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Givetian (Middle Devonian) sharks from Cairo, New York (USA): Evidence of early cosmopolitanism

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Whereas cosmopolitan distribution patterns are established for many Late Devonian vertebrates (e.g., placoderms, onychodontiforms), few palaeobiogeographic studies have considered chondrichthyans. Recent discoveries of shark material demonstrate that some chondrichthyans were cosmopolitan by the Middle Devonian. Abundant Givetian microremains have been recovered from the Cairo quarry in eastern New York State, USA. These include teeth of two shark species with Gondwanan affinities, the omalodontid *Portalodus mannoliniae* sp. nov. and the antarctilamnid *Wellerodus priscus*. Abundant teeth of *P. mannoliniae* sp. nov. are characterized by a smooth diplodont crown, polarized cusps, and a labially oriented base. The teeth demonstrate monognathic heterodonty. The juvenile morph is distinguished from the adult by smaller size, slender cusps, and variation in the shape of the base. *W. priscus* is represented by rare juvenile teeth. Two groups of scales that show affinity to material from northern (Spain) and East Gondwana (Antarctica) are tentatively attributed to the two described species. Antarctilamnid distribution suggests a north Gondwanan origin and a colonization of the margin of the landmass before dispersing to Laurentia by the Middle Devonian. This material further indicates that vertebrate global dispersal was initiated by the Middle Devonian, and emphasizes earlier palaeogeographic interpretations that the Middle Devonian “Hamilton fauna” of North American Laurussia originated in the Early Devonian in South American Gondwana.

Key words: Chondrichthyes, Elasmobranchii, Antarctilamnidae, Omalodontiformes, taxonomy, ontogeny, palaeobiogeography, Devonian, North America.

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Introduction

Current views on the distribution of Devonian vertebrates suggest a general transition from endemism in the Early Devonian to cosmopolitanism in the Late Devonian (Young 1990, 2003b; Young et al. 2000, 2010; Janvier 2007; Blicek 2011). Earlier studies on Devonian vertebrate dispersal were mostly conducted on agnathans and placoderms (reviewed in Lebedev and Zakharenko 2010), rather than chondrichthyans, which are mentioned only in comparative studies of ichthyofaunal assemblages (Schultze and Cloutier 1996; Anderson et al. 1999). Lebedev and Zakharenko (2010) expanded the stratigraphic scope by comparing dispersal patterns for the Givetian (387.7–382.7 Ma), Frasnian (382.7–372.2 Ma) and Famennian (372.2–358.9 Ma) (Cohen et al. 2013). While confirming that widespread dispersal became more common during the Late Devonian, they demonstrated that some vertebrates, in-

cluding such chondrichthyans as *Phoebodus*, *Omalodus*, and scale-based taxa such as *Ohiolepis*, were cosmopolitan by the Givetian (Lebedev and Zakharenko 2010). Cosmopolitanism, following Lebedev and Zakharenko (2010), is defined by presence across at least two realms. However, other chondrichthyans, namely the *Antarctilamna*–*Wellerodus* group and *Portalodus*, were also cosmopolitan by the Givetian.

Nomenclature is a problem in considering palaeogeographic distributions of such chondrichthyans. Notably, *Wellerodus* was erected by Turner (1997) based on teeth previously attributed to *Diplodus priscus*, *Diplodus striatus*, *Dittodus priscus*, and *Dittodus striatus* by Eastman (1899) and Hussakof and Bryant (1918). An important characteristic was the great similarity between the teeth of *Wellerodus* and the teeth of the East Gondwanan *Antarctilamna* (Turner 1997; Ginter 2004). A morphological distinction was based on the presence of intermediate cusplets in *Antarctilamna*

(Ginter 2004). However, Ginter et al. (2006) described *Wellerodus* teeth with intermediate cusplets, implying that *Antarctilamna prisca* and *Wellerodus prisca* are probably congeneric, but still represent two distinct species. Despite the fact that the two genera are now considered synonymous, Ginter et al. (2010) chose to maintain both of them to avoid nomenclatural confusion, as reuniting them under *Antarctilamna* would result in two species named *A. prisca* and *A. prisca*. Further work on both species should address this nomenclatural problem and clarify the taxonomy. *Portalodus*, also from East Gondwana (Young 1982; Long and Young 1995), was recently discovered in New York State (Ginter et al. 2006, 2010; Potvin-Leduc et al. 2010).

Here we describe Givetian chondrichthyan microremains from the Cairo quarry, New York, which are referred here to *Portalodus* and *Wellerodus*. We explore their affinities and implications for understanding of the Devonian palaeobiogeography of vertebrates.

Institutional abbreviations.—AMF, Australian Museum, Sydney, Australia; MGUV, Museo de Geología, Universitat de València, Valencia, Spain; NMV P, Museum Victoria Palaeontology Collection, Melbourne, Australia; NYSM, New York State Museum, Albany, USA; SMP-SMU, Shuler Museum of Paleontology, Southern Methodist University, Dallas, USA.

Geological setting

The Cairo quarry (Fig. 1), just south of New York State Route 145 at the Cairo Highway Department headquarters, is 3.22 km northwest of Cairo, Greene County, NY (42.32° N and 74.04° W, NAD 83). The quarry is located in the eastern part of the Devonian Catskill delta and exposes 12.0 m of sandstone and mudstone of the Plattekill Formation of the eastern Hamilton Group (Givetian).

Dark grey–black shale and siltstone lenses (Fig. 2) are interbedded with terrestrial red beds or fluvial sandstone. These fine-grained sedimentary rocks may reflect abrupt changes in base level (e.g., Bridge and Willis 1994) and deposition of estuarine or lacustrine sediments under oxygen-stratified water masses. Alternatively, they may reflect rapid deposition of flood plain muds or channel fills at the end of flooding events or with channel avulsion (e.g., Allen and Gastaldo 2006). Well-preserved plant material occurs locally in these shale and siltstone lenses (Hernick et al. 2008) with in situ bivalves (*Archanodon* in lighter grey, better oxygenated mudstone), abundant ostracodes and estherians, remains of drowned, subaerial arthropods, and fish debris.

Marine fish occur in a condensed sandstone, a fish bed, 4.75–5.1 m above the base of the section (Fig. 2; Ginter et al. 2006). The diverse fish assemblage includes the chondrichthyans described herein, with placoderms, acanthodians, actinopterygians, and sarcopterygians (Cloutier et al. 2010). A second fish bed, at 7.35 m, has articulated fish (placoderms and chondrichthyans, currently under study), ichthyoliths and

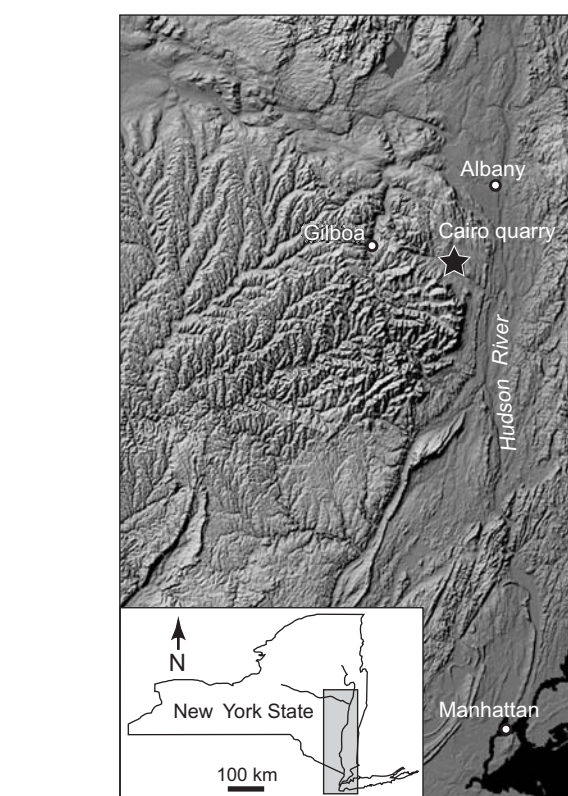


Fig. 1. Location of the Cairo quarry (star) (3.22 km northwest of Cairo, Greene County, 42.32° N and 74.04° W, NAD 83) in eastern New York State, USA (inset map); figure modified from Hernick et al. (2008: fig. 1).

the roots of a fossil forest (Cloutier et al. 2010). These black–dark grey shale to siltstone lenses feature a mixture of macro- to microscopic organisms from terrestrial and paludial, riverine, and coastal (estuarine to shallow littoral) communities.

The lack of burrows in the shale unit and its dark grey colour, which reflects abundant carbon, indicate dysoxic or anoxic conditions in the mud and probably at the sediment–water interface (e.g., Sagemann et al. 1991). The black colour of plant and shark debris at Cairo quarry reflects metamorphism of carbon to graphite and a ca. 6 km depth of burial during the Alleghanian orogeny (Sarwar and Friedman 1995). Diagenetic transformation of the bony material might have altered fine histological resolution.

The Cairo quarry succession, with a gentle northeast dip at the east end of the quarry and a gentle south dip in the central part of the quarry, records a southeast plunging anticline. More dramatic structural features include a high angle reverse fault that cuts out 0.75 m of black mudstone under the 9.0 m channel sandstone and produced a phacaloid cleavage in the mudstone at the northeast corner of the quarry (Fig. 2).

A problematical feature in the Cairo quarry stratigraphy follows from shallow rock cores drilled in September 2010 that reveal 3.0+ m of root-mottled palaeosols under the 7.35 m root surface. The 3.0+ m palaeosol interval is somehow replaced less than 150 m to the south by coarse-grained channel sandstone and the lower fish bed, as well as its accompanying black mudstone.

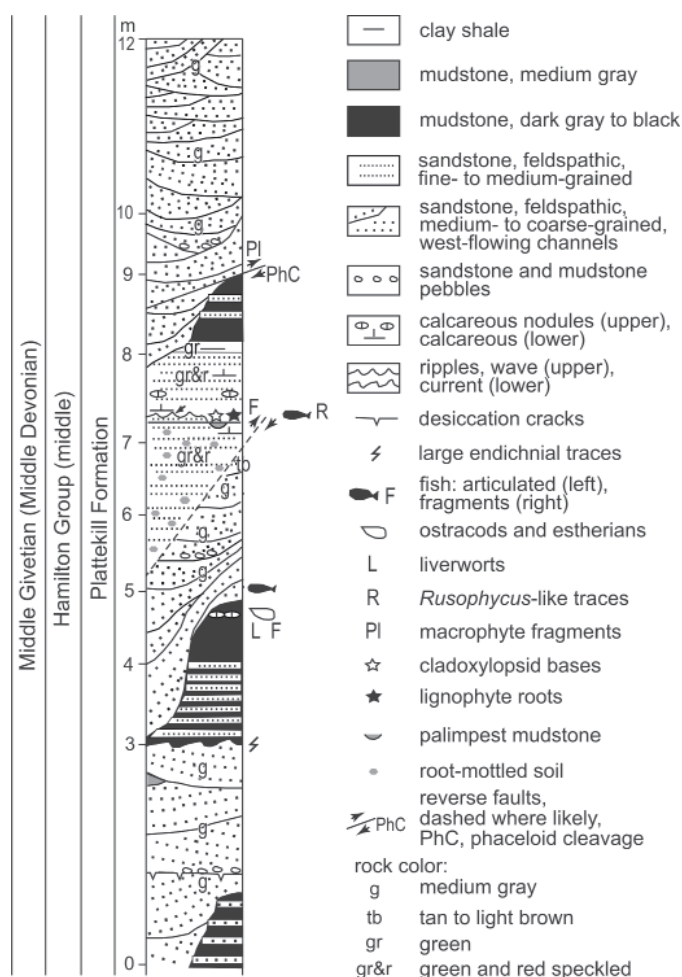


Fig. 2. Generalized stratigraphic section of the Plattekill Formation at Cairo quarry. Chondrichthyan specimens described herein originate from the 5-m level. The fish horizon at 7.35 m corresponds to the level of the fossilized forest mentioned by Cloutier et al. (2010).

