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A new aspinothoracid arthrodire from the Late Devonian of Ohio, U.S.A.

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ABSTRACT:

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The Cleveland Shale fauna represents a unique view of the time after a major Devonian extinction event (Frasnian–Famenian) with the recovery of arthrodires (Placodermi) best represented by this most specious North American fauna. This time was followed by an additional event (Hangenberg Biocrisis) leading to the extinction of arthrodires (and all other placoderms). An understanding of the diversity and interrelationships of North American arthrodires can aid our understanding of this critical time in vertebrate evolution. A new aspinothoracid arthrodire *Hlavinichthys jacksoni* gen. et sp. nov. is described from the Late Devonian of northern Ohio, U.S.A., which adds to our knowledge of this group. It provides a point of comparison to other members of the fauna whose interrelationships are poorly known. A phylogenetic analysis supports an assignment of *Hlavinichthys jacksoni* gen. et sp. nov. among the aspinothoracid arthrodires. This work has drawn attention to the continued need for descriptive and phylogenetic analyses of this unique fauna. Decades old species descriptions need revision along with preparation and description of new taxa. The work on *Hlavinichthys jacksoni* gen. et sp. nov. here is one step in that process.

Key words: Placodermi; New genus *Hlavinichthys*; New species *Hlavinichthys jacksoni*; Devonian; Famennian; Cleveland Shale; Ohio; U.S.A.

INTRODUCTION

The Cleveland Shale fish fauna represents the most speciose Famennian vertebrate fauna (66 species) with more than double the number of species than the next best-known fauna – the Tafilalt fauna (32 species), Morocco (Leliévre 2003; Carr and Jackson 2008). The fish fauna documents a post-extinction (Frasnian–Famennian) recovery that continued until the end-Devonian Hangenberg Biocrisis and the final extinction of the placoderms. The relatively large number of recorded species are a result of over a century and a half of collecting. The collections at the Cleveland Museum of Natural History represent a 90-year history of work on the Cleveland Shale. In 1965–1966, the Museum conducted the Interstate-71 Paleontological Salvage Project, a recovery effort conducted during the construction of the interstate. This project nearly doubled the Museum's collection, increasing the numbers of specimens for known taxa and adding new taxa to the faunal list. The size of the addition was such that much of the material remains to be prepared and/or described over four decades later. Included in the I-71 material is a new genus and species described here as *Hlavinichthys jacksoni* gen. et sp. nov.

INSTITUTIONAL ABBREVIATION: CMNH, Cleveland Museum of Natural History.

OTHER ABBREVIATIONS: **?**, unidentified; **ADL**, anterior dorsolateral plate; **AL**, anterior lateral plate; **AMV**, anterior median ventral plate; **Art**, articular;

av.w, anteroventral wing; **AVL**, anterior ventrolateral plate; **br.lam**, branchial lamina; **C**, central plate; **csc**, central sensory canal groove; **d.prp**, dermal preorbital process; **gr**, groove; **IG**, inferognathal; **IL**, interolateral plate; **ioc.ot**, otic branch of the infraorbital canal groove; **ioc.pt**, postorbital branch of the infraorbital canal groove; **ioc.sb**, suborbital branch of the infraorbital canal groove; **lc**, main lateral line groove; **M**, marginal plate; **MD**, median dorsal plate; **Nu**, nuchal plate; **oa.ADL**, overlap area for the anterior dorsolateral plate; **oa.AL**, overlap area for the anterior lateral plate; **oa.AVL**, overlap area for the anterior ventrolateral plate; **oa.MD**, overlap area for the median dorsal plate; **oa.PDL**, overlap area for the posterior dorsolateral plate; **oa.PVL**, overlap area for the posterior ventrolateral plate; **oa.SM**, overlap area for the submarginal plate; **oa.SO**, overlap area for the suborbital plate; **pbe**, postbranchial embayment; **PL**, posterior lateral plate; **pmc**, postmarginal canal groove; **PMV**, posterior median ventral plate; **PNu**, paranuchal plate; **PrO**, preorbital plate; **PSG**, posterior superognathal; **PSO**, postsuborbital plate; **PtO**, postorbital plate; **PVL**, posterior ventrolateral plate; **R**, rostral plate; **scler**, sclerotic plate; **SO**, suborbital plate; **soc**, supraorbital sensory canal groove; **sorc**, supraoral sensory canal groove; **th**, thickening.

SYSTEMATIC PALEONTOLOGY

Placodermi McCoy, 1848
Arthrodira Woodward, 1891
Eubrachythoraci Miles, 1971
Pachyosteomorphi Stensiö, 1944
Aspinothoracidi Stensiö, 1959 (*sensu* Miles and Dennis, 1979)

Genus *Hlavinichthys* nov.

HOLOTYPE: CMNH 9200, a single concretion containing most of the plates from a single specimen.

ETYMOLOGY: Named after Dr. William J. Hlavin.

REMARKS: Dr. William J. Hlavin was the supervisor of the I-71 Paleontological Salvage Project (1965–1966) that recovered the specimen. He provided the early analyses of the material recovered from the project and has continued his support of research on the Cleveland Shale fauna (Hlavin 1973, 1976; Hlavin and Boreski 1973; Yochelson and Hlavin 1985; House *et al.* 1986; Carr and Hlavin 1995, 2010; Gale *et al.* 1998, 1999; Gall *et al.* 1998, 1999).

TYPE SPECIES: *Hlavinichthys jacksoni* sp. nov., by monotypy; see below.

DIAGNOSIS: As for species, by monotypy.

TYPE LOCALITY: Excavation site for Interstate-71 at the intersection of Bellaire and Memphis Roads, on the boundary of Cleveland and Linndale, Ohio, U.S.A.

TYPE HORIZON: Cleveland Shale Member, Ohio Shale Formation, Ohio, U.S.A. Upper Famennian; *aculeatus* to *costatus–ultimus* Conodont Zones (Spalletta *et al.* 2017). The top of the Cleveland Member is not clearly defined.

REFERRED MATERIAL: CMNH 9200 is the only known specimen.

Hlavinichthys jacksoni sp. nov.

ETYMOLOGY: Named for Gary L. Jackson (1950–2017).

REMARKS: This is the occasion to recognize the memory of Gary Jackson. Gary Jackson was a former preparator and collections manager at the Cleveland Museum of Natural History (CMNH). The fossil material from the Cleveland Shale presents a difficult challenge for any preparator. Modes of preservation include carbon films, prismatic cartilage, perichondral ossifications, soft tissues, and crushed and scattered bones all preserved in a hard shaley matrix requiring mechanical preparation. It is the rare individual that can master the necessary skills for this arduous work. His preparation of fossils for the CMNH for 29 years was a major contributing factor for published works (e.g., Carr 1988, 1991, 2009; Williams 2001). He was also coauthor for a number of publications (Carr and Jackson 2002, 2005, 2005b, 2008; Carr *et al.* 2010; Boyle *et al.* 2011; Scott *et al.* 2012) and senior author (Jackson and Carr 2006; Jackson 2007; Jackson *et al.* 2012). His contribution to research on the Cleveland Shale fauna will be missed.

DIAGNOSIS: Based on the published character-set of Rücklin *et al.* (2015) and the lack of resolution among the aspinothoracid arthrodires (refer to Phylogenetic Position section below), *Hlavinichthys jacksoni* gen. et sp. nov. is unambiguously characterized by a single character: character 14, the embayment of the C plate by the PNu plate. Five characters appear as ambiguous characters in over 50% of the 34 equally parsimonious trees: (i) character 24, a reduced participation of the M plate along the lateral border of the skull roof; (ii) character 30, the absence of a postnuchal process of the PNu plate on the dermal surface; (iii) character 31, an anterior position of the C/PNu/M plate junction relative to the PNu/C/Nu plate junction; (iv) character 47, the presence of an IL plate branchial lamina; and (v) character 84, the termination of the groove for the supraorbital canal (soc) on the PtO plate, i.e., not extending onto the C plate.

Due to poor preservation in the region of the marginal-central plates' contact, the one unambiguous apomorphic character is unclear. Thus, *Hlavinichthys jacksoni* gen. et sp. nov. may represent a metaspecies (a species that lacks any apomorphies) based on the published data matrix of Rücklin *et al.* (2015). However, other characters (not included in the published analysis of Rücklin *et al.* 2015) that distinguish *Hlavinichthys jacksoni* gen. et sp. nov. from other members of the fauna include: (i) inferognathals (IG) with an acute occlusal surface without denticles (teeth of Rücklin *et al.* 2012); (ii) posterior superognathals (PSG) with an elongate dorsal process; (iii) the central sensory line grooves (csc) limited to the PtO plates, i.e., not extending onto the central plates; (iv) a bifurcated branchial lamina (br.lam) on the AL plate; and (v) a posterior lobe of the central plate extending along the entire lateral margin of the nuchal plate and beyond, extending onto a recessed overlap area on the paranuchal plate. The extent of insertion for the posterior lobe of the central plate was reported to be quite variable among the arthrodires from Gogo (Trinajstic and Dennis-Bryan 2009: "reduced" to "extended"). In the case of *Eastmanosteus calliaspis* (Dennis-Bryan 1987, text-fig. 4) the central-nuchal plate contact extends just over half the length of the lateral margin of the nuchal plate (Carr 1991, character 21). In *Hlavinichthys jacksoni* gen.et sp. nov. the process extends beyond the posterolateral corner of the nuchal plate, distinct from the range of variation seen in other arthrodires.

