A NEW SELENOSTEID ARTHRODIRE (‘PLACODERMI’) FROM THE LATE DEVONIAN OF MOROCCO

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ABSTRACT—A new genus and species of selenosteid arthrodire is described from the Late Devonian of Morocco. Driscollaspis pankowskiorum, gen. nov. sp. nov., is defined as a selenosteid with a shallow preorbital plate emplacement of the central plate, a paranal plate emplacement of the central plate as a deep embayment determined by the lateral and posterior lobe, a central plate expanded at the contact with the pinal plate as transverse anterior border, and a suborbital plate overlapping the postorbital plate. The dermal ornamentation is tubercular, forming patches of reticular ridges clustered around sensory-line canal junctions in plate centers. The sensory-line canals are distinctly raised just above the level of the dermal ornamentation, a unique character not previously recognized in any arthrodire but seen in some ptyctodontids. A new phylogenetic hypothesis supports the monophyly of the Selenosteidae within which this new taxon is resolved, but emphasizes also unresolved relationships among aspinothoracid arthrodires. The paleogeographic distribution of the Frasnian vertebrates from Morocco and especially the selenostoids on the western margin of Gondwana and Laurussia are discussed, and the indication for a contact of both continents during the late Frasnian is emphasized.

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SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

Placoderms are an extinct group of armored jawed fishes, constituting the first jawed vertebrates. The relationship of placoderms remains contentious, with some recent phylogenies showing placoderms as a paraphyletic series of evolutionary grades along the stem gnathostome lineage (Brazeau, 2009; Davis et al., 2012; Zhu et al., 2013) whereas others indicate placoderm monophyly supported by a number of synapomorphies, in particular a ring of tightly interlocking and strongly overlapping dermal bones that form a distinct trunk shield that articulates in most forms with a dermal head shield (Goujet, 2001; Goujet and Young, 2004; Young, 2010). There is some consensus, with phylogenetic analysis resolving ptyctodonts and arthrodires as a clade more closely related to crown-group gnathostomes (Brazeau, 2009; Davis et al., 2012). The discovery of Entelognathus led to a new phylogeny with a polytomy of arthrodires, ptyctodonts, and Entelognathus (Zhu et al., 2013). The recent discovery of sexual dimorphism and viviparity in arthrodires (Ahlberg et al., 2009; Long et al., 2009) provides additional character support for the clade ‘Ptyctodontida + Arthrodira.’

Much of our knowledge of the arthrodires, the most diverse group within the placoderms, is based on several key faunas that have produced both a large diversity of forms and superb three-dimensional (3-D) preservation, such as the Early Devonian fauna of Taemas-Wee Jasper, New South Wales (Young, 1979, 1981, 1988), Spitsbergen (Goujet, 1984), the Bad Wildungen fauna of Germany (Gross, 1932; Stensiö, 1963), the Gogo fauna of Western Australia (Long, 1988, 1990, 1994, 1995; Trinajstic and Hazelton, 2007; Trinajstic and Dennis-Bryan, 2009; Long and Trinajstic, 2010), and the eastern Anti-Atlas region of Morocco (Lehman, 1956, 1976, 1977; Lelièvre et al., 1993; Lelièvre, 1995; Rücklin, 2010, 2011). The arthrodires represent around 72% of known placoderm taxa (Denison, 1978), and there is consensus regarding the phylogenetic relationship of various subgroups. Within the eubrachythoracids, a sister-group relationship between the pachyosteomorphs and coccosteomorphs is supported by the majority of recent phylogenetic analyses (Trinajstic and Hazelton, 2007; Trinajstic and Dennis-Bryan, 2009; Carr and Hlavin, 2010); however, there remains instability within the basal members of both these groupings and within ingroup relationships of the pachyosteomorphs (Carr and Hlavin, 2010).

The most recent hypothesis of eubrachythoracid relationships (Carr and Hlavin, 2010) places the Selenosteidae within the Aspinothoracid sensu Miles and Dennis, 1979, of the Pachyosteomorphi Stensiö, 1944, although it was suggested that a new analysis of the European and North American taxa was required to resolve questions regarding the monophyly of the Selenosteidae (Lelièvre et al., 1987). A more recent phylogenetic analysis, using new specimens recovered from the Late Devonian of Morocco and including a redescription of the Bad Wildungen
selenosteids (Rücklin, 2011), supported the monophyly of the Selenosteidae. However, it has been noted (Maisch, 1998) that phylogenetic resolution requires further well-preserved material.