The Plattekill Formation is dominated by channel sandstone that would have undergone minimal compaction, and it is unlikely that the 3.0+ m-thick palaeosol was forced downward by compaction. The best interpretation of this 3.0+ m palaeosol interval is that it is the upper plate of a thrust or high angle reverse fault (Fig. 2). Indeed, comparable tectonic features such as decollements, thrust faults, and high angle reverse faults are known in the generally flat-lying Devonian successions across New York. These structural features produced by the Late Palaeozoic Alleghanian orogeny in eastern and southern North America (e.g., Engelder et al. 1987).

Material and methods

Rock samples, all from the same stratigraphic horizon, were sieved with the 2 mm and 15 µm screens of the Canadian Standard sieve series (number 10 and 18, respectively). The sieved rock residues were then sorted using a Leica MZ9.5 binocular microscope. Isolated fish remains were cleaned by mechanical preparation with 22 gauge medical syringes and

entomological needles. Formic acid (7–14%) immersion was tried without conclusive results. Photography was done with a model JEOL JSM-6460LV scanning electron microscope (SEM). The tooth terminology is as in Ginter et al. (2010). The cusps are distinguished as major and minor. The major cusp is bigger and, when asymmetry is observed, presents the most pronounced deflection from the labio-lingual axis.

Light photomicrographs of the specimens were made with a QImaging QIcam mono 10-bit camera mounted on a Leica MZ16 binocular. Measurements were taken on the images using ImageJ (<http://imagej.nih.gov/ij>). The width (latero-medial) and length (labio-lingual) of the base were measured for the teeth of *Portalodus manoliniae* sp. nov. and *Wellerodus priscus*. The cusp and base-to-cusp apex lengths were not measured because most of the cusps are broken or abraded. This decision was also motivated by the fact that the cusps diverge, and their measurement on a planar image would underestimate their length as the cusps project into a tridimensional space. The mode of growth of likely adult and juvenile morphotypes in *P. manoliniae* sp. nov. was established by plotting basal width against basal length of the teeth. All values were transformed into $\log_{10}(x + 1)$. Linear regressions for adult and juvenile morphotypes were compared using an ANCOVA (Sokal and Rohlf 2012). Residuals were normally distributed and independent from the dependent variable; the residual variance was homogenous. Statistical analysis was performed using the R software (<http://www.R-project.org>).

Internal structure of the specimens of *Portalodus manoliniae* sp. nov. and *Wellerodus priscus* was investigated using a micro-CT scan Skyscan 1173. Micro-CT-scan results were sufficient to expose internal structure of the specimens. However, for smaller specimens, the resolution was insufficient to clearly identify histological details. Exposure time, accelerating voltage, and current varied among specimens and are indicated in figure captions; all image acquisitions were done using a 1.0 mm thick aluminium filter. Reconstruction of the micro CT-scan data was done using the NRecon software (provided with the Skyscan). Animations of the 3D reconstructions used for the Supplementary Online Material (SOM, available at http://app.pan.pl/SOM/app60-Potvin-Leduc_etal_SOM.pdf) were done using CTVox (software provided with the Skyscan). Images used for figures were modified in Adobe Photoshop CS3 to adjust contrast. For the scales referred to Elasmobranchii indet. fam., gen. et sp. B of Burrow et al. (2009), two incomplete specimens were cleaned by immersion in 30% H₂O₂, followed by a short immersion in 5% HCl. The exposed internal structure was photographed with a JEOL JSM-6460LV SEM.

Systematic palaeontology

Class Chondrichthyes Huxley, 1880
 Subclass Elasmobranchii Bonaparte, 1838
 Order Omalodontiformes Turner, 1997

Family Omalodontidae Ginter, Liao, and Valenzuela-Rios, 2008

Remarks.—The order Omalodontiformes is characterized by a tooth base that either extends labially or labio-basally or a relatively symmetrical base without a labial or lingual extension (Ivanov et al. 2011) and is subdivided into two families, Aztecodontidae and Omalodontidae. The Aztecodontidae is characterized by a subrectangular root situated directly under the crown and includes *Aztecodus/Anaerodus* (probably synonymous; Ginter et al. 2010) and *Manberodus* (Ginter et al. 2008, 2010). The Omalodontidae is characterized by a tooth base with a labially directed lobe (Ginter et al. 2008, 2010) and includes *Doliodus*, *Omalodus*, and *Portalodus* (Ginter et al. 2008). The Omalodontiformes also includes a genus of uncertain affiliation, *Siberiodus* (Ivanov and Rodina 2004). The teeth of *Karksiodus* from the Givetian of Estonia (Ivanov et al. 2011) also present a labially directed base but have not yet been affiliated to any order.

Although a base not lingually directed is a rare character among chondrichthyans, using it as a common denominator to unite the taxa has been questioned on the basis of differences in external and internal morphology (Ivanov et al. 2011). For example, the histology of *Omalodus* is extremely similar to the histology of *Phoebodus* (Hampe et al. 2004) and it has also been suggested that *Omalodus* could represent elements associated with the dermal skeleton of *Phoebodus fastigatus* rather than its teeth (Ginter et al. 2010). In *Karksiodus*, while the base is labially directed, the structure of the crown is more comparable to the structure of the crown in antarctilamnids (Ivanov et al. 2011). The scales that we tentatively attribute to *Portalodus* in the present paper are different from the ctenacanth-type scales of the geologically older *Doliodus problematicus*. The scales of *D. problematicus*, as well as other morphological characters, are closer to what is observed in antarctilamnids (Miller et al. 2003; Gess 2011). Obviously, more material, and hopefully articulated, will be needed in order to establish with certainty the phylogenetic relationships of these sharks.

Genus *Portalodus* Long and Young, 1995

Type species: *Portalodus bradshawae* Long and Young, 1995; Aztec Siltstone, Middle Devonian (Givetian), Portal Mountains, southern Victoria Land, Antarctica.

Emended diagnosis.—Sharks with large diplodont teeth, devoid of intermediate cusps. Cusps divergent, twisted in different planes in occlusal view, and polarized. Labial surface smooth. Cusps almost rounded in cross-section, slightly compressed with cutting edges developed along mesial and marginal edge. Base with a prominent labial platform, and lacking a projection on lingual face and an articular structure. Underside of base simple, without well-defined ridges or transverse groove. At least one large nutritive foramen and rostrocaudal groove on ventral surface.

Portalodus manoliniae sp. nov.

Figs. 3–6; SOM 1, 2.

2006 *Portalodus bradshawae*; Ginter et al. 2006: 33.

2010 *Portalodus bradshawae*; Ginter et al. 2010: 30, fig. 23.

2010 *Portalodus* sp. nov.; Potvin-Leduc et al. 2010: 148A.

Etymology: In memory of Sharon M. Mannolini (1968–2003), NYSM, who initiated some of the work at the Cairo locality.

Type material: Holotype NYSM 17715; paratypes NYSM 17722, 17726, 17736 (a juvenile specimen).

Type locality: Cairo quarry, Cairo, Greene County, New York State, USA.

Type horizon: Plattekill Formation, Givetian (Middle Devonian).

Material.—78 teeth: NYSM 17695–17772, 17959–17964 from type locality.

Diagnosis.—Species of *Portalodus* with cusps smooth on labial and lingual sides. Crown clearly delimited from the tooth base by a collar-like section. Base with at least one, but possibly up to four lingual foramina, with an equal number of labial notches and aboral rostrocaudal grooves. Teeth display a variation in crown and base morphology that is consistent with a monognathic heterodonty. Juvenile teeth smaller (Fig. 5), with cusps more delicate with more pronounced sigmoid shape. Only one lingual foramen present, aboral side almost smooth, without a groove.

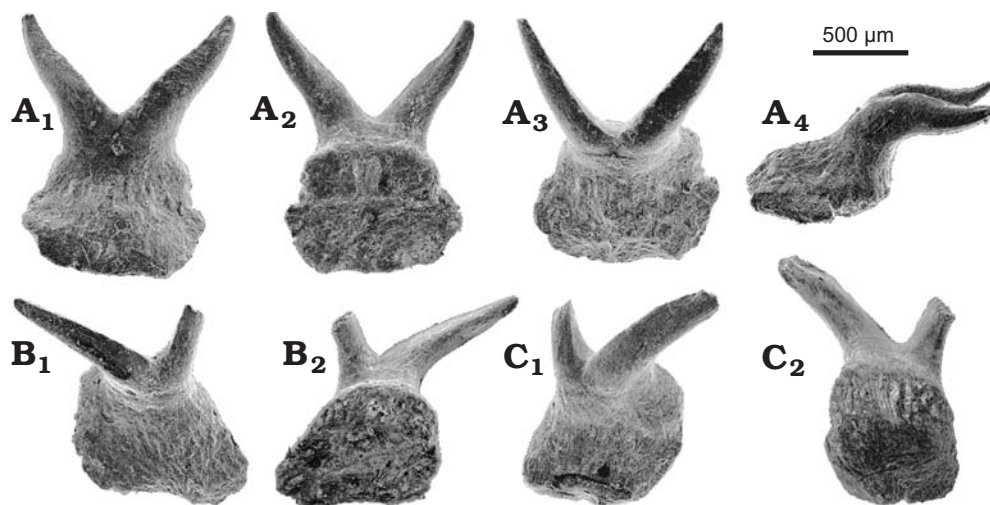


Fig. 3. Juvenile morphotype of the teeth of omalodontid shark *Portalodus manoliniae* sp. nov. from the Givetian of the Cairo quarry, New York, USA. **A.** NYSM 17736, paratype, in labial (A_1), lingual (A_2), occlusal (A_3), and lateral (A_4) views. **B.** NYSM 17756, in occlusal (B_1) and lingual (B_2) views. **C.** NYSM 17752, in occlusal (C_1) and lingual (C_2) views.