Due to a lack of resolution of the phylogenetic position for other taxa in the fauna, some additional features may represent autapomorphies of the new species or synapomorphies uniting members of the fauna. These additional features include: (i) the presence of a descending lamina along the posterior margin of the skull roof (not reported in other members of the fauna, but shared with *Paramylostoma arcualis*); (ii) a short posteriorly directed process on the posterior lateral plate similar to the condition in *Stenosteus angustopectus*; (iii) pointed anterior margin of the nuchal plate, distinct from the condition in *P. arcualis* and *Gymnotrachelus hydei*; and (iv) extension of the anterior median ventral plate anterior to adjacent anterior ventrolateral plates paralleling the condition in *Heintzichthys gouldii*.

METHODS AND MATERIALS

Originally, for the single specimen (CMNH 9200) of *Hlavinichthys jacksoni* gen. et sp. nov., both part and counterpart were recovered, and latex peels were made from the exposed surfaces. Subsequently the parts of the concretion were glued back together (permanently obscuring the surfaces preserved on the peels). The concretion was mechanically prepared using air abrasion, air scribes, and grinding wheels to the level of the bones exposing a dorsal view of the skull roof.

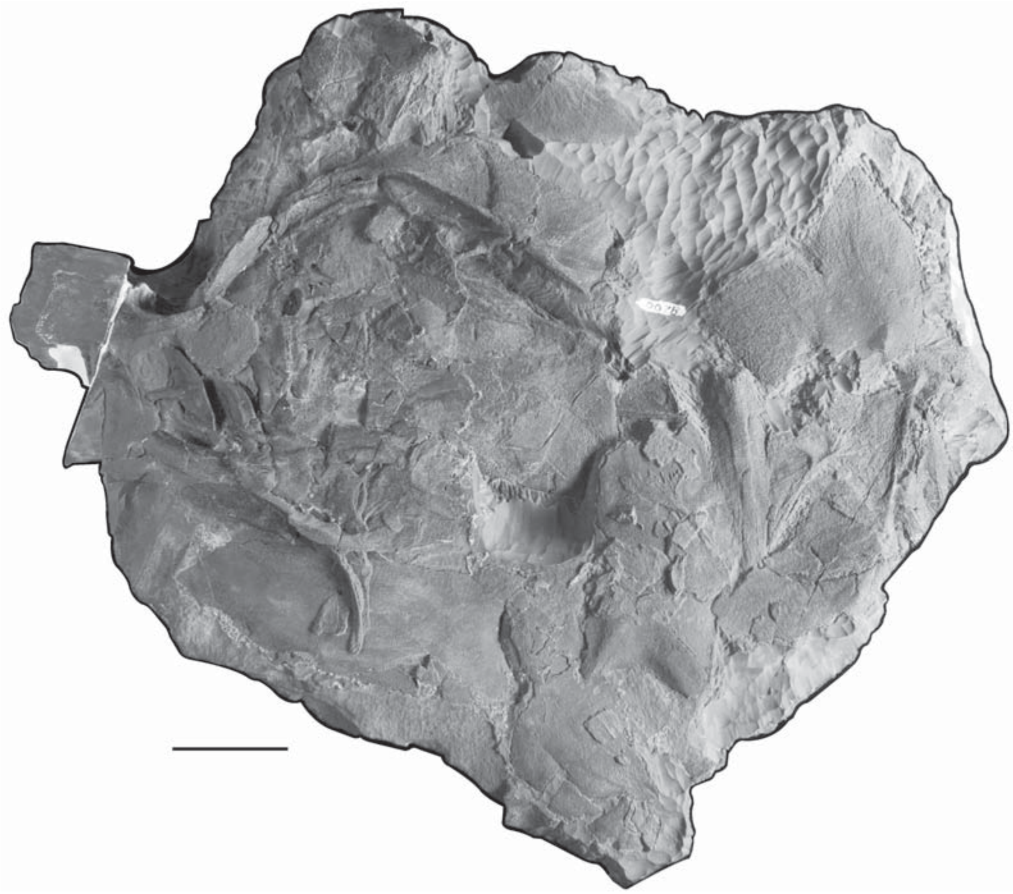
Hlavinichthys jacksoni gen. et sp. nov. was compared to other members of the fauna to potentially elucidate new anatomical characters for use in future phylogenetic analyses. A phylogenetic analysis was conducted using PAUP* v. 4.0b (Swofford 2002) based on the published data matrix of Rücklin *et al.* (2015, 27 taxa and 98 characters) with the addition of *Hlavinichthys jacksoni* gen. et sp. nov. to the analysis.

DESCRIPTION

The single specimen of *Hlavinichthys jacksoni* gen. et sp. nov. is preserved on the prepared surface of a concretion (Text-figs 1, 2). Although disarticulated, the skull roof, cheek plates, sclerotics, gnathal elements, and thoracic armor are preserved, as well as a number of unidentified plate fragments. The plates are disarticulated and displaced on the surface of the concretion (labeled in Text-fig. 2).

Skull roof

General features: The skull roof within the Eubrachythoracidi typically consists of four median plates (internasal, rostral, pineal, and nuchal) and seven paired plates (postnasal, preorbital, postorbital, central, marginal, paranuchal, and postmarginal). The skull roof of *Hlavinichthys jacksoni* gen. et sp. nov. appears intact and is preserved in dorsal view; however, parts of the roof are obscured by overlying plates or buried in matrix (Text-fig. 3). The internasal, postnasal, pineal, and postmarginal plates are not visible in this one and only specimen. A possible rostral plate (Text-fig. 2, R) has been displaced and sits atop the right preorbital plate. No clear details of



Text-fig. 1. *Hlavinichthys jacksoni* gen. et sp. nov., CMNH 9200. Scale bar equals 5 cm

its shape can be discerned. Additional unidentifiable fragments are associated with the skull roof.

Nuchal plate (Nu, Text-figs 1, 2, 3A, D): The nuchal plate is triangular in shape with a deep posterior embayment. Medially, there is a posterior dermal process that is laterally bounded superficially by shallow fossae (interpreted as areas covered by "soft tissue"; Stensiö 1963, text-fig. 102, a.dn) and ventrally by deep fossae that are bounded by the medial process and laterally by the vertical face of the nuchal thickening (homologous to the levator fossae of Goujet 1984). Posterolaterally, the nuchal plate extends as alia. The nuchal plate forms ca. 57.5% of the lateral border of the nuchal gap (measured between the articular fossa and the anterior-most extent of the gap). A prominent descending posterior lamina is present that continues onto the paranuchal plate (Text-figs 2, 3D). The transition from the paranuchal-contribution to the nuchal-contribution of the descending lamina is unclear. The depth of the lamina decreases as it approaches the midline. A similar condition is seen in some European Selenosteidae (the medial and lateral nuchal thickenings of Stensiö 1963, text-fig. 95). In *Paramylostoma arcualis* (a potentially related taxon in the Cleveland Shale fauna), Dunkle and Bungart (1945, p. 87) noted "little apparent ventral thickening" however, the paratype (CMNH 6054, not described in detail) possesses a vertical lamina that has been flattened some during preservation (Text-fig. 4).