Despite many forms having been described from the Late Devonian of Morocco, only in a few localities is material well preserved in carbonate facies that enables 3-D acid preparation. Here we describe one such specimen, from the Late Devonian of Morocco, and present a new hypothesis of relationship of the pachyosteomorphs within the euarchichthyac arthrodiras. The importance of the Selenosteidae is found in their phylogenetic position as one of the most derived forms in the diverse arthrodire clade. Therefore, they are an ideal group to help determine character polarities and autapomorphic character stages for arthrodires and ‘Placoderm.’

Institutional Abbreviation—LACM, Natural History Museum of Los Angeles County, Los Angeles, California, U.S.A.

Anatomical Abbreviations—ant.p.r., depression for anterolateral corner of endocranium; art.PN, articulation for paranuchal plate; art.PNu, articulation for paranuchal plate; art.R, articulation for rostral plate; art.SO, articulation for sublingual lamina of suborbital plate; ch.dpts, channel for dorsal region of supravagal process of endocranium; csl, central sensory-line canal; Ce, central plate; Ce.dept., depression on the central plate; cdec, depression for cucullaris muscles; d.end.i, ductus endolympathicus internus; dep., depressions on the nuchal plate; dp.obtm., interorbital concavity situated above main part of probable orbitotemporal fontanelle; H, height; ifo.ot, otic branch of the infraorbital sensory-line canal; ifo.pt, postorbital branch of the infraorbital sensory-line canal; L, length; laf, lateral articular fossa; Mg, marginal plate; mII, main lateral-line canal; m.sept., median septum; Nu, nuchal plate; P, pineal plate; pap, par-articular process; pdd, postrostral depression; pfI, pineal foramen; pmc, postmarginal sensory canal; PM, postmarginal plate; PNu, paranuchal plate; P.pr, posterior median process; Pro, preorbital plate; Pto, postorbital plate; pt.p.pr, ridge for postorbital process of endocranium; ptu, paired pits on visceral surface of nuchal; R, rostral plate (restored); res, resin; r.m, rostral margin; sk, skull roof; soc, supraorbital sensory-line canal; suov, suprarobital vault; th.seth, transverse supraethmoidal thickening; tri, triangular depression on posterior region of supravagal vault; W, width.

MATERIALS AND METHODS

The specimen (LACM 154677) was acid prepared (8–10% acetic acid) using the methodology of Toombs and Rixon (1959) and Rixon (1976) to free the plates of the head shield from the carbonate matrix. The exposed bones were hardened with paraloid. The specimen was radiographed with the Natural History Museum of Los Angeles County X-Ray machine in the Department of Ichthyology by Mr. Howell Thomas using a Faxitron cabinet X-ray model 43855C with a NTB digital X-ray scanner EZ 320. Settings were as follows: 50 kVp for 9 minutes for the dorsal-ventral perspective. Skull measurements are provided in Appendix 1.

SYSTEMATIC PALEONTOLOGY

PLACODERMI McCoy, 1848

ARTHRODIRA Woodward, 1891

SELENOSTEIDAE Dean, 1901

DRISCOLLASPIAS, gen. nov.

Type and Only Included Species—Driscollaspis pankowskiorum, sp. nov. (Figs. 1–4)

Diagnosis of Species—Tubercular dermal ornament forming reticular ridges; raised sensory-line canals; shallow preorbital plate embayment of the central plate; paranuchal plate embayment of the central plate as deep embayment determined by the lateral and posterior lobes; central plate expanded at the contact with the pineal plate as transverse anterior border and suborbital plate overlapping postorbital plate. Differs from Rhinosteus, Gymnotrachelus, Draconichthys, Microsteus, Enseosteus, and Stenosteus: skull roof as long as posteriorly broad, with wide and gently concave posterior margin. Differs from Pachyosteus, Microsteus, Walterosteus, Gymnotrachelus, and Stenosteus: rostral and pineal separated by preorbital plates with mesial contact. Differs from Stenosteus and Gymnotrachelus: postorbital plate with elongated posteroventral process. Differs from Enseosteus, Walterosteus, and Draconichthys: central and marginal plates in contact.

Holotype—Specimen LACM 154677. Incomplete head shield. Skull roof comprises paired preorbital, postorbital, central, paranasal plates and single medial pineal and nuchal plates. Cheek comprises marginal and postmarginal plates. Gnathal plates and parashpennoid not preserved. Trunk shield not preserved.

Etymology—in honor of Mark Pankowski and his family who donated the specimen to the Natural History Museum of Los Angeles County.

