, ne possèdent pas de dents, d'aiguillons ou de structure endosquelettique identifiables mais leurs écailles rappellent un modèle chondrichthyen (Märss *et al.*, 2006). *Kathemacanthus rosulentus*, du Dévonien inférieur, est de toute évidence édenté mais présente une série complète d'aiguillons pairs et médians en plus d'un endosquelette reconnaissable; ses écailles, toutefois, sont similaires à celles des chondrichthyens (Hanke & Wilson, 2010). Des écailles de type chondrichthyen retrouvées en association avec un ensemble d'aiguillons typique des acanthodiens est aussi retrouvé chez *Seretolepis elegans* (Hanke & Wilson, 2010). *Lupopsyryrus pygmaeus* (Bernacsek & Dineley, 1977; Hanke & Davis, 2012), *Lupopsyroides macrancanthus* et *Obtusacanthus corroconis* (Hanke & Wilson, 2004) présentent un ensemble complet d'aiguillons mais leurs écailles, bien que plus rapprochées de celles des chondrichthyens, ne rassemblent aucune des caractéristiques habituellement attribuées aux écailles de chondrichthyen ou d'acanthodien. *Polymerolepis whitei* présente un ensemble complexe et varié d'écailles de type chondrichthyen en plus d'un aiguillon anal (Hanke *et al.*, 2013). *Brochoadmones milesi* est encore considéré comme un acanthodien (Hanke & Wilson,

2006), quoique particulier et est pourtant récupéré parmi les chondrichthyens basaux dans les phylogénies récentes (Zhu *et al.*, 2013; Burrow *et al.*, 2016, King *et al.*, 2016, Qiao *et al.*, 2016). Globalement, plusieurs de ces taxons semble partager des caractères acanthodiens et chondrichthyens.

La présence de caractères acanthodiens chez des chondrichthyens, les combinaisons transitionnelles de caractères retrouvées au sein des formes putatives de chondrichthyens et les rapprochements phylogénétiques récurrents entre les acanthodiens et les chondrichthyens suggèrent l'existence d'autres espèces comblant ces lacunes. La récente découverte à Cairo, dans l'état de New York, d'un surprenant assemblage Givétien de placodermes et de chondrichthyens (Cloutier *et al.*, 2010) pourrait permettre de combler une partie de cette lacune. Le site de Cairo est connu depuis déjà plusieurs décennies, et ce principalement grâce à des recherches en paléobotanique (Matten, 1968a; 1968b; 1973; 1974; 1975; Banks *et al.*, 1975; VanAller Hernick *et al.*, 2008; Labandeira *et al.*, 2014; Feist & VanAller Hernick, 2014. La présence d'ichthyolithes est connue depuis longtemps (Matten, 1968a), mais les premières recherches portant sur certains de ces spécimens ont été publiées beaucoup plus tard. Ginter *et al.* (2006) ont présenté la première occurrence nord-américaine de dents de requin attribuées à *Portalodus bradshawae*, une espèce auparavant trouvée en Antarctique (Long & Young, 1995). Il est intéressant de noter que cette présentation mentionnait aussi la découverte de dents attribuées à *A. prisca* à Athol Springs, un autre site de l'état de New York. D'autres travaux ont permis de révéler un plus grand nombre de spécimens de *Portalodus* en plus de dents attribuées à *Wellerodus* et deux lots distincts d'écailles identifiées comme appartenant à des chondrichthyens (Potvin-Leduc *et al.*, 2010). Les dents de *Portalodus* ont finalement été attribuées à une nouvelle espèce, *P. manoliniae* (Potvin-Leduc *et al.*, 2015). Entre temps, durant l'été 2009, une nouvelle section du site a été révélée, exposant sur une surface de 675 m² le tracé complexe du réseau racinaire d'un ancien peuplement forestier. Cette découverte est en soi spectaculaire, puisque cette forêt est potentiellement la plus ancienne, sinon contemporaine au site de

Gilboa, la plus ancienne forêt actuellement connue (Stein *et al.*, 2007; 2012). Toutefois, au-delà de ce réseau forestier, le site présente aussi des dizaines de spécimens articulés et partiellement articulés de gnathostomes, témoignant probablement d'un épisode catastrophique (Cloutier *et al.*, 2010). La plupart des spécimens sont des placodermes, mais une vingtaine de chondrichthyens, attribués à *Wellerodus priscus*, ont aussi été identifiés (Cloutier *et al.*, 2010; Potvin-Leduc *et al.*, 2011). *Wellerodus priscus* est un chondrichthyen qui était jusqu'à tout récemment connu uniquement par des dents isolées initialement décrites par Eastman (1899) et Hussakof & Bryant (1918) puis extensivement réétudiées par Turner (1997). Les dents de *Wellerodus* sont diplodontes et correspondent à la diagnose d'*Antarctilamna*, ce qui a mené à leur union sous la famille des *Antarctilamnidae*. *Wellerodus* était déjà connu au sein du site de Cairo grâce à des microrestes isolés comprenant des dents, des écailles et l'extrémité distale d'un aiguillon. Des travaux préliminaires sur le matériel articulé ont permis de révéler la présence d'aiguillons pairs chez *W. priscus* (Potvin-Leduc *et al.*, 2011).

Dans ce mémoire est fournie la première description anatomique de *Wellerodus priscus* à partir de matériel partiellement articulé. Le matériel, malgré son mauvais état de préservation, comprend de nombreuses dents (y compris des familles), des aiguillons qui incluent, et ce sans ambiguïtés, des aiguillons dorsaux et pectoraux en plus de possibles aiguillons prépelviens, ainsi qu'un couvert squameux étendu permettant de documenter les variations et la régionalisation de l'écaillage. Les implications phylogénétiques seront discutées en effectuant des comparaisons avec les chondrichthyens basaux, les chondrichthyens putatifs et les acanthodiens. Finalement, une partie de la discussion portera sur les informations taphonomiques et leurs implications quant à la biologie de *Wellerodus* en tant qu'animal vivant.

CHAPITRE 1
WELLERODUS PRISCUS, UN CHONDRICHTHYEN AVEC AIGUILLONS
PAIRS DU DÉVONIEN MOYEN (GIVÉTIEN) DE L'ÉTAT DE NEW YORK,
ÉTATS-UNIS

1.1 RESUME EN FRANÇAIS DU PREMIER ARTICLE

Récemment, plusieurs découvertes ont mené à la réorganisation des hypothèses classiques concernant la phylogénie des gnathostomes basaux. Dans le cas des chondrichthyens, le scénario, imprécis, pourrait être appelé à changer avec les récurrentes unions des acanthodiens aux chondrichthyens et le nombre grandissant de taxons identifiés comme chondrichthyens putatifs. Un nouveau *Konzentrat-Lagerstätte* du Dévonien moyen découvert à Cairo, N.Y., É.-U., a révélé plusieurs gnathostomes articulés, dont des spécimens du chondrichthyen *Wellerodus priscus*. Trois spécimens décomposés partiellement articulés ont été préparés et ont révélé une combinaison de traits anatomiques, dont des familles dentaires et suffisamment de spécimens pour caractériser une variation dans la morphologie dentaire qui suggère la synonymie du genre avec *Antarctilamna*. *Wellerodus priscus* présente de façon non ambiguë des aiguillons dorsaux et pectoraux, ainsi que de possibles aiguillons pré-pelviens. Les aiguillons sont caractérisés par une insertion superficielle et des crêtes composées d'une succession de nodosités, elles-mêmes ornementées de crêtes longitudinales. Les aiguillons pectoraux sont plus courbés et présentent une rangée distale de denticules postérieurs. Les aiguillons pré-pelviens putatifs sont plus trapus et leur ornementation plus simple. L'écaillage est composée d'écailles de type cténacanthé présentant des odontodes sub-parallèles. La diversité de l'écaillage couvre une variation dans l'organisation des odontodes au sein des écailles du

corps et des écailles plates et arrondies, possiblement céphaliques, présentant un motif “étoilé”. La régionalisation dans l’écaillage implique un couvert d’écailles réduit au niveau de la tête, un corps couvert (flancs et dos) par des écailles de type cténacanthé et une transition au niveau pelvien vers des écailles plus plates avec crêtes. La taille relativement petite des spécimens (ca. 50 à 70 cm en longueur totale), l’état de décomposition dans la préservation des fossiles et l’environnement estuarien interprété pour Cairo suggèrent que les spécimens de *Wellerodus* pourraient être des juvéniles. La combinaison d’aiguillons pairs avec des caractères chondrichthyens distinctifs tels que des familles de dents et des écailles avec croissance aréale argumentent en faveur d’un lien entre les chondrichthyens et les chondrichthyens putatifs en plus de démontrer une distribution phylogénétique plus large de caractères “acanthodiens”. Ces caractères pourraient de plus définir le Baüplan du requin basal.

L’article intégré à ce mémoire s’intitule « *Wellerodus priscus, a chondrichthyan with paired fin spines from the Middle Devonian (Givetian) of the New York State, USA* » et sera corédigé par moi-même ainsi que par le docteur Richard Cloutier, de l’UQAR et le docteur Ed Landing, du NYSM. Au moment du dépôt de ce mémoire, l’article est encore en préparation de soumission. En tant que premier auteur, j’ai réalisé l’essentiel de la recherche, soit la préparation des spécimens, leur représentation, leur interprétation et la rédaction du présent article. Le docteur Richard Cloutier a participé à l’acquisition de données, a fourni assistance méthodologique et conseils et a participé à l’interprétation, la rédaction et à la révision de l’article. Éventuellement, le docteur Ed Landing se joindra au projet en tant que troisième auteur, contribuera à la rédaction de la section « *Geological and paleoenvironmental setting* » et participera à la rédaction et à la révision de l’article. Une partie des résultats a été présentée lors de la conférence 12th International Symposium on Early/Lower Vertebrates à Dallas (É.-U.) en mai 2011.

1.2 *WELLERODUS PRISCUS*, A CHONDRICHTHYAN WITH PAIRED FIN SPINES FROM THE MIDDLE DEVONIAN (GIVETIAN) OF NEW YORK STATE, USA

1.3 INTRODUCTION

Relationships among stem gnathostomes, as well as the characters defining them, have recently entered a state of flux and change (reviewed in Brazeau & Friedman, 2015). Adding to the conundrum is the problematic identification of the basal characters of each gnathostome lineage (Brazeau & Friedman, 2014). Understandably, any information that can be gained on how to polarize characters of early members of any gnathostome group will also inform on stem gnathostomes themselves. This search has been coupled with the search for the taxa, or group of taxa, that would be deemed the most representative of the stem gnathostomes. Given their purported basal position in the gnathostome relationships chondrichthyans used to be considered as a potential key group showing characters that would be representative of the stem gnathostome archetype (Maisey, 2012; Janvier & Pradel, 2015). This relative basal position, as well as the topography of the gnathostome relationships, has been challenged by recent discoveries (Brazeau & Friedman, 2015; Janvier & Pradel, 2015). One example of such challenges is the intricate relationships of chondrichthyans and acanthodians (Brazeau, 2009; Davis *et al.*, 2012; Burrow *et al.*, 2016, Qiao *et al.*, 2016). Originally considered as “spiny sharks”, acanthodians were considered until recently as a monophyletic group (Denison, 1979; Long, 1986; Janvier, 1996; Hanke & Wilson, 2004). Recent studies on the acanthodians *Ptomacanthus* (Brazeau, 2009) and *Acanthodes* (Davis *et al.*, 2012) reevaluated the acanthodians as paraphyletic, distributed either as stem chondrichthyans, stem osteichthyans or stem gnathostomes. A step towards a resolution of these problematic relationships was made with the discovery of *Entelognathus primordialis*, a placoderm with osteichthyan-like jaw bones, the study of which resulted in new phylogenetic analyses that grouped chondrichthyans with acanthodians, the latter being resolved as stem chondrichthyans (Zhu *et al.*, 2013). This relationship was also

recovered in subsequent analyses (Dupret *et al.*, 2014; Brazeau & de Winter, 2015; Giles *et al.*, 2015; Long *et al.*, 2015b, Qiao *et al.*, 2016). Phylogenetic analyses by Burrow *et al.* (2016) also recovered acanthodians as paraphyletic within a clade that comprises monophyletic chondrichthyans; a subgroup of acanthodians is recovered at the stem of «classic» chondrichthyans.

Positioning acanthodians as stem chondrichthyans raises more questions and, as systematically mentioned in numerous recent publications tackling this issue, new articulated specimens are sorely needed to further understand basal chondrichthyans as well as their relationships with other gnathostomes, namely acanthodians. The task is complicated by the scarcity of articulated material of early chondrichthyans, which are known for only a few specimens and fewer species (Grogan *et al.*, 2012). The oldest known articulated chondrichthyan is the Early Devonian *Doliodus problematicus* (Miller *et al.*, 2003). One of the surprising contributions of this discovery was the presence of paired pectoral fin spines. Until this discovery, paired fin spines were considered as an acanthodian synapomorphy (Denison, 1979; Janvier, 1996). Their presence in *D. problematicus* contributed to their reinterpretation as a basal gnathostome character (Miller *et al.*, 2003). *Doliodus problematicus* is well established as a chondrichthyan by the presence of prismatic calcified cartilage (Miller *et al.*, 2003; Maisey, 2013), but also by the presence of tooth whorls (Miller *et al.*, 2003; Turner, 2004, Maisey *et al.*, 2014), a character that is more common to acanthodians and basal osteichthyans (Brazeau & Friedman, 2015). Its braincase presented both basal and derived characters, while being closer to a shark *Gestalt* than what is observed in the neurocranium of the Early Devonian *Pucapampella*, the second oldest chondrichthyan known from articulated material (Maisey *et al.*, 2009).

Pucapampella is a genus known from diverse braincases from the Emsian of South Africa (Maisey & Anderson, 2001) and the Emsian–Eifelian of Bolivia (Maisey, 2001; Janvier & Maisey, 2010). Additional specimens include jaw elements, parts of the visceral

skeleton and possibly pectoral elements [depending whether or not *Zamponiopteron* is the same animal as *Pucapampella*, a still unresolved situation (Janvier & Maisey, 2010)]. The presence of osteichthyan characters in the braincase, such as a cranial fissure, a posterior dorsal fontanelle and a palatobasal articulation, suggests these features could be evolutionary relics from a plesiomorphic condition (Maisey & Anderson, 2001). However, different cranial characters observed in *D. problematicus* (Maisey *et al.*, 2009) reinstated confusion, notably because of the difficulty to reconcile the characters of both taxa within a phylogeny. As concluded by Maisey *et al.* (2009), while either *Doliodus* or *Pucapampella* could represent the basal chondrichthyan form, both cannot as they do not reunite a single set of plesiomorphies. *Pucapampella* is generally recovered as basal to all other chondrichthyans (Pradel *et al.*, 2011; Janvier & Pradel, 2015; Burrow *et al.*, 2016), although this position has only marginally clarified the phylogeny of basal chondrichthyans.

Other known articulated Paleozoic chondrichthyans have provided ambiguous morphological information. Some of these species establish a phylogenetic trajectory for an apparently already well-established shark-like *Gestalt*. Species such as *Tamiobatis vetustus* (Schaeffer, 1981; Williams, 1998), *Cladoselache* sp. (Dean, 1909; Bendix-Almgreen, 1975; Tomita, 2015), and the Carboniferous *Akmonistion zangerli* (Coates & Sequeira, 2001), *Kawichthys moodiei* (Pradel *et al.*, 2011), *Onychoselache traquairi* (Coates & Gess, 2007) and Bear Gulch ichthyofauna (e.g. *Thrinacoselache gracia* (Grogan & Lund, 2008); see reviews in Lund, 1990, and Grogan *et al.*, 2012), despite enabling the polarization of certain characters, are too derived to help in reconstructing the basal chondrichthyan organization. Granted, certain Devonian taxa might exhibit basal characters, such as *Antarctilamna prisca* (Young, 1982), for which was evocated the possible presence of paired fin spines (Miller *et al.*, 2003, Wilson *et al.*, 2007; Hanke & Wilson, 2010), or *Gogoselachus lynbeazleyae* (Long *et al.*, 2015a), a specimen demonstrating a possible evolutionary transition towards prismatic calcified cartilage. On the other hand, other

chondrichthyan species are too poorly known to clarify the hypotheses, such as the apparently toothless *Gladbachus adentatus* (Heidtke & Krätschmer, 2001), for which certain characters make its association with chondrichthyans more problematic (its squamation, for instance; see Burrow & Turner, 2013).

Current understanding of chondrichthyan evolution traces it back to still hypothetical relationships between *D. problematicus* and *Leonodus carlsi*, a chondrichthyan known for the oldest shark teeth (Mader, 1986; Botella, 2006; Botella *et al.*, 2009a, b). *Doliodus*, however, already appears to be shark-like, while *Leonodus*, also known from scales (Soler-Gijón & Hampe, 2003; Botella *et al.*, 2005) and fin spines (Soler-Gijón & Hampe, 2003), presents similarities with *A. prisca* (Soler-Gijón *et al.*, 2003; Botella *et al.*, 2005). By presenting traits suggesting a shark-like Baüplan (e.g., shark teeth, placoid scales), the oldest known species do not directly enable us to reconstruct a hypothetical basal form. Taxa filling the gaps at the base of stem gnathostomes, chondrichthyans and acanthodians are difficult to pinpoint. While there have been suggestions that the basal characters can be identified in iniopterygians, an otherwise derived clade known mainly from the Carboniferous (Grogan & Lund, 2009; Grogan *et al.*, 2012), another solution involves taxa attributed to putative chondrichthyans. Many of those putative taxa are based on scale characters and Hanke & Wilson (2010) provided an efficient review of the current state of knowledge on the scale characters and how they apply to putative taxa. Since then, more chondrichthyan-like scales have been recovered from the Ordovician (Sansom *et al.*, 2012; Andreev *et al.*, 2015), further arguing for a deep emergence of this type of scale. Of adamant interest to the current research are the putative chondrichthyans known from articulated material that still generate many interrogations. Taxa such as the Lower Silurian *Frigorilepis caldwelli* and *Wellingtonella gagnieri* lack teeth, fin spines or identifiable endoskeletal structure (Märss *et al.*, 2006), although their scales fit a more chondrichthyan-like model. The Early Devonian *Kathemacanthus rosulentus* is apparently toothless but supports a full complement of median and paired fin spines and an identifiable

endoskeleton; its scales, however, are similar to those of chondrichthyans (Hanke & Wilson, 2010). Chondrichthyan-type scales associated with an “acanthodian” set of fin spines are also found in *Seretolepis elegans* (Hanke & Wilson, 2010). *Lupopsyrus pygmaeus* (Bernacsek & Dineley, 1977; Hanke & Davis, 2012), *Lupopsyroides macracanthus* and *Obtusacanthus corroconis* (Hanke & Wilson, 2004) share a full complement of fin spines but also simple, monodontode scales that, while being closer to the chondrichthyan type, lack the classic characters used to distinguish chondrichthyans from acanthodians. *Polymerolepis whitei* presents a complex and varied set of chondrichthyan-like scales, but with an anal fin spine (Hanke *et al.*, 2013). *Brochoadmones milesi* was still considered as an acanthodian in the latest revision (Hanke & Wilson, 2006), although a peculiar one, and is recuperated as a stem chondrichthyan in recent phylogenies (Zhu *et al.*, 2013; Burrow *et al.*, 2016, Qiao *et al.*, 2016). Overall, many of these taxa appear to share both acanthodian and chondrichthyan apomorphies.

The presence of acanthodian characters in chondrichthyans, the transitional character combinations found in putative chondrichthyans and the recurring phylogenetic relatedness between acanthodians and chondrichthyans argue in favor of the existence of additional taxa bridging this gap. Among these potential transitional taxa, the recent discovery in Cairo, NY, of a Givetian assemblage with articulated placoderms and chondrichthyans (Cloutier *et al.*, 2010) could help filling this gap. The articulated chondrichthyan specimens belong to *Wellerodus priscus* (Cloutier *et al.*, 2010; Potvin-Leduc *et al.*, 2011), a chondrichthyan that was until recently only known by isolated teeth, initially described by Eastman (1889) and Hussakof & Bryant (1918) and extensively revised by Turner (1997). The teeth of *W. priscus* are diplodont and fall within the diagnostic range of *Antarctilamna*, uniting both under the *Antarctilamnidae*. *Wellerodus* was previously known from the Cairo locality through isolated remains that included teeth, scales and a broken fin spine tip (Potvin-Leduc *et al.*, 2010; 2015) and preliminary work on the articulated material revealed the presence of paired fin spines in *W. priscus* (Potvin-Leduc *et al.*, 2011).

In this paper, we provide the first anatomical description of the Givetian *W. priscus* from partially articulated material. This material, despite its poor state of preservation, presents numerous teeth, including tooth families, unambiguous dorsal and pectoral spines as well as putative prepelvic spines, and extensive scale covering enabling the documentation of squamation variation and regionalisation. Phylogenetic implications will be discussed by comparison with early chondrichthyans, putative chondrichthyans, and acanthodians. Taphonomical information will be discussed pertaining to the biology of *Wellerodus* as a living animal.

1.4 GEOLOGICAL AND PALEOENVIRONMENTAL SETTINGS

The specimens were recovered in the Cairo municipal quarry, located in the town of Cairo in southern New York State (Fig. 1A). The site exposes a 12 m deep sequence of the Platekill Formation from the eastern Hamilton group. The exposed sequence is made mostly of sandstone and mudstone (Fig. 1B); further information regarding the localization and the stratigraphy of the site can be found in Potvin-Leduc *et al.* (2015). The age is Givetian (Middle Devonian) [387.7–382.7 MA (Cohen *et al.*, 2013)].

The site is located in the eastern part of the Devonian Catskill Delta. The general Devonian environment of the site is interpreted as a sea bound shoreline, bordering the North American epeiric sea that covered most of the actual New York State (Gates, 2000). The shoreline, influenced by the sedimentary input from the Catskill Delta, went during the Middle and Upper Devonian through a transgressive motion, alternating sequences of marine and non-marine environments (Miller and Woodrow, 1991; Rickard, 2000). The Cairo facies, consequently, is characterized by two depositional environments: one associated with estuarine or lacustrine conditions and the other with infilling by flooding events (VanAller Hernick *et al.*, 2008; Potvin-Leduc *et al.*, 2015).