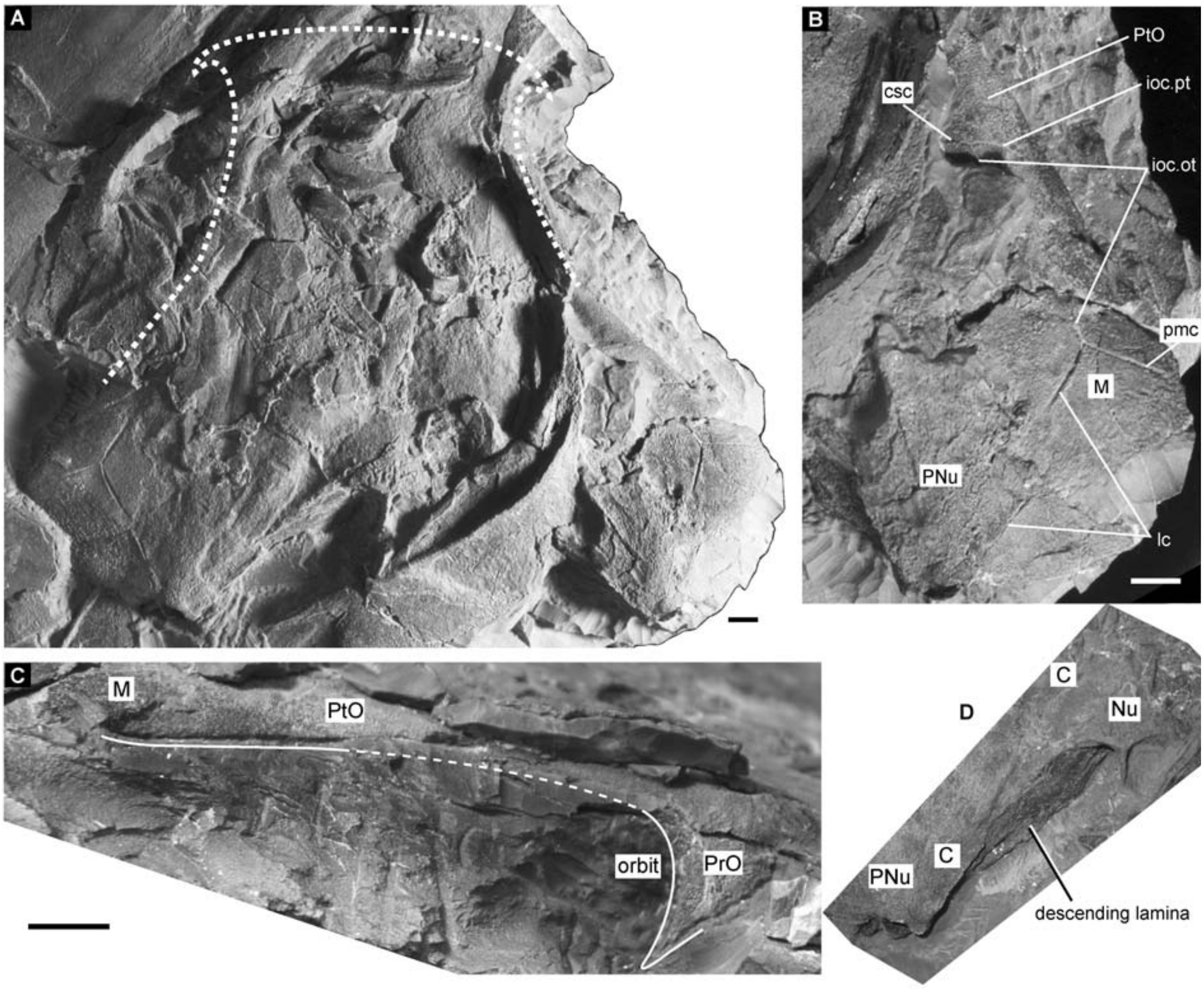
The anterior margin of the nuchal plate in *Hlavinichthys jacksoni* gen. et sp. nov. is pointed, differing from the transverse margin in, e.g., *P. arcualis* (Dunkle and Bungart 1945, text-fig. 3) and *Gymnotrachelus hydei* (Carr 1994, text-fig. 4B). The plate in the new genus and species occupies ca. 29% of the midline length of the skull roof (based on an estimated position of the rostral plate).

Preorbital plates (PrO, Text-figs 1, 2, 3A–C): The right preorbital plate is only partially exposed with

Text-fig. 2. *Hlavinichthys jacksoni* gen. et sp. nov., CMNH 9200. Outline of individual plates in Text-fig. 1. Scale bar equals 5 cm. Abbreviations: ? – unidentified; ADL – anterior dorsolateral plate; AL – anterior lateral plate; AMV – anterior median ventral plate; Art – articular; av.w – anteroventral wing; AVL – anterior ventrolateral plate; br.lam – branchial lamina; C – central plate; csc – central sensory canal groove; gr – groove; IG – inferognathal; IL – interolateral plate; ioc.ot – otic branch of the infraorbital canal groove; ioc.pt – postorbital branch of the infraorbital canal groove; ioc.sb – suborbital branch of the infraorbital canal groove; M – marginal plate; MD – median dorsal plate; Nu – nuchal plate; oa.MD – overlap area for the median dorsal plate; pbe – postbranchial embayment; PL – posterior lateral plate; PMV – posterior median ventral plate; PNu – paranuchal plate; PrO – preorbital plate; PSG – posterior superognathal; PSO – postsuborbital plate; PtO – postorbital plate (the right PtO plate is labeled both anterior and posterior to the sensory line grooves of the plate); PVL – posterior ventrolateral plate; R – rostral plate; scler – sclerotic plate; SO – suborbital plate; soc – supraorbital sensory canal groove; th – thickening

the medial and posterior edges obscured. A prominent dermal preorbital process is directed ventrally (Text-fig. 3C, outlined in white), similar to *P. arcualis* (Text-fig. 4, d.prp). A supraorbital sensory line groove (soc) crosses the plate. Only a small portion of the left plate is exposed with the supraorbital sensory line groove visible. Posteriorly, the groove on the left appears to end at the plate margin, but on neither side does the groove extend onto the central plate or its ossification center.

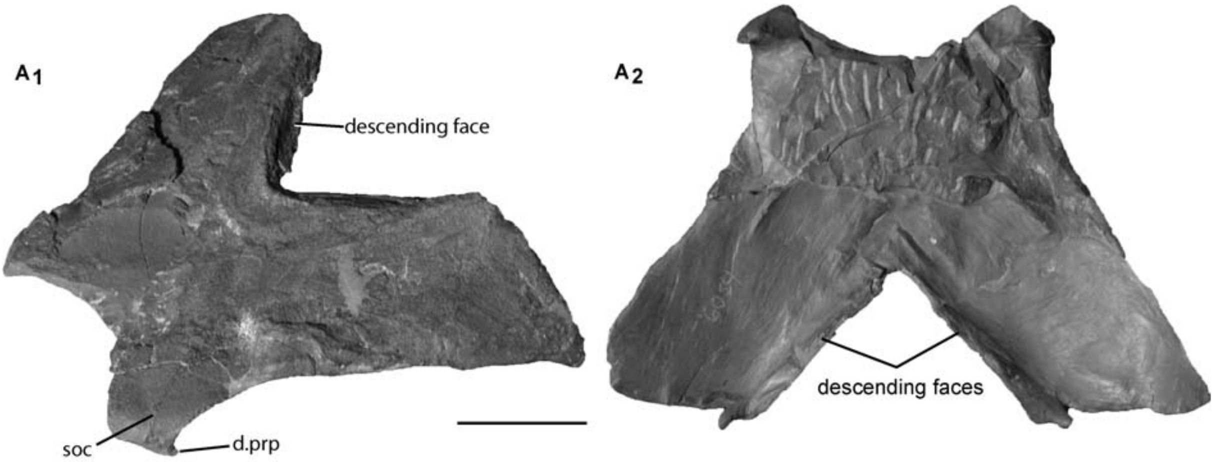
Postorbital plates (PtO, Text-figs 1, 2, 3A–C): Only the lateral part of the right postorbital plate and the postorbital-marginal plate contact on the left are visible. A groove (Text-figs 2, 3B) for the right postorbital branch of the infraorbital sensory canal (ioc.pt) is directed posteriorly and meets the groove for the otic branch (ioc.ot) initially at an angle of ca. 80 degrees, but rapidly arches posteriorly to form an effective angle of ca. 46.5 degrees. This deflection is similar to the case in several selenosteids with large orbits. A groove for the central sensory canal (csc) is present with its medial extent obscured by overlying bone and matrix. There is no evidence for the extension of this canal on to the central plate. No dermal postorbital process is present. The orbits represent an estimated 41% of the distance from the preorbital process to the posterior edge of the paranuchal plate (for comparison, mea-



Text-fig. 3. *Hlavinichthys jacksoni* gen. et sp. nov., CMNH 9200. A – close-up of the skull roof region of the concretion with an estimate of the covered outline indicated by a dashed line. B – close-up of the right postorbital, marginal, and paranuchal plates. C – close-up of left central, marginal, postorbital, and preorbital plates in lateral view with a line drawn parallel to the margin to emphasize the dermal preorbital process. D – close-up of the left side of the nuchal gap in a posterior dorso-medial view. Scale bars equal 1 cm. Abbreviations: C – central plate; csc – central sensory canal groove; ioc.ot – otic branch of the infraorbital canal groove; ioc.pt – postorbital branch of the infraorbital canal groove; lc – main lateral line groove; M – marginal plate; pmc – postmarginal canal groove; PNu – paranuchal plate; PrO – preorbital plate; PtO – postorbital plate

surements were determined for three species in the fauna, estimates include 23% in *Dunkleosteus terrelli*, CMNH 7054; 41% in *P. arcualis*, CMNH 6054; and 49% in *Stenosteus angustopectus*, CMNH 8043).