Occurrence and Stratigraphy—Mr. Mark Pankowski of Rockville, MD, acquired it by sale from a fossil dealer in Europe. The carbonate matrix was a black shale typical for the Late Devonian Kellwasser horizon in the eastern Anti-Atlas, Morocco (Wendt and Belka, 1991; Lubeseder et al., 2010). No conodonts were recovered from the limestone sample, so the age of the specimen is inferred solely from its host lithology.

DESCRIPTION

The holotype of Driscollaspis pankowskiorum (LACM 154677) is represented by a partial skull missing the gnathals, parashpennoid, postnasal, rostral, suborbital, and submarginal plates (Figs. 1, 2). None of the trunk shield plates have been recovered. The sensory line system in the new genus is reduced on the posterior part of the head shield (Fig. 1E, F) when compared with other selenosteids; the exception being Gymnotrachelus, which shows a reduction of the posterior sensory line system. The sensory lines follow the typical arthrodiran pattern (Heintz, 1932), but are raised above the dorsal ornament (Fig. 3), a characteristic of the ptyctodonts. Furthermore, the ornamentation in Driscollaspis with elongated ridges that become reticulate close to the path of the sensory lines is distinct from all other selenosteids (Fig. 3B). In contrast, it resembles the ornamentation in Holoneoma (Miles, 1971), but Driscollaspis differs completely in cranial osteomorphology.

Dermal Bones of the Skull and Cheek—The skull roof is posteriorly broad and strongly arched (length/width [L/W] ratio = 1), becoming narrower and flattening above and anterior to the orbits (Figs. 1, 2, 4), and in this respect is most similar to Pachyosteus Jaeckel, 1901, and Melanoosteus Lelièvre et al., 1987. The anterior skull margin has a convex curve. In Rhinosteus Jaeckel, 1911, Gymnotrachelus Dunkle and Bungart, 1939, Draconichthys Rücklin, 2011, and Microsteus Gross, 1932, the skull roof is more slender and the area between the orbits across the skull roof is much narrower. The posterior margin of the skull roof is wide and gently concave in contrast with Stenosteus Jaeckel, 1901, and Draconichthys, which has a narrow and deeply embayed posterior margin of the skull roof (Carr, 1996:fig. 1A, B; Rücklin, 2011:fig. 19E, F). The orbits are large, constituting
FIGURE 1. *Driscollaspis pankowskiorum*, gen. et sp. nov. **A-D**, skull roof in **A**, left lateral; **B**, dorsal; **C**, anterior; and **D**, posterior views. **E, F**, interpretation of skull plates; skull roof in **E**, lateral and **F**, dorsal views. **G**, lateral view of left postmarginal plate in detail.
almost half the total cheek length, with the marginal plate constituting the majority of the posterior cheek (Fig. 1A). The cheek is large compared with *Enseosteus* Jaekel, 1919, primarily as a result of the size of the marginal plate.

The anterior margin of the skull comprises the preorbital and rostral plates, although the latter is not preserved but is reconstructed as subtriangular based on the space between the preorbital plates.

The pineal plate is large, occupying approximately one-third of the area the postorbital plate does, which is large in comparison with other eubrachythoracid arthrodires. *Rhinosteus* possesses a much smaller pineal plate. In the new species, the pineal plate is anteriorly broad with an acute point and very small external pineal foramen, but in ventral view shows a wide (3 mm) pineal foraminal embayment in the center of the plate (Fig. 2B). Posteriorly, the pineal plate tapers to three-quarters the anterior width of the plate. There is a small break in the posterior margin, which is generally concave where it meets the central plates.

The preorbital plates are preserved, with each plate being roughly triangular, with jagged pineal and postorbital contact margins. Both preorbital plates contact each other mesially, separating the rostral and pineal plates. Within the selenosteids, mesial contact between the preorbital plates is known in *Enseosteo*, *Rhinosteus*, *Draconichthys*, and *Melanosteus*. The anterior margin of the plate curves downwards, forming part of the anterior margin of the orbit and the contact face for the suborbital plate (not preserved). The depth of the curvature is approximately one-third the length of the plate and in this extent resembles *Rhinosteus* Gross, 1932. The surface of the plate is crossed by the supraorbital sensory groove, the walls of which are raised above the level of the dermal ornament. On the visceral surface there is a pronounced dermal preorbital process, which thickens to form the anterior margin of the supraorbital vault. Mesially, there is a pronounced channel for the neurocranial preorbital process and anterior to this is a well-defined supraethmoid crista.