The Cairo quarry yielded diversified Devonian flora and fauna. The first publications related to this site concerned paleobotanical remains (Banks *et al.*, 1985; VanAller Hernick *et al.*, 2008; Feist & VanAller Hernick, 2014; Labandeira *et al.*, 2014). Subsequently fish microremains were described, mainly focusing on shark remains (Ginter *et al.*, 2006; Potvin-Leduc *et al.*, 2010, 2015). Ichthyolith diversity is however much diverse, with an assemblage composed of placoderms, acanthodians, actinopterygians and sarcopterygians (Cloutier *et al.*, 2010). These specimens were recovered from the first of two ichthyolith-yielding horizons, situated at 4.75-5.1 m from the base of the section (Fig. 1B). The second of these horizons, at 7.35 m, was discovered in the summer of 2010 and presented both the fossilized roots of ancient paleotrees (as well as evidence of vegetal succession) and the

remains of tens of articulated fishes, including mostly placoderms but also around nineteen specimens of *Wellerodus priscus*. The whole site was mapped in minute details during the summers of 2010 and 2011. Part of this map encompassing the specimens under study in the current paper is presented in Fig. 2. The studied material was sampled from seven out of 112 quadrates that correspond to the quadrates coded on the field as F6, I5, M10–11 and N9–11.

A major area of the floor of the Cairo quarry is characterized by the presence of the fossilized traces of the root systems of an ancient “forest”, including stumps and ramifying roots. The larger root systems are identified as archaeopterid lignophytes (*Archaeopteris*-like). Archaeopterid root length (for the 11 main root systems) varies between 0.53 and 12.84 m (N = 173). The root system is preserved as “hollowed” traces, but in the western side of the site, plant debris can be observed at the bottom of the roots, and the surrounding reddish sediment is extensively littered with minute plant debris. The superposed greenish mudstone layer contains the articulated fish specimens as well as abundant ichthyoliths [more than 3200 ichthyoliths in 112 quadrats (675 m²)]. With the exception of stump-root systems, plant debris are rare. Articulated fish specimens are mainly associated to the roots (with one preferential direction). This mass mortality is interpreted as being the result of a single catastrophic event (e.g., tidal wave) that transported these fishes against the roots, slowly decaying in dwindling ponds until a mudflow-type event provided correct fossilization conditions. The scarcity of plant remains in that layer suggests that the trees were dead at the time of the event. A younger stratigraphic layer covers part of the site, within which are found stump traces of a second plant species assigned to cladoxylopsids. The two plant species observed are temporally and geologically distinct, suggesting recolonization and vegetal succession. This specific vegetal succession, from archaeopterids to cladoxylopsids also hints at a transition from a well-drained environment to wetland conditions (Mintz *et al.*, 2010).

Research on the vertebrates from this horizon has included preliminary studies on the fish assemblage, revealing two groups of fish with affinities for estuarine and marine faunas (Cloutier *et al.*, 2010). Preliminary taxonomic work on the placoderms, encompassing specimens from both horizons, has been initiated by Lavoie *et al.* (2011), while first data regarding the *W. priscus* articulated specimens was presented by Potvin-Leduc *et al.* (2011).

1.5 MATERIAL AND METHODS

The *Konzentrat-Lagerstätte* section of the quarry floor was mapped during the summers of 2009 to 2011, resulting in a detailed map of the stump-root systems and the associated micro-remains and articulated specimens. This map provided a detailed portrait of the fossilization event and the distribution of the articulated fishes. Numerous specimens were then extracted from the site, including approximately ten *Wellerodus priscus* specimens, making this discovery possibly the oldest occurrence of an assemblage of at least partly articulated chondrichthyans. The site and its taphonomy are currently under study, as are some of the extracted placoderm specimens. Of the extracted chondrichthyans, three specimens have been so far prepared for this publication. Part of the site map is shown in Fig. 2, showing the selected specimens *in situ*.

The studied specimens were extracted from the Cairo quarry during the summers of 2010 and 2011. Excavation of the articulated specimens from the quarry floor necessitated extraction through the use of rock saw and hammer drill and plastering of a massive rock block to preserve the integrity of the specimen due to the crumbly nature of the matrix. Since most of the specimens were still partly, or mostly, covered with matrix, and given the impossibility to prepare in the field, preliminary delimitation of specimens for cutting and removal had to be conducted by deduction from the exposed parts. At the time, there was no indication of the extent to which a specimen could be covered and hidden. This resulted in certain specimens showing, once prepared, truncated sections of their endoskeleton. Preparation in the laboratory revealed, in all the studied specimens, that extensive and significant sections of the fossils were covered with sediment and could not be identified as such in field conditions. Consequently, missing parts may have been caused by the removal procedure. Since the site was found in a municipal quarry, not much protection was possible for the exposed surface. While the surface of interest was delimited and presence of field workers insure some supervision during the field sessions, little could be done in

terms of protection outside of that limited time frame. This meant that the fossils were exposed to weathering, but also to human intervention, as the quarry was the local *nec plus ultra* of quad and motocross riding.

Because the matrix (mainly mudstone) does not react to formic or acetic acids, the specimens were mechanically prepared using entomological needles (.0 and .00) mounted on pin vises. As this implied extremely long preparation times, only three articulated specimens were completely prepared for this publication. Selection of the specimens was based on characters of interest that were apparent before preparation, including the presence of pectoral fin spines and teeth families. Specimens were drawn using a camera lucida mounted on a Leica binocular (MZ6 and MZ9.5). The drawings were vectorized by hand using Adobe Illustrator CC. Pictures were taken with Nikon cameras (models D300 and P350). Scanning electron microphotographies (SEM) were performed with a model JEOL JSM-6460LV.

1.6 SYSTEMATIC PALEONTOLOGY

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Order Antarctilamniformes Ginter, Liao, and Valenzuela-Ríos, 2008

Family Antarctilamnidae Ginter, Liao, and Valenzuela-Ríos, 2008

Remarks.— As defined by Ginter *et al.* (2008), the family diagnosis pertains to teeth characters. We consider that most of the diagnosis is still valid with a few exceptions. The new material described herein provides new information concerning scales at this taxonomic level. Characters pertaining to the ornamentation of the fin spines will also be added, although the exact number of fin spines and their position remain unclear at this level and might represent distinction criteria between *Antarctilamna* and *Wellerodus*.

Emended diagnosis.— The antarctilamid tooth-bases are lingually directed, usually broad, from oval to trapezoidal with the wider lingual side, and provided with an oval articular boss. The two main lateral cusps are triangular in labial view, labio-lingually compressed, and may or may not be slightly sigmoidal at the tips. There are no more than five (usually one or three) smaller cusps in between, the median cusp being larger than the intermediate cusplets. The labial face of the main cusps is ornamented with straight to spiral cristae whose number and form depend on the width and direction of the cusps. Body scales are of

the ctenacanth type and present areal growth through the addition of odontodes, although some disparity is observed among genera and variations among body zones of an individual. Fin spines are present and include at least one dorsal fin spine, although full complement of fin spines is likely variable among genera and species. The fin spines are ornamented with ridges composed of odontodes following a “peg-in-peg” motif. The ridges connect alternatively to the leading edge. The insertion zone of the spines is either shallow or almost unapparent.

Genus *Wellerodus* Turner, 1997

Remarks.— Current taxonomic status of the genera *Wellerodus* and *Antarctilamna* is that the two are synonymous but kept distinct for reasons of nomenclatural clarity (Ginter, 2004; Ginter *et al.*, 2006; 2010). The initial distinctive character concerned the presence of intermediate cusplets on the teeth of *Antarctilamna*, although Turner (1997) noted them and intermediate cusplets were further documented in *Wellerodus* by Ginter *et al.* (2006; 2010) and also supported by other material presented by Potvin-Leduc *et al.* (2011) and this publication. Differences between the two genera now encompass variation in the height of the median cusps and the size of the coronal button (Ginter *et al.*, 2010). The known repartition of antarctilamnids seems to hint at a geographical distinction, with *Antarctilamna* occupying Gondwana and *Wellerodus* found in Laurentia (Potvin-Leduc *et al.*, 2015), although Ginter *et al.* (2010) identified some New York specimens as *A. prisca*.

There is currently one species of *Wellerodus* (*W. priscus*) and three species attributed to *Antarctilamna*. *A. prisca*, from the Middle and Late Devonian of Australia and Antarctica, is known by isolated teeth, fin spines, and scales, as well as articulated material, including a braincase and jaw elements (Young, 1982, 2011; Long & Young, 1995; Burrow

et al., 2009). *A. ultima*, from the Famennian of South Africa, is known by material that includes teeth, a fin spine, a neurocranium and jaw elements (Gess & Coates, 2015), while *A. seriponensis*, from the Early Devonian of Bolivia, was erected based on a fin spine (Gagnier *et al.*, 1988). Teeth of *Wellerodus* have also been recovered from Poland (Liszkowski & Racki, 1993; Ginter, 2004) and Russia (Ivanov, 2008). Note, however, that other remains have been attributed to antarctilamnids, mostly scales and fin spines; a list of occurrences is available in Potvin-Leduc *et al.* (2015; Table 1). As no other articulated specimen of *Wellerodus* species has been discovered to date, it is impossible to confirm that the European specimens belong to *W. priscus* and that the taxonomic characteristics described for *W. priscus* can be extended to the genus. Given the available material, any generic diagnosis at this point should be limited to teeth and thus we chose to leave the genus diagnosis for *Wellerodus* unchanged, as posited by Turner (1997).

While the diagnosis for *Wellerodus* is based solely on tooth characters, the original diagnosis for *Antarctilamna* initially encompassed characters from partially articulated material as it was defined by the diagnosis of the type species, *A. prisca* (Young, 1982). The diagnosis of *Antarctilamna* was emended in Burrow *et al.* (2009) to encompass a second tooth morphotype, new data on tooth histology and precision on scale morphology. Gess & Coates (2015) did not emend the genus diagnosis when they described *A. ultima*. As currently defined, the generic diagnosis for *Antarctilamna* does not accurately represent *Wellerodus*, while still, as far as the authors of the present paper understand it, cover the variation observed in *A. ultima*. Burrow *et al.* (2009) describe teeth with 4–7 cusps, while *Wellerodus* shows 3–5, meaning that a *Wellerodus* tooth could not be distinguished from an *Antarctilamna* one. The characters that can be established as different between the genera appear to be constrained to the extremes of known variation, meaning that these differences may not be present in each individual. The current criteria can only confirm the identification of *Antarctilamna* if teeth present the full complement of intermediate cusplets. Possible distinctions can also be observed in structures other than the teeth. The

odontodes forming the crown of the scales are semiconcentric in *Antarctilamna* but subparallel in *Wellerodus*. Some differences in the general organisation of the fin spines are also observed. It is unclear whether these differences justify a separation at the generic level, but as mentioned, *Wellerodus* and *Antarctilamna* cannot be synonymized without creating a problematic nomenclature.

Wellerodus priscus Eastman, 1899

Figures 3–16

2015 Compound chondrichthyan scales Type 1 *sensu* Liao *et al.* 2007; Potvin-Leduc *et al.* 2015: 192

Material.— NYSM 19051a–c, a partially articulated specimen in three parts (cephalic region (NYSM 19051a), median dorsal fin spine (NYSM 19051b) and fragments of the pelvic region (NYSM 19051c); NYSM 19052, the anterior part of a partially articulated specimen; NYSM 19053, the anterior part of a partially articulated specimen; NYSM 19054, a pectoral fin spine and an incomplete median fin spine; NYSM 19055, the basal part of an incomplete fin spine in posterior view; NYSM 19056, the basal part of an incomplete fin spine in lateral view; NYSM 19057, the basal part of a fin spine in anterior view; NYSM 19058, a scale patch; NYSM 19059, indeterminate fossilized organic matter with semi articulated teeth; NYSM 19060–19068; isolated teeth from one individual; all the specimens can be attributed to *Wellerodus priscus* due to their association, or the association of similar material, with unambiguous teeth.

Emended diagnosis.— Antarctilamnid bearing paired pectoral fin spines, at least one median fin spine, and at least two pairs of prepelvic fin spines. Fin spines are ornamented with ridged odontodes. The pectoral fin spines have a posterior row of median denticles on the distal third of the spine. These denticles are absent in the median fin spines, where the distal posterior face is smooth, almost concave surface, as opposed to the keel observed in *Antarctilamna* fin spines. Teeth are diplodont, with one median, always smaller cuspid. Intermediate cusplets may be present, but never more than one between the lateral and the median cusp. Distribution of intermediate cusplets can be uneven, with one present on only one side. The total number of cusps varies between three and five. Squamation is mainly composed of compound scales of the ctenacanth type. The crown of the scales is characterized by sub-parallel odontodes. Squamation also includes rare scales with the aforementioned semi-concentric pattern, but with a doubled main odontode centerpiece, and round, flat plates with a stellate pattern. Squamation transits towards the posterior half to scales with a flat crown covered with ridges.

1.6.1 Description

The studied material includes three articulated specimens; the first specimen, NYSM 19051, is divided in three sections that include part of the cephalic region (NYSM 19051a; Fig. 3), a median dorsal fin spine (NYSM 19051b; Fig. 4) and possibly part of the pelvic region (NYSM 19051c; Fig. 5) while the two other specimens, NYSM 19052 (Fig. 6, 7) and NYSM 19053 (Fig. 8, 9), are whole and consist of the section located anterior to the pectoral region. The localisation of the specimens NYSM 19051a–c in the field is constrained by roots and prevents it from mixing with other individuals; this is considered sufficient to interpret the presented three pieces as belonging to a single individual (Fig. 2).

The studied material also includes one scale patch (NYSM 19058), teeth (*in situ* within a fragment of organic matter, NYSM 19059; isolated, NYSM 19060–19068) and fin spines (NYSM 19055–19057). All articulated specimens are flattened, with the body shape poorly preserved. The general state of preservation is poor, making the identification of anatomical endoskeletal elements difficult. Specimen NYSM 19052 appears as if its endoskeleton has completely “disintegrated” into multiple micro-pieces of variable sizes, sometimes under a millimeter-wide. Specific boundaries of anatomical elements are few and unclear, with some anatomical reliefs found in what were probably endoskeletal margins. Our observations suggest that a fair amount of decomposition had taken place before the material was fossilized, thus explaining the difficulty in identifying clear endoskeletal structures and outlines. The bigger, thicker endoskeletal elements that could be expected to be present, namely those in the cephalic region (e.g., Meckel’s cartilage, palatoquadrate) are, if not missing, at least difficult to discriminate. The articulated specimens are preserved laterally. The specimens are incomplete but total body length is estimated at 50 to 70 cm.

Teeth.—

The teeth of *Wellerodus priscus* have been extensively described by Turner (1997). Most of the material described by Turner (1997) came from Eighteen Mile Creek, New York State, but some specimens were also recovered from Elmhurst, Illinois. The material most recently described by Potvin-Leduc *et al.* (2015) from the Cairo quarry completed Turner’s work by adding variation that was considered as characteristic of juveniles – notably, teeth that would fit all diagnostic criterion but differ in being smaller and more delicate. The description included here will add to the known range of morphological variation and the *in situ* organisation of the teeth.

Teeth are abundant in the articulated specimens; there are approximately 209 teeth in specimen NYSM 19051, 169 teeth in specimen NYSM 19052 and 64 teeth in specimen NYSM 19053. The basal width of the teeth in the partially articulated material ranges from approximately 5 to less than 1 mm. Sizes are unclear in the material revised by Turner (1997); measurements given for *W. priscus* include height (from 5 to 10 mm) and basal width (4 to 8 mm). The measure provided for *Wellerodus wellsii* [prior to the fusion of the three species erected by Turner (1997)] corresponds to the width between the cusps (ranging from 5 to 14 mm). In *Antarctilamna prisca*, the biggest teeth have a basal width of 4 mm and a cusp length of ca. 2.5 mm. The basal width for the smallest teeth was less than 1 mm, while most of the teeth measured about 3 mm (Young, 1982).

The teeth are diploidont; note that all the following described variation can also be observed in the documented dentition within the illustrated partially articulated specimens (Fig. 3, 7, 9). There are two main lateral cusps lingually oriented and one, always smaller, median cusp (Fig. 10, 11; note that all described variation can also be observed. There has been no observation of specimens where that median cusp would be missing. There are cristae on the lingual and labial sides of the cusps, although they may be missing on the labial side (Fig. 10A, C). The cristae are straight which slightly differs from *Antarctilamna prisca*. The two lateral cusps point towards the lateral sides of the teeth. They are either symmetrical or one of the lateral cusp may be more laterally oriented than the other (Fig. 10D, G). Monognathic heterodonty has been described for Paleozoic sharks in general (Zangerl, 1981) and specifically in *Doliodus problematicus* (Maisey *et al.*, 2014). A similar slanting has also been documented in *Portalodus manoliniae* (Potvin-Leduc *et al.*, 2015), a chondrichthyan that co-occurs with *W. priscus* in the Cairo site. It is consequently assumed that the asymmetry is related to a more lateral position within the jaw. Intermediate cusplets are rarely present. The median cusp is always smaller than the lateral cusp, but always bigger than the intermediate cusplets. A tentative distinction between *W. priscus* from *A. prisca* considered the absence of intermediate cusps between the laterals

and the median, although Turner (1997) mentions the presence of occasional intermediate cusplets. New specimens of *W. priscus* presented by Ginter *et al.* (2006; 2010) showed intermediate cusps and confirmed that this character could not discriminate between both genera. Confirming this information, other teeth recovered from the Cairo site presented intermediate cusplets (Fig. 10A–C, E–F) (also mentioned in Potvin-Leduc *et al.*, 2011). However, the maximum number of cusplets is always one per side, lower than what is observed in *Antarctilamna* (up to two per side; Ginter *et al.*, 2010). When present, intermediate cusplets are on the same level as the other cusps.

The occurrence of intermediate cusplets varies among specimens. This is noteworthy, as in the articulated specimens studied herein, teeth with intermediate cusplets were rare and only found in NYSM 19052 (Fig. 7). While not clearly associated with one of the articulated specimen, many of the isolated teeth presenting the intermediate cusplets were found in proximity of each other; given the organization of the fossils on the site, they most certainly belong to a single individual. Contrary to most of the isolated teeth, with the exception of NYSM 19065 (Fig. 10E), the position of the intermediate cusplets in specimen NYSM 19052 was asymmetrical, meaning that only one would be found on one side of the median cusp, with the other side being bare. A similar organisation is seen in some teeth of *A. prisca* (Young, 1982; text-fig. 3A). While this might be indicative of positional asymmetry, the teeth showing this variation were not the biggest observed in the specimen. Accordingly, this might still be related to the position, but possibly farther towards the lateral end of the mouth. While the presence of intermediate cusplets in *W. priscus* is clear, they could be much less frequent within an individual's dentition than in *A. prisca*, resulting in a diagnostic character applicable to an articulated specimen but possibly useless for isolated teeth. All the material revised by Turner (1997) included few specimens showing possible intermediate cusplets, demonstrating that they are not as abundant within an individual as teeth without intermediate cusplets. Absence of teeth with intermediate cusplets within some individuals could also be possible.

The shape of the base ranges from oval to relatively rectangular. None presented the C-shaped base noted in the diagnosis provided by Turner (1997); incidently, the C-shape is never mentioned in the specific diagnoses. The base is broader in the lateral axis than in the labio-lingual axis. The teeth possess a coronal button and a basal concavity, with a slight basolabial extension observed in some specimens [Fig. 10D, E]. Ginter *et al.* (2010) suggested that the coronal button could be used as a distinction between *Antarctilamna* and *Wellerodus*, with the button being bigger in *Wellerodus*, although it should occupy a smaller oral-lingual area. Buttons observable in the articulated specimens vary in size. It should consequently be considered whether button size might be better explain by variables such as the position within a tooth family, which would imply factors like the age of the tooth and the exposure to wear damage.

The familial organization of teeth, implying the junction of the coronal button of one tooth inside the basal concavity of another (Fig. 11), is observed in some tooth families of specimen NYSM 19051a. As suggested from the morphology of the base – the presence of a coronal button and a basal concavity – the teeth are organized in such a way that the base of one tooth fits over the coronal button of the subsequent. The teeth are not fused at the base; given the extensive surveying of the site and the available material on the specimens, tooth whorls are absent in *Wellerodus*. The families are likely incomplete as they encompass only two to three teeth. This low number is smaller than the number of teeth per family observed in other Paleozoic sharks; tooth families share up to six teeth in *A. ultima* (Gess & Coates, 2015), between four to possibly seven teeth per family in *D. problematicus* (Maisey *et al.*, 2014) and a minimum of four teeth per family in *Onychoselache traquairi* (Dick & Maisey, 1980; Gess & Coates, 2001). Tooth whorls in *Akmonisition zangerli* included up to five teeth (Coates & Sequeira, 1998). Tooth families are unknown in *A. prisca*.

In vivo position of the teeth in specimens NYSM 19051, NYSM 19052 and NYSM 19053 is unclear. The general position of the head is suggested by a greater concentration of teeth, but clear limits of cranial endoskeletal elements are missing or difficult to ascertain. The right section of specimen NYSM 19051a presents a potential marginal arrangement of teeth at its lower margin (Fig. 11), but this is difficult to reconcile with the dense organisation observed in the center of that section. There is no structure that could be assigned to a dental furrow. The exact number of teeth position per jaw section is unknown but is estimated to approximately 14 families of four teeth based on specimen NYSM 19051. For comparison purposes, 12 to 14 teeth were found in *D. problematicus* (Maisey *et al.*, 2014), 6 or 7 with symphyseal tooth whorls in *Akmonistion zangerli* (Coates & Sequeira, 2001) and at least 15 teeth per jaw ramus in *Onychoselache traquairi* (Dick & Maisey, 1980).

Overall, most of the teeth observed in the partially articulated specimens, while still fitting the systematic description of Ginter *et al.* (2010), are closer to the smaller morphotype described in Potvin-Leduc *et al.* (2015) and the smaller and more slender teeth of the sample revised by Turner (1997). However, some of the teeth recovered from quadrate F6 are more similar to the bigger teeth figured in Turner (1997); they also present the highest prevalence of teeth with intermediate cusplets in the studied Cairo specimens.