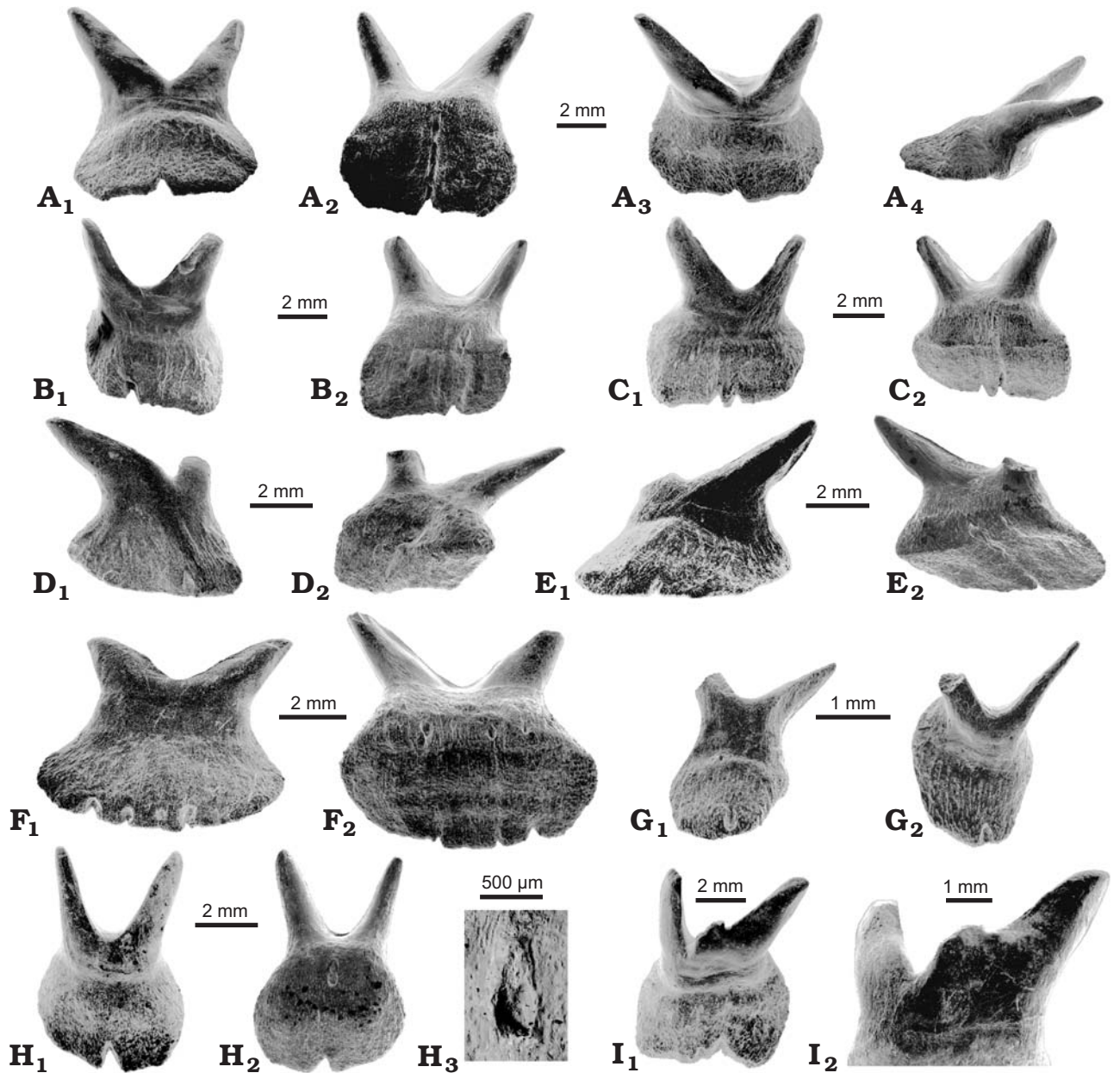


Fig. 4. Adult morphotype of the teeth of omalodontid shark *Portalodus mannoliniae* sp. nov. from the Givetian of the Cairo quarry, New York, USA. **A.** NYSM 17715, holotype, in labial (A₁), lingual (A₂), occlusal (A₃), and lateral (A₄) views. **B.** NYSM 17714, in occlusal (B₁) and lingual (B₂) views. **C.** NYSM 17737, in occlusal (C₁) and lingual (C₂) views. **D.** NYSM 17710, in labial (D₁) and lingual (D₂) views. **E.** NYSM 17701, in labial (E₁) and lingual (E₂) views. **F.** NYSM 17718, in labial (F₁) and lingual (F₂) views. **G.** NYSM 17758, in labial (G₁) and occlusal (G₂) views. **H.** NYSM 17726, paratype, in labial (H₁) and lingual (H₂) views, with close-up of the vertically superposed lingual foramen (H₃). **I.** NYSM 17719, in occlusal view (I₁), with close-up of the crown (I₂).

Description

General appearance.—The teeth are diplodont, with lingually oriented united cusps. The major and minor cusps are easily distinguished by their asymmetry in size, shape, and orientation; they diverge apically in occlusal and lateral views. Lateral deviation from the base is more pronounced in the major cusp. The cusps are smooth and circular or oval in cross-section. A cutting edge runs along the lateral and mesial edges. The mesial cutting edge is continuous between the cusps. There are no intermediate cusps or crenulations between the cusps. The crown is clearly delimited from the

base by a groove. In lateral view, the labial side of the base forms an obtuse angle with the crown; the angle ranges between 122° and 173° (mean = 148°; n = 73). The angle varies with the side of the tooth base, with one part of the tooth base with a slightly more obtuse angle than the other. There is no relation between this angle variation and the major/minor status of the cusps. Part of the base beneath the crown is continuous with it, forming a collar-like section. The base is labially oriented and is devoid of an apical button and basal tubercle. At least one lingual foramen is present.

Two morphotypes were identified based on their size and

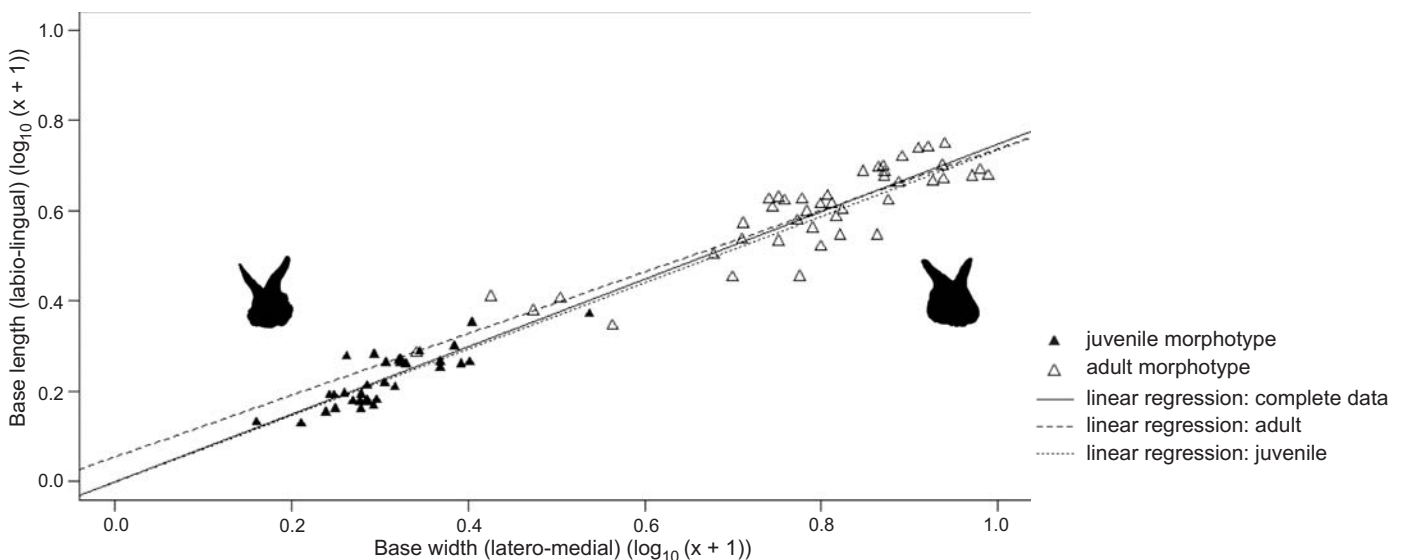


Fig. 5. Relationship between width and length of the tooth base for *Portalodus manoliniae* sp. nov. Regression lines are represented for the juvenile ($n = 32$ teeth) and adult ($n = 43$ teeth) morphotypes as well as for the complete sample.

shape. The smaller one is interpreted as that of a juvenile (Fig. 3) and the larger one is interpreted as adult (Fig. 4). The proportion of the tooth base, the shape of the crown, and the shape of the cusps also differ between the morphotypes. The ratio of base width to base length is smaller in the juvenile morphotype. The ratio increases linearly with the size of the teeth, without demonstrating different rates of increase between the two morphotypes (Fig. 5). A linear regression for all specimens was significant ($F_{(1,75)} = 1516$, $p < 2.2e-16$), but these regressions were not significantly different when comparing the juvenile and adult morphotypes (ANCOVA: $F_{(3,73)} = 525.8$, $p = 0.1410$) (Fig. 5). This increase indicates that growth of the base featured a greater increase in width than in length.

Juvenile morphotype.—The teeth of the juvenile morphotype are similar to the adult morphotype but are much smaller. The width of the base ranges from 0.4 to 2.4 mm and the length of the base ranges from 0.3 to 1.3 mm. The cusps are slender, more compressed laterally, and their sigmoid shape is more pronounced. Distinction between the major and minor cusp is observed but is not as pronounced as in the adult morphotype (Fig. 3B, C). Distinction between the cusps relies mostly on orientation asymmetry. The junction between the crown and the base appears more constricted than in the adult morphotype. The shape of the base is trapezoidal in aboral view. The base widens in the labial direction. The aboral face of the base is smooth. The notch of the labial margin and the basal groove are either absent or barely noticeable. There is a single lingual foramen.

Adult morphotype.—The size of the interpreted adult teeth is variable. The width of the base ranges from 1.2 to 8.8 mm, and the length of the base ranges from 0.9 to 3.7 mm. The cusps tend to be labio-lingually compressed at the base. The relative compression increases as the cusp increases in size. The lingual half of the cusp is more rounded transversally. The cutting edge separates the two sides of the tooth. The cusps

are slightly sigmoid in shape, but the minor cusp is straighter. The cusps are either symmetrical (Fig. 4A, H) or show a slight (Fig. 4B, C) to pronounced asymmetry (Fig. 4D, E). The base extends labially; this extension is similar to, or slightly greater than, what is observed in the juvenile morphotype. Its oral surface is covered with low ridges and crevices that begin at the junction of the base and the crown, and radiate from the margin of the base to the crown. The same relief is found on the underside, where it parallels the labio-lingual axis. The base is either round or oval in shape, with its longer axis generally in the medio-lateral axis. In occlusal view, the base may be asymmetrical and extends labially away from the apex of the major cusp. The degree of asymmetry increases with increased deflection of the major cusp (Fig. 4A–E).

The teeth vary in cusp size, orientation, and degree of lateral deflection. This variation is comparable to the monognathic heterodonty found in the Early Devonian *Doliodus problematicus* (Miller et al. 2003; Maisey et al. 2009) and *Protodus jexi* (Turner and Miller 2008). The variation in *P. manoliniae* sp. nov. teeth is also similar to that described by Johnson (1999) for the Permian xenacanthiform *Orthacanthus texensis*.