Central plates (C, Text-figs 1, 2, 3A, B, D): Only the central portion of the right central plate is visible. The left central plate consists of the central portion, the posterior portion of a possible lateral lobe, and an elongate posterior lobe. A lateral lobe is typically delineated anteriorly by an embayment of the postorbital plate (separating an anterior lobe from lateral lobe). This portion of the central and postorbital plates is not exposed in *Hlavinichthys jacksoni* gen. et sp. nov. In other arthrodires, as well as in *Hlavinichthys jacksoni* gen. et sp. nov., the posterior lobe of the central plate is formed by an embayment of the paranuchal plate. The posterior lobe in the new species uniquely extends nearly to the articular fossa on the paranuchal plate (paralleling approximately 82% of the nuchal gap lateral-length). Despite the expansion of the posterior lobe it does not form a direct boundary for the nuchal gap, since a narrow process of the paranuchal plate extends anteriorly separating



Text-fig. 4. *Paramylostoma* arcualis, CMNH 6054. A_1 – an anterior dorsal-oblique view of the skull roof and A_2 – ventral view. Scale bar equals 5 cm. Abbreviations: d.prp – dermal preorbital process; soc – supraorbital sensory canal groove

the lobe from the gap. No sensory line grooves are visible on the exposed surface of the central plates. Each plate is centrally elevated as a compression artifact suggesting the presence of the endolymphatic thickenings internally.

Marginal plates (M, Text-figs 1, 2, 3A–C): Both marginal plates are visible, each with three sensory line grooves present (otic branch of the infraorbital sensory line [ioc.ot], postmarginal canal [pmc], and main lateral line [lc], Text-fig. 3B). The main lateral line groove forms an angle of ca. 121 degrees with the otic branch of the infraorbital sensory line groove and an angle of ca. 98 degrees with the postmarginal canal groove. The region of confluence for the postorbital, marginal, paranuchal, and central plates is unclear; however, it appears that lateral lobe of the central plate is in contact with the marginal plate, thus eliminating a postorbital-paranuchal plate contact. In comparison, there is a clear postorbital-central plate contact in *P. arcualis* (Dunkle and Bungart 1945, text-fig. 3).

Paranuchal plates (PNu, Text-figs 1, 2, 3A, B, D): The paranuchal plates are irregular in outline with a post-marginal process, an anterior embayment between lateral and posterior lobes of the central plate, and a narrow extension along the nuchal gap. No post-nuchal process on the dermal surface is present. The main lateral line groove (lc) traverses the plate with an endolymphatic pore present medial to the groove. Articular fossae are present with well-developed para-articular processes. The articular fossae are deflected from horizontal (ca. 40 and 33 degrees left and right, respectively) indicating extensive flattening during preservation.

The posterior descending lamina begins at the dorsomedial corner of the articular fossa and increases in depth medially where it appears to be continuous with the nuchal lamina (Text-fig. 3D). In *P. arcualis* the paranuchal plate forms the greater portion of the lamina, well beyond the dermal surface contact of the two plates.

Cheek and sclerotic plates

General features: The cheek in eubrachythoracids consists of three plates (suborbital, postsuborbital, and submarginal). The plates form an overlapping single unit as seen in *Gymnotrachelus hydei* and *Stenosteus angustopectus* (Text-fig. 5B, C, respectively), unlike some taxa where the submarginal plate simply abuts the other two overlapping plates (e.g., *Heintzichthys gouldii* and especially in *Dunkleosteus terrelli* (Text-fig. 5D, E respectively). In the only specimen of *Hlavinichthys jacksoni* gen. et sp. nov., the submarginal plate is not preserved, although an overlap impression of the submarginal plate on the posterior suborbital plate provides information on how the cheek plates are organized.

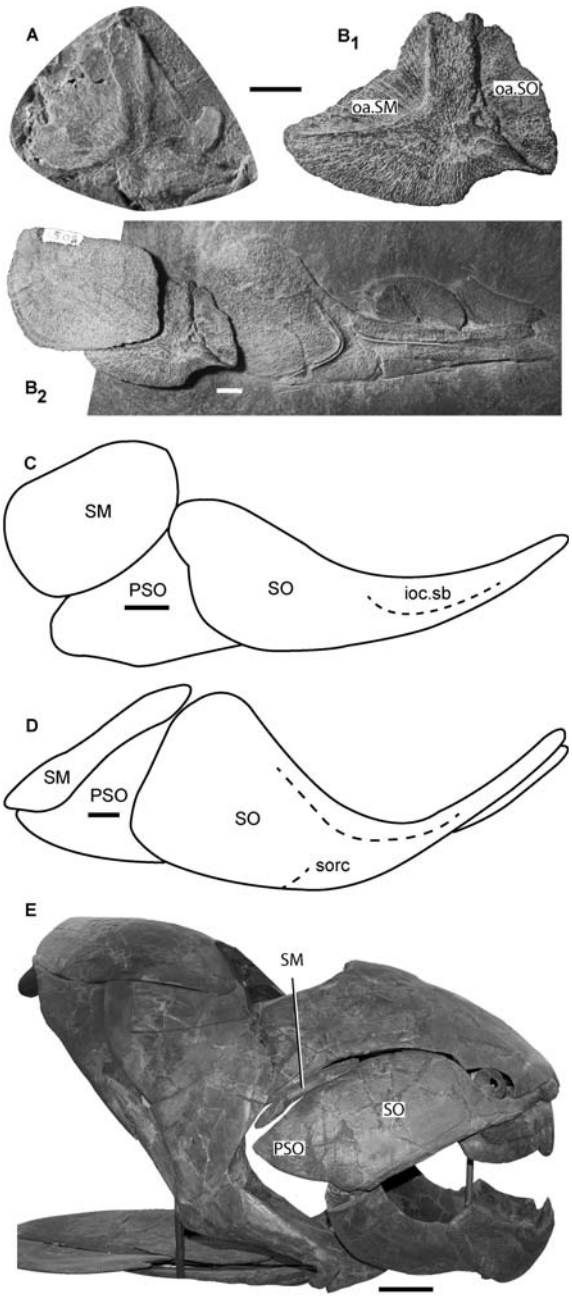
Suborbital plates (SO, Text-figs 1, 2): The suborbital plate consists of ‘blade’ and ‘handle’ regions, typical among the Aspinothoracidi (*sensu* Miles and Dennis, 1979). Seen in external view, a groove for the suborbital branch of the infraorbital sensory line (ioc.sb) is present. The low angle between the ‘blade’ and ‘handle' along with the posterior deflection of the groove for the postorbital branch of the infraorbital sensory line (ioc.pt) suggest the presence of relatively large orbits despite the lack of a dermal postorbital process. Internally, a large suborbital shelf is present. Other internal features are not visible.

Postsuborbital plates (PSO, Text-figs 1, 2, 5A): The left postsuborbital plate is seen in internal view (Text-fig. 5A). Compression artifacts indicate the overlap areas for the suborbital and submarginal plates. The ventral edge of the plate is notched. Internally, a slight thickening at the ossification center may indicate the position of the quadrate.

The postsuborbital plate outline and areas of overlap with adjacent plates parallel the condition in *G. hydei* (Text-fig. $5B_1$). It appears that the organization of the cheek plates also parallels the condition seen in *G. hydei* (Text-fig. $5B_2$), where the suborbital and submarginal plates are externally separated by the postsuborbital plate. As in *G. hydei*, it appears this organization would leave a gap between these three plates and the skull roof.

Submarginal plates (SM): Although this plate is not preserved, its form can be inferred based on its relation to the postsuborbital plate. It appears that the condition in *Hlavinichthys jacksoni* gen. et sp. nov. parallels that in *G. hydei* where the plate is rectangular in shape (Text-fig. $5B_2$). It is clear that the condition in *Hlavinichthys jacksoni* gen. et sp. nov. is unlike that in, e.g., *Dunkleosteus terrelli* where the submarginal plate simply abuts the other two plates of the cheek (Text-fig. 5E).