Fin spines.—

Wellerodus priscus is characterized by the presence of median (dorsal) and paired (pectoral and prepelvic) fin spines. Unequivocal presence of paired pectoral fin spines is demonstrated in specimen NYSM 19052; the specimen, laterally preserved, presents both fin spines side to side (Fig. 7). In specimen NYSM 19052, the left pectoral fin spine is found in lateral position and lying atop a layer of organic matter and cartilage that is

covering the second, right pectoral fin spine, positioned with its posterior concavity facing up. Similar organisation of paired fin spines is found in laterally preserved acanthodians [for example, *Brochoadmones milesi*, in Hanke & Wilson (2006: Fig. 3)]. Cartilaginous endoskeletal elements, identified as radials based on their shape and position are associated with the overlaying fin spine; thus also suggesting that the fin spines are pectoral spines (Fig. 12A, B; see Pectoral girdle). Radials form a series of at least five square-shaped blocks of cartilage linearly organized. Size is approximately 2 x 2 mm; one rectangular element could represent a fusion of two smaller radials.

A comparable organization of fin spines is found in NYSM 19053, where one preserved spine is found with its ventral side facing up and is therefore interpreted as a pectoral spine (Fig. 9). Similar organization of fin spines has also been found on the field and within specimens that are still unprepared (DPL, RC, pers. obs.), further confirming that, at least within the conditions of the Cairo *Konzentrat-Lagerstätte*, this layout is a common occurrence. There are no prepectoral, nor admedian fin spines.

The pectoral fin spines are straight and relatively narrow compared to *Antarctilamna*. Their size ranges from 53 to 75 mm. There is a slight curving along the leading edge of the pectoral spine, although the anterior edge of the dorsal spines is straighter (Fig. 4). The fin spines appear slender than the fin spines of *A. prisca* and are pointier. In lateral view, the apex of the fin spine is not as curved as the tip of the fin spines in *A. prisca*, where the leading edge curves at the tip to join the straight posterior axis (Young, 1982). This general shape also distinguishes the fin spines of *W. priscus* from the almost conical dorsal fin spine of *A. ultima* (Gess & Coates, 2015). The fin spines are covered by straight, ornamented costae that are oriented towards the leading edge at a very low angle (Fig. 4, 13A, B). The ridges follow the length of the spines on a relatively straight trajectory, generally following the long axis of the spine and ultimately connecting in an alternate manner at the leading edge (Fig. 13A). This pattern is observed in *A. prisca*, as well as in

the antarctilamnid spines from Venezuela (Young & Moody, 2002). The taxonomic value of this pattern is unclear. The dorsal fin spine described for *A. ultima* (Gess & Coates, 2015) is preserved in lateral view, meaning that the pattern of the leading edge is undetermined. As the general organisation of the ridges seems comparable between the fin spines of those species, the alternating pattern might be recovered on *A. ultima* as well and, as such, the alternating ridge pattern at the leading edge might be characteristic of antarctilamnids. This pattern is not observed in *Doliodus problematicus* (R. C., pers. obs.); determining the presence of this pattern in the fin spines associated with *Leonodus* will be consequential in evaluating if the pattern is basal for crown-group chondrichthyans or plesiomorphic for total group chondrichthyans.

The alternating ridge pattern is found in certain acanthodians, such as *Lupopsyrus pygmaeus* (Bernacsek & Dineley, 1977; Hanke & Davis, 2012), *Parexus recurvus* (Burrow *et al.*, 2013) and *Ankylacanthus* (Burrow *et al.*, 2008). The acanthodians spines appear to differ from the chondrichthyan ones by the presence of incomplete or stunted ridges near the basal end of the spine, as opposed to ridges extending all the way to the anterior edge in *W. priscus* and *A. prisca*. This character cannot be confirmed in *A. ultima*, as the basal portion of the ornamentation is incomplete in the figured spine (Gess & Coates, 2015: Fig. 6 A, B). Of interest is the combination of the extension of the ridges to the leading edge and the shallow insertion, noted by Gess & Coates (2015) as a possible character of *Antarctilamna*.

Ridges are of relatively equal width but tend to get narrower as they are closer to the posterolateral edge of the fin spine (Fig. 13B), a character also observed in *A. prisca*. The ridges are made of a succession of odontodes, showing the “cone-in-cone” organization described for *A. prisca* (Young, 1982). Each odontode is on the same level as the ones from the adjacent ridges; this is mostly apparent in specimen NYSM 19057 (Fig. 13A), but less so in laterally preserved fin spines (for example, specimen NYSM 19054; Fig. 12C). There

might have been some skewing of the rows as a result of compression of the fossils during fossilization and slight displacement of the structure. The odontodes are ornamented with small subparallel ridges that converge toward the distal tip of the odontode (Fig. 13C, D). In specimen NYSM 19056, a small, lateralized projection can be observed on the lateral side of the odontodes (Fig. 13D). This asymmetry is present in the ridges closer to the leading edge and is not observed in the ridges located posteriorly. The function of this asymmetry is unknown, but given that its presence appears dependant on the proximity of the leading edge, hydrodynamic constraints are expected. The taxonomic significance of this ornamentation is unknown; to our knowledge, such a projection has never been described in other taxa.

The insertion zone is narrow, its depth ranging from 2 to 4 mm, both in pectoral and median fin spines. The insertion zone appear slightly more extensive, while remaining short, in dorsal fin spines, as is observed in NYSM 19051b (Fig. 4). A narrow insertion zone has been generally observed in antarctilamnid fin spines, the only exception being two specimens described by Young (1982; Pl. 87, Fig. 3) and presenting a more extensive insertion zone. The extensive insertion zone has not been observed in any of the Cairo *W. priscus* specimens. The spine is opened posteriorly. The concavity extends for at least half the length of the spine; however, specimens NYSM 19052 and NYSM 19053 hint at possibly two thirds of the length (Fig. 7, 9). The distal end of the posterior side does not present a median ridge as in *A. prisca* and *A. ultima*. This character is absent in the dorsal fin spines (see specimen NYSM 19051b); the closed section of the posterior side appears smooth, even slightly concave (Fig. 5). However, in the pectoral fin spines, the closed, distal section of the posterior wall is adorned with a single median row of retrorse denticles (Fig. 12C, D). The median row is unique as indicated by the embedded denticles associated with the tip of a fin spine in specimen NYSM 19053 (Fig. 9; in the top right section of the specimen). A posterior median ridge has not been observed in the similar antarctilamnid fin

spines from Venezuela described by Young & Moody (2002), possibly hinting at a distinguishing character between *Antarctilamna* and *Wellerodus*.

Only specimen NYSM 19051c shows part of the posterior half of the body including four smaller fin spines (Fig. 5, 14). Each fin spine is broken; complete length is estimated at 1 cm for the biggest. Their position, relative to the cephalic remains of specimen NYSM 19051a and the median fin spine in specimen NYSM 19051b, suggests a posterior, post-median fin spine position. The spines are straight and covered by straight, unornamented ridges. The posterior side is opened on a substantial length of the fin spine. There is no apparent insertion zone. The number of elements, as well as their shape morphologically distinct from the pectoral and median fin spines, suggests that these elements are prepelvic fin spines. In acanthodians, intermediate spines are described as asymmetrical, stubby and cone-like (Jerve, 2016), a general description that is congruent with the putative prepelvic fin spines of *W. priscus*. In other gnathostomes with paired fin spines, pelvic fin spines are not fundamentally different from pectoral fin spines, but Burrow *et al.* (2016) note that prepectoral, admedian and prepelvic fin spines often have a different ornamentation than the median and paired fin spines. There are no endoskeletal elements associated with the prepelvic fin spines, but a thick, incomplete plate-like remain, covered with scales, is found relatively close to them (Fig. 5). Presence of typical *Wellerodus* scales in association with the spinelets argues in favour that they belong to the same animal. Other alternatives include the possibility that these would represent remains from within the digestive track. This hypothesis is rejected due to the organization of the spines relatively to the scales, which are surrounding but not covering while showing their crown. The possibility that these spines could belong to an *in utero* juvenile is also rejected, for the morphology of the spines does not fit our developmental knowledge of fin spine growth. Discovery of a smaller fin spine attributed to *W. priscus* would also support our understanding that younger fin spines would remain morphologically similar. If the described smaller spines are accepted as prepelvic (based on similarity with acanthodian morphology), then pelvic

fin spines are to be considered as present in *Wellerodus* (although none has been identified as such). To our knowledge, there are no Paleozoic vertebrates in which prepelvic fin spines are present and pelvic fin spines absent. Hence, *W. priscus* is purported to possess pelvic fin spines, even if these have not been found yet. As pelvic fin spines share a morphology similar to pectoral fin spines, and different from prepelvic fin spines, this also leads to the conclusion that they are not among the putative prepelvic fin spines. If isolated, they might be mistaken for pectoral fin spines, unless the retrorse denticles character is restricted to the pectoral fin spines, a logical assumption given that in acanthodians presenting this trait it is limited to the pectoral fin spines.

The presence of a second dorsal fin spine is unknown. Specimen NYSM 19052 shows a partial fin spine posterior to the pectoral fin spines that could either be a second dorsal or a pelvic fin spine. Orientation of the fin spine appears more congruent with a dorsal position, but relative size might be smaller than expected when compared with the dorsal fin spine found in specimen NYSM 19051b. If the presence of prepelvic fin spines in specimen NYSM 19051c is representative of the *W. priscus* condition, then their presence might be expected in specimen NYSM 19052 if the incomplete spine is indeed a pelvic fin spine. However, given that there is no known endoskeletal support for prepelvic spines, they could also have been displaced by the decay processes. Note however that no prepelvic fin spines have been found in association with specimens NYSM 19052 and NYSM 19053; there is also good reason to believe that the posterior half of the shark is missing in these two specimens. If the difference in estimated size is relevant, the third fin spine of specimen NYSM 19052 might be a second dorsal fin spine, with the first one missing from the recovered remains. The presence of two dorsal fin spines is considered as the basal gnathostome condition (Janvier, 1996; Larouche *et al.*, 2017) and, incidentally, is the condition most common in acanthodians (Denison, 1979) and the oldest complete chondrichthyans (Zangerl, 1981). Maisey (2009) noted that the first and second dorsal fin spines are usually similar, with eventual differences limited to size and curvature. Cases of

important disparity, such as the presence of a spine associated with the first dorsal fin and the absence of a spine associated with the second dorsal fin, is considered a derived condition (Maisey, 2009). The alternative, a first dorsal fin without a spine and second dorsal with one, has never been observed.

The plesiomorphic condition for fin spines in chondrichthyans is still hypothetical. There are to date no known cases within acanthodians or chondrichthyans of the presence of paired fin spines without median ones, although the alternative is possible (Hanke, 2002). Beyond its pectoral fin spines (Miller *et al.*, 2003), *Doliodus problematicus* is now known as possessing a full, “acanthodian”-like complement of fin spines, including dorsal, prepectoral, admedian, prepelvic and pelvic fin spines (Maisey *et al.*, 2017). Available articulated remains of *Antarctilamna prisca* support either a first median fin spine (Young, 1982) or one pectoral fin spine if the alternative suggestion of Miller *et al.* (2003) proves correct. Young (1982) suggested the presence of two median fin spines but concluded in that direction based on the presence of two different sets of characteristics within the recovered fin spines. In *A. ultima*, only one fin spine was recovered and interpreted as a dorsal fin spine; we have no reason to question this interpretation. The Devonian juvenile chondrichthyan from South Africa described by Gess & Coates (2015) shows two dorsal fins but only one spine associated with the first dorsal fin. Conservative appraisal would lead to conclude on at least one dorsal fin spine on *W. priscus*, with the presence of more than one still unclear.

The presence or absence of an anal fin spine cannot be confirmed at this point in *Wellerodus priscus*. While such a spine has been presented as an acanthodian synapomorphy (Denison, 1979, Maisey, 1986), its presence in the putative chondrichthyan *Polymerolepis whitei* suggests that it could be a more widespread character among early gnathostomes (Hanke *et al.*, 2013). Given the presence of characters previously considered

as “acanthodian” in *W. priscus*, the presence of an anal fin spine should be considered as a possibility.

Specimen NYSM 19052 presents clear evidence of the characters enabling distinction between (at least) the paired pectoral fin spines and the median ones. Median fin spines are found not as tightly attached (see NYSM 19051b, where the median fin spine is found by itself, with only a partly attached fin web) or completely missing (NYSM 19052). Paired pectoral fin spines, given their close relationship with the endoskeletal structure of the pectoral girdle, would be expected to stay at least partly articulated with the specimen, compared to a fin spine that is only superficially inserted in the skin and superficial muscular tissues of the animal. No evidence for a basal plate for the median fin spines has been found.

Scales.—

The articulated specimens and isolated remains of *Wellerodus priscus* enable us to describe the variation in scale morphology. Part of this variation is associated to body regional distinction. Patterns of position and orientation are difficult to discern since it appears that there was at least some level of displacement pre-burial. The scales of *Wellerodus priscus* are of the ctenacanth type (*sensu* Reif, 1978; Karatajūtė-Talimaa, 1992) (Fig. 15A–G). The crown is composed of at least one, but up to three and possibly four rows of subparallel odontodes. Width of the odontode row is variable. The variation suggests growth by addition of odontodes, either laterally or by a superposition initiated on the anterior side. The purported mode of odontode addition suggested for *Wellerodus* might well be plesiomorphic for chondrichthyans, as this is likely the one identified in the Ordovician *Tezakia* (Andreev *et al.*, 2015). The odontodes project posteriorly, beyond the posterior margin of the base. The base of the scales is generally rhomboid but can be

rectangular or oval (Fig. 15C). It often appears flat or concave, but rare instances of convex bases have been observed. A flat or slightly concave surface on the anterior side followed by a marginal depression (convex) just anterior to the posterior margin is the common pattern. Neck canals were not observed in the studied specimens but were identified in other *Wellerodus priscus* scales found as isolated microremains in the Cairo quarry (Potvin-Leduc *et al.*, 2015).

Six morphotypes, mostly based on crown morphology, are observed in the material. Morphotype 1 is characterized by a large central odontode sitting atop the other rows. The main odontode is wider anteriorly, at its point of initiation, but narrows as the external surface of the odontode curves towards the horizontal plane. This widened section is ornamented with small ridges (Fig. 15A, B). Taxonomic value of this ornamentation is unclear, given that ctenacanth-type scales mostly reflect environmental constraints (Fletcher *et al.*, 2014). However, similar scales found in Spain, along with antarctilamnid teeth, present the same ornamentation, alongside similar scales that do not possess it (Ginter *et al.*, 2008; Fig. 2K). The initiation point of this odontode is also located at the anteriormost apex of the scale (Fig. 15A, D). This remains true if there are other main odontodes lateral to the central one. This variation most likely results from the growth pattern of the scales, with the lateral overlaying odontodes present in wider scales. In morphotype 2, the main odontode remains alone atop the crown (Fig. 15D). In morphotype 3, some scales show three main odontodes, with the central one appearing retracted, so that the initiation point of the lateral main odontodes are positioned more anteriorly (Fig. 15E). In some scales, the main odontode presents side flanges that converge towards the posterior end of the scale. Their point of origin is evident but they tend to fuse at mid-odontode as they progress towards the posterior end.

Morphotype 4 is characterized by a heart-shaped crown with a central section made of two parallel odontodes. A depression is found between the two odontodes; however, it is

unclear if it corresponds to a pore opening. The surrounding odontodes are organized concentrically around this central section (Fig. 15F). The organisation of these odontodes is closer to what is described for *A. prisca* (Young, 1982) and *Doliodus problematicus* (R.C., pers. obs.). Although rare, the occurrence of scales exhibiting this morphotype does not suggest a pathological morphology, but they are too few to be confidently interpreted as sensory pore openings. Their organization may appear similar to the neuromast-protecting scales in thelodonts (Turner, 2004). While the thelodont scales exhibit a symmetrical separation in the crown, the two sections do not re-unite distally, contrary to the *Wellerodus* scale. If there is a pore in the scale, it is completely surrounded by the odontodes.

Morphotype 5, identified in specimen NYSM 19051c, is characterized by a flatter, more rectangular crown ornamented by parallel straight ridges or straight odontodes oriented anteroposteriorly (Fig. 15G). These scales are found in the articulated material that includes morphotype 1 as well as teeth; they confidently belong to *W. priscus*. This type of scales has also been observed in other, undescribed specimens from the site (D. P.-L., R. C., pers. obs.). Localization of these scales on specimen NYSM 19051c would suggest that they occur towards the posterior half of the shark, or at least beyond the first dorsal fin spine. Morphotype 4 is similar to the ventral scales of *Ctenacanthus costellatus* (Reif, 1978; Fig. 1A, B).

Morphotype 6 occurs in specimen NYSM 19052 and corresponds to platelets similar to stellate scales (Fig. 15H). They have not been identified in specimens NYSM 19051a–c and NYSM 19053 but have been observed elsewhere in the field and in still undescribed specimens (D. P.-L., R. C., pers. obs.). They are generally round in shape, thin and flattened, with an elevated central point. Ridges run from the central point towards the margin. The margin is finely crenulated, with crenulations being more numerous than the number of ridges. No specific base has been observed on these scales and they are consequently interpreted as flat. The position of the structures in *W. priscus* cannot easily

be ascertained but the greater concentration of these scales is found dorsal to the pectoral spines. They are generally found isolated, except for a small group on the middle left margin of specimen NYSM 19052 (Fig. 7). This group is probably located dorsally, approximately at the level of the pectoral girdle, and appears organized.

The scales of morphotype 6 are somewhat reminiscent of the mucous membrane denticles seen in *Doliodus problematicus* (Miller *et al.*, 2003; Fig. 2C) but are bigger and not as numerous. In *D. problematicus*, the mucous membrane denticles are inside the mouth and anterior to the neurocranium. The radiating pattern of the *W. priscus* scales is different from the oriented odontodes usually seen in mucous membrane denticles. Given the distinctiveness of these structures and the fact that the function and morphology of mucous membrane denticles is more akin to oral teeth (Butler, 1995), the identification of morphotype 6 as such appears doubtful because of their position and their morphology. Because of their flatness, they cannot be associated to the scales generally described as “stellate” for chondrichthyans. The surface ridges are radiating from a central point, a pattern different from the irregular one found in the rare stellate scales described for *Tamiobatis vetustus* (Williams, 1998; Fig. 6H). The closest scales are some of the head scales from *Obtusacanthus corroconis* (Hanke & Wilson, 2001; Fig. 9C, E), although the relief of the *O. corroconis* scales appears more pronounced. There is a superficial similarity in the morphology with the crown pattern of the head scales of *Polymerolepis whitei* (Hanke *et al.*, 2013; Fig. 2C, D), but the *Wellerodus* scales do not appear to have a base or one that compares to the base of the head scales of *P. whitei*. The crenulated margin has been observed in other chondrichthyan head scales, but in those cases, the radiating crown is either accompanied by a distinct base or by a towering element at the center of the scale (*e.g.* *Lissodus sardiniensis* (Fisher *et al.*, 2010). Similar elements have been documented in Carboniferous iniopterygians. The tuberculated plates found in the buccal cavity of *Sibyrrhynchus denisoni* (Zangerl & Case, 1973) share a comparable radiating pattern, but the marginal crenulation is much more pronounced. The bigger size, the relative number of

similar plates and the position within the animal appears different from the condition in *W. priscus*. Snowflake-like denticles covering parts of the head and the body have been described in *Iniopera richardsoni*, with some occurring in the skin behind the head region (Zangerl & Case, 1973), a position that could be comparable to the greatest concentration of these scales in specimen NYSM 19052.

An anterior transition in squamation appears to be from the anterior to the posterior region of the head. The head appears to be mostly scaleless, although it is unclear if the transition towards a complete scale cover is progressive or abrupt. Few scales were identified in specimen NYSM 19051a, the section most likely to present cephalic elements, while they become slightly more abundant in sections NYSM 19051b (the dorsal fin spine) and NYSM 19051c (the general prepelvic region, also supporting a subsequent transition in scale morphology). Distribution of the scales in specimen NYSM 19052 also supports the transition at the cephalic level, as scales are much more abundant over the pectoral region and become progressively more dispersed and less abundant towards the anterior of the animal.

The “classic” ctenacanthiform scales (morphotypes 1–3) are found in the post-cranial section. Based on specimens NYSM 19052 and NYSM 19053, the bigger body scales are more abundant in the pectoral region, but also in what would correspond to the flanks and back of the animal. Bigger ctenacanth-type scales have been associated with the leading edge of fins in chondrichthyans and acanthodians, it is suggested that this distribution might also be found within *Wellerodus priscus*. The scale patch found between the two pectoral fin spines of specimen NYSM 19053, consequently suggests that these scales were associated with the fin itself. These scales are isolated as opposed to the tissue impression found in association with the dorsal fin spine in specimen NYSM 19051b. One specimen of fin spine preserved with its posterior face upwards, specimen NYSM 19055 (Fig. 15B), has body scales lying inside the posterior concavity. This association is not found in the

similarly positioned fin spines in articulated specimens NYSM 19052 and NYSM 19053 because the spines are covered by organic tissue.

A second transition occurs in the vicinity of the pelvic region towards morphotype 5. No intermediate crown morphotype has been identified so far. This regionalization could be compared to what is observed in terms of regional scale pattern in *Diplodoselache woodi* where rhomboid scales appear at the pelvic level and extend to the caudal peduncle (Hampe, 2003). The pattern of squamation for Paleozoic chondrichthyans consists of simple lepidomoria on the ventral side, scales of moderate complexity on the flanks and highly specialized, compound scales on the dorsal side (Zangerl, 1981). The scales ascribed to the body and the back in *Wellerodus* appear more complex, but clearly morphotype 5 is also more complex than simple lepidomoria.

