

Scheenstia bernissartensis (Actinopterygii: Ginglymodi) from the Early Cretaceous of Bernissart, Belgium, with an appraisal of ginglymodian evolutionary history

Lionel Cavin, Uthumporn Deesri & Sébastien Olive

To cite this article: Lionel Cavin, Uthumporn Deesri & Sébastien Olive (2019): *Scheenstia bernissartensis* (Actinopterygii: Ginglymodi) from the Early Cretaceous of Bernissart, Belgium, with an appraisal of ginglymodian evolutionary history, Journal of Systematic Palaeontology, DOI: [10.1080/14772019.2019.1634649](https://doi.org/10.1080/14772019.2019.1634649)

To link to this article: <https://doi.org/10.1080/14772019.2019.1634649>

 View supplementary material 

 Published online: 22 Jul 2019.

 Submit your article to this journal 

 View Crossmark data 



Scheenstia bernissartensis (Actinopterygii: Ginglymodi) from the Early Cretaceous of Bernissart, Belgium, with an appraisal of ginglymodian evolutionary history

Lionel Cavin^{a*} , Uthumporn Deesri^{b,c} and Sébastien Olive^d

^aDepartment of Geology and Palaeontology, Muséum d'Histoire Naturelle, CP6434, 1211 Geneva 6, Switzerland; ^bDepartment of Biology, Faculty of Science, Mahasarakham University, Khamriang, Kantarawichai District, Maha Sarakham 44150, Thailand; ^cPalaeontological Research and Education Centre, Mahasarakham University, Khamriang, Kantarawichai District, Maha Sarakham 44150, Thailand; ^dPalaeobiosphere Evolution, OD Earth and History of Life, Royal Belgian Institute of Natural Sciences, Rue Vautier 29, 1000 Brussels, Belgium

(Received 12 March 2019; accepted 6 June 2019)

Lepidotes bernissartensis is a species of holostean ray-finned fish from the Barremian–Aptian of Bernissart, Belgium, described by Traquair in 1911. We provide here a revision of its anatomy, which led us to include this species in the genus *Scheenstia*, and to consider *L. brevifulcratus* and *L. arcuatus*, both from the same site, synonymous with *S. bernissartensis*. We performed two cladistic analyses in order to assess the phylogenetic position of *S. bernissartensis* and to do an updated appraisal of the evolutionary history of the ginglymodians. *Scheenstia* is included in the Lepidotidae, and placed in a pectinated position between the basal genus *Lepidotes* and the more derived members of the family (other species of *Scheenstia*, *Isanichthys* and *Camerichthys*). The nodes within the lepidotids are weakly supported. Although *S. bernissartensis* is not directly related to *S. mantelli* from the Wealden of Europe, the two species have similar palaeoenvironments and stratigraphical ranges. Taken as a whole, the ginglymodians experienced several episodes of diversification that are spatially and temporally restricted. The oldest episode involved basal ginglymodians and occurred in the Middle Triassic, in marine environments along the northern margin of the Tethys. A second episode affected the Semionotidae and occurred in freshwater environments of North America and Europe in the Late Triassic and Early Jurassic. The remaining Semionotiformes, Macrosemiidae and Callipurbeckidae, ranged from the Triassic to the Early Cretaceous and were mostly marine. Among the Lepisosteiformes, two clades, the Lepidotidae and the Lepisosteoidi, show episodes of diversification, first in marine and then in freshwater environments.