Most teeth have one or two foraminal openings on the lingual margin of the base (Fig. 4A–C), but up to four have been observed (Fig. 4F). The openings on the lingual face are either nearly circular or ovoid and surrounded by a thickened margin that forms a tubercle over the foramen. In rare cases, two superposed openings are present (Fig. 4H₂, H₃), a condition also observed in the omalodontid *Omalodus schultzei* (Hampe et al. 2004). The number of lingual foramina observed in *P. manoliniae* sp. nov. is greater than that noted in *P. bradshawae*, and appears to be variable and possibly size-related in *P. manoliniae* sp. nov. Thus, the number of lingual foramina is not regarded as a diagnostic feature. However, it is interesting that the biggest specimen found at Cairo is about half as large as the largest specimen from Antarctica. Labial notches are present on the labial margin and their number is equal to

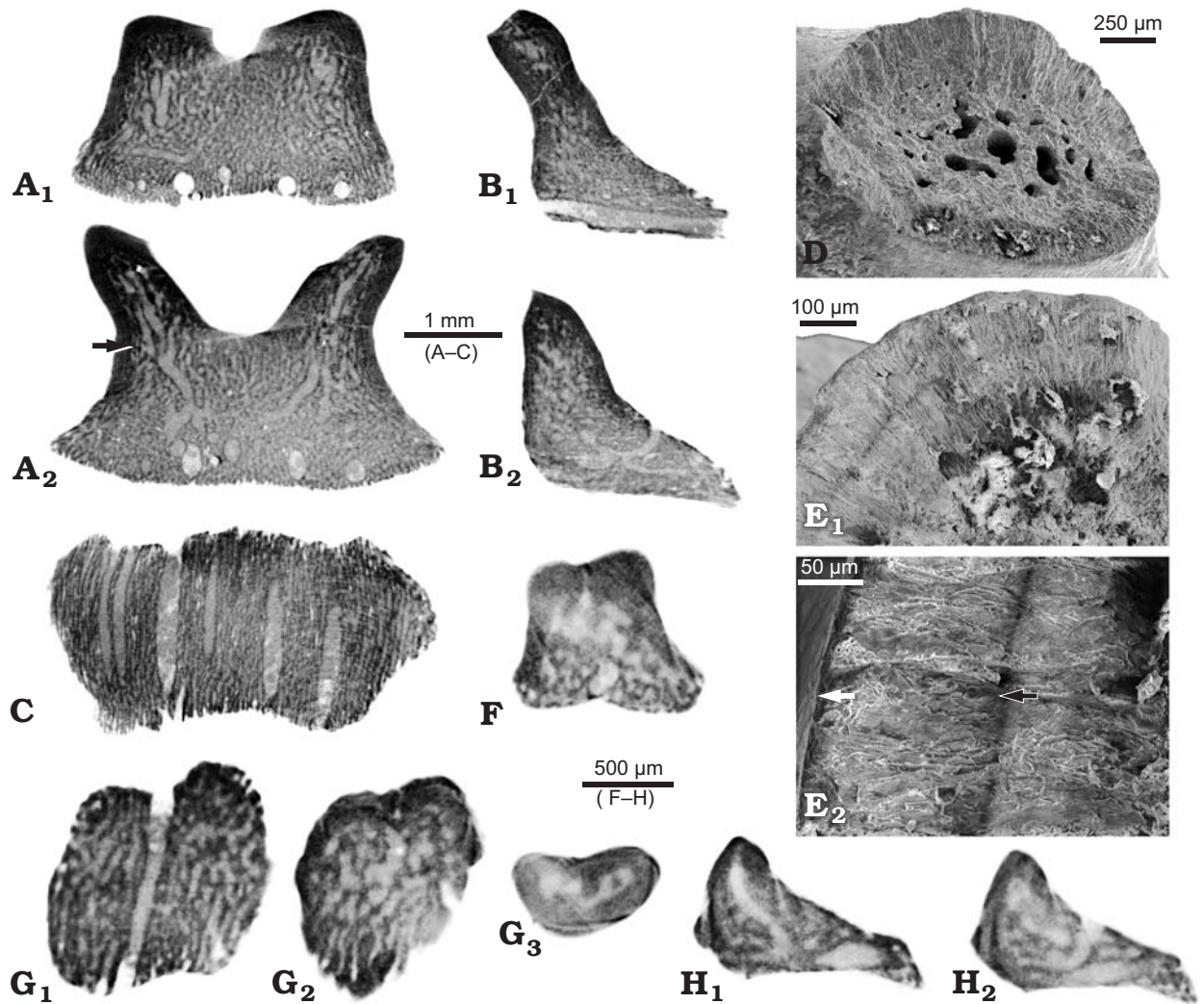


Fig. 6. Internal structure of the teeth of omalodontid shark *Portalodus manoliniae* sp. nov. from the Givetian of the Cairo quarry, New York, for the adult (A–E) and the juvenile (F–H) morphotypes. **A–C.** NYSM 17718; images acquired by micro CT-scan (exposure time: 1300 ms; accelerating voltage: 75kV; current: 106 μ A). **A.** Coronal planes angled through the crown and the base, near the lingual margin, with the base horizontal (A_1) and along the plane of the cusps (A_2), black arrow indicates a possible growth line in the orthodontine outer layer. **B.** Transverse planes through the right (B_1) and the left (B_2) cusps when looking from the labial side. **C.** Horizontal plane through the base. **D–E.** NYSM 17716; images acquired by SEM. **D.** Break facet of the right cusp when looking from the labial side. **E.** Close-up view of the margin of the left cusp (when looking from the labial side) (E_1) and of the orthodontine external layer (E_2); white arrow indicates the enamel outer layer, black arrow shows separation line between the two main orthodontine layers. **F–H.** NYSM 17699; images acquired by micro CT-scan (exposure time: 1000 ms; accelerating voltage: 70kV; current: 114 μ A). **F.** Coronal plane angled through the crown and the base. **G.** Horizontal planes through the base, near the bottom of the base (G_1), at about mid-base (G_2), and at the bottom of the crown, underneath the forking of the cusps (G_3). **H.** Planes along the labio-lingual axis through the left cusp (when looking from the labial side), near its median side (H_1), and inbetween the two cusps (H_2).

the number of lingual foramina. The position of the notches varies along the margin; they are usually located in the minor cusp region. Grooves of variable depth that connect a notch to a foramen are often found on the underside of the base, in some cases only weakly developed. The connecting grooves generally parallel the axis of deflection of the major cusp. The number of grooves is equal to the number of foramina.

Two specimens slightly differ from the above-described morphology of the adult morphotype. Specimen NYSM 17758 (Fig. 4F) has a narrow base, as opposed to the broader, rounded base that is more common. Specimen NYSM 17719 (Fig. 4I) shows a secondary cusp that emerges from the mesi-

al side of the major cusp base. A similar feature has been described in *Orthacanthus platypternus* (specimen SMP-SMU 64308 of Johnson [1987: fig. 3P, R]). Comparable deformed and fused teeth may result from disease, mutation, and trauma (Johnson 1987; Hampe 1997; Becker et al. 2000), or simple juxtaposition during ontogeny. In this case, trauma or ontogenetic variation is more likely the cause, given that disease and mutation would probably induce more extensive and longer-lasting effects on the whole tooth file rather than on a single tooth (Becker et al. 2000).

Internal structure.—Both the mature and juvenile morphotypes of *Portalodus manoliniae* sp. nov. were investigated

by micro-tomodensitometry. Two components were readily identifiable in the teeth: (i) an inner part composing the majority of the tooth, and (ii) an outer layer limited to the crown (Fig. 6A–C). Based on the histology of *P. bradshawae* (Hampe and Long 1999), the internal part of the tooth of *P. manoliniae* sp. nov. is identified as trabecular dentine whereas the outer layer would be orthodentine. Hampe and Long (1999) identified in *P. bradshawae* a third, external layer of enameloid; this layer is not visible in the CT-scan of *P. manoliniae* sp. nov. but can be observed in SEM images (Fig. 6E₂).

The outer layer of orthodentine is denser and appears darker (Fig. 6A, B). It is present only in the crown, distinguishing it from the base. Hampe and Long (1999) described parallel growth lines in the orthodentine layer in *P. bradshawae*. One main line is barely distinguishable in the adult morphotype of *P. manoliniae* sp. nov. (Fig. 6A₂). This line is evident in the SEM pictures (Fig. 6E) and appears to mark a separation between two main layers of orthodentine. The outer layer of the cusp shows the parallel alignment of the dentine tubules (Fig. 6E₁).

In *Portalodus manoliniae* sp. nov., the cavities of the trabecular dentine are elongated. In the base, they are mostly organized in a lingual to labial direction (Fig. 6C). The cavities become more vertical and wider as they are closer to the crown (Fig. 6A, B), as is the case in *P. bradshawae* (Hampe and Long 1999). One main luminal canal is found within each cusp (Fig. 6A₂), but these are accompanied by a network of thinner, vertical cavities (Fig. 6A₂, D).

Six vascular canals, rather than the four identified by external inspection, cross the base in the labio-lingual axis (Fig. 6A, C). Two main canals appear to be associated with the median side of each of the cusps. The other four are not symmetrically organized; the left side is irrigated by two small canals, as opposed to a larger single one on the right side (Fig. 6C). The network of cavities is connected to these canals. The basic architecture of the canals is formed by the transverse canals, with the canals extending to the apex of the cusps (Fig. 6A₂, B₁) and canals connecting the transverse blood canals to the oral surface of the base (Fig. 6B₂; see also the video information in SOM).

The cavity network of the trabecular dentine is simpler and the interior of the base appears more porous in the juvenile tooth of *Portalodus manoliniae* sp. nov. Otherwise, the organization of the cavities is similar (Fig. 6G). The network formed by the cavities is connected to the single median canal that crosses the base from the lingual to the labial side (Fig. 6G₁). The network of luminae separates into two main canals inside the crown (Fig. 6F, G₃) making the cusps more closely connected when compared to the wider separation observed in the base of adult tooth. The cusps are occupied by a single central canal (Fig. 6H), indicating that growth of the tooth was accompanied by addition of canals in the cusp peripheral to the main one. The canal in the cusp connects directly to the median transverse canal (Fig. 6H₁). As in the adult morphotype, the median transverse canal is connected by another canal to the oral surface of the base (Fig. 6H₂).

Remarks.—*Portalodus* teeth from the Plattekill Formation identified by Ginter et al. (2010) as *P. bradshawae* are interpreted herein as those of a new species. This identification is based on the absence of striations on the lingual side of the cusps in *P. manoliniae* sp. nov. Variation in the number of cristae is not considered as a valid criterion to distinguish *Portalodus* species because it is often size-dependent (Ginter 2004). However, we interpret the cristae by their presence (*P. bradshawae*) or absence (*P. manoliniae* sp. nov.), and regard this character as a valid criterion for specific distinction (Ginter and Ivanov 1996). While separation between the crown and the tooth base is apparent in *P. bradshawae*, delimitation is more definite in *P. manoliniae* sp. nov. The crown in *P. manoliniae* sp. nov. is continuous with a collar-like section of the base that is not seen in described specimens of *P. bradshawae* (Long and Young 1995).

The relative size between the two taxa could support the distinctiveness of the two taxa. In *Portalodus bradshawae*, the minor cusp is described as at least 33% shorter than the major cusp. Most of the available specimens of *P. manoliniae* sp. nov. have either one or both cusps broken. On specimens with fairly well preserved cusps, wear damage was evident, thus indicating that the observed length of the cusp is not representative of its initial length. Consequently, it is not possible to determine if the size relationship described for *P. bradshawae* holds true for *P. manoliniae* sp. nov. However, the few complete teeth of *P. manoliniae* sp. nov. either do not present as important a difference between the cusps or have cusps of similar length, both in the juvenile (Fig. 3A) and the adult morphotypes (Fig. 4A, B, H). Teeth showing cusps of similar size could either be symphyseal teeth, or it is possible that *P. manoliniae* sp. nov. differs from *P. bradshawae* by the fact that the minor and the major cusps are of comparable size. None of the specimens, even among the damaged ones, appear to show size discrepancies as important as that seen in specimen AMF 54330 of Long and Young (1995: fig. 7A, D; identified as SN96a [Gavin Young, personal communication 2013]).