The scales of *W. priscus* differ from those of *Antarctilamna prisca* by presenting crown with subparallel odontodes rather than semiconcentric ones. The scales demonstrate a regularity that seems more common than what is observed in similar ctenacanth-type growing scales. In *W. priscus*, the odontodes from a same row are generally identical, with little variation in size and length. Most of the scales are symmetrically organized along a longitudinal mid-scale axis. Antarctilamnid scales are similar to those of a wide variety of Devonian chondrichthyans; examples include *Altholepis composita* (Martínez-Pérez *et al.*, 2010) *Gogoselachus lynbeazleyae* (Long *et al.*, 2015a), *Phoebodus rayi* (Ginter & Turner, 1999) and *Tassioliodus lessardi* (Derycke & Goujet, 2011). Additionally, similar scales have been regularly found as isolated microremains in the Givetian of Spain (Liao *et al.*, 2007; Ginter *et al.*, 2008), the Middle Devonian of Antarctica (Burrow *et al.*, 2009), the Frasnian of Australia (Trinajstić & George, 2009) and the Frasnian and Famennian of Iran (Yazdi & Turner, 2000; Hairapetian & Ginter, 2009).

Braincase.—

Cartilaginous elements that could be associated to the cephalic region, if not a neurocranium, are considered to be present in specimen NYSM 19051a and possibly specimen NYSM 19052. In specimen NYSM 19051a, the important concentration of teeth and tooth families suggest that the dispersion was not as important as the one observed in other specimens. Consequently, the associated elements would represent endoskeletal elements of the cephalic region.

The lower part of specimen NYSM 19053 is of interest, as it is superposed over another part of the specimen. This is suggested by an apparent delimitation and the fact that there are no teeth overlying this section, compared to their abundance in the left section of the specimen (Figs. 8, 9).

In specimen NYSM 19053, there are no regions akin to what is observed in specimen NYSM 19051a. Teeth in specimen NYSM 19053 are comparatively disorganized and typical body scales (morphotypes 1–3) are abundant. If specimen NYSM 19051a is a good reference, then fewer scales should be associated with the cephalic region. Consequently, the intense number of scales in specimen NYSM 19052 could be indicative that the neurocranium and jaw elements are missing, leaving us mainly with parts of the branchial apparatus and the pectoral girdle.

The neurocranium is known in both species of *Antarctilamna* (Young, 1982; Gess & Coates, 2015); however, the original interpretation of the neurocranium of *A. prisca* (Young, 1982) was inverted (Hampe & Long, 1999; Gess & Coates, 2015). *A. prisca*, and probably *A. ultima*, present a fairly long otico-occipital region, closer to ctenacanth, rather than the larger, less elongated neurocranium seen in *Doliodus*, a shape that is probably plesiomorphic. Hanke & Davis (2012) described the braincase of *Lupopsyrus pygmaeus* as

broad and depressed and mentioned, citing Janvier (1996), that these are characteristics found in various clades and could therefore be primitive for gnathostomes.

Jaws and visceral arches.—

No cartilaginous elements associated to the jaw or the visceral arches have been identified with certainty in our specimens of *Wellerodus*. A “cleaver”-shaped palatoquadrate is expected since it has been described in *Antarctilamna prisca* (Young, 1982) and *A. ultima* (Gess & Coates, 2015). This shape is also characteristic of certain Paleozoic chondrichthyans, notably those with amphistylic jaw suspension (Zangerl, 1981). In *A. ultima*, ceratohyals are blade-like with a distal tapering, and their length is about two thirds of the length of the Meckel’s cartilage (Gess & Coates, 2015).

As suggested for the neurocranium, jaws and visceral arch elements are most likely preserved in specimen NYSM 19051a but too altered to be identified properly. The abundance of teeth in the lower part of specimen NYSM 19052 and the bottom left section of specimen NYSM 19053 also point towards that region for a potential position of the suspensorium. In both cases, position relative to the pectoral region is also indicative of where to find the elusive jaw-related elements. The situation is complicated in specimen NYSM 19052 by the apparent fracturation of the endoskeletal elements into multiple small pieces.

Pectoral girdle and fins.—

Scapulocoracoids have not been clearly identified yet. Endoskeletal structures of the pectoral fin remain elusive, but in specimen NYSM 19053, a flat, partly rectangular but incomplete endoskeletal plate accompanies the pectoral fin spine preserved in posterior

view (Figs. 8, 9). Part of it is broken and missing, thus limiting the interpretation of its shape and of its association with other elements. Anterior to the right pectoral fin spine in specimen NYSM 19052, there is a sub-rectangular, partly degraded structure in a similar position. It is possible that these structures represent basal elements. A polybasal (likely tribasal) condition is expected in *Wellerodus*, as it is the purported basal condition and that a monobasal condition is considered derived for chondrichthyans (Lund & Grogan, 1997; Coates, 2003; Zhu & Yu, 2009; Pradel *et al.*, 2010; Tomita, 2015); a basal element, either a meso- or a metapterygium, is known in *Doliodus* (Miller *et al.*, 2003). There is also a thin, long and narrow unidentified element at the upper right of the fin spine with its leading edge up in specimen NYSM 19053, but it has not been identified yet.

In NYSM 19052, the greater concentration of cartilaginous elements around the pectoral fin spines corresponds most likely to the pectoral girdle. Given the anatomical position, as indicated by the presence of the pectoral fin spines, it suggested that the immediate region represents a decomposed pectoral girdle and fin endoskeleton. This assumption is supported by the presence of a pectoral fin endoskeleton composed of five radials associated to the left pectoral fin spine (Fig. 12B). These serial elements are linked to the fin spine in a way much similar to the radials in *Acanthodes* (Miles 1973), although their number is greater in *Wellerodus*. These elements might be similar to the posteriorly extended serial elements seen in the pectoral fin of '*Ctenacanthus*' *costellatus*, or simply the radials in the same shark (see Fig. 4 in Coates, 2003).

Compared to clear-and-stained juvenile specimens of *Centroscyllium fabricii* (Émilie Lebel, 2016, unpublished MSc memoir), a striking similar situation is established with a pectoral fin of one of the specimens (#253; total length = 28.2 cm). The *C. fabricii* specimen shows an unmineralized pectoral fin endoskeleton, while a series of radials are mineralized. This ontogenetic condition could be compared to the condition observed in *Wellerodus* (specimen NYSM 19052) (Fig. 16). If the *Wellerodus* specimens are juveniles,

and hence incompletely mineralized, this could be an alternate explanation for the presence of a preserved series of radials without evident basal plates.

Pelvic girdles.—

The pelvic region is unknown beyond the identification of the small prepelvic spines suggested in specimen NYSM 19051c. Shapeless organic material associated with scales and a thick plate are located at the right of the prepelvic fin spines (Fig. 5). A similar thick plate is seen in association with other spines, including one fin spine interpreted as paired and probably pectoral in specimen NYSM 19054. These thick plates in the vicinity of the prepelvic fin spines could potentially be interpreted as the pelvic girdle; chondrichthyan pelvic girdles are basically a pair of plates (Zangerl, 1981). The posterior half of other older chondrichthyan articulated material (*i.e.*, *Doliodus*, *Pucapampella* and *Antarctilamna*) is unknown while little is known about the pelvic girdle of *Gladbachus* (Heidtke & Krätschmer, 2001). Similar elements, in terms of relative size and shape, are found in younger forms such as in stethacanthids (Lund, 1985) and in *Akmonistion* (Coates & Sequeira, 2001). The foramen usually present in the middle of the pelvic basal plate has not been observed in the thick plates of *Wellerodus*. The plesiomorphic pelvic girdle in chondrichthyans is presented as a small triangular element that is not fused to its contralateral counterpart (Lund & Grogan, 1997).

Median fins.—

Knowledge of the dorsal fins is sparse given that the dorsal fin spines are often found isolated. Fossilized tissue associated with the dorsal fin spine of specimen NYSM 19051b is identified as part of the dorsal fin web (Fig. 4). The area is composed of disorganized

organic matter with a few scattered scales of morphotype 1. The fin web is connected to the fin spine at the point where the posterior cavity of the spine closes, indicating that the distal part of the fin spine would have been free from the median fin web. No radials are found in association with the fin web.

Cartilage.—

The nature of the cartilage of *Wellerodus priscus* remains unclear although it is assumed that it is a prismatic calcified cartilage as in other chondrichthyans. There is no region of the prepared specimens displaying tessellated mineralization. The cartilage seems to be composed of small blocks (<0.5 mm) juxtaposed against each other. Tessellated mineralization is known in older and coeval chondrichthyans, including the *Antarctilamna prisca*. Two braincases attributed to *A. prisca* were considered as possibly showing prismatic calcified cartilage, based on the observation of fine ridges (Young, 1982; Text-fig. 6; Maisey, 2013). In *A. ultima*, the specimens were preserved as a whitish clay infilling the compressed lower and upper impressions of the specimens (Gess & Coates, 2015). Original endoskeletal tissue was dissolved, hence the impossibility to confirm the presence of any type of cartilage mineralization (Gess & Coates, 2015). There is clear evidence, in *D. problematicus*, of prismatic calcified cartilage (Miller *et al.*, 2003; Maisey, 2013). However, Burrow *et al.* (2016) suggested that the cartilage found in *Doliodus* is closer to the acanthodian tessellated cartilage than to the clear polygonal organization of elasmobranchs and younger chondrichthyans. There are also reports of prismatic calcified cartilage in *Pucapampella* (Maisey & Anderson, 2001; Maisey, 2013). The cartilage observed in *W. priscus* is superficially similar to the globular calcified cartilage found in acanthodians such as *Climatius reticulatus* (Burrow *et al.*, 2015) and putative chondrichthyans such as *Seretolepis elegans* (Hanke & Wilson, 2010).

1.7 DISCUSSION

This description of articulated specimens of *W. priscus* has yielded extensive information on intraspecific and intraindividual variation in tooth morphology and organization, obscuring the distinction between *Wellerodus* and *Antarctilamna*. Fin spines have been described for *W. priscus*, making it the second unambiguous case of pectoral fin spines in a chondrichthyan. Prepelvic fin spines have also been described, as well as the differences in morphology among the three types of fin spines. A qualitative description of the variation in scale morphology has been provided (five morphotypes), as well as regionalisation in the squamation. The relevance of these new data is demonstrated by providing a more evident transition between some acanthodians, putative chondrichthyans and early Paleozoic sharks. Further investigation of the endoskeleton is compromised by the poor state of preservation of the specimens, although this consequently fuels reflection on the paleobiological implications of this, notably in the context of evaluating the Cairo specimens as juveniles. Conceptually, our paper follows on the conclusions of Hanke & Wilson (2010).

1.7.1 Diplodont teeth in Devonian chondrichthyans

Many Early and Middle Devonian chondrichthyans, including taxa known from isolated teeth, have been compared to antarctilamnids, suggesting that the diplodont morphology is common in early chondrichthyans, or at least more typical than the other known morphologies (Ginter, 2004; see *Mcmurdodus whitei* (Burrow *et al.*, 2008) and *Protodus jexi* (Turner & Miller, 2008)). The most ancient known chondrichthyan teeth belong to *Leonodus*, a taxon that has been interpreted as basal relative to *Antarctilamna-Wellerodus* (Ginter, 2004; Ginter *et al.*, 2010). While it shares with antarctilamnids a

diplodont crown with cups covered with striae, it differs by the shape of the base and the absence of intermediate cusps, although the tricuspid specimen figured in Ginter *et al.* (2010; Fig. 20 E, F) looks like an antarctilamnid tooth, apart from the bi-bulbous oral side of the base. Closeness to antarctilamnids has also been suggested for *Doliodus* despite its quite distinct labially oriented tooth base. The labially-oriented tooth base has been considered as a distinct character to warrant the existence of the Omalodontidae, as defined by Ginter *et al.* (2008; 2010), although doubt has been raised regarding the monophyly of this group (Ivanov & Rodina, 2004; Ivanov *et al.*, 2011). *Doliodus* shares crown characters with *Antarctilamna* and *Wellerodus* (Turner, 2004). Known histology yields an orthodontine structure, with a thin layer of enameloid (Turner, 2004). This is somewhat different from *Antarctilamna*, but the importance of this difference depends on the absence (Hampe & Long, 1999) or the presence (Burrow *et al.*, 2009) of an outer layer of enameloid on the crown. The organic histological components are otherwise relatively common in Paleozoic sharks (Zangerl, 1979; Hampe *et al.*, 1999).

Teeth of the Givetian *Karksiodus mirus* from Estonia (Ivanov *et al.*, 2011) and northwestern Russia (Ivanov & Märss, 2014) present a crown organisation similar to those of antarctilamnids, with two main lateral cusps and one median, smaller cusp. Specimens with intermediate, although asymmetrically positioned intermediate cusps have also been described (Ivanov & Märss, 2014). Other similarities with the *Antarctilamna-Wellerodus* include the histology of their cusps, which compares to the data published by Burrow *et al.* (2009). *K. mirus* differs from other coeval chondrichthyan teeth by its arched base without labial or lingual extensions, the presence of a single encapsulated basal canal and the very fine and dense striation of the cusps.

Tassiliodus lessardi (Derycke & Goujet, 2011), an Emsian chondrichthyan from Algeria, is an important tooth taxa that fills a geographical gap in the paleobiogeography of Early and Middle Devonian chondrichthyan, notably given the suggested presence of

antarctilamnids, or related taxa, along the coast of Northern Gondwana (Potvin-Leduc *et al.*, 2015). It is characterized by a general crown morphology similar to antarctilamnids, in that the teeth present two main lateral cusps with one median, smaller median cusp. The teeth also possess intermediate cusplets between the median and the laterals; contrary to antarctilamnids, the intermediate cusplets are not on the same plane as the main and the median ones. Number of intermediate cusplets in the available specimens can be higher than in antarctilamnids (five in *T. lessardi*) and they are asymmetrically distributed. The cusps lack striae which differs from antarctilamnids. Some of the associated scales also present morphological similarity to the scales of *Wellerodus* (Derycke & Goujet, 2011: Fig. 6D). Other scales seem to present the flat crown with straight ridges organization (mostly Fig. 6) while others display crown morphology similar to the stellate scales but differ by the presence of a base. The scales associated to *T. lessardi* by Derycke & Goujet (2011) display important variation, providing more evidence that early chondrichthyans can possess a diverse squamation, just as is seen in *W. priscus*.

The diplodont crown appears to have spread during the Early and Middle Devonian, hinting at a period of evolutive fine tuning over a basic diplodont design. Finding diplodont teeth within chondrichthyans characterized by basal gnathostome apomorphies (i.e., paired fin spines in *Doliodus*, *Wellerodus* and possibly *Leonodus*) argues in favour of this being the basal tooth design for chondrichthyans (Ginter, 2004). *Wellerodus* also demonstrates the presence of shark-like tooth families in basal chondrichthyans.

1.7.2 The case of *Ctenacanthus wrighti*

When describing the fin spines of *A. prisca*, Young (1982) noted the similarities between them and the North American fin spines identified as *Ctenacanthus wrighti*. *C. wrighti* was initially described by Newberry (1884), but later excluded from *Ctenacanthus*;

while similar, differences in ornamentation were considered sufficiently important to warrant the exclusion (Maisey, 1981; 1984b). “*Ctenacanthus*” *wrighti* has not been reaffiliated to any taxa, but Turner (1997) mentioned that the fin spines affiliated to this taxon were found within the same horizon as *Wellerodus priscus*. She suggested that their affiliation to *Wellerodus priscus* should be seriously considered and investigated, a point also supported by Ginter *et al.* (2006).

The original description of “*C.*” *wrighti* is based on the apical part of a spine (Newberry, 1884). The spine of “*C.*” *wrighti* is straight with an angular cross-section and straight ridged ribs. The holotype came from the Moscow Shale, in the Hamilton Group, New York State, making it contemporaneous to *W. priscus* (Newberry, 1884). The spine, with a 5-cm wide base, is much bigger than the fin spines found at Cairo. The anterior margin of “*C.*” *wrighti* is straight and the spine is laterally compressed; there is a posterior cavity, opened up to the middle of the spine. The fin spines are ornamented with pectinated ridges that are almost of uniform width. They become narrower and less distinctly pectinated near the posterior margin. When compared to the *Wellerodus* from Cairo, these characters could easily describe a *W. priscus* median fin spine. In the illustration of Newberry (1884), the organisation and overall morphology of the odontodes could correspond to what is observed in antarctilamnids. The Cairo specimens, in confirming the presence of fin spines in *Wellerodus*, makes it even more possible that the association suggested by Turner (1997) and Ginter *et al.* (2006) is correct. Reappraisal of the “*C.*” *wrighti* material is necessary to determine if its characters correspond to the characters of *Wellerodus*, which, if they do, should lead to the renaming of “*C.*” *wrighti*.

1.7.3 Comparison of fin spines within antarctilamnids

Following the description of *Doliodus problematicus*, it was suggested by Miller *et al.* (2003) that *Antarctilamna prisca* had pectoral fin spines. *A. prisca* was initially characterized as possessing two dorsal fin spines, although only one fin spine was associated with the holotype (Young, 1982). Given the lateralized position of the fin spine relative to the head on the holotype (CPC 21187; Young, 1982) and its similarity with what was observed on the articulated specimen of *Doliodus problematicus*, Miller *et al.* (2003) suggested that the fin spine from the holotype might represent a pectoral spine rather than a dorsal fin spine. The specimen of *Antarctilamna ultima*, from South Africa, has only one fin spine, interpreted as a dorsal fin spine (Gess & Coates, 2015). In their South African material, Gess & Coates (2015) found no evidence in favor of fin spines being positioned in front of the pectoral fins. While we accept the dorsal fin spine interpretation, we believe that the current material might be insufficient to conclude on the absence of pectoral fin spines in *A. ultima*.

Given the organization of the fin spines in *W. priscus*, we cannot provide further evidence to corroborate or not Miller *et al.*'s (2003) interpretation. Fin spines found in similar position in *W. priscus* are interpreted as dorsal; however, the studied specimens appear to be preserved in lateral position, *contra D. problematicus* and *A. prisca* which are preserved dorso-ventrally. Presence of pectoral fin spines in *W. priscus* could imply their presence in *A. prisca*, but since they might be absent in *A. ultima*, the final implications for diagnosis purpose remain to be determined. The spines described by Young (1982) present variation related to their insertion zone, some being almost inexistent (Young, 1982; fig. 5), while in others being more extensive (Young, 1982; Pl. 87, fig. 3). Young (1982) suggested that this variation was position-related, with the longer insertion zone associated to the second dorsal fin (probably due to the fact that the fin spine of the holotype is close to the head while presenting almost no insertion zone). This variation was noted and reinterpreted

by Wilson *et al.* (2007) and restated by Hanke & Wilson (2010), where the authors suggested that the spines with shallow insertion were paired while the deeper inserted ones would be median. Based on *W. priscus*, we agree with their hypotheses.

Based on our description of *W. priscus*, we consider that it will be worth re-evaluating *A. prisca*. These points follow, and mostly agree, with prior conclusions by Hanke & Wilson (2010). *W. priscus* clearly shows that the presence of paired fin spines is possible in antarctilamnids. The spines of *W. priscus* present a different morphology depending on their position, where the paired spines are characterized by a slightly shorter insertion zone compared to the dorsal spines. We believe that possible differences in fin spine morphology could be indicative of their body position and, as such, would warrant a re-evaluation of the fin spines ascribed to *A. prisca* so as to determine if the observed variation is indicative of topographical position (Wilson *et al.*, 2007; Hanke & Wilson, 2010) rather than disparity among species (Gess & Coates, 2015).

Isolated fin spines, mainly from Gondwana, have been tentatively attributed to antarctilamnids since the initial description by Young (1982). Fin spines from the Eifelian of Iran described in Blieck *et al.* (1980) were reinterpreted as *Antarctilamna* by Young (1989, 1991). They were originally described as ornamented similarly to *Ctenacanthus*, but differing from it by the rounded anterior edge. The published picture of the fin spine is small (Blieck *et al.*, 1980; Pl.1, fig. 20), but reveals a fin spine that, apart from a close-up examination of the ornamentation, looks much like *W. priscus*. It is interesting to note that the fin spine shows the slender look of *W. priscus* rather than the short, broad morph of *A. prisca*.

Other chondrichthyan fin spines are in need of reinterpretation. We suggest that the Venezuelan fin spines attributed to ?antarctilamnid gen. et sp. indet. by Young & Moody (2002) should officially be considered as an antarctilamnid. With the information on *Wellerodus*, the described fin spines present the required diagnostic features. As two

morphotypes were identified, we propose that the Venezuelan material is composed of both pectoral and median fin spines rather than variation of the median spines. One more time, the variation seems to take into account the presence or absence of an insertion zone and possible curvature of the anterior edge. We propose that the curved fin spines, such as MBLUZ P-5 (Young & Moody, 2002; Figs. 14B, 15A) are pectoral fin spines. The other morphotype, represented by MBLUZ P-7 (Young & Moody, 2002; Fig. 14A) is highly similar to the *Wellerodus* specimen NYSM 19057 (Fig. 13A). This specimen could consequently be considered as a median fin spine. Of interest is that they might be positioned somewhere between *Antarctilamna* and *Wellerodus* in their details – the general shape is more like *Wellerodus*, but absence of retrorse denticles is more akin to *Antarctilamna*. One major difference takes into account the width of the ridges. In the Venezuelan material, they are described as thinner towards the anterior edge, while the condition is the opposite in the Cairo *Wellerodus* material (Figs. 12C, 13B) and in *A. prisca* (Young, 1982) and *A. ultima* (Gess & Coates, 2015).

Furthermore, it is suggested that the chondrichthyan fin spine described by Maisey & Melo (2002; Fig. 2) from the Eifelian–Givetian Pimenteira Formation, in Brazil, belongs to antarctilamnids and is likely affiliated to *Wellerodus*. It is reinterpreted here as a pectoral fin spine, thus reflecting a hypothesis considered by Maisey & Melo (2002). The Brazilian spine, while not perfectly preserved, is ribbed with a possible pectinate ornamentation, akin to antarctilamnid ornamentation. The general shape of the spine, with the gentle distal curvature, and the posterior row of retrorse denticles reunite in a specimen almost identical to the pectoral fin spine of specimen NYSM 19052 preserved in a similar position. The bicuspid tooth recovered in the vicinity of the fin spine, while incomplete and not attributable with certainty, was compared to the teeth of *Antarctilamna*. While the tooth appears to be lacking a median cusp, sufficient variation has been documented to consider the possibility of an antarctilamnid tooth devoid of its median cusps. The antarctilamnid

affiliation is also supported by the description of a fragmentary fin spine from the same formation that presents ornamentation similar to antarctilamnids (Janvier & Melo, 1992).