Keywords: Lepisosteiformes; Lepidotidae; osteology; cladistic analysis; evolutionary history

Introduction

Bernissart is a former coal-mining village in western Belgium, situated less than 1 km from the Franco-Belgian frontier (Fig. 1A, B). In 1878, the Sainte-Barbe mine shaft started to produce one of the greatest palaeontological discoveries of all times: more than 20 complete articulated skeletons and several incomplete specimens of the dinosaur *Iguanodon* along with numerous remains of plants, crocodiles, turtles, rare amphibians, insects and about 3000 actinopterygians. Godefroit *et al.* (2012) documented the historical background of this discovery. In a detailed monograph, the actinopterygians were studied by Traquair (1911), who identified 11 genera. Further studies by Gaudant (1966), Taverne (1981, 1982, 1999), Grande & Bemis (1998), Poyato-Ariza & Wenz (2004) and Olive *et al.* (2017, 2019) revised some of the ray-finned taxa from the Bernissart

assemblage, but the revision of the ‘*Lepidotes*’ species from this site was still pending. Traquair (1911) recognized three species of *Lepidotes* in the Bernissart site, *L. bernissartensis*, *L. brevifulcratus* and *L. arcuatus*.

The genus *Lepidotes* was used for a long time as a wastebasket taxon containing several tens of species, mostly from the Jurassic and Cretaceous, poorly characterized by general features, such as thick rhomboid scales and, for most of the species, by semi-tritorial or strongly tritorial dentition. For two decades, several studies have revised species traditionally referred to *Lepidotes* and species related to the other wastebasket genus *Semionotus*, as well as other ‘semionotiform’ taxa mostly from Europe (Wenz 2003; López-Arbarello 2008, 2012; López-Arbarello & Sferco 2011; López-Arbarello & Wencker 2016; López-Arbarello *et al.* 2019), but also from North America (Gibson 2013) and South America (Wenz & Brito 1996; Gallo & Brito