Stratigraphic and geographical range.—Type locality and horizon only.

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

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

Genus *Wellerodus* Turner, 1997

Type species: *Wellerodus priscus* Eastman, 1899, Elmhurst, Illinois, USA, Middle to Late Devonian.

Wellerodus priscus Eastman, 1899

Fig. 7; SOM 3.

Material.—NYSM 17773–17779, juvenile teeth from Plattekill Formation, Cairo quarry, Greene County, New York, USA.

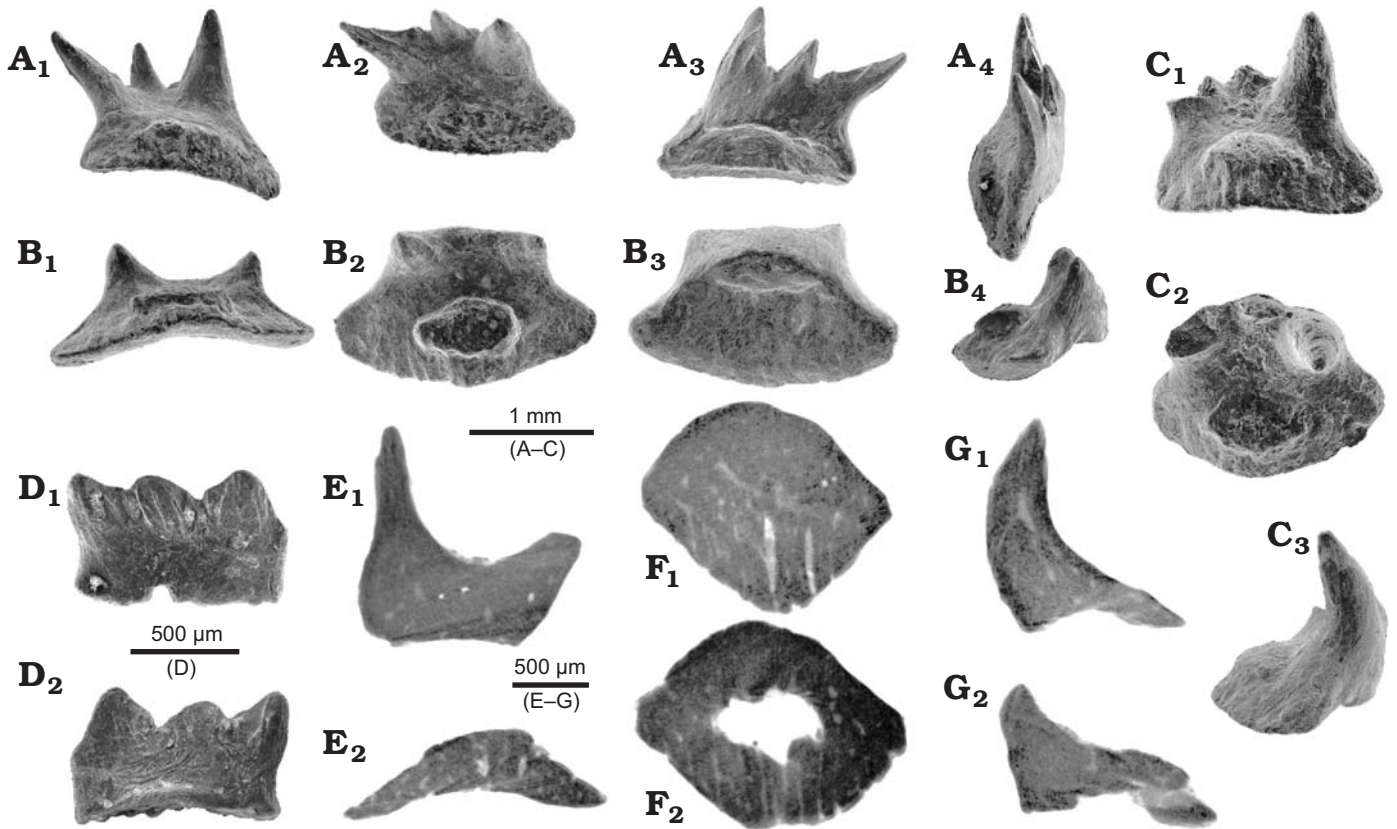


Fig. 7. Juvenile teeth of antarctilamid shark *Wellerodus priscus* from the Givetian of the Cairo quarry, New York. A–D, SEM micrographs. **A.** NYSM 17775 in lingual (A₁), occlusal (A₂), labial (A₃), and lateral (A₄) views. **B.** NYSM 17774 in lingual (B₁), occlusal (B₂), labial (B₃), and lateral (B₄) views. **C.** NYSM 17776 in lingual (C₁), occlusal (C₂), and lateral (C₃) views. **D.** NYSM 17779 in lingual? (D₁) and labial? (D₂) views. **E–G.** NYSM 17776; images acquired by micro CT-scan (exposure time: 1000 ms; accelerating voltage: 70kV; current: 114 µA). **E.** Coronal planes angled through the crown and the base, near the labial (E₁) and lingual (E₂) margins. **F.** Horizontal planes through the base, underneath the articular button (F₁) and through the depression underneath the base (F₂). **G.** Planes along the labio-lingual axis through the complete right cusp (G₁) and the broken median cusp (G₂) (when looking from the lingual side).

Description.—The teeth are diplodont with one intermediate cusp. When compared to the main cusps, the intermediate cusp appears to be bigger than observed in previously described specimens of *W. priscus* (Turner 1997: figs. 1, 5; Ginter et al. 2010: fig. 25C–H). Absence of the intermediate cusp in certain specimens appears to be the result of abrasion (Fig. 7B). The teeth are small and of approximately similar size. The base ranges in width from 1.0 to 2.3 mm and in length from 0.4 to 1.3 mm. The cusps are round in cross-section, but the minor cusps are occasionally compressed front to back. Only the main cusps have a cutting edge on the mesial and external side. A notch is seen in the cutting edge at the junction between the principal and the intermediate cusps. A comparison of cusp shapes is not easy because many specimens are damaged. In NYSM 17775 (Fig. 7A), the minor cusp is sigmoid, and the major cusp is straighter. The minor cusp diverges more strongly from the occlusal axis. The cusps are characterized by few cristae on the labial side. They originate at the level of the base of the intermediate cusp and begin to curve mesially at the mid-height of the principal cusps, then curve again towards the apex of the cusp. The cristae are straight on the labial side of the

cusp of NYSM 17775. The intermediate cusp shows two straight cristae that start at the cutting edge level and join at the cusp's apex. The lingual side of the cusps is smooth.

The tooth base is oval, lingually oriented, and has a well-developed oval button (Fig. 7B₂, C₂). A single notch is found on the lingual margin, except in NYSM 17778 where two are present. The base is arched in lingual view and expands laterally beyond the width of the principal cusp base. The base can narrow under the area of cusp insertion. The base can be asymmetrical, in which case it is more laterally extended in the direction opposite the apex of the minor cusp. In lateral view, the base has a labial concavity that would seem to fit into the articular button of the next tooth in the series. In some cases, a slight labial extension is present. Specimen NYSM 17779 differs from the other specimens in that the orientation of its base is not clearly defined (Fig. 7D). The orientation is inferred from the position of the marginal notch and the cristae which, based on NYSM 17775 (Fig. 7A₃), should be labially oriented. The cusps are flattened and triangular, and the size of the intermediate one is similar to the main cusps.

Histology.—Based on the similarity of general morphology, *Wellerodus priscus* is expected to share the same histological

structure as *Antarctilamna prisca* in possessing an internal layer of trabecular dentine with an outer layer of orthodentine at the crown level (Hampe and Long 1999). Micro-tomodensitometry of *W. priscus* teeth did not provide histological detail, but a few canals are apparent within the base (Fig. 7E₁, F). The cusps are characterized by one main canal (Fig. 7G₁) that connects to a more complex network located in the base underneath the articular button. In NYSM 17776, circulation at the level of the articular button is ensured by two main canals (Fig. 7E₂, F₁) that open in the lingual side of the depression seen underneath the base. Only one such canal was noted in *A. prisca* (Hampe and Long 1999). In situ, the basal depression would have been connected to the articular button of the following tooth in a tooth family, thus putting in contact the internal canals of one tooth with the straight canals crossing underneath the articular button of the following tooth (Fig. 7G₂; see also SOM 3). The lingual side of the base is crossed by smaller canals leading directly to the depression; there are no similar canals on the labial side of the base (Fig. 7F₂).

Subclass Elasmobranchii Bonaparte, 1838

Compound chondrichthyan scales Type 1 sensu Liao et al. 2007

Figs. 8, 9; SOM 4.

Material.—NYSM 17782–17789, scales; NYSM 17960, an incomplete fin spine with associated scales and smaller, rounder elements from Plattekill Formation, Cairo quarry, Cairo, Greene County, New York, USA.

Description.—The scales are of ctenacanth type (sensu Reif 1978). They have either two or three rows of ridge-ornamented odontodes (Fig. 8A, B). The main row is widest and composed of eight to ten odontodes (except for the smaller NYSM 17787; Fig. 8C). An underlying row can, in some cases, be distinguished by the apexes of odontodes on the posterior margin of the crown. The overlying, higher row is composed of either one, two, or three odontodes that are not in contact with each other. This higher row contains a main odontode

relatively central to the main row. This main odontode originates at the anteriormost point of the base. The odontodes of the higher row are characterized by a small triangular area with a pattern of ridges that occurs at their contact with the base (Fig. 8D, E₁). These ridges taper where the odontodes curve towards the posterior extremity. The base is more often concave (Fig. 8E₃), but a convex base is present in one specimen (NYSM 17788). The overall shape of the base varies between rhomboid and oval, with the anterior side sometimes irregular in outline. A row of vascular openings is present under the crown on the posterior side of the neck (Fig. 8E₂).

The associated scales appear identical to MGUV 5945 of Ginter et al. (2008: fig. 3) and to a specimen assigned to the chondrichthyan dermal denticle type 1 of Liao et al. (2007: fig. 4). In both cases, the specimens came from the Aragonian Pyrenees of Spain. Of interest is the triangular pattern found at the base of the odontodes of the higher row in the Cairo scales. This characteristic form is also present in MGUV 5945 of Ginter et al. (2008) but appears to be absent from the other scales figured by Liao et al. (2007) and Ginter et al. (2008). More specimens from either locality would help to establish if this represents a taxonomically diagnostic character. Liao et al. (2007) suggested an assignment to *Phoebodus*, but as this taxon has not been found in the Cairo assemblage, and given the similarity with the Cairo scales, it is possible that the ctenacanth-type scales from Cairo belong to *Wellerodus*. It is interesting to note that a tooth identified as *Antarctilamna* was also found in the Aragonian Pyrenees (Ginter et al. 2008).