1.7.4 Fin spines in chondrichthyans, putative chondrichthyans and acanthodians

Antarctilamnid fin spines have been compared to ctenacanth fin spines and share with them a similar ornamentation (Young, 1982). Based on Maisey (1981), antarctilamnids share with some ctenacanths the crenelated ridges, but in the latter the ridges are usually thinner and denser than in *W. priscus* and *Antarctilamna*. The large insertion zone of ctenacanth fin spines is absent in antarctilamnids. The presence of the leading edge pattern in ctenacanth fin spines is difficult to evaluate as they are often preserved in lateral views. It can, at least, be clearly distinguished from fin spines presenting a main ridge running along the leading edge, as in *Eunemacanthus costatus* (Maisey, 1982). Ctenacanth fin spines often present two rows of posterior denticles towards the tip of their dorsal fin spines. These rows are absent in dorsal fin spines of *Antarctilamna* and *Wellerodus*. Although a posterior row of denticles can be seen in fin spines of *Wellerodus*, this row is single and found on pectoral fin spines, which are absent in ctenacanths.

In *Doliodus*, the ornamentation of the pectoral fin spines is different from that of antarctilamnids (R. C., pers. obs.). The insertion zone is also more extensive. The left pectoral spine of *D. problematicus* has no posterior or trailing edge of denticles, but a spine near the posterior of the specimen presents denticles (Burrow *et al.*, 2008). In their phylogenetic matrix to evaluate the status of acanthodians, Burrow *et al.* (2016, character 258) coded for the presence of a posterior row of denticles in *Doliodus*. The fin spines identified as *Climatius latispinosus* from the Campbellton Formation, New Brunswick (Canada), have been suggested to belong to *Doliodus* because they are often found in association with *Doliodus* teeth and scales (Miller *et al.*, 2003; Maisey *et al.*, 2009). The

resolution of this question will be of interest, given that some fin spines referred to *C. latispinosus* are characterized by a single row of posterior denticles.

Two different morphotypes of fin spines have been assigned to *Leonodus* (Soler-Gijón & Hampe, 2003). Both are characterized by ornamentation similar to ctenacanth. One of the morphotypes is slender and curvier, with a relatively large insertion zone, while the other is straighter and broader with a poorly developed insertion zone. All spines are described as bearing a row of posterior denticles. The presence of denticles differs from the *Antarctilamna* material but is similar with the pectoral fin spines of *W. priscus*. Further data on *Leonodus* will be of essential to the comprehension of early chondrichthyan relationships.

Some of the fin spine characters described in *Wellerodus* are also observed in some acanthodians and putative chondrichthyans. The fin spines of the Lower Devonian acanthodian *Lupopsyrus pygmaeus* (Bernacsek & Dineley, 1977; Hanke & Davis, 2012) are characterized by a superficial insertion, a posterior row of denticles on the pectoral fin spines and a ridge pattern on the spines that is generally similar to *Wellerodus*, albeit the angle with the leading edge is more acute in some specimens. They differ from antarctilamnid spines by the presence, at the base of the spine, of short, incomplete ridges. The ridges in *L. pygmaeus* are also wider and coarser. The insertion zone is shallow and appears more pronounced in the median fin spines. The similarities between the fin spines of *Wellerodus* and *Lupopsyrus* suggest the existence of a basal pattern in fin spines.

The pectoral fin spines of the Early Devonian *Lupopsyroides macracanthus* and *Obtusacanthus corroconis* are described as having ridges that converge toward the leading edge (Hanke & Wilson, 2004), although it is unclear whether they connect alternatively at the leading edge. In *L. macracanthus*, the pectoral fin spine is also characterized by four posterior tubercles towards the tip. The fin spines of *Seretolepis elegans* (Hanke & Wilson, 2010) present an organisation of the ridges and ornament that superficially recalls what is

seen in *Wellerodus*. However, the ornamentation is not as delicate as in *Wellerodus* and the nodes are smooth and unornamented. Retrorse pectoral fin spine denticles are also known in the Early Devonian *Vernicomacanthus* (Newman & Davidson, 2010).

The two species of the Early Devonian *Ankylacanthus*, *A. incurvus* and *A. convexus* (Burrow *et al.*, 2008), have fin spines with a posterior row of denticles, but the pattern of ridges, apart from the leading edge alternate connecting, differs from *W. priscus* by the wide space separating each ridges. The angle of the ridges with the leading edge is also much more pronounced in *Ankylacanthus*. *Ankylacanthus* is described as having one posterior row of denticles and “protoctenacanth” ornamentation (Burrow *et al.*, 2008). Similarity between the spines of *Ankylacanthus* and *Doliodus* raise the possibility that *Ankylacanthus* could be a stem chondrichthyan, but the ossified scapulocoracoids of *Ankylacanthus* are not representative of chondrichthyan pectoral girdles (Burrow *et al.*, 2008). Burrow *et al.* (2008) place *Ankylacanthus* in acanthodians because of the similarities with the younger Gyraacanthidae. *Ankylacanthus* was not included in the phylogeny of Burrow *et al.* (2016), but given the recent discoveries and research, shared characters between some acanthodians and basal chondrichthyans strongly suggest a stem chondrichthyan position for *Ankylacanthus*.

The pectoral fin spines of the Late Devonian acanthodian *Diplacanthus ellsii* bear rows of denticles on the lateral margins of the distal two-thirds of the spine. The insertion zone is short contrary to the dorsal, and one specimen shows a fin web that ends where the denticles begin (Gagnier, 1996). All the spines, except the intermediate ones, have two to four grooves on each side. In the Late Devonian *D. horridus*, the pectoral fin spines bear two rows of posterior denticles that originate near the inserted part (no fin web is apparent). Insertion zone appears shallower in the pectoral fin spines than in median fin spines (Gagnier, 1996). The diplacanthids from the Middle Devonian of Scotland were recently revised by Burrow *et al.* (2016). In *D. crassisimus*, only the pectoral fin spines bear two

rows of posterior denticles. The prepelvic fin spines have no insertion zone and differ from the median and pectoral fin spines by being broad and flat proximally; their ornamentation is otherwise similar to what is observed on the other spines. A double row of posterior denticles is also found on the pectoral fin spines of *D. tenuistriatus* (Burrow *et al.*, 2016).

If acanthodians, or at least some of them, are indeed stem chondrichthyans, the presence of a posterior row of denticles could be plesiomorphic (if found in other basal chondrichthyans). The apomorphic condition would correspond to either the absence of posterior rows of denticles, as in *Antarctilamna* and other sharks, or the double row observed in certain ctenacanth and xenacanth. In Burrow *et al.* (2016), *Lupopsyrus* is considered to be basal to the chondrichthyan lineage. Although the gyracanthid *Ankylacanthus* is not included in the phylogeny presented by Burrow *et al.* (2016), the gyracanthid *Gyracanthides* is nevertheless closely related to chondrichthyans.

Paired pectoral fin spines were previously known in chondrichthyans only through the articulated specimen of *D. problematicus*. The presence of pectoral fin spines had also been suggested for *A. prisca* (Miller *et al.*, 2003, Wilson *et al.*, 2007, Hanke & Wilson, 2010), although they have not been described for *A. ultima* (Gess & Coates, 2015). Paired fin spines were otherwise unknown in early chondrichthyans, but with the added evidence of this character in *W. priscus*, it appears as if their presence should be strongly considered in early chondrichthyans. Prepelvic fin spines are considered plesiomorphic for acanthodians; they are also present in putative chondrichthyans from the Mackenzie Mountains (Hanke & Wilson, 1998; 2004). Their presence in *W. priscus* hints at this character being plesiomorphic for the clade acanthodians + chondrichthyans, supposing a close relationship between the two groups.

1.7.5 Taxonomic implications and the quest for the basal chondrichthyan

While some evident characteristics distinguish *W. priscus* from *Antarctilamna ultima*, a possible distinction at the generic level will depend on the presence or absence of pectoral fin spines in *A. prisca*. The presence of prepelvic fin spines in *W. priscus*, associated with paired fin spines, and, as far as is known, their absence in *A. prisca*, could indicate a deeper separation between the two, or at least hint at *Antarctilamna* being derived. Congruous with these reflections is the question regarding whether or not the Cairo material is conspecific with the other material described and revised by Turner (1997). There are arguments for uniting both; notably, the effort to limit the number of potentially “false” species erected from material ultimately belonging to the same taxa or susceptible to ontogenetic transformation. Since there are peripheral arguments for suggesting that the studied Cairo specimens of *Wellerodus* are juveniles, caution is even more relevant.

In Ginter *et al.* (2010), teeth from western New York State are presented as *Antarctilamna*, while others, also from New York State, are identified as *Wellerodus*. According to Ginter *et al.* (2010), the button of the teeth of *Wellerodus* is more prominent, although it occupies a smaller oral-lingual area than in *Antarctilamna*. The median cusplet can be higher in *Wellerodus* than in *Antarctilamna*. In most cases, intermediate cusplets are absent in *Wellerodus*. However, the Cairo material demonstrated that absence and presence of intermediate cusplets occur within the same dentition. Size ranges overlap, but *Wellerodus* can be bigger than *Antarctilamna* (Turner, 1997; Ginter *et al.*, 2010). Within the articulated specimens of *Wellerodus*, we have documented sufficient intra-individual variation that covers the supposed criteria to distinguish *Antarctilamna* and *Wellerodus*, implying that both morphotypes described by Ginter *et al.* (2010) occur within the same individual. Our data suggests that “diagnostic” tooth characters as currently defined cannot discriminate between both genera, further arguing, along the lines of Ginter (2004) and Ginter *et al.* (2006; 2010) that *Antarctilamna* and *Wellerodus* are synonymous. We suggest

that specific distinction might exist, but at the level of the whole dentition when considering the prevalence tooth morphotypes, implying that specific diagnosis based on teeth would require articulated, or at least almost-complete, material.

The proposed synonymy between the two genera and their diagnoses as currently defined do not cover characters that have otherwise been observed as divergent between the two genera. While in both genera the scales are compound, of the ctenacanth type, with a cup-shaped base, the semi-concentric and flatter organization of the odontodes appears to be characteristic of *Antarctilamna*, with *Wellerodus* being characterized by sub-parallel odontodes. While distinction is evident when comparing the scales of the holotype of *Antarctilamna* (Young, 1982) with the scales of *Wellerodus*, a possible overlap in crown morphology variation must be considered. The scales of the Elasmobranchii indet. fam. gen. et sp. A of Burrow *et al.* (2009) are closer to the typical *Wellerodus* body scales than the typical *Antarctilamna* scales. Crowns similar to that of *Antarctilamna* are known in Paleozoic taxa, such as in *D. problematicus* (Miller *et al.*, 2003), *L. carlsi* (Botella *et al.*, 2005), *Polymerolepis whitei* (Hanke *et al.*, 2013), *Seretolepis elegans* (Hanke & Wilson, 2010) and isolated ichthyoliths (e.g., Forey *et al.*, 1992). The ctenacanth-type ornamentation remains common and is probably influenced by hydrodynamic adaptation (Fletcher *et al.*, 2014).

Fin spines might provide the best evidence for a possible distinction at the generic level. Such distinction might be achieved on the basis of the presence of paired fin spines. *A. ultima* is described as lacking pectoral fin spines while their presence remains possible in *A. prisca*. However, the presence of prepelvic fin spines in *W. priscus* might provide more ground for generic distinctiveness as it may well yield more phylogenetic significance. The impossibility to establish endoskeletal comparisons due to the state of preservation of the articulated *W. priscus* material makes it difficult to assess whether more differences among *A. prisca*, *A. ultima* and *W. priscus* could lead to a distinction at the generic level. Since

there are sufficient elements to consider the possibility that the Cairo material belongs to juvenile individuals (see below), the possible distinctions beyond size changes that would exist between a juvenile and an adult *W. priscus* must also be taken into account. As the importance of these characters cannot be clearly evaluated, we cannot invalidate the synonymy of *Antarctilamna* and *Wellerodus*.

1.7.6 Phylogenetic implications

The first contribution of *Wellerodus priscus* to our understanding of basal chondrichthyans consists of the presence of paired fin spines, suggesting that their presence in *Doliodus problematicus* was not a random, eclectic evolutionary case while adding an argument to paired fin spines being, if not a basal gnathostome character (Grogan *et al.*, 2012), at least a basal chondrichthyan character. This evidence also tends to support a basal association between acanthodians and chondrichthyans, as suggested in recent works (Zhu *et al.*, 2013, Dupret *et al.*, 2014; Brazeau & de Winter, 2015; Giles *et al.*, 2015; Long *et al.*, 2015b, Burrow *et al.*, 2016, Qiao *et al.*, 2016, Chevriniais *et al.*, 2017, Larouche *et al.*, 2017).

When *Antarctilamna* was first described, Young (1982) considered a phylogenetic relationship with xenacanthid based on its bicuspid teeth. *Antarctilamna* was consequently considered as part of the xenacanth total group in Maisey (1984a), while Lund (1985) considered it as basal to all chondrichthyan clades with the exception of *Hybocladodus*. Mader (1986) proposed that all chondrichthyans with the exception of *Leonodus* emerged from stem Xenacanthiformes. This included *Antarctilamna* whose position, although uncertain, was suggested as being basal to *Phoebodus* and the other derived chondrichthyans. Long & Young (1995) presented *Antarctilamna* as belonging to a group of stem xenacanth alongside *Leonodus* and *Diplodoselache*. The position of the latter two

taxa was uncertain but suggested as falling between *Antarctilamna* and the crown group xenacanth. Janvier (1996) reconstructed *A. prisca* along the lines of *Diplodoselache woodi*, the most basal of the xenacanth; it was still considered as belonging to the Xenacanthiformes. While *D. woodi* still occupies the same position within xenacanth (Hampe, 2003), it is no longer considered a good proxy for the reconstruction of *Antarctilamna*. The original reconstruction of *A. prisca* has thus been invalidated (Hampe & Long, 1999; Hampe, 2003) because the reconstruction included elements from two different taxa (*Antarctilamna*'s braincase, distinct from the xenacanth ones, and the fin spine, which is closer to the ctenacanth). Hampe & Long (1999) proposed *Antarctilamna* as basal to *Diplodoselache* and other xenacanth. Their rejection of *Antarctilamna* as a xenacanthid was based on the variable number of intermediate cusplets on the teeth, the differences of ornamentation type for the fin spines, and neurocranial characters that did not fit a xenacanthid model. Hampe & Long (1999) considered the possibility that *Antarctilamna* could be a basal phoebodontid. Hampe (2003) rejected that *Antarctilamna* was related to xenacanthids, suggesting a sister group relationship with *Adamantina*. Soler-Gijón & Hampe (2003) presented *Antarctilamna* as belonging to a still undefined group of basal chondrichthyans that included *Leonodus*. Ginter (2004) suggested a phylogenetic scenario where the *Antarctilamna-Wellerodus* group is positioned at the base of chondrichthyans, between *Leonodus* and the remaining chondrichthyans. Characters that are absent in *Antarctilamna-Wellerodus* but present in phylogenetically derived taxa concern the cusps: the loss of the sigmoidality and labio-lingual compression. The same scenario is presented in Ginter *et al.* (2010), who position Antarctilamniformes towards the base of their scenario of tooth morphology evolution, beyond *Leonodus* and before Phoebodontiformes, Cladodontomorphi and Euselachii. In their phylogeny, the Antarctilamniformes follow the Omalodontiformes (although their position remains uncertain, owing to the uncertainty about their monophyly) and are the sister group of all

the other chondrichthyans. The *Antarctilamniformes* are characterized by the apparition of the primitive tooth base and the diplodont crown.

Many acanthodians and putative chondrichthyans that were positioned as stem chondrichthyans by Burrow *et al.* (2016; *Gyracanthides*, *Lupopsyrus*, *Obtusacanthus*, *Kathemacanthus* and *Brochoadmones*) share some characters with *Wellerodus*; many of these characters are related to fin spine position and characteristics. This stem, in all their analyses, include *Lupopsyrus*, but also *Pucapampella* as the sister group to all other chondrichthyans. *Pucapampella* is consistently basal to all other chondrichthyans. *Doliodus* and *Tamiobatis* are sister groups. Diplacanthids are resolved in all their trees in the branch that diverges from the lineage leading to chondrichthyans, possibly discriminating between the numbers of rows of retrorse denticles on the pectoral fin spines, with the single row are associated to the chondrichthyan lineage.

1.7.7 Speculations on chondrichthyan origin and distribution path

Hypotheses on chondrichthyan geographical origin have fluctuated with the discoveries of stratigraphically older chondrichthyan taxa. *Antarctilamna* suggested Gondwana as an important region for early chondrichthyan evolution, an assumption that would have been further supported by the *Pucapampella* material. The discovery of *Doliodus problematicus* led Miller *et al.* (2003) to suggest a Laurentian origin. The implications of the newly described characters of *Wellerodus priscus* helps in suggesting a new hypothetical biogeographical trajectory.

One of the most important contributions of our study of *Wellerodus* is to establish tentative new links between the putative chondrichthyan fauna from MOTH and the more “elasmobranch-like” remains found along the southern coast of Laurentia and the northern coast of Gondwana. Based on the Early Devonian *D. problematicus*, it is obvious that

elasmobranch characters (e.g., diplodont teeth, ctenacanth-like scales) evolved early during chondrichthyan evolution. Ctenacanth-like scales are a relatively common occurrence in various early chondrichthyans and, as previously mentioned, many of those are found in association, if not directly related, to diplodont teeth. In describing another taxa with pectoral fin spines, but also prepelvic fin spines, we further consolidate the existence of a plurality of early chondrichthyan taxa (already comprising *Doliodus* and quite probably *Leonodus*) displaying intermediate characters between crown chondrichthyans and a group formed by acanthodians and putative chondrichthyans

If a phylogenetic link is established between *Wellerodus* and the putative chondrichthyans from MOTH, this may lead to the consolidation of a biogeographical road of dispersal and evolution. Putative chondrichthyans would have developed in Laurussia, before dispersing towards the Tethys Ocean where an event of emerging “sharkness” would have occurred, as exemplified by the presence of various chondrichthyan remains sharing histological and morphological similarities with other early chondrichthyans such as *D. problematicus* and antarctilamnids on the Laurentian and Gondwanan shores of Tethys; this is also exemplified by our knowledge of antarctilamid distribution (Potvin-Leduc *et al.*, 2015). Finally, important morphological similarities between *Wellerodus* and *Doliodus*, two taxa attributed to two distinct orders, could potentially suggest a closer relationship between the two (*i.e.*, the basal shark *Baiüplan*) and support the paraphyly of the Omalodontidae.

1.7.8 Paleobiological reflections based on taphonomical considerations

Interpretation of the *Wellerodus* specimens was complicated by the state of preservation of the specimens. Although some of the specimens were almost complete and articulated or partly articulated, anatomical description of internal skeletal elements was

blured by the state of preservation. Clear limits of endoskeletal elements are rare and incomplete. In addition, clear limits seem to delimitate discrete elements within specific body regions where larger endoskeletal elements are expected. Hypotheses regarding this situation concern the nature of the endoskeleton and the ontogenetic stage of the shark. We propose that the discovered specimens of *Wellerodus* at Cairo are juveniles.

Chondrichthyans are phylogenetically characterized by the presence of prismatic mineralized cartilage (Maisey, 1986; Grogan *et al.*, 2012), a tissue that might easily lose its cohesiveness during decay (Schaeffer, 1965; Allison, 2001). As the mineralized layer is composed of a mosaic of tesserae, decomposition will lead to the separation of these units. However, it has often been possible to identify with confidence the main endoskeletal elements in the rare articulated specimens, namely parts of the head and pectoral girdle region. The state of preservation of *W. priscus* is comparable to the one observed in certain acanthodians, such as in articulated specimen of *Nostolepis scotica* (Burrow & Turner, 2010), *Climatius reticulatus* (Burrow *et al.*, 2015), *Seretolepis elegans* (Hanke & Wilson, 2010) and other specimens from the MOTH locality (M. V. H. Wilson, pers. comm.). In these cases, the main endoskeletal tissue consists of globular calcified cartilage.

Tesserae are made of both globular calcified and prismatic calcified cartilage (Dean & Summers, 2006). Since there is a gradation within tesserae from the globular cartilage of the inner surface to the prismatic calcification of the peripheral surface, it has been suggested that this might reflect ontogenetic stages of tissue mineralization (Dean & Summers, 2006). Could the endoskeleton of *W. priscus*, although mineralized, not be prismatic, either as an apomorphy of that species or as a consequence of the ontogenetic stage of the individuals when they died? The complete absence of prismatic calcified cartilage in a chondrichthyan, such as *Wellerodus*, would be surprising, as many other traits point to the shark-like status of *W. priscus* (e.g., the chondrichthyan-style organization of the teeth, the organization of the fin spines, the squamation). But as suggested by Burrow *et*

al. (2016) regarding the cartilage of *Doliodus problematicus*, it might be necessary to consider that the presence of prismatic calcified cartilage might not be a *sine qua none* condition in basal chondrichthyans.

In the Cairo specimens, cartilaginous structures often appear torn apart. While rare, endoskeletal structures in Paleozoic sharks still often appear as complete and “solid.” It is unclear how this observation must be interpreted. It is tempting to see it as indicative of a weaker internal composition when compared to the marginal layer of the same structure. Following what is known of the decay of the axial structures in the catshark (Sansom *et al.*, 2013), the internal components of a prismatically calcified cartilaginous endoskeleton might have decomposed before the outer layer, thus weakening the whole skeleton if further disturbance occurred.

Establishing that a fossilized specimen is a juvenile is, in the absence of an unequivocal growth series (Cloutier, 2010), at best supported by peripheral evidence. Reflection on whether or not our specimens of *Wellerodus* are juveniles can be paralleled with Maisey *et al.*'s (2014) comments regarding the age of the articulated specimen of *Doliodus problematicus*. Maisey *et al.* (2014) considered that it was unlikely that the complete *Doliodus* specimen be a juvenile given its size [estimated total length between 50 to 75 cm (Miller *et al.*, 2003)], its extensive endoskeletal mineralization, the size of the teeth approaching the maximum known size for that species, the large size of the fin spines and the presence of a continuous covering of dermal denticles on the head and body. The Cairo specimens are of comparable length (estimated at between 50 and 70 cm) and seem to possess relatively large fin spines. They present an extensive dermal denticles covering, though it is difficult to establish the completeness of this covering. While scales are often present almost everywhere on the specimens, a complete, unbroken covering is not observed. It is difficult to establish the extent to which there might have been reworking and post-mortem dispersal of the scales, but it is believed that there must have been at least

a minimum of reorganization. However, if the teeth described and revised by Turner (1997) are indeed conspecific, the specimens described herein are far from displaying the maximum known size. The juvenile chondrichthyan described by Gess and Coates (2015) had numerous structures present, although some were not preserved. Fossilization conditions are obviously different, making it difficult to make any assumptions regarding preservation of structures, their ontogenetic sequence and iff presence or absence in one is indicative of a similar state in the other.