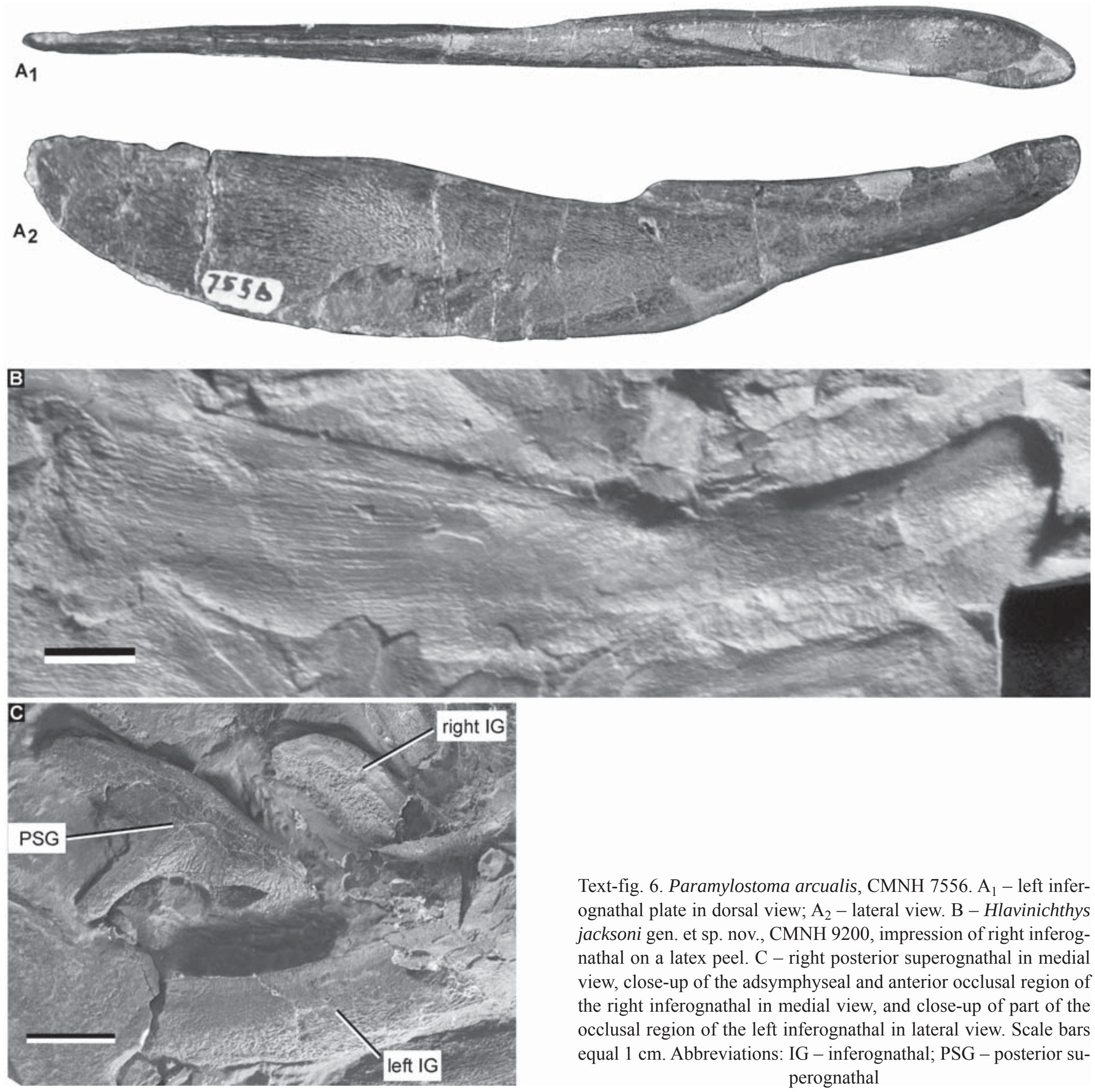
Sclerotic plates (scler, Text-figs 1–3): Four sclerotic plates are recognized with possible fragments of others also present. Based on the curvature of a single plate it appears four plates formed the sclerotic ring (a pattern common to arthrodires, Burrow *et al.* 2011). An estimated diameter for the opening of the ring is 35 mm. Along the border of the orbital aperture, each sclerotic plate is finely ornamented with punctate tubercles with some coalescence forming oval shaped tubercles.



Text-fig. 5. A comparison of cheek plates. A – *Hlavinichthys jacksoni* gen. et sp. nov., CMNH 9200, right postsuborbital plate in internal view. B – *Gymnotrachelus hydei*, CMNH 8051, B_1 – right postsuborbital plate in external view and B_2 – suborbital, postsuborbital, and submarginal plates in external view. C – *Stenosteus angustopectus* after Carr, 1996, text-fig. 1B. D – *Heintzichthys gouldii* after Carr, 1991, text-fig. 2. E – *Dunkleosteus terrelli*, CMNH 7054, in left lateral view, but graphically reflected to orient the cheek as in the images above. Scale bars for A-D equal 1 cm, scale bar for E equals 10 cm. Abbreviations: ioc.sb – suborbital branch of the infraorbital orbital canal groove; oa.SO – overlap area for the suborbital plate; oa.SM – overlap area for the submarginal plate; PSO – postsuborbital plate; SM – submarginal plate; SO – suborbital plate; sorc – supraoral sensory canal groove

Gnathal elements

General features: In the eubrachythoracids, the gnathal elements typically consist of paired anterior and posterior superognathals and inferognathals. In *Hlavinichthys jacksoni* gen. et sp. nov., the inferognathals are partially covered and the anterior superog-



Text-fig. 6. *Paramylostoma arcualis*, CMNH 7556. A$_1$ – left inferognathal plate in dorsal view; A$_2$ – lateral view. B – *Hlavinichthys jacksoni* gen. et sp. nov., CMNH 9200, impression of right inferognathal on a latex peel. C – right posterior superognathal in medial view, close-up of the adsymphyseal and anterior occlusal region of the right inferognathal in medial view, and close-up of part of the occlusal region of the left inferognathal in lateral view. Scale bars equal 1 cm. Abbreviations: IG – inferognathal; PSG – posterior superognathal

nathals are incomplete. *Hlavinichthys jacksoni* gen. et sp. nov. can be distinguished from *Paramylostoma arcualis* in the presence of acute occlusal surfaces on the inferognathals in contrast to the flattened durophagous pattern in *Paramylostoma arcualis* (Text-fig. 6A) and it differs in the form of the superognathals. *Hlavinichthys jacksoni* gen. et sp. nov. is distinguishable from the other members of the fauna by its lack of teeth/cusps on the gnathal plates and its lack of an anterior cusp on the inferognathal.

Inferognathals (IG, Text-figs 1–3, 6B, C): Right and left inferognathals are present consisting of posterior 'blade' (non-dental), dental, and adsymphyseal regions. Overlying plates mostly cover the left inferognathal and the right is fragmented with only pieces visible. A mold of the left inferognathal is present on the latex peel (Text-fig. 6B). The plate is ca. 10.8 cm long with the blade forming ca. 60% of the total length.

There is no tooth or cusp above the ossification center. The acute occlusal surface continues past the ossification center and ventrally onto the adsymphyseal region (Text-fig. 6C). An articular ossification (Art) of Meckel's cartilage (Text-figs 1, 2) is present and detached from the inferognathal.

Posterior superognathals (PSG, Text-figs 1, 2, 3, 6C): Both posterior superognathals are present in medial view and appear flattened. A prominent dorsal process is present and located mid-plate. A vertical thickening strengthens it medially. The distance from the occlusal surface to the tip of the process is ca. 61% of the length of the plate, with the process uniquely elongate compared to other members of the fauna. The occlusal surface, like the inferognathals, consists of an acute edge. *Paramylostoma arcualis* and *Heintzichthys gouldii*, in contrast, possess a very short dorsal process that is displaced anteriorly (Dunkle and Bungart 1945, text-fig. 2A; Carr 1991, text-fig. 8D; respectively).

Anterior superognathals (ASG, Text-figs 1, 2): A single anterior superognathal is present. A dorsal process is present extending posteriorly from the occlusal part of the plate. The anterior portion of the plate is triangular in cross-section. The medial base of the triangle forms an occlusal surface with the inferognathal. Laterally, the apex of the triangle adds structural support for the short cusp-like structure.

Thoracic armor

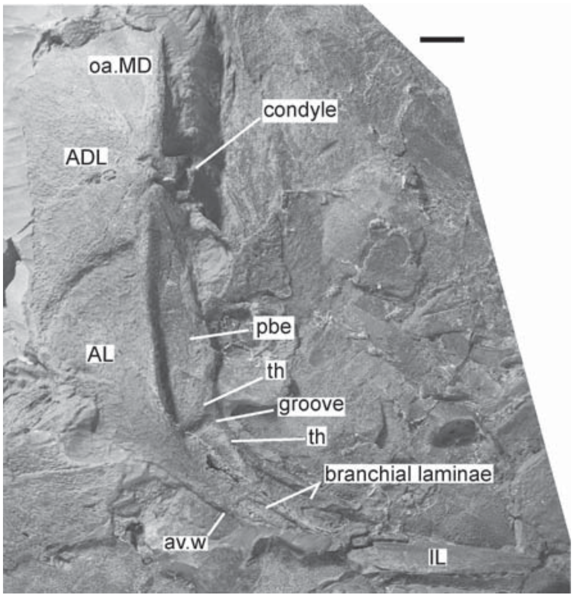
General features: The thoracic armor in aspinothoracid arthrodires consists of one dorsal median plate (median dorsal), four pairs of lateral plates (anterior dorsolateral, anterior lateral, posterior dorsolateral, and posterior lateral), two median ventral plates (anterior median ventral, posterior median ventral), and three paired ventral plates (interolateral, anterior ventrolateral, posterior ventrolateral). The posterior ventrolateral plates are fragmented, the presence of a posterior median ventral is only speculative (based on a fragment of the plate), and the posterior dorsolateral plates are missing. Both the anterior ventrolateral and posterior ventrolateral plates possess a few tiny punctate tubercles externally in the region of the ossification center. These tubercles lack the stellate radiations at the base as seen in some arthrodires. They are all isolated without coalescence (unlike some tubercles on the sclerotic plates).

Median dorsal plate (MD, Text-figs 1, 2): The median dorsal plate is short and broad (midline-length/width = ca. 0.68; maximum-length/width = ca. 0.74). The anterior margin is shallowly embayed with a small median process. The posterior margin is gently rounded with a shallow midline embayment above the presumed still buried carinal process.