The Cairo scales are also comparable to NMV P228929 of Elasmobranchii indet. fam. gen. et sp. A of Burrow et al. (2009: fig. 9) from the Aztec Siltstone in Antarctica, who noted a similar morphology in *Antarctilamna prisca* material. The scales described here, however, have a different morphology from the scales described in the holotype of *A. prisca* (Young 1982). The scales of *A. prisca* are rounder, flatter and show a circular pattern of ridges (Young 1982: pl. 87: 6, 7), more similar to the scales of *Doliodus problematicus* (Miller et al. 2003: fig. 1B) than to the scales found in

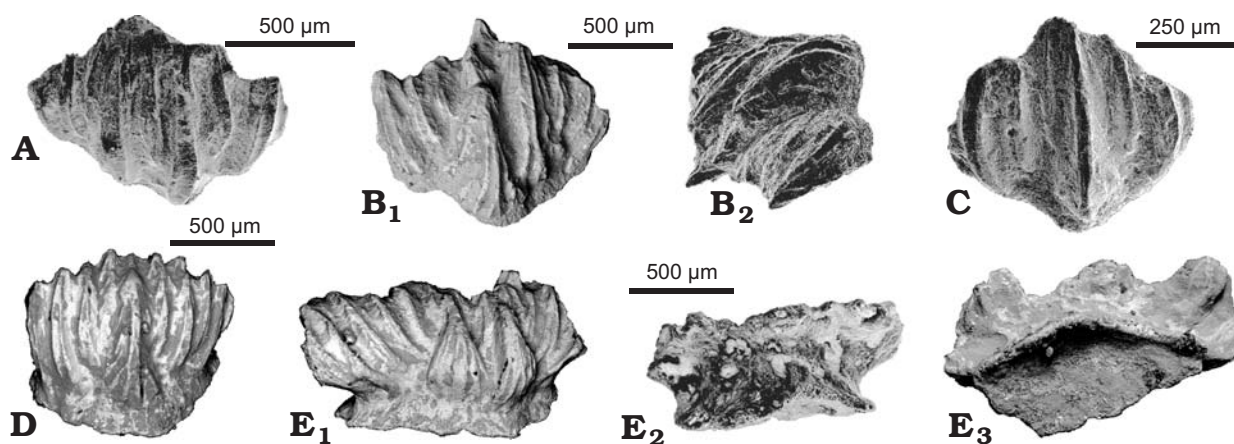


Fig. 8. Compound chondrichthyan scales Type 1 sensu Liao et al. (2007), attributed to *Wellerodus priscus*, from the Givetian of the Cairo quarry, New York. A. NYSM 17785 in dorsal view. B. NYSM 17782 in dorsal (under BES mode) (B₁) and dorso-lateral (B₂) views. C. NYSM 17787 in dorsal view. D. NYSM 17783 in dorsal view (under BES mode). E. NYSM 17786 in rostral (E₁), caudal (E₂), and basal (E₃) views (under BES mode).

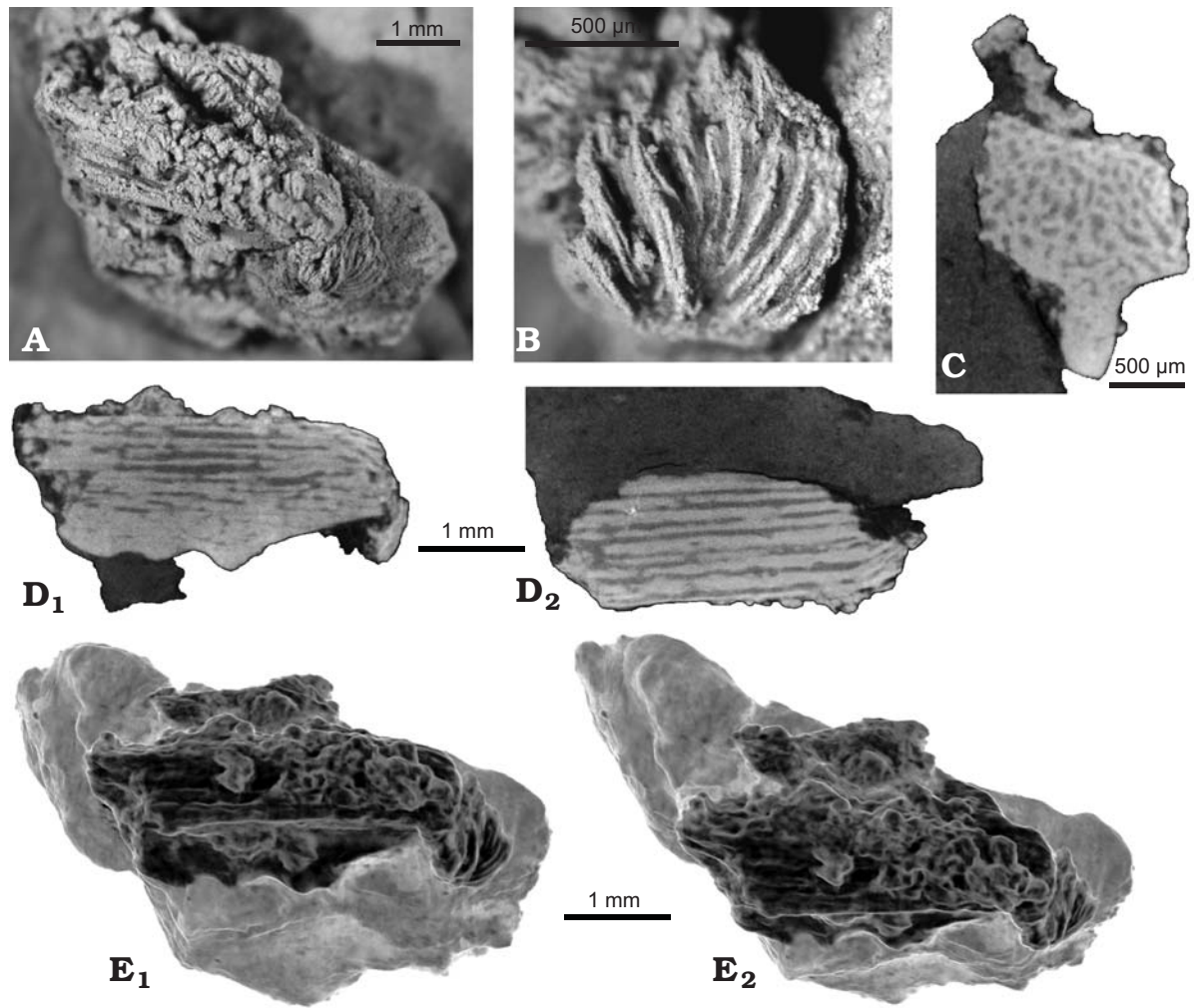


Fig. 9. Incomplete fin spine with compound chondrichthyan scales that are comparable to Type 1 sensu Liao et al. (2007) from the Givetian of the Aragonian Pyrenees, Spain, NYSM 17790. **A.** Specimen whitened with ammonium chloride. **B.** Close-up view of associated spine, associated to compound chondrichthyan scales Type 1 sensu Liao et al. (2007). **C.** Transversal section extracted from a reconstruction of the specimen from micro CT scan data (exposure time: 1650 ms; accelerating voltage: 65kV; current: 120 μA), showing the internal canals. **D.** Sections extracted from the reconstruction of the fin spine tip from micro-tomodensitometry data; lateral (D₁) and dorsal (D₂) views, showing the system of internal canals. **E.** 3D reconstructions of the fin spine tip from micro CT scan data (exposure time: 1650 ms; accelerating voltage: 65kV; current: 120 μA), in lateral (E₁) and dorso-lateral (E₂) views.

Cairo. Since then, new articulated material currently under study, including associated scales and dentition, confirms the affiliation of the compound scales with *W. priscus* (DP-L. and RC, personal observations).

The tip of a small fin spine was recovered in association with the scales just described (NYSM 17790; Fig. 9A, B). The spine is covered with longitudinal, relatively smooth ridges. The smoothness is likely owing to abrasion as a small section of a ridge at the spine's tip shows a short series of tubercles. A line of median denticles is present on the ventral face (Fig. 9D₂). The specimen is partly covered with compound chondrichthyan scales and small rounded elements (Fig. 9A, E₂). The interior of the spine, as revealed by micro-CT scan, is mostly occupied by numerous canals running parallel to the long axis of the spine, with the occasional perpendicular connection between canals (Fig. 9C, D₁, E₁; see also SOM 4). A specific pattern does not seem to be present in the organization of the canals.

Elasmobranchii indet. fam., gen. et sp. B sensu Burrow et al. 2009

Fig. 10.

Material.—NYSM 17791–17799; 17898–17958, scales from Plattekill Formation, Cairo quarry, Cairo, Greene County, New York State, USA.

Description.—The body scales are characterized by a simple rhomboid crown and, in most cases, bear lateral flanges. In lateral view, these flanges extend upwards from anterior to posterior (Fig. 10E–I). The crown can be asymmetric; in some cases only one flange is visible (Fig. 10F), while in others the lateral halves can be antero-caudally displaced relative to each other (Fig. 10G). The posterior edge tapers and extends only slightly beyond the base. The anterior edge generally has a single median depression; however, there might be from zero to three depressions (Fig. 10H). A concentric pattern is observed in the crown of some specimens