An incomplete endoskeletal mineralization can account for the lack of integrity of the specimens, but mineralization does not proceed as simply as being more extensive along the margins of endoskeletal elements; extensive mineralization is recorded in many Paleozoic chondrichthyans (Maisey, 2013). In modern elasmobranchs, multiple tessellated layers can be found in areas subjected to mechanical stress; this relationship is not found in extinct sharks where multiple layers can also be size-dependant and associated to growth (Maisey, 2013). However, this must be considered independently from the pattern of original mineralization in the juveniles. The ontogenetic sequence of mineralization might not reflect which zones are more likely to develop thicker mineralization. Interestingly, Maisey (2013) mentioned that stem chondrichthyans might not have developed tessellated mineralization, consequently making them difficult to identify as such. If this situation is true (and one could argue that it is supported by the condition in putative chondrichthyans), it may not necessarily imply that this would be the case in *W. priscus*. It is congeneric with *Antarctilamna prisca* for which tesserae are known; the geologically older chondrichthyans *Doliodus* and *Pucapampella*, also demonstrate this condition. It remains to be demonstrated whether the more basal states of character displayed by *Wellerodus priscus* are associated to a hypothetical plesiomorphic state in endoskeletal mineralization.

Comparison with extant juvenile specimens of *Centroscyllium fabricii* was made possible due to the availability of cleared and double stained specimens. An age-dependant

mineralization can also explain the absence of fully-developed prismatic calcified cartilage in a younger individual. The texture of the developing cartilage seen in the pelvic girdle of juvenile specimens of *C. fabricii* presents superficial similarities to the surface of the fossilized cartilage of *Wellerodus*. Also, a situation similar to the alignment of radials observed in NYSM 19052 (mineralized radials in an otherwise cartilaginous pectoral endoskeleton) is observed in a juvenile specimen of *C. fabricii* (Fig. 16).

Peripheral indices add to what is suggested by the structural data. Ecological cues are, if not neutral, at least coherent with the hypothesis of the specimens being juveniles. The material found in Buffalo, New York State, is pelagic and associated to bigger sharks, while smaller individuals are found along the coastline. This ontogenetic habitat partitioning has been documented for other Paleozoic sharks (Fisher *et al.*, 2011; Beck *et al.*, 2016).

1.8 CONCLUDING REMARKS

We provided the first description of articulated material of the Middle Devonian chondrichthyan *Wellerodus priscus*. This material is of utmost importance, given the scarcity of articulated chondrichthyan material, its closeness to conspecific *Antarctilamna prisca*, and the new morphological information contributing to support a close relationship between “acanthodians” and chondrichthyans.

Despite the generally poor preservation of the articulated fossils, it was possible to provide description of dentition variation as well as tentative positioning. The presence of intermediate cusplets was confirmed within the dentition of *W. priscus*. The observed intraspecific variation is sufficiently important to eliminate characters suggested as distinctive between *Antarctilamna* and *Wellerodus*.

Possibly the most evocative find with this material is the description of a complex combination of fin spines that includes at least one dorsal, paired pectoral fin spines and putative prepelvic fin spines. The pectoral fin spines further advocate this character as basal to chondrichthyans, stem chondrichthyans, and possibly gnathostomes. The presence of characters previously restrained to acanthodians, such as a posterior row of median denticles on the paired pectoral fin spines and the putative prepelvic fin spines, helps in uniting chondrichthyans to putative chondrichthyans.

The squamation of *Wellerodus priscus* is composed of polyodontode crowns of ctenacanth-type but reveals different morphotypes within the crowns, possibly reflecting the growth pattern of the dermal covering. Scale regionalisation is revealed, involving fewer scales in the head region and a transition towards flatter and simpler ornamentation towards the pelvic region.

W. priscus shares with putative chondrichthyans at least part of a set of fin spines usually attributed to acanthodians while being covered by a micromeric dermal skeleton

composed of areal growing scales. *Wellerodus* is distinguished from the putative chondrichthyans by a typical chondrichthyan dentition and body scales of ctenacanth type. Based on this, *W. priscus* seems to offer evidence for the transition towards the shark-like Baüplan and possibly help in establishing a phylogenetic link with, if not acanthodians, at least putative chondrichthyans. In-between the initial and the final deposit of this memoir, new research on *Doliodus* by Maisey *et al.* (2017) revealed that it possessed a full, acanthodian-like complement of fin spines, including prepectoral, admedian and prepelvic fin spines. This is clear support and validation of the hypotheses put forward within this research, further arguing in favor of the aforementioned phylogenetic links between chondrichthyans and at least some acanthodians.

Much remains to be done on *Wellerodus priscus* from Cairo. The first step should focus on the histology of cartilages, teeth, spines, and scales. Internal organization of acanthodian spines studied through synchrotron (Jerve, 2016) shows that internal organization and growth patterns are similar to those of chondrichthyan spines. The main difference is that the inner layer in acanthodians can be made of bone, while in chondrichthyans it will always be dentinous in nature (Jerve, 2016). As suggested by Jerve (2016), further studies on the internal composition of older fin spines would clarify whether or not there was an evolutive change in internal structure, possibly further linking acanthodians and chondrichthyans. Investigation on the composition of the endoskeleton would confirm whether or not prismatic calcified cartilage is present and if globular calcified cartilage is the main endoskeletal tissue. Secondly, in terms of anatomy, the endoskeleton of *W. priscus* is in need of better preserved specimens. A complete description, notably for the neurocranium, would offer invaluable information necessary for the validation of previously mentioned phylogenetic hypotheses. Once missing data would have been partly completed, it would be most appropriate to include *Wellerodus priscus*

into a phylogenetic matrix in order to investigate its phylogenetic position and clarify interrelationships among early chondrichthyans, putative chondrichthyans and acanthodians.

1.9 FIGURES

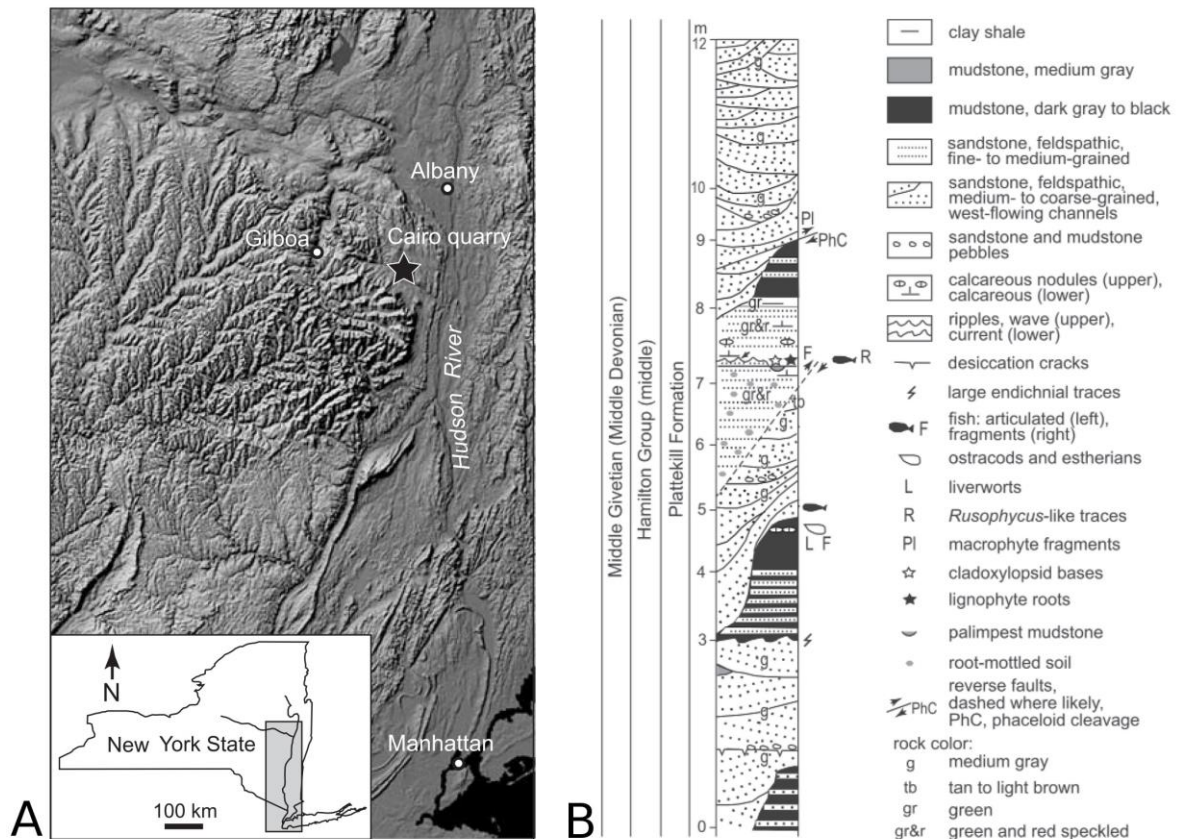
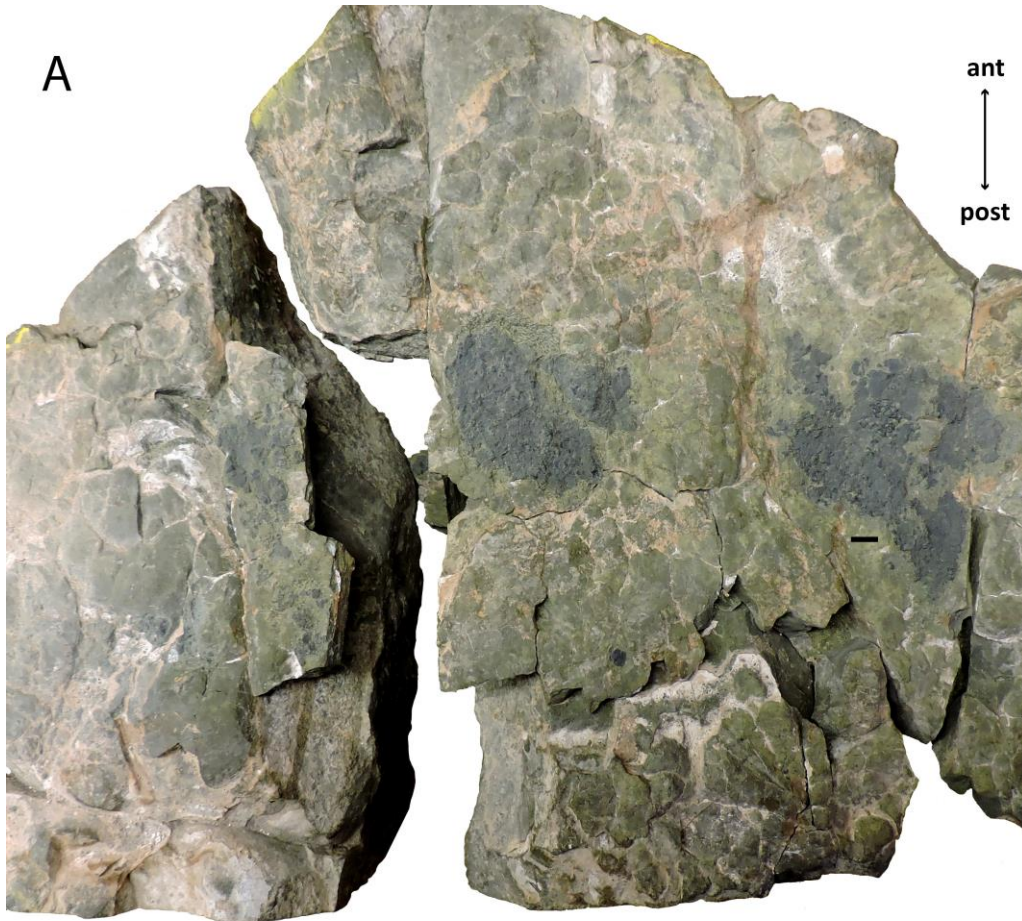


FIGURE 1: Geographical and stratigraphical information of the Cairo quarry, New York, USA. **A**: Location of the Cairo quarry (star) (3.22 km northwest of Cairo, Greene County, 42.32° N and 74.04° W, NAD 83) in eastern New York State, USA (inset map). **B**: Generalized stratigraphic section of the Plattekill Formation at Cairo quarry. Chondrichthyan specimens described herein originate from the 7.35-m level, which is also the level of the fossilized forest mentioned by Cloutier *et al.* (2010). The fish horizon at 5 m corresponds to the ichthyolith level that included the chondrichthyan remains described by Potvin-Leduc *et al.* (2015). Figures modified from Potvin-Leduc *et al.* (2015).



FIGURE 2: Selected section of the map of the Cairo *Lagerstätte* presenting the *in situ* position, prior to extraction, of the three prepared partially articulated specimens. The root system of archaeopterids is represented by the black lines; the grid code with the associated letter and number corresponds to the working grid used to cartography the site. The green triangles represent *W. priscus* fin spines and the black tooth a *Portalodus mannoliniae* tooth. **Color legend:** Green: *Wellerodus priscus*; Blue: placoderm indet.; Gray: Groenlandaspid placoderm; Purple: Cocosteid placoderm. Size of a quadrate (dotted rectangle) is 2 m wide by 3 m long.



← FIGURE 3: Specimen NYSM 19051a, the cephalic region of a partially articulated specimen of the antarctilamnid *Wellerodus priscus* from the Givetian of the Cairo quarry, New York, USA. **A**: Photograph of the prepared specimen. **B**: Drawing of the specimen. **Color legend**: Black: endoskeletal and/or cartilaginous elements and structures; Blue: scales (morphotypes 1–3); Orange: teeth. **ant**: anterior; **post**: posterior. Scale bars equal to 1 cm.

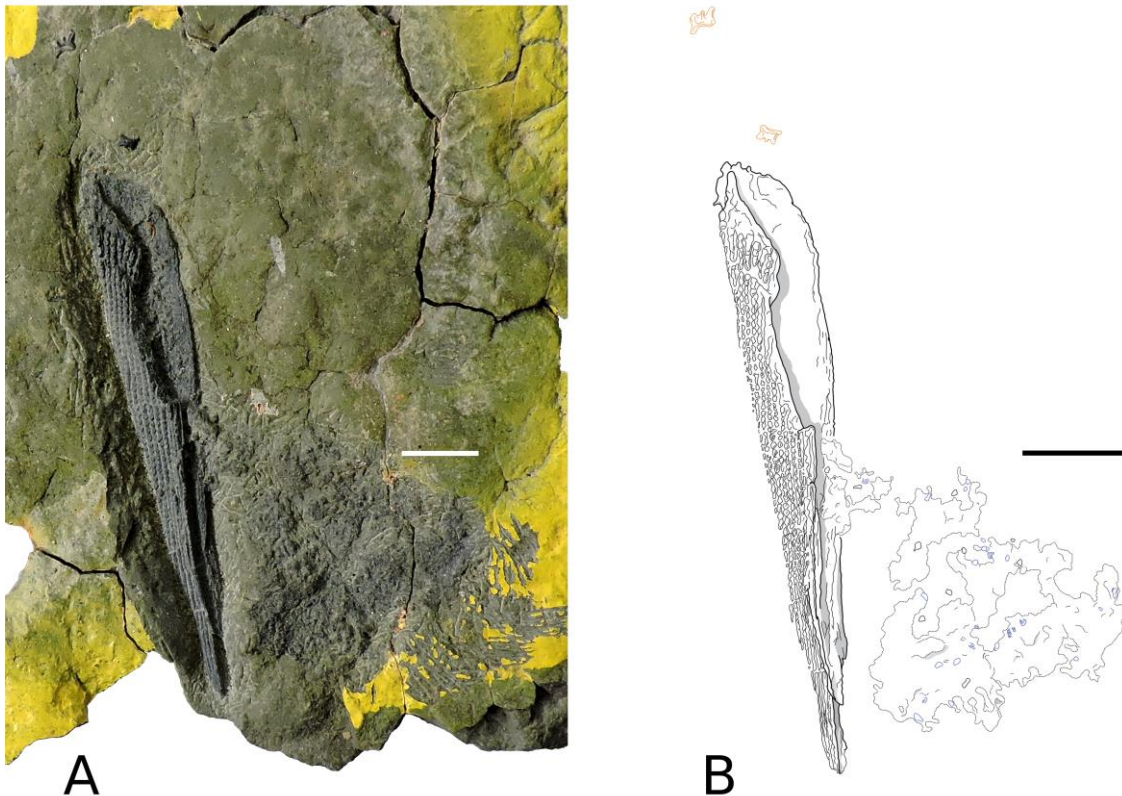
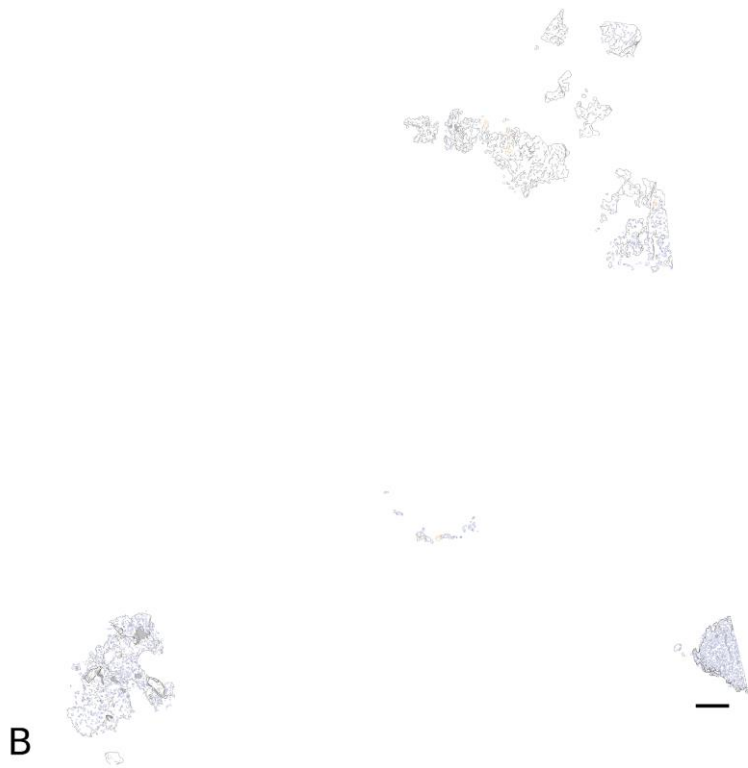
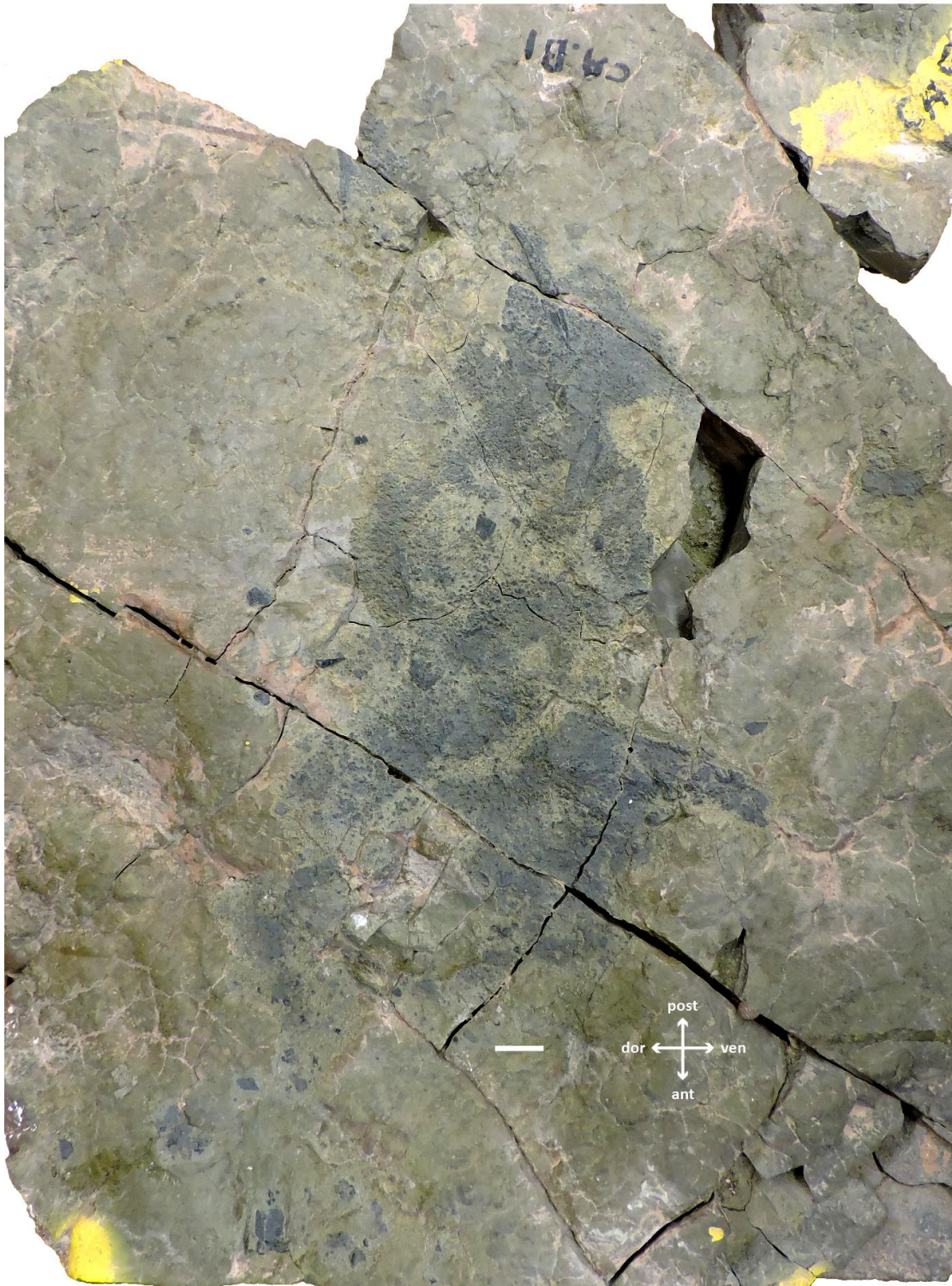


FIGURE 4: Specimen NYSM 19051b, a median dorsal fin spine with associated fin web of a partially articulated specimen of the antarctilamnid *Wellerodus priscus* from the Givetian of the Cairo quarry, New York, USA. **A**: Photograph of the prepared specimen. **B**: Drawing of the specimen. **Color legend**: Black: endoskeletal and/or cartilaginous elements and structures; Blue: scales (morphotypes 1–3); Orange: teeth. Scale bars equal to 1 cm.