Medially, a step is formed to the interorbital concavity housing the preorbital process of the endocranium with a pronounced anterolateral depression (Fig. 2B).

Postorbital plates are subtriangular to ‘D’-shaped, with a medium-sized postorbital process. There are three sensory-line grooves meeting at the center of ossification (Fig. 1). The central sensory-line bends posteriorly before it divides into the grooves for the otic and postorbital branches of the infraorbital canal, including an angle of approximately 45° (Fig. 1C). The postorbital branch of the infraorbital canal continues onto the marginal plate. Internally, the postorbital plate bears the posterior part of the supraorbital vault, which is deepest in the posterolateral corner. Posterolaterally, a triangular embayment is formed between the supraorbital vault and the lateral consolidated portion of the skull roof (Fig. 2B).

The subtriangular marginal plate (Figs. 1–3) is the largest plate in the cheek, approximately the same size as the paranuchal plates. Medially, the marginal and central plates have a short contact (Fig. 1), which is in common with *Rhinosteus* and *Pachyosteus*, but lacking in *Enseosteo*, *Walterosteus*, and *Draconichthys*. Three sensory-line grooves, the otic branch of the infraorbital canal, the main lateral line, and the postmarginal canal come in contact on the dermal surface of the marginal plate. Dermal ornamentation becomes more reticulate closer to the center of the plate.

The paired central plates (Figs. 1, 2) are the largest dermal plates of the skull roof. They are trilobed, although the lateral lobes that meet the marginal plates are short. There are well-defined posterior lobes separating the nuchal and paranuchal plates, and there is contact with both the marginal and postorbital plates laterally. The grooves for the central and supraorbital sensory canals are clearly seen, but the posterior pit-line canals cannot be distinguished. The plates are incomplete along the midline, but it appears from sections of contact preserved that it had an interdigitated suture. A postpineal foramen is not seen.
The paranuchal plates (Figs. 1, 2) are trapezoidal in dorsal view, with an anteriorly pointed margin that is 74% as wide as the posterior margin, which is marked by a short stout median process (Figs. 1B, D, 2B). The posterior margin is gently concave. The nuchal plate is shorter and triangular in *Pachyosteus*. Posterodorsally, the paired pre-endolymphatic thickenings extend posteriolaterally on the paranuchal plate to form the thick posterior margins of the plate. The margins form a narrow ridge in the midline (Fig. 1D) and lead to separate, deeply set paired pits (Fig. 2B). Into these pits the posterior division of the endocranial sensory canal groove crossing the plate. An anterior overlap for the paranuchal plate. There are well-developed para-articular processes and broad, horizontal lateral articular fossae (Figs. 1D, 2B) for the articulation of the trunk shield. The main lateral line groove (Fig. 2E) crosses the dorsal surface of the plate from the anterior margin to the posterior corner of the paranuchal plate. Posterior sensory-line grooves are reduced and no trace of the posterior margin to the posterior corner of the paranuchal plate. Posterior (Fig. 2E) crosses the dorsal surface of the plate from the anterior margin to the posterior corner of the paranuchal plate. Posterior sensory-line grooves are reduced and no trace of the posterior margin to the posterior corner of the paranuchal plate. Posterior sensory-line grooves are reduced and no trace of the posterior margin to the posterior corner of the paranuchal plate.

The paranuchal plates (Figs. 1–3) are only slightly smaller than the central plates and larger than the preorbital plates. There is a deep embayment where the posterolateral corners of the nuchal plate overlap. There are well-developed para-articular processes and broad, horizontal lateral articular fossae (Figs. 1D, 2B) for the articulation of the trunk shield. The main lateral line groove (Fig. 2E) crosses the dorsal surface of the plate from the anterior margin to the posterior corner of the paranuchal plate. Posterior sensory-line grooves are reduced and no trace of the posterior margin to the posterior corner of the paranuchal plate. Posterior sensory-line grooves are reduced and no trace of the posterior margin to the posterior corner of the paranuchal plate.

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the lateral cusp on the lateral face of the anterior supragnathal (character 88, 0→1); and (9) lack dermal plate ornament (character 91, 0→1).

Clade 6 is supported in all trees by (1) large orbit size (character 28, 1→2); (2) position of the PrO/PtO/C triple point over the orbit (character 33, 0→1, also present in the camuropiscids); (3) loss of the interolateral branchial lamina (character 47, 1→0, although this character was unable to be scored for the majority of taxa); and (4) closed angle between the postorbital and otic branches of the infraorbital sensory-line groove (character 75, 0→2).