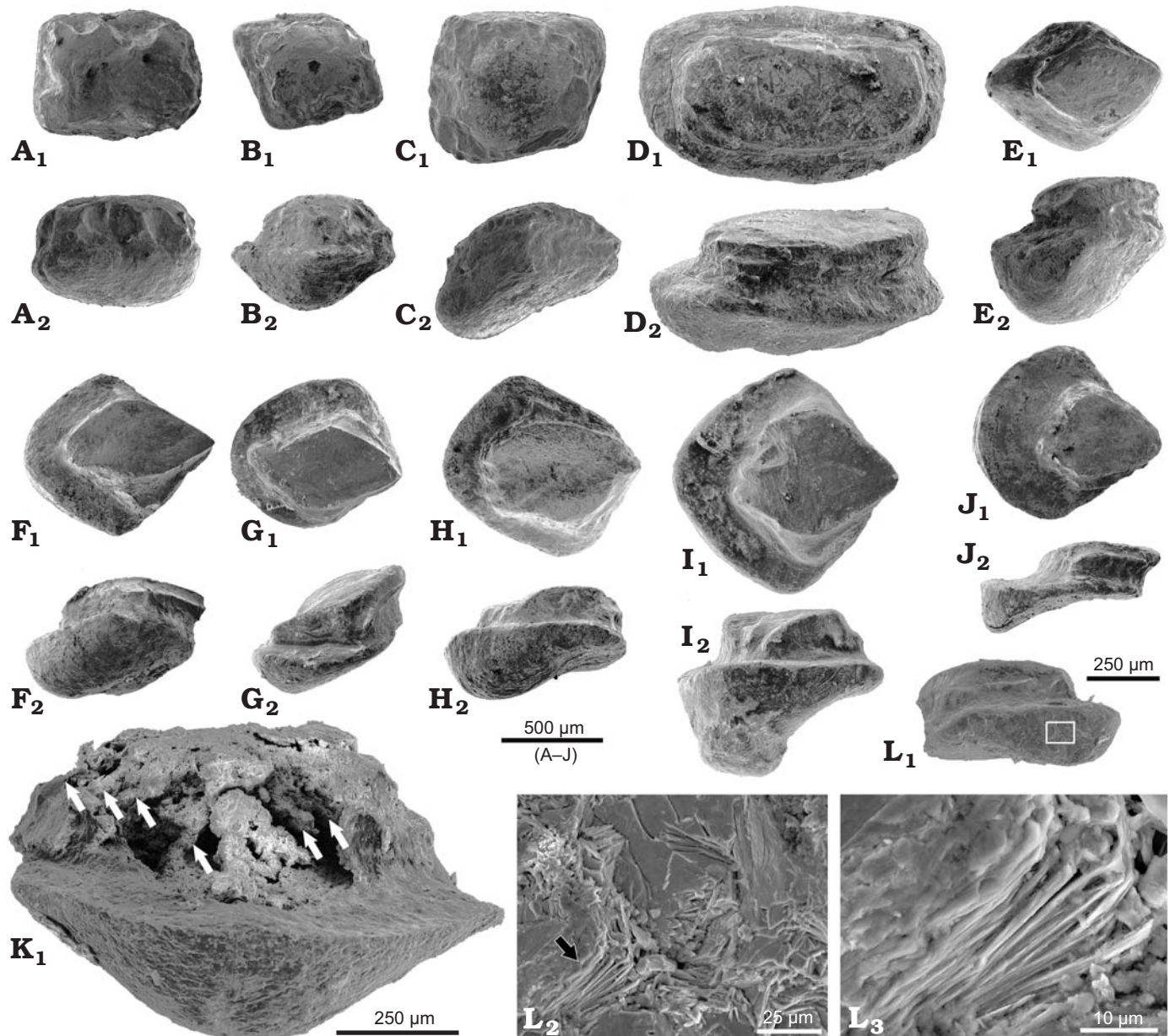


Fig. 10. Scales of Elasmobranchii indet. fam., gen. et sp. B sensu Burrow et al. 2009 from the Givetian of the Cairo quarry, New York, tentatively assigned to omalodontid shark *Portalodus mannoliniae* sp. nov. **A.** NYSM 17899. **B.** NYSM 17898. **C.** NYSM 17900. **D.** NYSM 17958. **E.** NYSM 17791. **F.** NYSM 17796. **G.** NYSM 17927. **H.** NYSM 17795. **I.** NYSM 17944. **J.** NYSM 17798. **K.** NYSM 17934, white arrows indicate the superposed internal layers in the crown. **L.** NYSM 17918 (**L**₁), with magnification of framed section (**L**₂); the close-up on the bundle of fibres (**L**₃) corresponds to the section identified by the arrow in **L**₂. In crown (**A**₁–**J**₁), lateral (**A**₂–**C**₂, **E**₂–**H**₂, **J**₂, **L**), postero-lateral (**D**₂), antero-lateral (**I**₂), and anterior (**K**) views.

and suggests areolar growth. The crown is smaller than the base, and its anterior edge does not reach the anterior margin of the base. Consequently, the base has an anterior U-shaped plateau when viewed from above. The base is smooth and generally rhomboid, but rounded in some specimens. In lateral view, the anterior half of the base is bulbous whereas the posterior half is flattened. The bulbous part generally occupies about half of the length of the base, but variation is observed among the scales (Fig. 10E, I, J). One specimen (Fig. 10D) is a flattened, very wide scale that appears to be the result of a fusion, as the base of the scale has three bulbous structures that are aligned laterally.

Scales identified as head scales are characterized by an irregular, almost stellate crown (Fig. 10A–C). The crown outline varies from oval to circular, and may cover the whole surface of the base, but can also recede from the anterior margin of the base. The base may be more rounded and symmetrical, but in some cases retains the shape described above for the body scales. In lateral view, the base ranges in shape from that present in body scales to a massive, block-like form (Fig. 10A–C).

Although investigation with the micro-CT scan was inconclusive, the internal structure was partly revealed by SEM of damaged specimens (Fig. 10K, L). The crown ap-

pears to be composed of superposed layers (Fig. 10K); these layers are organized similar to the semicircular growth zone observed in the crown of Elasmobranchii indet. fam., gen. et sp. B of Burrow et al. (2009: fig. 10m). Unoriented bundles of fibres are observed in the base (Fig. 10L).

Similar head and body scales have been described from the Middle Devonian of Antarctica (Burrow et al. 2009). Burrow et al. (2009: 86) mentioned that these specimens could belong to either *Portalodus* or *Aztecodus*. As *Aztecodus* has not been identified at Cairo, despite extensive sampling and fieldwork, these scales are tentatively assigned to *P. manoliniae* sp. nov. However, the pustulous base, one of the characteristics noted by Burrow et al. (2009), is not observed in the Cairo material.

Discussion

Ontogenetic perspective.—Ontogenetic variation is well known in extant and fossil sharks (Raschi et al. 1982; Gottfried and Francis 1996; Adnet 2006; Purdy and Francis 2007). For this reason, we regard the smaller specimens that appear to be variants of *Portalodus* and *Wellerodus* as juveniles.

The shape of the crown, the size of the tooth, the shape and thickness of the base, the number of cusps, and the presence of serrations are morphological characters known to change during ontogeny (Peyer 1968; Ginter and Ivanov 1992; Gottfried and Francis 1996; Johnson 1999; Adnet 2006; Purdy and Francis 2007). Teeth of juveniles have been described for such Devonian taxa as *Phoebodus gothicus* (Ginter 1990) and *P. bifurcatus* (Ginter and Ivanov 1992; Turner and Youngquist 1995). Characters known to be modified in the ontogeny of Devonian shark teeth (Ginter 1990; Ginter and Ivanov 1992), as well as in *Portalodus manoliniae* sp. nov., include modification in cusp shape and angle of divergence, as well as size of the base and differences in shape, texture and thickness. It is unlikely that the juvenile teeth of *P. manoliniae* sp. nov. represent embryonic tooth buds leading to the adult morphotype because both types of teeth appear completely formed, and morphologically transitional forms are unknown. Sexual dimorphism can explain differences in size and shape in dentition (Peyer 1968); however, the absence of size overlap and the linear regression similarity (Fig. 5) reject this hypothesis.

Teeth of the juvenile morphotype of *Portalodus manoliniae* sp. nov. are generally well preserved (Fig. 3). The cusps are almost always complete and do not show wear. The broken cusps likely resulted from damage during preparation. All the teeth of the adult morphotype show wear; most have broken cusps, but the broken surfaces are often polished and eroded (Fig. 4). The wear appears mostly limited to the cusps, and the damaged cusps are not blunt as would be expected from abrasion (Irmis and Elliott 2006). The wear is compatible with the slower rate of tooth replacement proposed for Palaeozoic sharks (Williams 1990; Botella et al. 2009), as teeth with a rapid replacement rate and a shorter

functional stage would exhibit little wear (Zangerl 1981; Downs and Daeschler 2001).

As an ontogenetic shift in diet is known among some extant sharks and bony fish (Wetherbee and Cortés 2004; Newman et al. 2011), the difference between juvenile and adult morphologies in *Portalodus manoliniae* sp. nov. could have been associated with a modification of the feeding habits. This could suggest one of three interpretations to explain the reduced tooth wear: (i) a juvenile diet with lesser abrasive effects; (ii) faster tooth replacement in juvenile sharks; (iii) a short duration of the juvenile period. An alternative hypothesis would be that these teeth are embryonic rather than juvenile; this would mean that the teeth were shed before being used, hence the absence of wear (Shimada 2002; Purdy and Francis 2007).

Previous descriptions of *W. priscus* (Eastman 1899; Husakof and Bryant 1918; Turner 1997) encompassed variation that might have included ontogenetic variation. The teeth described here, however, differ from this material by the smaller size of the specimens. Numbers of cristae are also different, as the observed numbers are less than those described by Turner (1997), but this character may be size-related (Ginter 2004). The morphology of the base differs slightly from the description of Turner (1997); the base widens in the lingual direction (Fig. 7). Ontogenetic heterodonty is suggested as the source of this variation because modification of the base and differences in ornamentation are observed in other juvenile Devonian shark teeth (Ginter and Ivanov 1992).

The juvenile teeth of *Wellerodus priscus* show wear. Except for NYSM 17775 (Fig. 7A), the cusps are often eroded and blunt, and their outer surface seems abraded. The level of abrasion is greater than that observed on teeth of similar size of *Portalodus manoliniae* sp. nov. This difference between the types of damage and the fact that the teeth of *W. priscus* are approximately all of the same size (as opposed to the variation seen in *P. manoliniae* sp. nov.) suggests post mortem transport or in situ abrasion (Anderson 2001).

Palaeobiogeographical perspective.—Vertebrate faunas became more and more cosmopolitan by the Late Devonian, with the suggestion of global dispersal beginning during the Middle Devonian (Young 1990, 2003b; Young et al. 2000, 2010; Janvier 2007; Blicek 2011). The record of the Middle Devonian is not as well documented as the Late Devonian, and it is difficult to establish with certainty the chronology of dispersal. Current knowledge suggests that, among vertebrates, chondrichthyans appear to show the oldest record of widespread dispersal because a number of taxa, such as *Phoebodus*, *Omalodus*, and *Ohiolepis* were cosmopolitan already by the Givetian (Lebedev and Zakharenko 2010). The presence of *Portalodus* and the *Antarctilamna–Wellerodus* group in the Givetian of the northeastern United States adds two more taxa.

The geographical and stratigraphical record of *Portalodus* is limited. *Portalodus* was previously known from the Givetian of Antarctica (Young 1982; Long and Young 1995) and South Africa (Anderson et al. 1999). A tooth impression

from Colombia was also referred to *Portalodus* (Janvier and Villarreal 2000).

The record of remains assigned to the Antarctilamnidae is more abundant and suggests that antarctilamnids colonized an important part of the shores of Palaeotethys (Fig. 11; occurrences of the Antarctilamnidae are listed in Table 1). Not included in the distribution is the alternative interpretation of scales and fin spines from the Australian Silverband Formation as *Antarctilamna* (Turner 1986), which has since then been confirmed otherwise by Burrow (2003) (*Radioporacanthodes* sp. cf. *R. qujingensis* and *Sinacanthus? micracanthus*, respectively).

Also of interest is the mention of *Diplodus* sp. cf. *D. priscus* in the Famennian Daihua assemblage of South China (Wang and Turner 1985, 1995; Zhao and Zhu 2010). As *D. priscus* was subsequently revised by Turner (1997) as *Wellerodus priscus*, it should be reinterpreted as well as *W.* sp. cf. *W. priscus*. Zhao and Zhu (2010) also mentioned the presence in the same assemblage of “cf. *Dittodus grabau*.” This identification should be corrected to “cf. *Omalodus grabau*” for the same reason (Turner 1997).

Two particularities emerge from the distribution of *Antarctilamna*, *Wellerodus*, and *Portalodus* (Fig. 11). The first is that, except for the uncertain specimen from the Famennian of China, *Wellerodus* appears to be found only within Laurentia, whereas *Antarctilamna* appears to be restricted to Gondwana. However, this should be considered with care: both taxa occur between latitudes 30–60°S, and *Wellerodus* has so far only been recognized from teeth that are morphologically similar to the teeth of *Antarctilamna*. The second

particularity is that, although based on only three occurrences, all remains of *Portalodus* so far have been found alongside antarctilamnid remains. This suggests that *Portalodus* remains could serve as an indicator of antarctilamnid presence. It is important to note, however, that the relationship is not reciprocal, as antarctilamnid remains are not necessarily accompanied by *Portalodus*.

Lebedev and Zakharenko (2010) regarded *Portalodus* and *Wellerodus* as local, endemic genera, and *Antarctilamna* as a polydemic genus. With the discovery of North American *Portalodus* and *Wellerodus*, and considering *Antarctilamna* and *Wellerodus* as synonymous (Ginter et al. 2010), *Portalodus* and sharks associated to the *Antarctilamna*–*Wellerodus* group are herein reconsidered as cosmopolitan, as defined by Lebedev and Zakharenko (2010).