FIGURE 5: Specimen NYSM 19051c, the pelvic? region of a partially articulated specimen of the antarctilamnid *Wellerodus priscus* from the Givetian of the Cairo quarry, New York, USA. **A**: Photograph of the prepared specimen. **B**: Drawing of the specimen. **Color legend**: Black: endoskeletal and/or cartilaginous elements and structures; Blue: scales (morphotypes 1–3, 5); Orange: teeth. **ant**: anterior; **post**: posterior. Scale bars equal to 1 cm. →





← FIGURE 6: Partially articulated specimen NYSM 19052 of the antarctilamnid *Wellerodus priscus* from the Givetian of the Cairo quarry, New York, USA. Photograph of the prepared specimen. **ant**: anterior; **post**: posterior; **dor**: dorsal; **ven**: ventral. Scale bar equals to 2 cm.

FIGURE 7: Partially articulated specimen NYSM 19052 of the antarctilamnid *Wellerodus priscus* from the Givetian of the Cairo quarry, New York, USA; interpretative illustration. **Color legend**: Black: endoskeletal and/or cartilaginous elements and structures; Blue: scales (morphotype 1–5); Green: scales (morphotype 6); Orange: teeth; Purple: placoderm indet. element. **fs**: fin spine; **lpfs**: left pectoral fin spine; **rpfs**: right pectoral fin spine. Scale bar equals to 1 cm. →

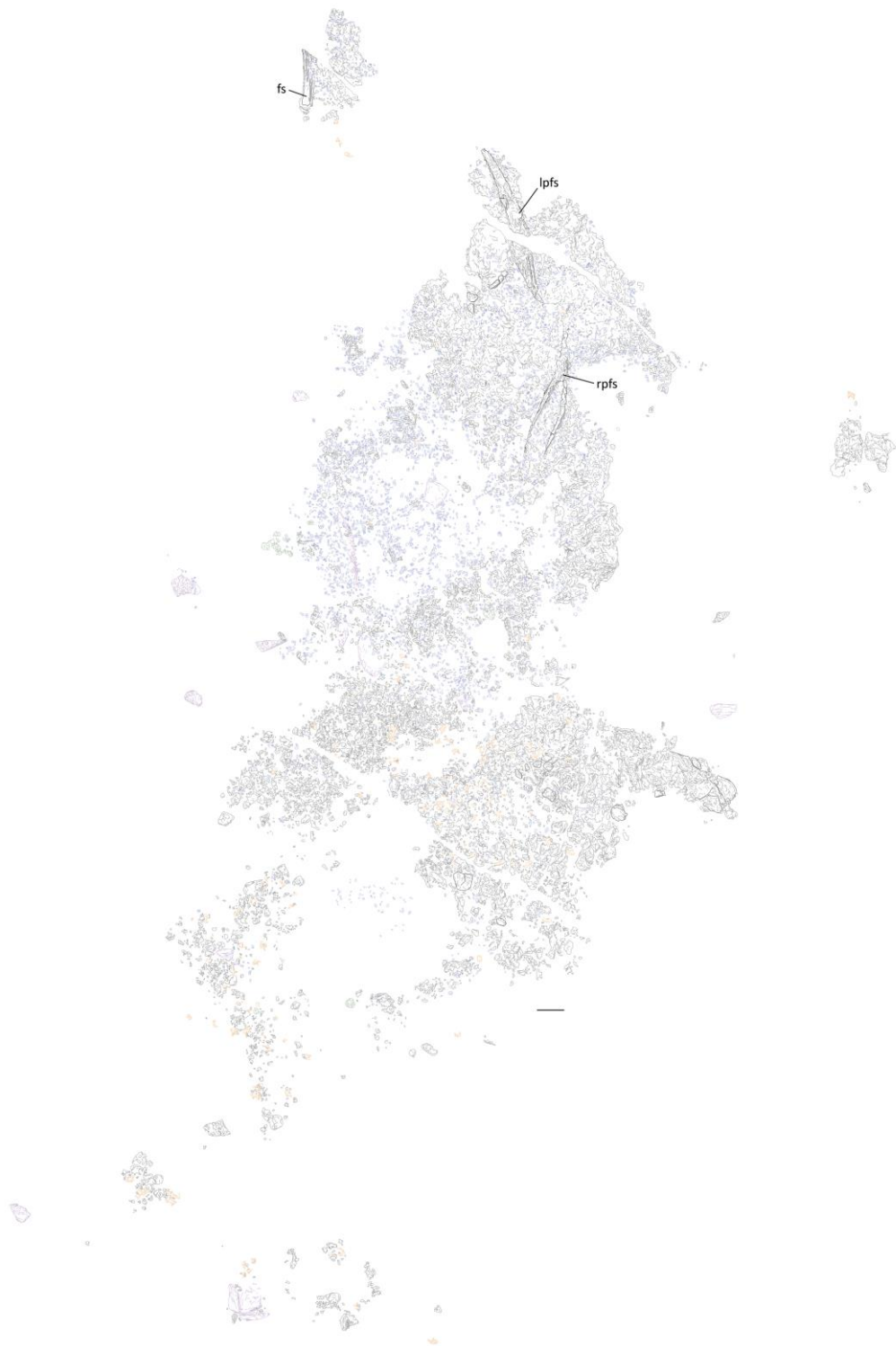




FIGURE 8: Partially articulated specimen NYSM 19053 of the antarctilamid *Wellerodus priscus* from the Givetian of the Cairo quarry, New York, USA. **ant**: anterior; **post**: posterior; **dor**: dorsal; **ven**: ventral. Interpretation of the orientation of the specimen is a general suggestion. Scale bar equals to 1 cm.

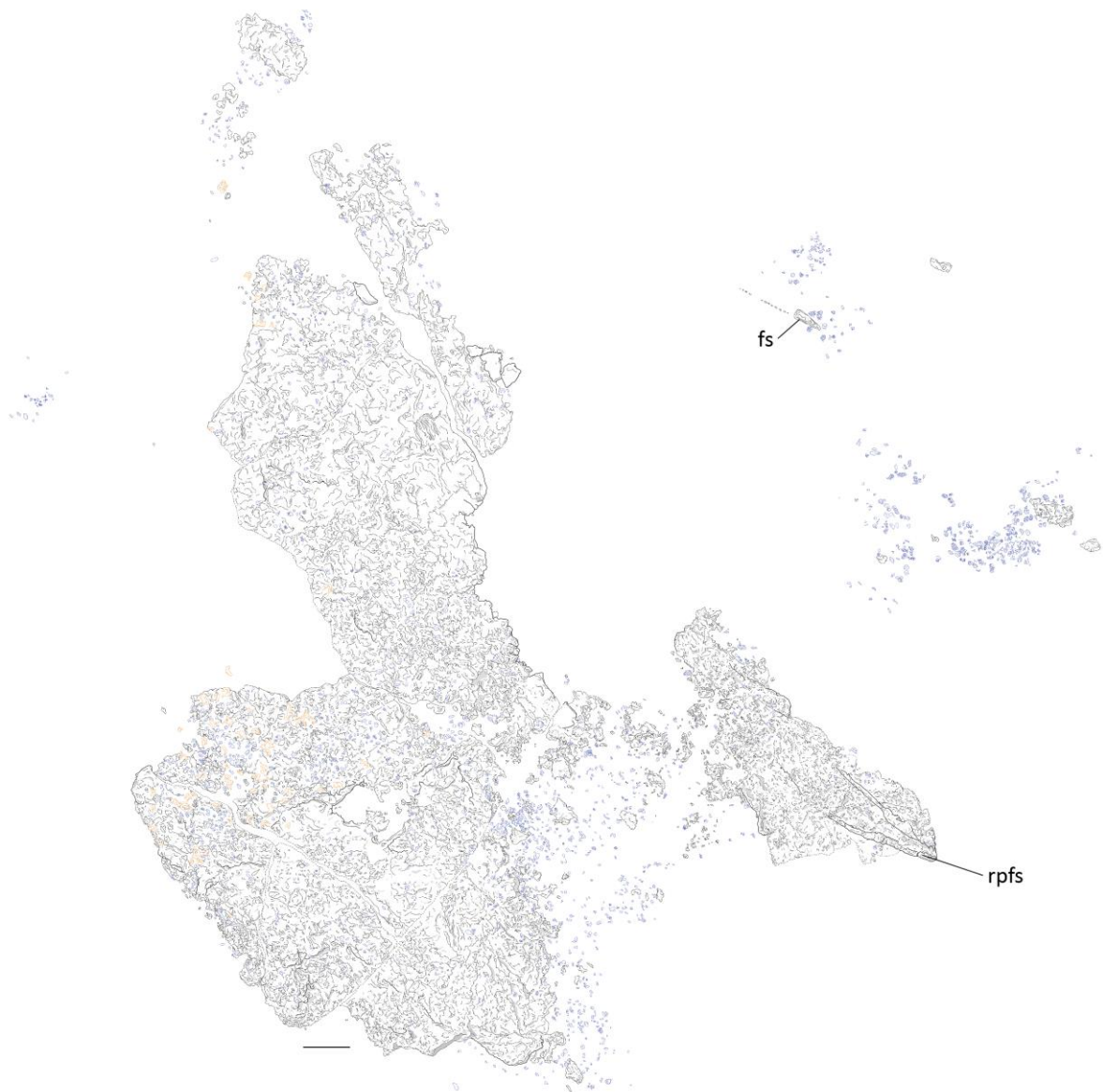
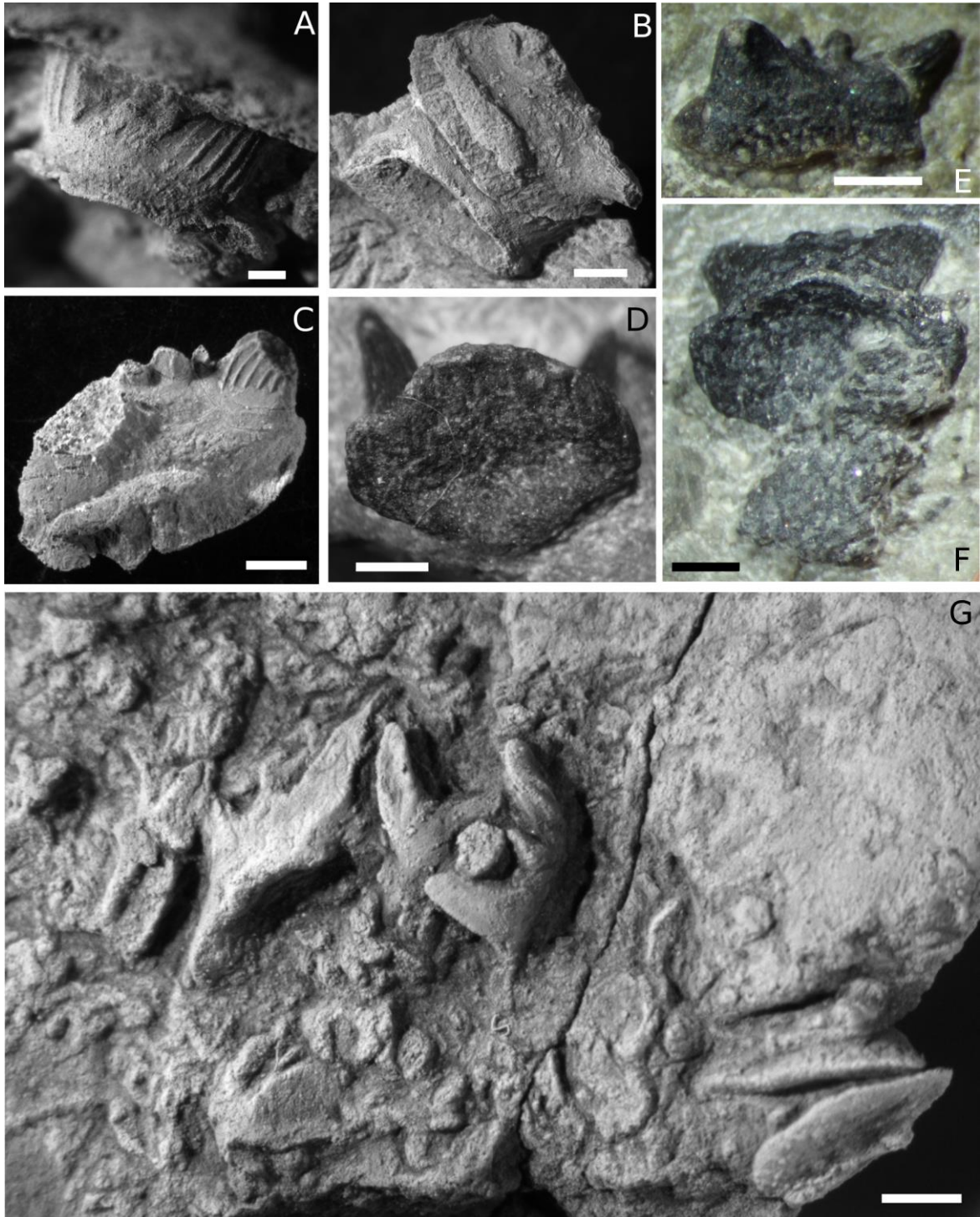


FIGURE 9: Partially articulated specimen NYSM 19053 of the antarctilamid *Wellerodus priscus* from the Givetian of the Cairo quarry, New York, USA; interpretative illustration. **Color legend:** Black: endoskeletal and/or cartilaginous elements and structures; Blue: scales (morphotypes 1–4); Orange: teeth. **fs:** fin spine; **rpfs:** right pectoral fin spine. Scale bar equals to 1 cm.



← FIGURE 10: Teeth, isolated and *in situ*, of the antarctilamnid *Wellerodus priscus* from the Givetian of the Cairo quarry, New York, USA. **A, F**: Photographs of specimen NYSM 19068, in labial (**A**) and labiobasal (**F**) views. **B**: Photograph of specimen NYSM 19067, two teeth semi-articulated, in oro-lingual view. **C**: Photograph of specimen NYSM 19061, in oral view. **D**: Photograph of specimen NYSM 19064, in basal view. **E**: Photograph of specimen NYSM 19065, in lingual view. **G**: Specimen NYSM 19059, a small sample of semi articulated teeth with fossilized organic matter. Scale bars equal to 1 mm.

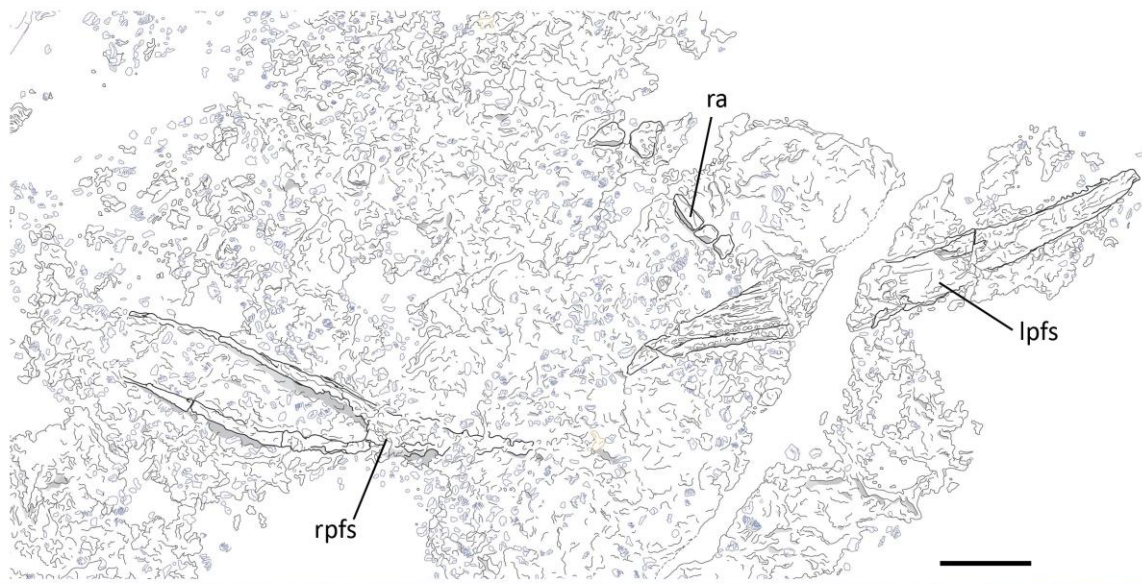
FIGURE 11: *In situ* teeth organisation within specimen NYSM 19051a of the antarctilamnid *Wellerodus priscus* from the Givetian of the Cairo quarry, New York, USA. Photograph (**A**) and illustration (**B**) of same area with organized tooth. **Color legend**: Black: endoskeletal and/or cartilaginous elements and structures; Blue: scales (morphotypes 1–3); Orange: teeth. Scale bar equals to 1 cm. →



A

B





← FIGURE 12: Pectoral fin spines of the antarctilamnid *Wellerodus priscus* from the Givetian of the Cairo quarry, New York, USA. **A, B**: Specimen NYSM 19052; **A**: photograph of the pectoral fin spines showing the right pectoral fin spine in posterior view and the left pectoral fin spine in lateral view. **B**: illustration of the pectoral fin spines. Color code: Black: endoskeletal and/or cartilaginous elements and structures; Blue: scales (morphotypes 1–3). Orange: teeth. **C, D**: Specimen NYSM 19054; photograph of an isolated pectoral fin spine in lateral view. **D**: Detail of the retrorse pectoral denticles on the posterior side of the distal tip of the fin spine. **lpfs**: left pectoral fin spine; **ra**: radial; **rpfs**: right pectoral fin spine. Scale bars equal to 1 cm in **A–C**, 1 mm in **D**.

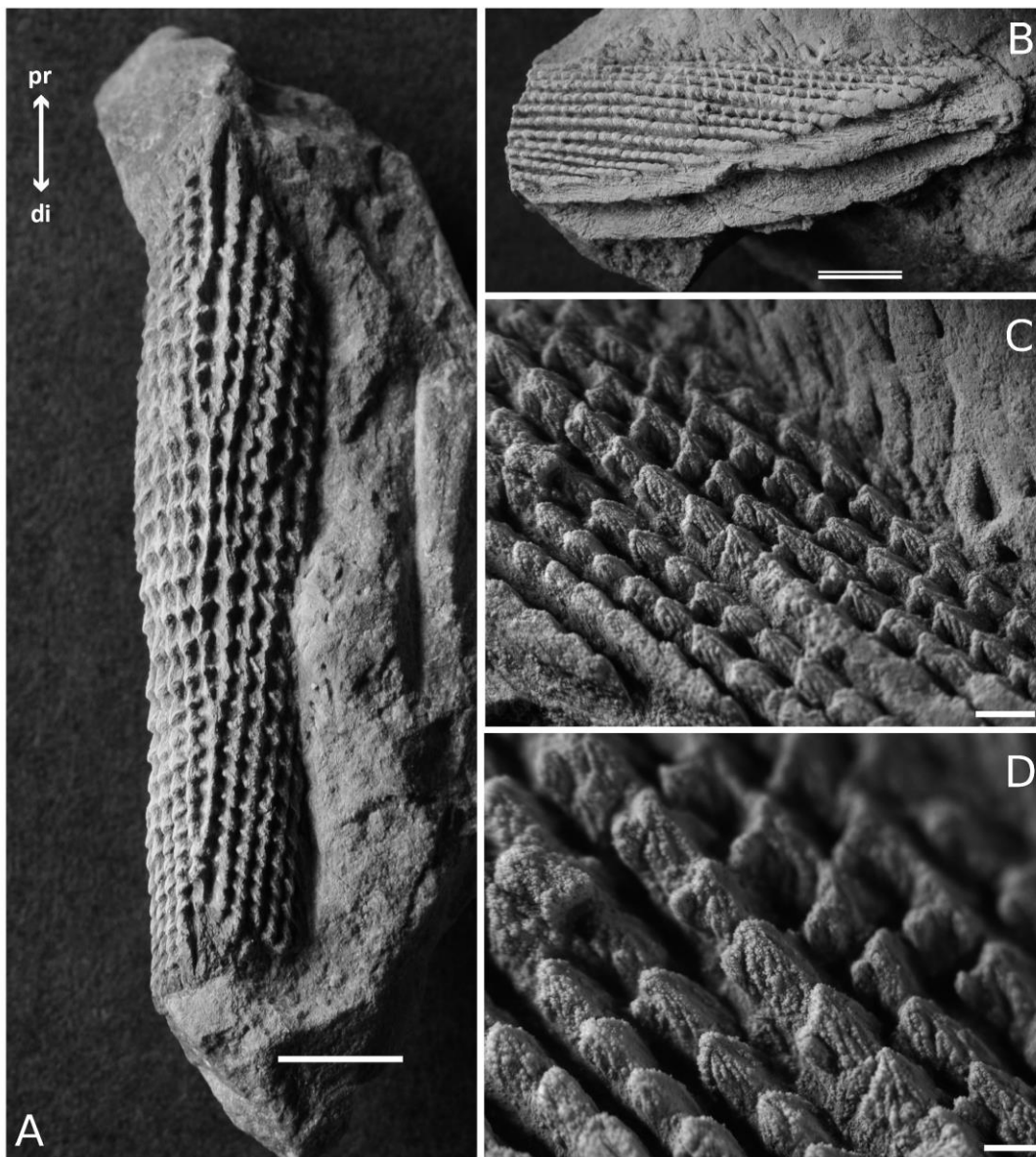


FIGURE 13: Ornamentation and details of the ornamentation in the fin spines of the antarctilamnid *Wellerodus priscus* from the Givetian of the Cairo quarry, New York, USA. **A**: Specimen NYSM 19057 in leading edge view, showing the pattern of ridges fusing into each other in an alternate sequence. **B–D**: Specimen NYSM 19056 in lateral view, showing variation in width of ridges (**B**), detail of the ornamented nodes forming the ridge (**C**) and a close-up view of the odontodes with the asymmetrical projection (**D**). **pr**: proximal; **di**: distal. Scale bars equal to 5mm (**A**, **B**), 1 mm (**C**) and 500 μm (**D**).