The relationship of Gorgonicthys, Heintzichthys, and Gymnotrachelus, clade 7, is also supported in all trees by (1) loss of the marginal plate contact with the central plate (character 23, 1→0, which also occurs in the coccosteomorphs); (2) character 56, 1→0, (3) shortening of the cheek length (character 61, 0→1, also present in the camuropiscids); and (4) position of the posterolateral corner of the skull roof (character 92, 2→1); characters 69, 83, and 89 were coded as missing for the majority of the taxa and are therefore uninformative here.

Clade 9 is resolved by (1) character 4, 0→1; (2) medial contact between the preorbital plates in front of the pineal

FIGURE 4. Driscollaspis pankowskiorum gen. et sp. nov.: X-ray images of holotype. A, skull roof in dorsal view and B, skull roof in right lateral view.
plate (character 18, 2→1, also present in the camuropiscids and polymorphic for the incisoscutids and Compagopiscis); (3) suborbital marginal contact (character 55, 0→1, also present in the camuropiscids); (4) loss of the dentent process on the quadrate (character 58, 2→1, although this character could only be coded for Selenosteus; and (5) well-bound
resolved within the Selenosteidae, similar to the analysis of Carr and Hlavin (2010).

Characters Rücklin (2011) used to diagnose the Selenosteidae Dean, 1901, comprised the following: possessing large orbits, with the marginal plate forming the posterior orbital margin; the development of a large submarginal plate; and a short, rigid cheek region in addition to a closed angle between postorbital and otic branches of the infraorbital sensory-line grooves. However, no camuropiscids were included in this analysis (Rücklin, 2011). When the camuropiscids are considered, a number of characters, probably associated with the increased size of the orbits in each family (Trinajstic and Dennis-Bryan, 2009; Carr and Hlavin, 2010), are found to be common, including the position of the PrO/PtO/C triple point over the orbit, a broad submarginal plate, and the marginal plate participating in the orbit. Additionally, in Driscollaspis, the participation of the marginal plate in the orbit is not certain and this character is ambiguous for several of the North American taxa. The most robust character to define the Selenosteidae appears to be character 75, the angle between the postorbital and otic branches of the infraorbital sensory-line groove. However, this character is also present in Brachydeirus along with a number of other characters considered synapomorphies for the Selenostidae that are related to the enlargement of the orbit. The Brachydeiridae have been considered the sister group to the Selenostidae (Lelièvre et al., 1987; Carr, 1991, 1994, 1996; Rücklin, 2011); however, the group requires revision (K. Dennis-Bryan, pers. comm.).

In contrast to the earlier analysis of selenosteid placoderms (Rücklin, 2011), there is no clear separation between the North American taxa and the Moroccan and European taxa. The addition of a new Moroccan taxon has not clarified the taxonomy of the selenosteid placoderms forming a clade with Gymnotrachelus as sister group to all remaining selenosteiids is similar to the analysis of Carr and Hlavin (2010:fig. 9, clade 8). The position of Stenosteus, basal to this clade, is in contrast to the analysis of selenosteid placoderms by Carr (1996), where Stenosteus and Selenosteus are the most derived selenosteids. In the analysis of Rücklin (2011), Steno- steus is part of a basal clade including also Gymnotrachelus and Selenosteus. One problem is that even though additional taxa have been recovered, these are often incomplete, and in comparison to the coecomucoid taxa there are many characters, especially gillarch and trunk shield characters that cannot be coded. The North American taxa still require revision (Carr and Hlavin, 2010), as do some of the European taxa.

Paleobiogeography of Frasian Vertebrates

The utility of fishes in determining biogeographic relationships is limited because fishes are nektonic marine animals, inhabiting the shelf regions of the oceans. The arthrodirans discussed here were probably not able to cross large oceans and, therefore, were assigned to category ‘d’ of biogeographic utility after McKerrow et al. (2000). Consequently, a comparison of their occurrences can be used to infer oceanic barriers (Rücklin, 2010). An argument for the apparent provincialism of arthrodirans and ptyctodont placoderms might be their reproductive strategy as live-bearing organisms without widespread larval stages (Long et al., 2008, 2009). Therefore, different placoderm ranges might be explained in paleobiogeographic terms.