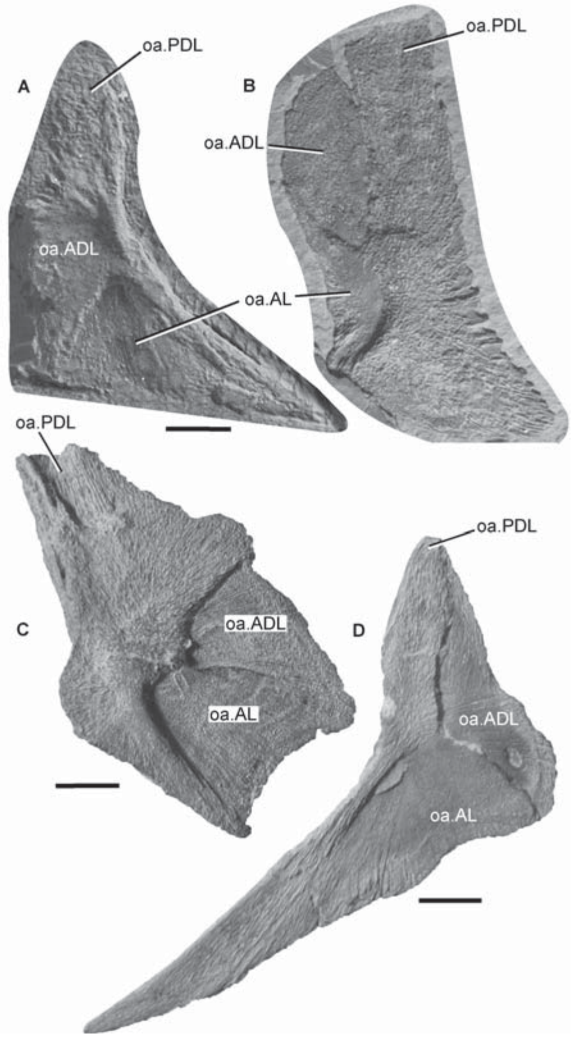
In the holotype (CMNH 5284) for *Paramylostoma arcualis*, the anterior process of the median dorsal plate is not described by Dunkle and Bungart (1945, 87), but is present on the paratype (CMNH 6054). The process represents an anterior extension of the internal median keel, which is not exposed in *Hlavinichthys jacksoni* gen. et sp. nov.

Anterior dorsolateral plates (ADL, Text-figs 1, 2, 7): On the right side, the anterior dorsolateral and anterior lateral plates are fused as a single complex (the left complex is mostly obscured by overlying plates, assumed to represent fragments of the posterior ventrolateral plate, Text-fig. 2). On the external surface are overlap areas for the median dorsal and anterior lateral plates. The posterior margin of the plate is likely incomplete. Processes of the anterior dorsolateral plate extend anterior to both the median dorsal and anterior lateral plates. There is no indication of a sensory groove on the plate. A glenoid condyle and subglenoid process is present.

Anterior lateral plates (AL, Text-figs 1, 2, 7): The anterior lateral plate is triangular in outline with the posterior margin apparently incomplete. The anterior margin is gently curved with no obstantic process. The postbranchial embayment (pbe) extends the length of the plate with two obstantic thickenings (th)



Text-fig. 7. *Hlavinichthys jacksoni* gen. et sp. nov., CMNH 9200. Right anterior dorsolateral, anterior lateral, and interolateral plates in lateral view. Scale bar equals 1 cm. Abbreviations: ADL – anterior dorsolateral plate; AL – anterior lateral plate; av.w – anteroventral wing; gr – groove; IL – interolateral plate; oa.MD – overlap area for the median dorsal plate; pbe – postbranchial embayment; th – thickening



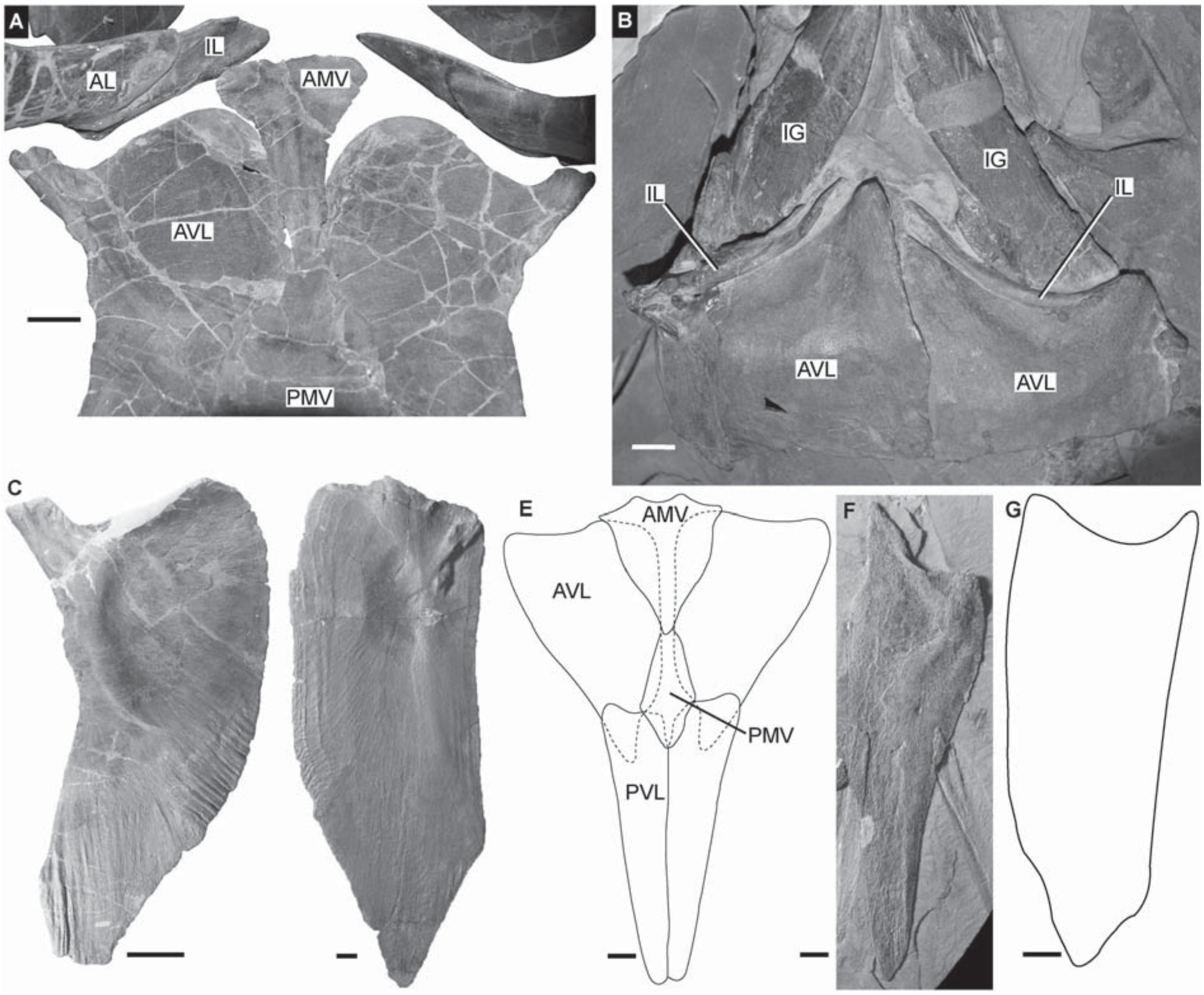
Text-fig. 8. A comparison of posterior lateral plates in lateral views. A – *Hlavinichthys jacksoni* gen. et sp. nov., CMNH 9200, left plate. B – *Stenosteus angustopectus*, CMNH 8043, left plate. C – *Gymnotrachelus hydei*, CMNH 8051, right plate. D – *Heintzichthys gouldii*, CMNH 8057, right plate. Scale bars equal 1 cm

separated by a shallow groove (Text-figs 2, 7). The embayment extends dorsally onto the anterior dorsolateral plate. The anteroventral wing (av.w) of the dermal surface tapers to a point (supporting an interpretation of the absence of a spinal plate). The branchial lamina continues ventrally from the lower obstantic thickening and bifurcates. The apparent contact for the interolateral plate lies within a depression formed by the bifurcated branchial lamina. This is in contrast to the typical condition where the contact lies between the dermal lamina and a single branchial lamina (e.g., *Dunkleosteus terrelli*, Heintz 1932, text-fig. 51).

Posterior lateral plates (PL, Text-figs 1, 2, 8A): Both posterior lateral plates are preserved in external view. The plates are triangular in outline with an irregular anterodorsal edge. The posterior border is gently curved. Anteriorly there is an overlap area for the anterior dorsolateral plate (oa.ADL, Text-fig. 8A) and anteroventrally an area for the overlap of the anterior lateral plate (oa.AL). The dorsal apex of the plate is assumed to contact the posterior dorsolateral plate (not preserved or represented by unidentifiable fragments). Posterior and ventral to the anterior lateral plate overlap, the plate forms a short posteriorly directed process. This pattern of overlaps and a process (of varying lengths) is seen in *Stenosteus angustopectus*, *Gymnotrachelus hydei*, and in *Heintzichthys gouldii* where the process is elongate (Text-fig. 8B, C, and D, respectively).