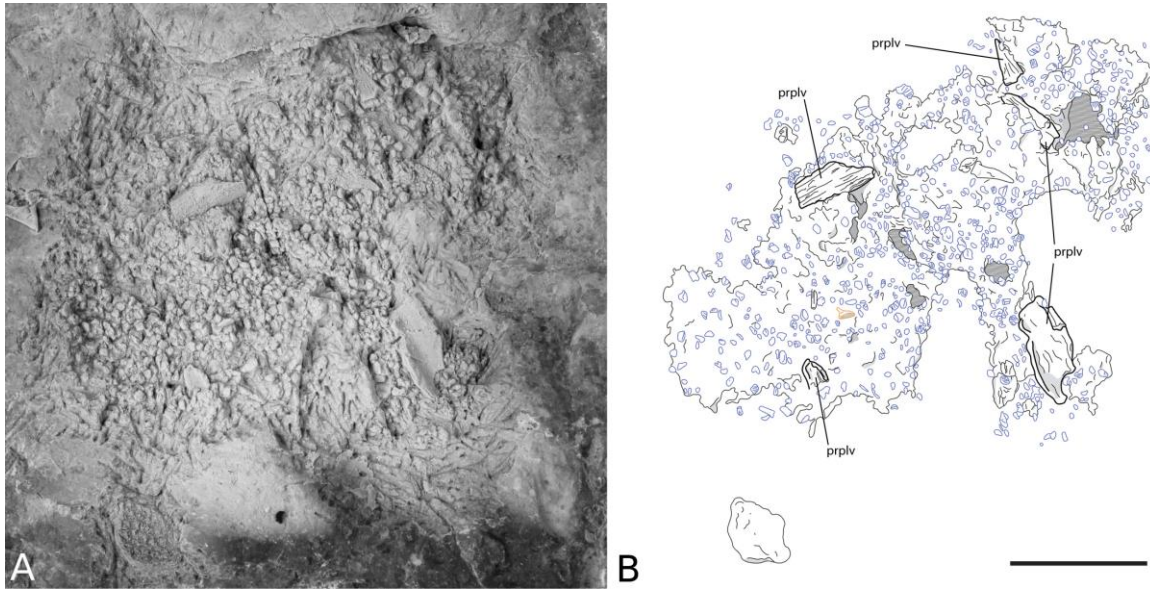


FIGURE 14: Putative prepelvic fin spines of the antarctilamnid *Wellerodus priscus* from the Givetian of the Cairo quarry, New York, USA. Close-up of the region showing the putative prepelvic (**prplv**) fin spines on specimen NYSM 19051c. **Color legend:** Blue: scale; Orange: tooth. Dashed lines represent sediment. Scale bar equals 1 cm.

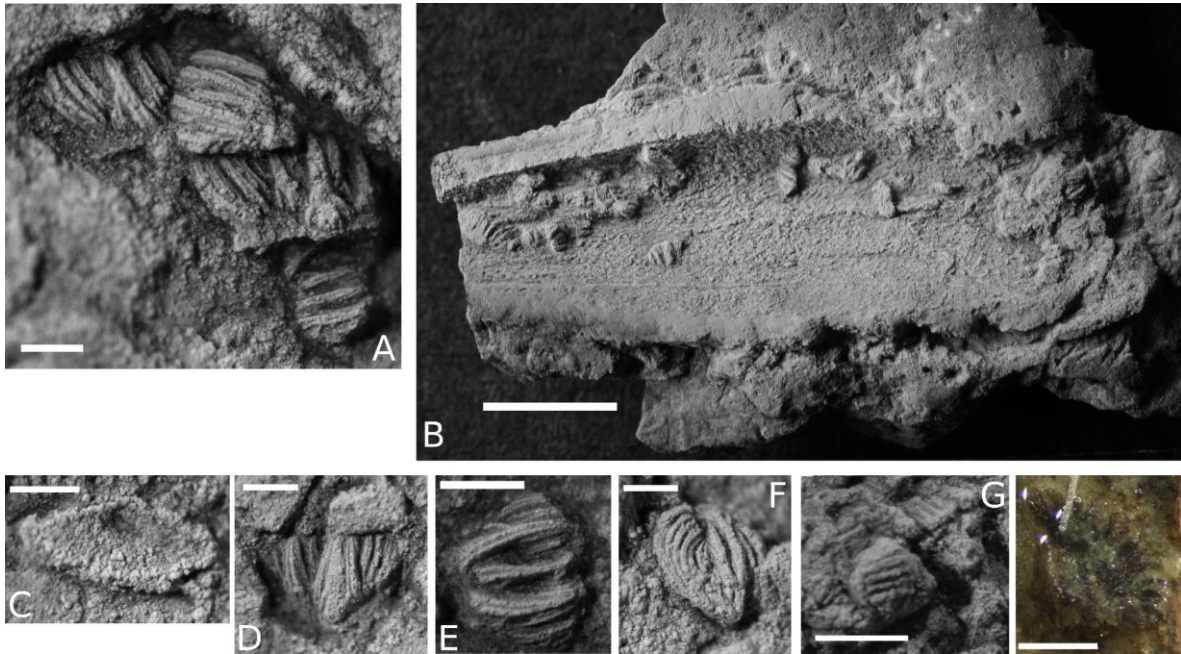
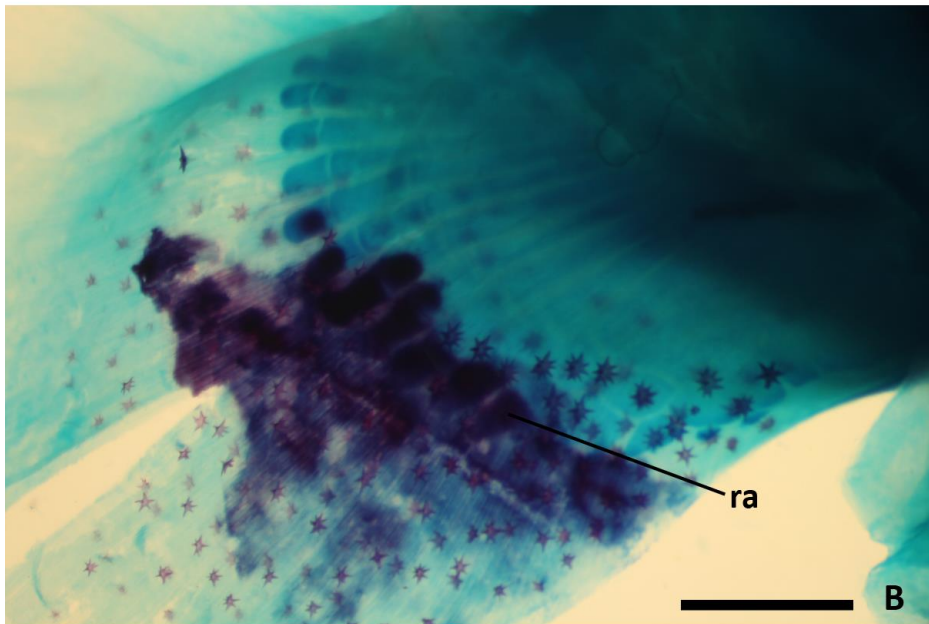
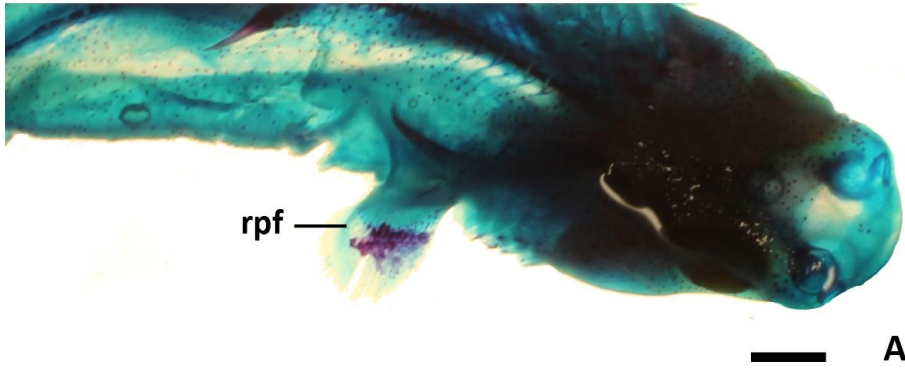


FIGURE 15: Scale morphotypes of the antarctilamnid *Wellerodus priscus* from the Givetian of the Cairo quarry, New York State, USA. **A–G**: Ctenacanth-type scales from specimen NYSM 19058 (a scale patch; **A**, **C–F**), specimen NYSM 19055 (a fin spine in posterior view; **B**) and specimen NYSM 19051c (pelvic? region of a partially articulated specimen; **G**). **A**: Morphotype 1. **B**: Morphotype 1. **C**: Base of scale. **D**: Morphotype 2. **E**: Morphotype 3. **F**: Morphotype 4. **G**: Morphotype 5. **H**: Morphotype 6; stellate, flat scale from partially articulated specimen NYSM 19052, possibly a head scale. Scale bars equal to 5mm (**B**), 1 mm (**G**, **H**) and 500 μ m (**A**, **C–F**).

FIGURE 16: Comparison of mineralized radials in the pectoral fins of chondrichthyans. **A**, **B**: Juvenile specimen of chondrichthyan *Centroscyllium fabricii*. **A**: Anterior half of the specimen, showing the right pectoral fin with partially mineralized radials. **B**: Close-up of the right pectoral fin; unmineralized cartilage is colored blue while the mineralized elements are red. A single line of radials is mineralized in an otherwise unmineralized pectoral fin endoskeleton. **C**: Left pectoral fin spine of specimen NYSM 19052 of antarctilamnid *Wellerodus priscus* from the Givetian of the Cairo quarry, New York State, USA. The pectoral fin spine is associated to a series of mineralized elements interpreted as radials; no other adjacent structures are displaying mineralization despite the purported presence of the pectoral girdle and fin endoskeleton. **lpfs**: left pectoral fin spine; **ra**: radial; **rpf**: right pectoral fin. Scale bars equals to 1cm in **A**, 5 mm in **B** and **C**. →



CONCLUSION GÉNÉRALE

Ce mémoire a été initié avec la présentation d'un projet assez large : dans l'optique d'établir une phylogénie complète des gnathostomes, identifier les formes basales des grands groupes de gnathostomes et déterminer les traits les caractérisant, en plus de définir les relations présentes entre ces groupes. Au sein de ce défi était soulignée la problématique entourant la définition des formes basales des chondrichthyens, et ce dans le contexte d'un lien phylogénétique avec les acanthodiens de plus en plus souvent retrouvé dans les études phylogénétiques. Ces formes basales, enfin, peuvent-elles être réconciliées avec les chondrichthyens putatifs, soit des formes présentant des caractères appartenant soit aux acanthodiens, soit aux chondrichthyens? Comme les spécimens fossiles de chondrichthyens basaux sont rares, la description de nouveaux spécimens amène nécessairement de nouvelles et pertinentes informations. Ce cas de figure est très bien illustré par notre description de *Wellerodus priscus*, la première impliquant des spécimens partiellement articulés du récemment découvert *Konzentrat-Lagerstätte* de Cairo, dans l'état de New York. Il apparaît, au final, que le matériel, le travail et les conclusions présentées dans ce mémoire sont pertinents et originaux de plusieurs façons.

Nous avons fourni la première description de la dentition *in situ* pour *W. priscus*. Cette dentition confirme l'organisation des dents sous forme de familles; leur nombre abondant (jusqu'à approximativement 209 au sein du spécimen NYSM 19051) permet d'estimer que la dentition pourrait déjà être comparable, en termes de quantité (environ 14 emplacements dentaires sont estimés par section de mâchoire), à celle d'autres chondrichthyens paléozoïques (Dick & Maisey, 1980; Maisey *et al.*, 2014). La variation de la morphologie de la couronne dentaire au sein d'un même individu a pu être documentée. Ces observations tendent vers la conclusion qu'il n'existe pas de critères diagnostiques dentaires permettant de distinguer entre *Antarctilamna* et *Wellerodus*, à l'exception du nombre maximal de cuspides intermédiaires, soit jusqu'à quatre chez *Antarctilamna*

contrairement à un maximum de deux chez *Wellerodus*. Cette situation n'est cependant retrouvée que chez un certain nombre de spécimens et il est aussi observé que les cuspidés intermédiaires ne sont pas répartis de façon systématique au sein de la dentition d'un même individu chez *W. priscus*.

Les dents de *Wellerodus* et d'*Antarctilamna* présentent un *Gestalt* diplodonte qui pourrait représenter la forme basale pour les chondrichthyens. Elles sont documentées chez plusieurs taxons du Dévonien, tels que *Leonodus* (Mader *et al.*, 1986), *Doliodus* (Miller *et al.*, 2003; Turner, 2004; Maisey *et al.*, 2014), *Karksiodus mirus* (Ivanov *et al.*, 2011; Ivanov & Märss, 2014) et *Tassiliodus lessardi* (Derycke & Goujet, 2011), et leur répartition phylogénétique comme paléogéographique contribue à dresser le portrait d'une émergence et distribution initiale sur les rives de la Laurussie et du Gondwana, de chaque côté de l'océan Rhéique. Cette distribution est aussi en accord avec la répartition des fossiles attribués aux antarctilamnides, qui suggèrent soit cette distribution pour les antarctilamnides, soit la distribution de chondrichthyens présentant des caractères semblables et conséquemment probablement plésiomorphes (Potvin-Leduc *et al.*, 2015).

Nous avons décrit les aiguillons chez *Wellerodus priscus*; ces aiguillons sont caractérisés par leur ornementation, composée de crêtes formées d'une série successive de cônes, eux-mêmes ornements de lignes convergentes vers la pointe distale de chaque cône. Les crêtes convergent vers le bord d'attaque où elles se rejoignent de façon successive et alternée. Ce patron d'ornementation et d'organisation des crêtes semble être commun aux antarctilamnides et, de ce fait, a été ajouté à la diagnose de la famille. Nous avons aussi documenté la présence d'excroissances asymétriques latérales chez certains de ces odontodes; à notre connaissance, il s'agit de la première fois qu'un tel caractère est noté chez des aiguillons de chondrichthyens. Point crucial, les spécimens de Cairo ont révélé chez *W. priscus* la présence non ambiguë d'aiguillons pectoraux pairs. Ce caractère avait été révélé chez *Doliodus problematicus* (Miller *et al.*, 2003), soulevant de ce fait qu'il

s'agisse d'une synapomorphie des gnathostomes basaux et non seulement des acanthodiens (Zhu *et al.*, 1999; Grogan *et al.*, 2012). *W. priscus* est le premier chondrichthyen depuis *D. problematicus* chez qui la présence d'aiguillons pairs est indubitablement confirmée. De plus, les aiguillons pectoraux sont caractérisés par une rangée unique retrouvée au niveau de la marge postérieure distale de l'aiguillon. Ce caractère est probablement plésiomorphe; il a été documenté chez le chondrichthyen *Doliodus problematicus* (Burrow *et al.*, 2008; 2016) et est probablement présent chez le chondrichthyen *Leonodus carlsi* (Soler-Gijón & Hampe, 2003). Ce caractère est aussi décrit chez plusieurs acanthodiens (Bernacsek & Dineley, 1977; Gagnier, 1996; Hanke & Wilson, 2004; Burrow *et al.*, 2008; Newman & Davidson, 2010; Hanke & Davis, 2012; Burrow *et al.*, 2016); plusieurs de ces acanthodiens ont été retrouvés à la base des chondrichthyens lors de récentes analyses phylogénétiques (*i.e.* Zhu *et al.*, 2013; Burrow *et al.*, 2016).

De potentiels aiguillons pré-pelviens ont aussi été observés au sein du spécimen NYSM 19051c. Les aiguillons prépelviens sont considérés comme un caractère plésiomorphe pour les acanthodiens mais sont aussi retrouvés chez certains chondrichthyens putatifs (Hanke & Wilson, 1998; 2004). Chez les chondrichthyens, leur présence a été récemment démontrée chez *Doliodus* (Maisey *et al.*, 2017), mais n'a jamais été autrement documentée. La présence d'aiguillons prépelviens chez *Wellerodus* est inattendue et phylogénétiquement significative puisqu'elle documente une nouvelle plésiomorphie pour les chondrichthyens basaux tout en établissant un lien supplémentaire avec les acanthodiens et chondrichthyens putatifs, un lien aussi soutenu par la présence des aiguillons pectoraux pairs et la présence de denticules postérieurs sur les aiguillons pectoraux.

Compte tenu des différences de positionnement des spécimens lors de la fossilisation de *Wellerodus* et d'*Antarctilamna*, il nous est impossible de confirmer la suggestion qu'*Antarctilamna* posséderait des aiguillons pectoraux pairs (Miller *et al.*, 2003; Wilson *et*

al., 2007; Hanke & Wilson, 2010). Toutefois, compte tenu de la variation documentée chez *Wellerodus*, nous croyons que les différents morphotypes d'aiguillons documentés chez *Antarctilamna* (Young, 1982) sont mieux expliqués par une divergence entre aiguillons médians et pairs qu'entre premier et deuxième aiguillons dorsaux (Young, 1982). Bien que nous acceptions l'identification de l'aiguillon découvert en association avec *Antarctilamna ultima* comme étant dorsal (Gess & Coates, 2015), nous ne croyons pas que le matériel connu permet d'exclure la présence d'aiguillons pairs chez *A. ultima*, et encore moins chez *A. prisca*. Enfin, la variation observée chez *Wellerodus* devrait aussi pouvoir permettre de compléter le travail d'identification mené sur les deux morphotypes d'aiguillons associés à *Leonodus* (Soler-Gijón & Hampe, 2003).

Nous suggérons qu'il est tout à fait plausible que les aiguillons identifiés sous le nom de « *Ctenacanthus* » *wrighti* appartiennent à *Wellerodus*, comme l'ont suggéré Young (1982), Turner (1997) et Ginter *et al.* (2010). Nous considérons de plus que l'attribution aux antarctilamnides devrait être confirmée pour des aiguillons retrouvés au Venezuela (Young & Moody, 2002) ainsi qu'en Bolivie (Janvier & Melo, 1992; Maisey & Melo, 2002).

Les écailles de *Wellerodus* sont de type cténacanthé et caractérisées par plusieurs odontodes organisés de manière parallèle, contrairement à l'organisation concentrique généralement attribuée à *Antarctilamna* (Young, 1982). Six morphotypes ont été identifiés, caractérisant des variations dans la distribution des odontodes probablement dues à la croissance de l'écaille (morphotypes 1 à 3), une forme rare où les odontodes sont organisés de manière plus concentrique (morphotype 4), une forme plus petite et plus simple (morphotype 5) et une forme plus ronde, plate et d'organisation étoilée (morphotype 6). Nous avons décrit un premier aperçu de la régionalisation de l'écaillage; les écailles des morphotypes 1 à 4 sont surtout retrouvées sur les flancs et le dos de l'animal, avec une prédominance des types 1 à 3. Les écailles sont moins nombreuses au niveau de la tête, là

où pourrait aussi se retrouver le morphotype 6, tandis que le morphotype 5 est associée à une transition associée au niveau pelvien et ventral. *Wellerodus* démontre une écaillage complexe et diversifiée au sein d'un même individu. De plus, l'écaillage de type polyodontode à croissance aréale apparaît chez plusieurs taxons, notamment certains chondrichthyens putatifs, soulignant l'émergence d'un type d'écaillage propre aux chondrichthyens basaux.

Plusieurs indices périphériques laissent supposer que les spécimens de *W. priscus* de Cairo pourraient être des individus juvéniles. Le piètre état de conservation de l'endosquelette des spécimens pourrait être expliqué par une minéralisation incomplète associée à un stade ontogénétique juvénile. Les dimensions des spécimens de Cairo sont inférieures à celles d'autres spécimens retrouvés en d'autres endroits de l'état de New York, laissant supposer une croissance incomplète. De plus, ces autres spécimens sont retrouvés dans un milieu interprété comme pélagique, tandis que le site de Cairo correspond à un environnement estuarien et plus près des côtes, ce qui est géographiquement cohérent avec un partitionnement d'habitat ontogénétique, dans lequel les adultes sont retrouvés en eaux plus profondes et les juvéniles et subadultes plus près des côtes sont des comportements qui ont été identifiés chez des espèces actuelles et fossiles (Fisher *et al.*, 2011; Beck *et al.*, 2016). L'hypothèse voulant que les spécimens de Cairo soient des individus juvéniles de *W. priscus* est la plus simple, mais sans écarter la possibilité que les chondrichthyens de Cairo soient associés à une nouvelle espèce. La possibilité qu'il y ait plus d'une espèce parmi les spécimens de Cairo ne peut aussi être écartée, et ce jusqu'à ce que le travail de préparation et d'analyse des autres spécimens soit complété.

Au-delà de cette étude de nouveaux spécimens, permettant de mieux caractériser l'endosquelette, des travaux subséquents devront porter sur la composition interne et la structure histologique des dents, des aiguillons, des écailles et de l'endosquelette. Un assemblage de traits caractéristiques aux chondrichthyens basaux semble se préciser,

impliquant notamment les dents diplodontes, les aiguillons pairs et les écailles polyodontodes, mais cette similarité morphologique doit être appuyée par une similarité dans la composition interne. Une fois ces informations acquises, elles devront être intégrées à une analyse phylogénétique, afin de déterminer la position de *Wellerodus* et d'évaluer si se confirme l'impression d'une combinaison de caractères permettant de définir les relations et les transitions entre acanthodiens, chondrichthyens putatifs et chondrichthyens.

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