The Moroccan fish-fauna exemplifies a paleobiogeographic change during the Devonian. In the Emsian and Eifelian, the placoderm fauna of Morocco, and their association with the acanthodian Machaeracanthus, a typical Gondwanan element (Klug et al., 2008), is indicative of a Gondwanan affinity (Young, 1987). The arthrodiran genus Atlantidosteus is present in Morocco as well as in Australia, indicating a probable continuity of a
marine environment along the northern margin of Gondwana (Young, 2003b), whereas there is no overlap between the arthrodiran faunas of Gondwana and Laurussia currently documented.

These affinities apparently change in the Late Devonian, with the occurrence of arthrodirans common to Laurussia and Gondwana in the Frasnian of Morocco. This supports the hypothesis that no paleobiogeographic barrier existed and probably the ocean between Laurussia and Gondwana narrowed in the Late Devonian (Rücklin, 2010). Further palaeontological data supporting this hypothesis include the distribution of trilobites in the Rhenish Massif and Morocco (Feist, 2002) and logs of wood (mainly *Archaeopteris*) from the Anti-Atlas and Dra Valley of Morocco (Meyer-Berthaud et al., 1997, 2004) that are similar to floras in Laurussia. In addition, the distribution of the antiarcan *Bothriolepis*, which occurs from the late Givetian–early Frasnian onwards in Gondwana and Laurussia (Young, 2003a), supports a close relationship. Even vertebrate assemblages from northern South America support this hypothesis with a dispersal of marginal marine and possibly freshwater fishes in the Late Frasnian or Early Famennian (Janvier and Villarroel, 2000; Young et al., 2000; Young and Moody, 2002; Young, 2003a; Janvier and Maisey, 2010). The occurrence of *Asterolepis* and *Holoptichius* in the Frasnian of Colombia even suggests a southward dispersion of Euramerican taxa towards Gondwana (Janvier and Maisey, 2010) and supports the idea of an interchange of faunas and close relation.

However, the comparison of the Moroccan placoderm fauna with Australian vertebrate assemblages from Gogo Formation shows a difference. Both assemblages are from the Frasnian and situated on the northern margin of Gondwana. The change from a possible continuity of a marine environment in the Early Devonian along the northern margin of Gondwana to a western and eastern direction might indicate a paleobiogeographic barrier in the Frasnian (Rücklin, 2010). Iran would form a terrane east of the barrier; this is in accordance with the overlapping chondrichthyan, acanthodan, conodont, and thelodont faunas of Iran and Western Australia (Turner et al., 2002; Hairapetian et al., 2006; Trinajstic and George, 2009). This is also indicated by phyllolepid placoderms from non-marine sediments, which are restricted to Gondwana in the Givetian (Australia, Antarctica, Turkey, Venezuela), but present in Laurussia (Europe, Russia, Greenland, North America) from the Late Devonian (Famennian) onward. A Gondwanan origin and later spread to Laurussia via a land connection is suggested. Therefore, a closure of the ocean between Gondwana and Laurussia and a continental connection at or near the Frasnian-Famennian boundary has been postulated (Young, 2003a, 2005). An opposing view concerning the ecology of Middle to Late Devonian fishes is given by the study of Schultz and Cloutier (1996) who doubt restriction of any genus to a freshwater environment.

In the Famennian, a western fish fauna dominated by the large arthrodirans *Dunkleosteus* and *Titanichthys* is common in Morocco, North America, Belgium, and Poland. Therefore, a contact of Gondwana and Laurussia in the east is indicated, forming a biogeographic barrier in the Famennian (Young, 1987). With further investigation and description of thelodonts and arthrodirans from Western Australia, this hypothesis might be tested.

CONCLUSIONS

*Driscollaspis* is a new taxon of the diverse arthrodiran Kellwasser fauna from the eastern Anti-Atlas of Morocco. This new genus and species demonstrates an even larger diversity of the selenosteid fauna than recently proposed (Rücklin, 2011). Therefore, even more new placoderm taxa should be expected because the sampling curve for Devonian vertebrates in Morocco is still rising. With this high diversity of Paleozoic fishes, the localities in Morocco are comparable to the Late Devonian faunas at Bad Wildungen in Germany and from the Gogo Formation in Australia. Currently the Moroccan fauna is described as being dominated by arthrodirans (Rücklin, 2010) and lacking other osteichthians.

Unfortunately, the new genus has not preserved some important characters; nevertheless, an inclusion in the existing data matrix resulted in a phylogenetic position inside Selenosteidae as sister group to *Rhinosteus*.