The oldest Antarctilamnidae occur in the late Lochkovian–early Pragian (Santa Rosa Formation at Seripona; Janvier and Maisey 2010) and late Emsian–early Eifelian (Belén Formation; Janvier and Maisey 2010) of Bolivia, in the Pragian (Emsian in Burrow et al. 2006) of Saudi Arabia (Forey et al. 1992) and in the Pragian of Australia (Burrinjuck; Young 2011). This last occurrence also indicates an older age for the Australian Bunga Beds specimens of *A. prisca* (Young 2007, 2011). This suggests a peri-Gondwana early dispersion, but without a hypothetical centre of origin. The observed distribution, however, suggests that antarctilamnid, or antarctilamnid-like, remains should be found in North Africa. It is interesting then to note the recent discovery in the Emsian of Algeria of the chondrichthyan *Tassiliodus lessardi* (Derycke and Goujet 2011). Although its phylogenetic relationships

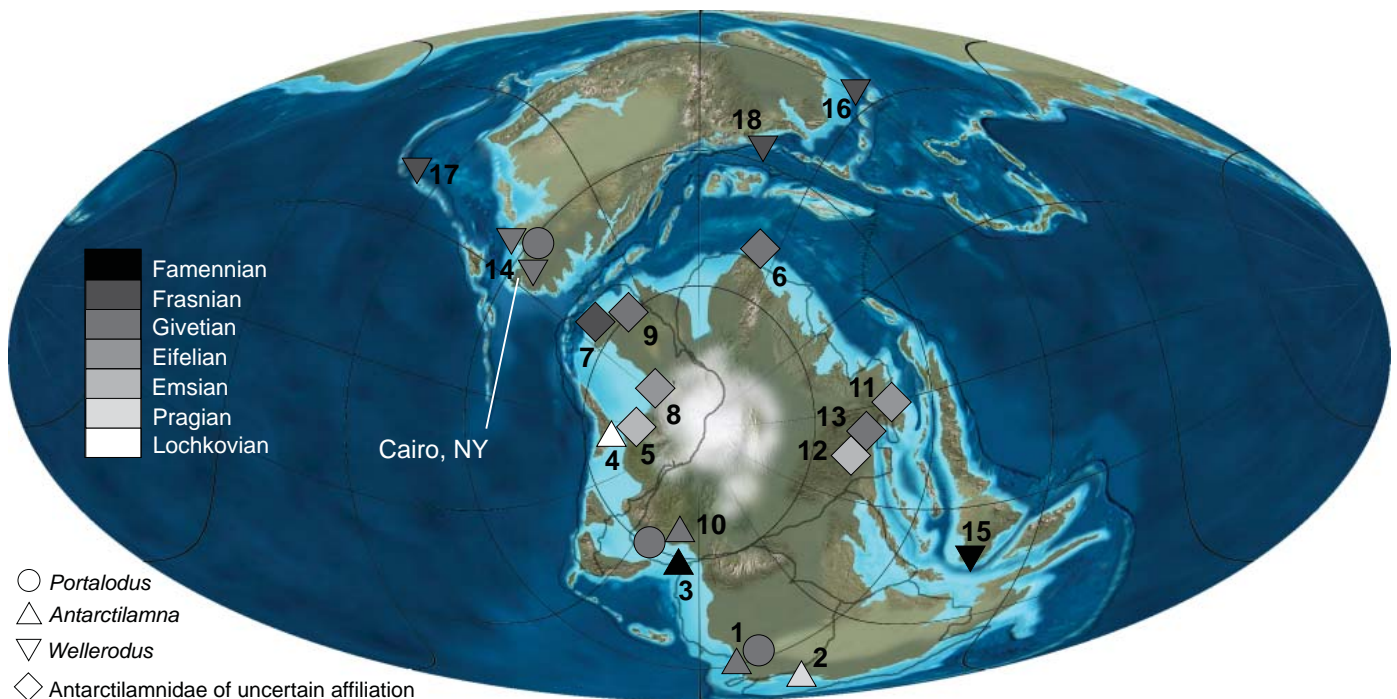


Fig. 11. Early Devonian (400 Ma) map in South Polar Mollweide projection with occurrence of remains currently assigned to the Antarctilamnidae and *Portalodus*. Locality numbers for the Antarctilamnidae refer to Table 1; when more than one locality are represented by the same symbol, the oldest one is depicted. *Portalodus* was reported in Antarctica (Young 1982; Long and Young 1995; localities 1.1–1.3 in Antarctilamnidae), South Africa (Anderson et al. 1999; locality 9 in Antarctilamnidae), and New York (this paper; locality 14 in Antarctilamnidae). Map modified from Blakey (2008: fig. 8B).

Table 1. List of taxa affiliated to the Antarctilamnidae with localization, age, kind of material known, and references. ¹ age from Young (2007); ² age from Janvier and Maisey (2010); ³ age from Forey et al. (1992); ⁴ age from Burrow et al. (2006); ⁵ age from Forey et al. (1992); ⁶ age from Ginter (2004).

Number	Identification	Localization	Age	Material	References
1.1	<i>Antarctilamna prisca</i>	Antarctica (Southern Victoria Land)	Late Givetian, Early Frasnian	partially articulated specimen including neurocranium; teeth, scales, fin spines	Young 1982
1.2			Middle/Late Devonian	teeth	Long and Young 1995
1.3			?Late Givetian	teeth, scales?	Burrow et al. 2009
2.1	<i>Antarctilamna prisca</i>	Australia (Bunga Beds, NSW)	Emsian–Eifelian ¹	teeth, fin spines, endocrania and jaw remains	Young 1982
2.2		Australia (Burrinjuck, NSW)	Pragian	Meckel's cartilage	Young 2011
3	<i>Antarctilamna ultima</i>	South Africa	Famennian; Witpoort Formation	mandibular arch, ceratohyals, fin spine, teeth	Gess 2007, 2011
4	<i>Antarctilamna seriponensis</i>	Bolivia	Late Lochkovian–Early Pragian ² ; Santa Rosa Formation (Seripona)	fin spine	Gagnier et al. 1988
5	Antarctilamnidae	Bolivia	Late Emsian–Early Eifelian ² ; Belén Formation	fin spines	Gagnier et al. 1989
6	<i>Antarctilamna?</i> sp.	Spain (Aragonian mountains, Pyrenees)	Givetian	tooth	Ginter et al. 2008
7	Antarctilamnidae	Colombia	?Late Frasnian	spine, tooth	Janvier and Villarroel 2000
8	<i>Antarctilamna</i>	Brazil	Eifelian–Givetian	tooth, spine	Maisey and Melo 2005
9	Antarctilamnidae	Venezuela	Givetian–Frasnian	spines	Young and Moody 2002
10	<i>Antarctilamna</i> sp.	South Africa	Givetian; Adolphspoor and Klipbokkop Formations	teeth	Anderson et al. 1999
11	<i>Antarctilamna</i> sp.	Iran	Eifelian	spine	Blieck et al. 1980; reinterpreted in Young 1989, 1991
12	<i>Antarctilamna</i> sp.	Saudi Arabia	Pragian ³ or Emsian ⁴ ; Wajid Sandstone	compound scales, fin spines	Forey et al. 1992
13		Saudi Arabia	Pragian ⁵ or Middle Devonian ⁶ ; Jawf Formation	tooth	Forey et al. 1992; reinterpreted in Ginter 2004
14	<i>Wellerodus priscus</i>	USA (Illinois, New York)	Givetian, lower Frasnian	teeth	Turner 1997; this paper
15	<i>Wellerodus</i> sp. cf. <i>W. priscus</i>	China	Famennian	tooth	Wang and Turner 1985; Zhao and Zhu 2010
16	<i>Wellerodus</i>	Russia (Middle Urals)	Frasnian	teeth	Ivanov 2008
17	<i>Wellerodus</i>	USA (Nevada)	Frasnian	teeth	Ginter 2004
18	<i>Wellerodus</i>	Poland	Frasnian	teeth	Liszkowski and Racki 1993; Ginter 2004

remain undetermined, *T. lessardi* has an organization of the cusps and of the base that is close to that of antarctilamnids.

Occurrences of antarctilamnids are relatively frequent along the coast of West Gondwana, but are rarer in East Gondwana. This is compatible with the suggestion that antarctilamnids in Australia suggests an incursion from the Malvinokaffric Realm (Young 2003b). The late occurrence of an antarctilamnid in China, if confirmed, would be consistent with the interpretation that faunal exchanges between Asia and the rest of Gondwana only occurred by the Famennian (Young 2003b; Young et al. 2010). If antarctilamnid populations were still present in the Arabian region by the end of the Middle Devonian, dispersal along the northeastern Gondwana continental shelf might have been possible. Marine continuity by the Middle Devonian is implied for North

and East Gondwana (Young 2003a) and is supported by the similarity of Late Devonian vertebrate assemblages between Iran and Australia (Burrow et al. 2010).

The presence of older antarctilamnid remains in Antarctica than in North America suggests that occupation of the Gondwanan coastline would have occurred before the colonization of Laurussia. It is important to note that a chondrichthyan able to disperse along most of the coasts of Gondwana by the Emsian did not cross to Laurussia before the end of the Middle Devonian. This would suggest that by the Middle Devonian global dispersal was not constrained by continental distances any more, as argued by McKerrow et al. (2000). Middle Devonian palaeogeographical reconstructions suggest that Laurussia and Gondwana were in proximity, with the closest regions being the eastern part of USA and the northwest region

of South America (Scotese and McKerrow 1990; Keppie and Ramos 1999; McKerrow et al. 2000; Torsvik and Cocks 2004). This proximity is supported by ichthyofaunal (Schultze and Cloutier 1996; Young et al. 2000; Young 2003b; Rücklin 2010; Dupret et al. 2011) and palaeobotanical data (Streel et al. 1990; Berry et al. 1993; Meyer-Berthaud et al. 2003). However, some geophysical studies support the opposite hypothesis of a wide ocean between Laurussia and Gondwana in the Middle Devonian (Van der Voo 1993; Tait et al. 2000; Li and Powell 2001). Tait et al. (2000) remarked that biological dispersion can be influenced by factors not related to geographical distance, such as oceanic transport. While both hypotheses are considered legitimate, we prefer the hypothesis of proximity of Laurussia and Gondwana by the Middle Devonian because it integrates more interpretive factors.

The Cairo site is interpreted as presenting two depositional environments, one estuarine or lacustrine and the other flooding, as observed on the Middle and Upper Devonian shoreline of the Catskill Delta. As previously described material of *Wellerodus* from New York State was from a marine environment (Hussakof and Bryant 1918; Schultze and Cloutier 1996; Turner 1997), *W. priscus* presumably occupied either a marine or marine-connected environment.

Our study supports an earlier interpretation of Middle Devonian biotic migration that involves Laurussia and Gondwana. Clarke (1913) first noted that elements of the classic Middle Devonian (Givetian) Hamilton Group assemblage of eastern North America had their oldest known representatives in the Amazon and Parará basins of South American Gondwana. Later, Arden and Rehrig (1964) commented on the faunal similarities between the North African margins of North Gondwana and the Hamilton Group assemblages of North America in the Middle Devonian. The progressive collapse of faunal provincialism persisted into the Late Devonian, with a number of groups (e.g., ammonoids, conodonts) showing cosmopolitan distribution after the Frasnian–Famennian extinctions (e.g., House 1971; Klug et al. 2010).

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