Interolateral plates (IL, Text-figs 1, 2, 7, 9A): Both interolateral plates are preserved. The right plate (Text-fig. 7) maintains its association with the anterior lateral plate with the left plate isolated and in ventral view (Text-fig. 9A). Its identification is further confirmed by comparison to *Paramylostoma arcualis*, where the two plates are preserved *in situ* (Text-fig. 10B). The interolateral plate in *P. arcualis* consists of two laminae that appear to overlap and under lap the leading edge of the anterior ventrolat-

Text-fig. 9. *Hlavinichthys jacksoni* gen. et sp. nov., CMNH 9200, A_1 – right anterior ventrolateral plate in external view with the left interolateral plate on top; A_2 – latex peel of the internal view. Scale bar equals 1 cm. Abbreviation: IL – interolateral plate

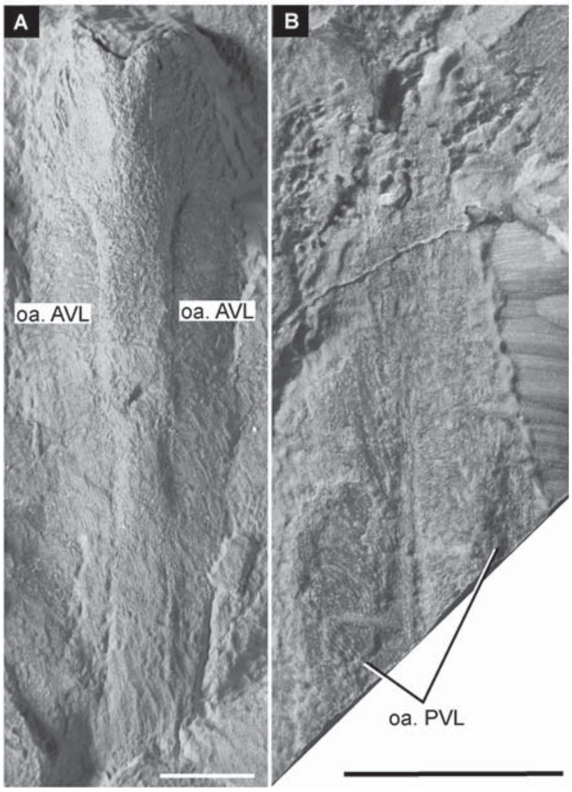


Text-fig. 10. A comparison of anterior ventrolateral plates. A – *Dunkleosteus terrelli*, CMNH 7954, anterior ventral plates (internal view) of the thoracic armor of a mounted specimen. B – *Paramylostoma arcualis*, CMNH 5284, anterior ventral plates and inferognathals (ventral view). C – *Dunkleosteus terrelli*, CMNH 5997, left anterior ventrolateral plate in internal view. D – *Heintzichthys gouldii*, CMNH 9388, left anterior ventrolateral plate in internal view. E – *Gymnotrachelus hydei*, ventral plates of the thoracic armor (internal view), after Carr, 1994, fig. 2C. F – *Stenosteus angustopectus*, CMNH 8042, right anterior ventrolateral plate in internal view. G – *Hlavinichthys jacksoni* gen. et sp. nov., CMNH 9200, latex peel tracing of right anterior ventrolateral plate in internal view. A, C, scale bars equal 5 cm; B, D-G scale bars equal 1 cm. Abbreviations: AL – anterior lateral plate; AMV – anterior median ventral plate; AVL – anterior ventrolateral plate; IG – inferognathal; IL – interolateral plate; PMV – posterior median ventral plate; PVL – posterior ventrolateral plate

eral plate. In *Hlavinichthys jacksoni* gen. et sp. nov. the dorsal lamina is expanded. It is likely that the dorsal lamina represents the branchial lamina that has been flattened in preservation. The laminae of the interolateral plates are unornamented. The nature of the overlap with the anterior lateral plate is unclear, but it is assumed that the lateral end of the interolateral plate fits in the space between the two branchial laminae of the anterior lateral plate (an atypical pattern among the Pachyosteomorphi, e.g., *D. terrelli*, Heintz 1932, text-fig. 53).

Anterior ventrolateral plates (AVL, Text-figs 1, 2, 9, 10G): Both plates are preserved and are at least 2.5 times longer than wide (max. length = 13.8 cm; max. width = 5.5 cm; it is not clear that the posterior end of the right AVL is complete). The anterior margin consists of anterolateral and anteromedial processes with a shallow nearly transverse embayment between the two processes. Externally there are punctate tubercles in the region of the ossification center on both the right and left plates.

Internally, growth lines are visible along the me-

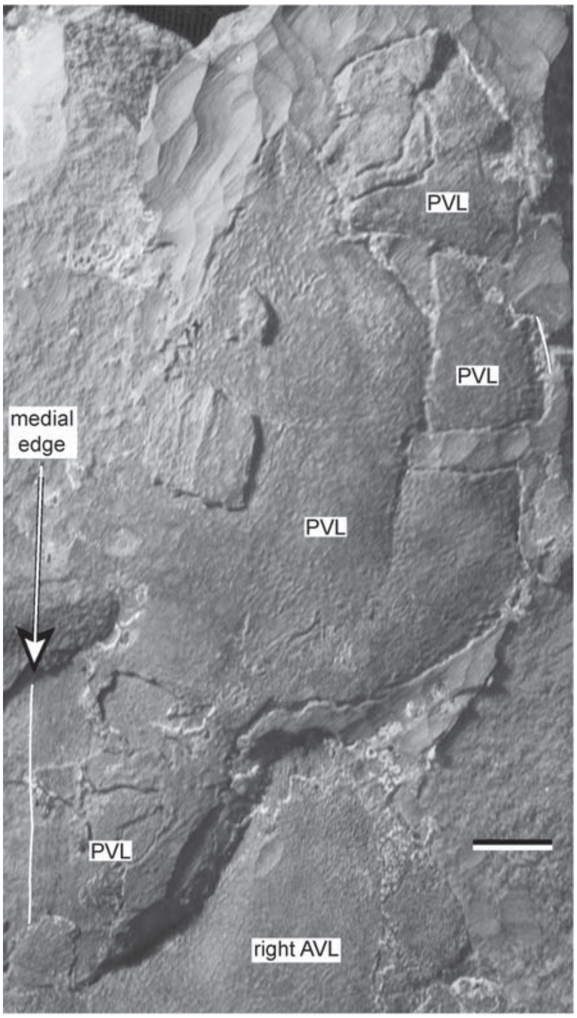


Text-fig 11. *Hlavinichthys jacksoni* gen. et sp. nov., CMNH 9200, A – anterior median ventral plate in external view. B – posterior median ventral plate in external view. Scale bar equals 1 cm. Abbreviations: oa.AVL – overlap area for the anterior ventrolateral plate; oa.PVL – overlap area for the posterior ventrolateral plate

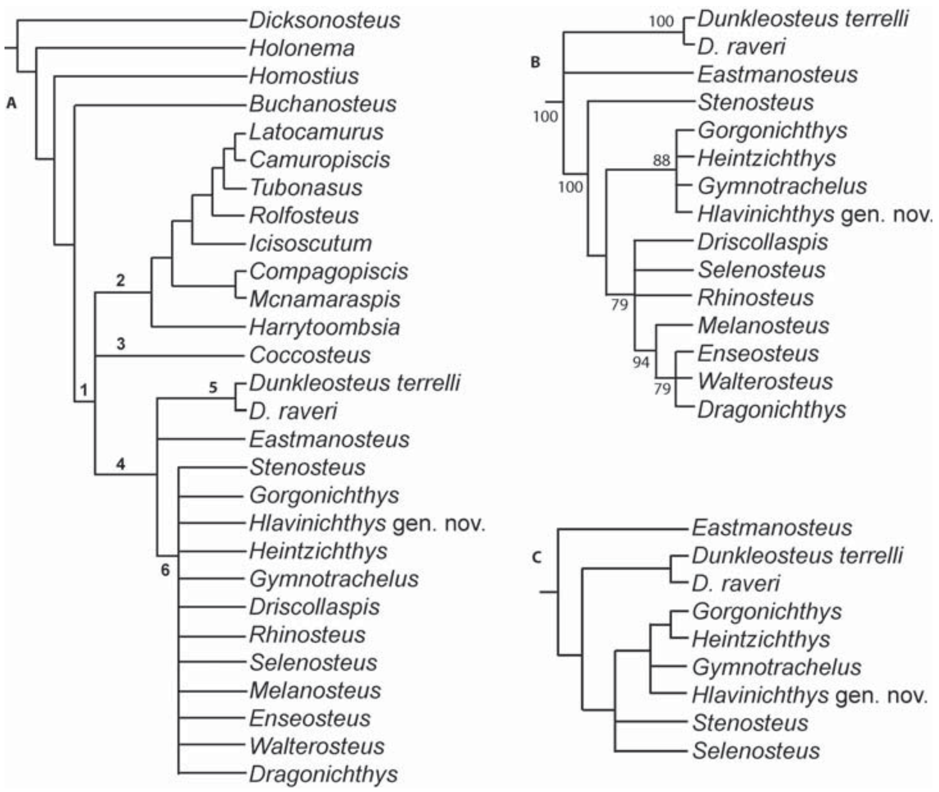
dial and lateral edges of the plate and three thickenings extend from the ossification center (Text-fig. 9A$_2$; the Y-shaped thickenings of Dennis-Bryan 1987). The pattern of processes and the orientation of the anterior portion of this plate are variable within members of the Cleveland Shale fauna (Text-fig. 10). Among these taxa, the ossification center is positioned anterolateral as in *Hlavinichthys jacksoni* gen. et sp. nov.