The occurrence of another selenosteid arthrodiran from Morocco emphasizes the wide distribution of selenostoids in Gondwana and Laurussia in the Frasnian and the close paleobiogeographic position of both continents. Also, the wide distribution of selenostoids on the western margin of Gondwana and Laurussia and the absence on the eastern margin of Gondwana might be an indication for a contact of Gondwana and Laurussia during the late Frasnian forming a biogeographic barrier.

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APPENDIX 1. Measurements.

Skull roof: L = 134 mm; W = 134 mm
W across anterior orbit = 70 mm; L orbit = 50 mm
W between lateral articular fossa on posterior margin = 63 mm
Depth skull roof (as preserved) without postmarginal plate = 70 mm
Nuchal plate: L = 37 mm; W = 50 mm (posterior); anterior W (dorsal) = 29 mm
Nuchal thickening max. depth = 17 mm
Paranuchal plate: (right) L = 57 mm; W (depth) = 64 mm
Central plate: (right) L = 68 mm; W = 34 mm
Marginal plate: (right) L = 41 mm; W = 60 mm (max. dimension measured)
Postmarginal plate: (left) L = 28 mm; H = 30 mm
Postorbital plate: (right) L = 45 mm (max. dimension measured orbit); W = 25 mm
Preorbital plate: (right) L = 49 mm; W = 36 mm
Pineal plate: L = 30 mm; W = 19 mm

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APPENDIX 2  Character-taxon matrix used for phylogenetic analysis. Polymorphic character states A, (0, 1); B, (0, 2); C, (1, 2). Abbreviations: DunkleosteusR, Dunkleosteus raveri; DunkleosteusT, Dunkleosteus terrelli.

| 10 | 20 | 30 | 35 |
|----|----|----|----|
| Dicksonosteus | 120000-101 | 0000200010 | 1-100120000 | 11010 |
| Holonema | 020020-011 | 10110-02-0 | 0000000100 | 11010 |
| Buchanosteus | 0-0-0-0-00 | 10012-0010 | 0-110-001 | 01012 |
| Homosteus | 100000-100 | 00012-12-0 | 00110-010 | 01-0 |
| Harzytoombsia | 101120-000 | 010110110 | 0000011110 | 11012 |
| Rolfosteus | 1111011000 | 0110111010 | 0000111101 | 11-2 |
| Tubonasus | 1101111002 | 2111011110 | 000-011110 | 111-2 |
| Coccosteus | 100020-000 | 0112011800 | 0111001101 | 11012 |
| Eccaliaspis | 101020-012 | 011201112 | 1110001-101 | 11012 |
| DunkleosteusT | 100210-011 | 21000112-1 | 111100-000 | 11012 |
| DunkleosteusR | -00220-01- | -----12-1 | -11-000-00- | -11- |
| Gorgonichthys | 110010-101 | 01000-12-0 | 1100-101 | 11112 |
| Heintrizhthys | 11-010-001 | 21002-12-2 | 1001-200 | 11102 |
| Rhinosteus | 1-1-10001 | 2-002-1112 | 101110-201 | 10102 |
| Gymnotrichelaus | 100100-000 | 21000-12-1 | 0010-101 | 11101 |
| Stenosteus | --0-11001 | 2-000-1200 | -010-10111 | 01000 |
| Incissocutum | 1111CA-00B | 1110000001 | 0000101110 | 11211 |
| Latocamurus | 111110-102 | 2111-01100 | 0001111100 | 11102 |
| Camuropiscis | 1111010002 | B11110110 | 001110110 | 11002 |
| Melanosteus | 1702100000 | 2100271110 | 001110200 | 01110 |
| Compagopiscis | 11111C0000B | B111001200 | 010002101 | 11012 |
| Mcnamaraspis | 1011210000 | 011010108 | 01000-101 | 10101 |
| Driscollaspis | 10012100001 | 21120-1100 | 111100-201 | 1130- |
| Enaeosteus | 1001110001 | 21102-1100 | 00010-200 | 11110 |
| Walterosteus | 10-110001 | 2-002-12-1 | 00011-200 | 11110 |
| Dragonichthys | 1-1000000 | 2-000-0110 | 100110-200 | 1111- |
| Selenosteus | ---0-00011 | 2-002-12-0 | 10A-1-201 | 021- |