Anterior median ventral plate (AMV, Text-figs 1, 2, 11A): Preserved in external view, the anterior median ventral plate is at least 3.5 times longer than wide. The anterior part of the plate extends anterior to the adjacent anterior ventrolateral plates, similar to the condition in *H. gouldii* (Carr 1991, text-fig. 9D). A small indentation is present on the anterior edge. Overlap areas for the adjacent anterior ventrolateral plates (oa.AVL) are present.

Posterior ventrolateral plates (PVL, Text-figs 1, 2, 12): A right posterior ventrolateral plate can be recognized in external view. A left plate consists of isolated fragments. Neither plate has defining anterior or posterior features, so right/left was determined by their nearness to the right and left AVL plates. Isolated punctate tubercles are noted on the external surface. The medial/lateral determination is based on comparisons with other taxa where, if there is a difference, the lateral margin is more convex than the medial margin (e.g., *H. gouldii*, Carr 1991, text-fig. 12 and *P. arcualis*, Dunkle and Bungart 1945, text-fig. 3). From the preserved portion of the right plate, the plate is longer than wide. The anterior borders of the posterior ventrolateral plates in *Hlavinichthys jacksoni* gen. et sp. nov. are fragmented and incomplete (with no indication for an overlap area for the anterior ventrolateral plate).



Text-fig 12. *Hlavinichthys jacksoni* gen. et sp. nov., CMNH 9200, fragmented right posterior ventrolateral plate in external view. Clear plate boundaries are indicated by white lines. Scale bar equals 1 cm. Abbreviations: AVL – anterior ventrolateral plate; PVL – posterior ventrolateral plate



Text-fig. 13. A – a strict consensus tree of all 28 taxa based on 34 equally parsimonious trees. Eubrachythoracidi; node 2, Coccosteomorphi (with *Coccosteus*, node 3, unresolved); node 4, Pachyosteomorphi; node 5, Dunkleosteidae; and node 6 Aspinothoracidi. B – a 75% majority tree for the pachyosteomorph portion of the tree in Text-fig. 13A. C – a strict concensus tree, again showing only the pachyosteomorphs, but with the Moroccan and European aspinothoracid arthrodires removed from the analysis (6 trees, TL = 309, CI = 0.3825, HI = 0.6052, RI = 0.5505)

Posterior median ventral plate (Text-figs 1, 2, 11B): A fragment of a single plate showing bilateral symmetry and overlap areas (oa.PVL) is present and may represent a fragment of the posterior median ventral plate.

PHYLOGENETIC POSITION

The determination that *Hlavinichthys jacksoni* gen. et sp. nov. is a member of the Aspinothoracidi Stensiö, 1959 *sensu* Miles and Dennis, 1979, was based on an analysis using PAUP* v. 4.0b (Swofford 2002). The data matrix of Rücklin *et al.* (2015, 27 taxa and 98 characters) was used as published with *Hlavinichthys jacksoni* gen. et sp. nov. added to the taxonomic data set. Parameters for PAUP followed those of Rücklin *et al.* (2015): *Dicksonosteus arcticus*, *Holonema westolli*, *Homostius*, and *Buchanosteus confertituberculatis*, set as outgroups; rooting was based on a monophyletic ingroup and paraphyletic outgroup; all characters set as unordered; random stepwise addition with 10 repetitions (holding 100 trees at each step); with the addition of the following characters scores for *Hlavinichthys jacksoni* gen. et sp. nov. – 1????0N001 21?22?1??? 1?100??200 0110?0000N 1?000?100? 010100???0 101101?101 ????100??0 0N?010??01 10?11???.

The analysis of Rücklin *et al.* (2015) produced four equally parsimonious trees (text-fig. 5, 349 steps, CI = 0.3467, HI = 0.6590, RI = 0.5649). A reanalysis of the matrix revealed a conflict between the published results and the current analysis. The tree topology within the coccosteomorph arthrodires is not consistent between the two analyses (likely due to unordered characters related to the development of the tubular snout in *Rolfosteus* and *Tubonasus*, K. Trinajstic, personal communication, 2018; resulting, in part, in the difference in tree lengths, 357 versus 349, and topology). The strict concensus trees for the pachyosteomorph arthrodires correspond; however, only three of the four trees are an exact match. The fourth tree (Rücklin *et al*. 2015, text-fig. 5D) differs in the switched positions of *Walterosteus* and *Dragonichthys*.

After adding *Hlavinichthys jacksoni* gen. et sp. nov. to the data matrix, the PAUP Heuristic Search analyses resulted in a variable number of equally parsimonious trees (17–34) with a tree length of 368 steps. The largest group of trees had a consistency index (CI) of 0.3315, homoplasy index (HI) of 0.6685, and retention index (RI) of 0.5519 (Text-fig. 13A, a strict concensus tree with six nodes indicated). Within the Eubrachythoracidi (node 1), the results support the sister group relationship of Coccosteomorphi Stensiö, 1944 (node 2, however with *Coccosteus* unresolved, node 3) and Pachyosteomorphi (node 4). Among the pachyosteomorph arthrodires there are three monophyletic groups: (i) Dunkleosteidae Stensiö, 1963 (node 5), (ii) *Eastmanosteus*, and (iii) Aspinothoracidi (node 6). With the addition of *Hlavinichthys jacksoni* gen. et sp. nov. to the analysis there is a complete loss of resolution of relationships among the aspinothoracid arthrodires. A 75% majority rule tree (Text-fig. 13B) suggests that *Hlavinichthys jacksoni* gen. et sp. nov. is most likely related to a group of Cleveland Shale arthrodires (*Gorgonichthys*, *Heintzichthys*, *Gymnotrachelus*, and *Hlavinichthys* gen. nov.). Text-fig. 13C shows the results of an analysis excluding the European and Moroccan aspinothoracid arthrodires. Again, *Hlavinichthys jacksoni* gen. et sp. nov. is an unresolved member of the same monophyletic group. This lack of resolution both within the Cleveland Shale fauna and the more global analysis of aspinothtoracid arthrodires is a testament to the need for further study of unprepared Cleveland Shale fish fossils, continuing review of poorly known members of the fauna, and comparisons beyond the Cleveland Shale fauna.

A case in point is the needed reanalysis of *Paramylostoma arcualis*, which superficially shares a number of features with *Hlavinichthys jacksoni* gen. et sp. nov. The description of *P. arcualis* by Dunkle and Bungart (1945) lacks sufficient descriptive data (i.e., missing data or not mentioned) to be included in a phylogenetic analysis. It is the lack of such data that Rücklin *et al.* (2015) attributed to the poor resolution of North American taxa. Also critical to the phylogenetic analysis of Cleveland Shale fishes is the recent discovery of one or possibly two potentially new species of aspinothoracid arthrodires recovered from the laterally equivalent Chagrin Shale Member (Ohio Shale Formation). Further hindering an analysis of the relationships among the aspinothoracid arthrodires is the exclusion of North American families, such as the Mylostomatidae Woodward, 1891, Titanichthyidae Dean, 1975 and Bungartiidae Denison, 1975 as well as several Arthrodira *insertae sedis*. Continued work on North American, Moroccan, and European aspinothoracid arthrodires offers great potential toward understanding the systematics and evolution of this diverse group at a critical time in vertebrate evolution.

CONCLUSIONS

In the Famennian, there was a major diversification of aspinothoracid arthrodires following the Frasnian–Famennian extinction (Kellwasser event). The Cleveland Shale fauna has provided the best picture of this time. The new taxon, *Hlavinichthys jacksoni* gen. et sp. nov., adds to our understanding of the aspinothoracid arthrodires. However, recent phylogenetic analyses have failed to resolve the relationships among this diverse group of fishes with many important taxa still excluded from analyses. With the extensive unprepared collections from the Cleveland Shale and the potential for new taxa or new information on poorly known taxa, continued research on the Cleveland Shale fauna can offer a unique view of the Famennian. Finally, the Hangenberg Biocrisis began in the Famennian and is recorded in the sediments of the Cleveland Shale (Baird 2013). Thus the Cleveland Shale not only documents the diversification of the North American aspinothoracid arthrodires, but their end-Devonian extinction as well.

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