| 40 | 50 | 60 | 70 |
|----|----|----|----|
| Dicksonosteus | 11000 | 0000111110 | 010000-10 | 00-000-0 |
| Holonema | 10011 | 0010111100 | 1000000100 | 00-000-0 |
| Homosteus | 1-00- | ------1-1 | -11000-11 | 00-000-1 |
| Holonema | 00001 | 1---101-1- | -10100---1 | 01-0------ |
| Heintrizhthys | 11011 | 0-11111110 | 21-00011-1 | 001001010 |
| Rholfosteus | 10110 | 0011111110 | 211010110 | 0110-0101 |
| Tubonasus | 1-11- | 001111-00 | 21-01-110 | 0110-0101 |
| Coccosteus | 11001 | 000111100 | 21100111 | 00101-0111 |
| Eccaliaspis | 10000 | 11-010111 | 1101011111 | 00101C0111 |
| DunkleosteusT | 00000 | 11-010101 | 11010111-11 | 0010020111 |
| DunkleosteusR | ---0--- | ------- | ------ | -0------ |
| Gorgonichthys | 0000- | 1---0----- | ------- | -001011101 |
| Rhinosteus | 0000- | 10-10-010- | 1101011111 | 1010011110 |
| Gymnotrichelaus | 0000- | 10000-0000 | -1011----0 | 111111110 |
| Stenosteus | 01010 | ---0-1-01 | -00101111 | -00-0-0-0- |
| Incissocutum | 01110 | --11110-01 | 00001111AA | A01001A101 |
| Latocamurus | 11011 | 0-011-01-1 | 21-010110 | 0110000101 |
| Camuropiscis | 11110 | 0011111111 | 211010110 | 0110010101 |
| Melanosteus | 0717777777 | 170777777 | 710777777 | 010077777 |
| Compagopiscis | 11110 | 0011111100 | 2110011110 | 0000101010 |
| Mcnamaraspis | 11011 | 0011111000 | 21110010 | 0000101101 |
| Driscollaspis | ------ | ------- | -1111---- | 01------- |
| Enaeosteus | 01--- | 000------- | 10110000 | 011111111 |
| Walterosteus | 001--- | ------- | 10110000 | 0111------- |
| Dragonichthys | ------ | ------- | 10110000 | 0111------- |
| Selenosteus | 1-00- | 1---0----- | 11011-01-1 | 01-01111 |

(Continued on next page)
| APPENDIX 2 (Continued) |
|------------------------|
|                         | 80          | 90          | 98          |
| Dicksonosteus          | 0000000010  | 00010-------0 | 12200-------0 |
| Holonema               | ---1001A1A  | 10011-------0 | 133000-------0 |
| Buchanosteus           | 1-------001 | 1A0110-------1 | 12201-------1 |
| Homosteus              | ---001-------0 | 11001-------1 | 12101-------0 |
| Harrytoombsia          | 0010010000 | 00111-------1 | 1-------1     |
| Rolfosteus             | ---1101101  | 00010-------1 | 133-------0---0 |
| Tubonaseus             | 000---101000 | 00010-------1 | 122-------0---0 |
| Coccoesteus            | 001---011001 | 001110-------01 | 12211-------1 |
| Ecalliapis             | 1111000010  | 000110-------0 | 122-------0---0 |
| Dunkleosteust          | 0100000-------0 | 00111110111 | 02101-------01 |
| DunkleosteusR          | 0-------000---0 | ---1111-------1 | 1-------1     |
| Gorgonichthys          | ---100-------0 | ---1101-------1 | 000-------011 |
| Heintrichthys          | 01------0100000 | 000110------101 | 011-------11 |
| Rhinosteus             | ---200000---0 | 00111-------11 | 02201-------0 |
| Gymnotrachelus         | 3-------200000 | 000100-------01 | 011-------11 |
| Stenosteus             | 000001-------0 | 10-------10 | --------- |
| Incisoscutum           | 10111111000  | 000111-------1 | 1-------1     |
| Latocamuratus          | 31111101000  | 00110-------1 | 1-------1     |
| Camuropiscis           | ---10101000  | 10111011111 | 112-------011 |
| Melanosteus            | 1711277777  | 11111077001 | 10000??71 |
| Compagopiscis          | 111110A000A  | 00111111111 | 133-------011 |
| McNamaraaspis          | 11111101000  | 00111111111 | 133-------011 |
| Driscollaspis          | ---10-------0 | ---11------1 | ---A-------11 |
| Enseosteus             | ---2000-------0 | 100------11 | 101-------011 |
| Walterosteus           | ---2-------0 | --------1 | 101-------0-- |
| Dragonichthys          | ---1-------001 | 1100-------1 | 101-------0-- |
| Seleinosteus           | --------2 | --------001 | -----1--