*Corresponding author. Email: lionel.cavin@ville-ge.ch

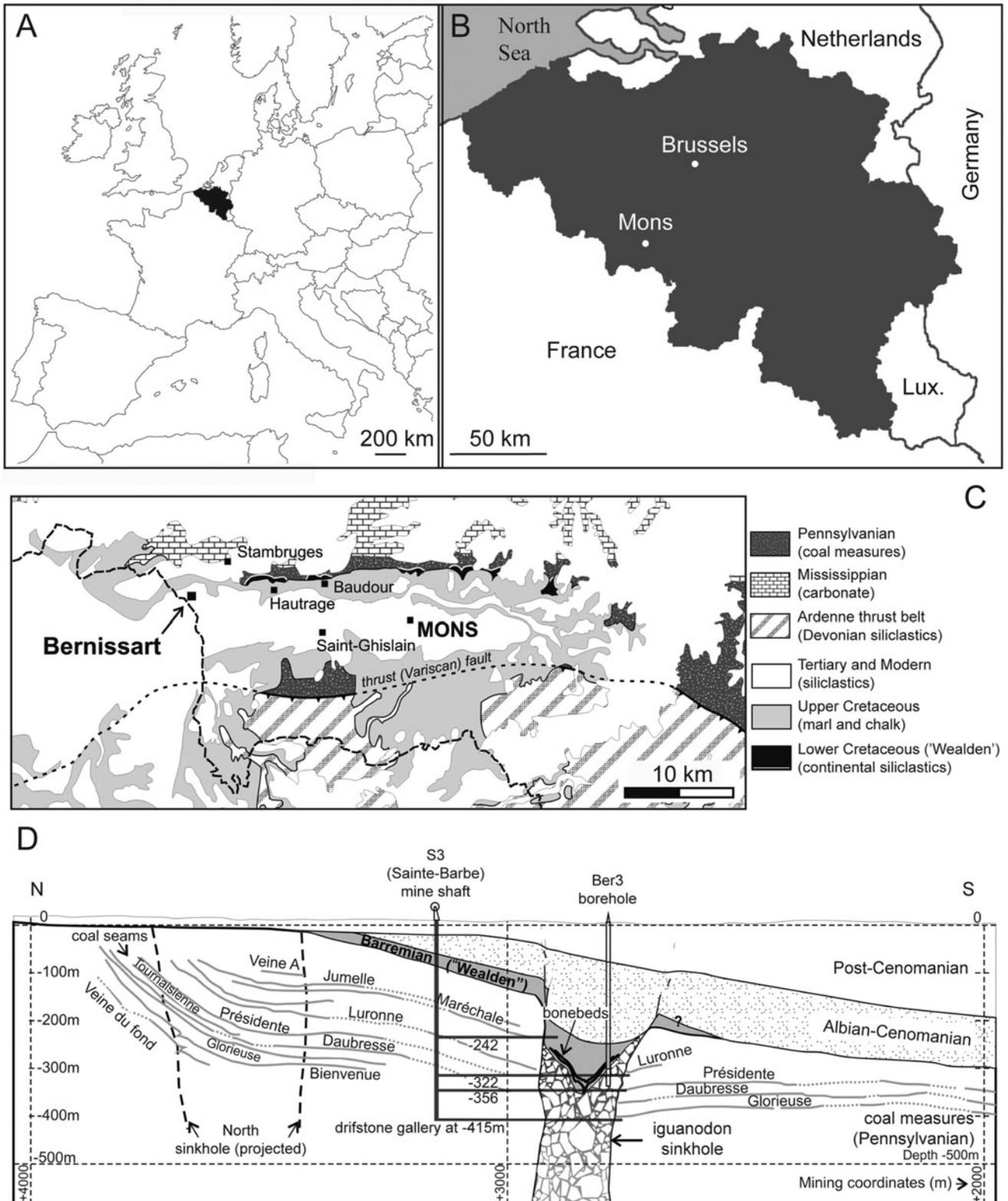


Figure 1. Location and geological framework of the Bernissart locality. **A**, location of Belgium in Western Europe. **B**, location of Bernissart within Belgium. **C**, location of Bernissart within the Mons Basin, from Baele *et al.* 2012b. **D**, cross-section of the Bernissart area showing the geological setting of the *Iguanodon* Sinkhole, from Baele *et al.* 2012b, who adapted the figure from Delmer & Van Wichelen 1980. **Abbreviation:** Lux., Luxemburg.

2004; López-Arbarello & Codorniú 2007; Lins de Paiva & Gallo 2018). In parallel, the discovery of new material has allowed the recognition of new taxa related to *Lepidotes* and *Semionotus*, in particular from the Triassic of Europe (Tintori & Lombardo 2007) and China (López-Arbarello *et al.* 2011; Wen *et al.* 2011; Xu & Wu 2011; Sun & Ni 2017; Xu *et al.* 2018), from the Early Cretaceous of Mexico (López-Arbarello & Alvarado-Ortega 2011), from the Late Jurassic–Early Cretaceous of Southeast Asia (Cavin & Suteethorn 2006; Cavin *et al.* 2013, 2019; Deesri *et al.* 2014, 2016), and eventually from the Cretaceous of Africa (Wenz 1999; Forey *et al.* 2011).

The systematic affinities of *Lepidotes* and *Semionotus* have been discussed for a long time. Since the resurrection of Holosteii by Grande (2010), most studies resolved *Semionotus*, *Lepidotes* and related taxa as stem gars (e.g. Cavin 2010). This clade, named Ginglymodi by Grande (2010), was split in two clades by López-Arbarello (2012): the Lepisosteiformes, which include the extant gars and a series of genera from the Early Jurassic to the present, and the Semionotiformes, which include extinct Triassic to Cretaceous genera. This pattern was then recovered in most subsequent studies. Recently, the lepisosteiform clade was enriched by genera closely related to modern gars discovered in the Cretaceous of North America (Alvarado-Ortega *et al.* 2016) and South America (Wenz & Brito 1992; Grande 2010), in the Cretaceous of Africa (Cavin & Brito 2001; Grande 2010) and, more surprisingly, in marine sediment of the Late Jurassic of Mexico (Brito *et al.* 2017).

The anatomical revision of '*Lepidotes*' *bernissartensis*, its inclusion in a phylogenetic framework and the discussion of its position in the evolutionary history of ginglymodians are proposed here.

Geological setting and locality

Geologically, Bernissart is situated in the north-western part of the Mons Basin, an east-west synclinal structure filled with Meso–Cenozoic deposits (Fig. 1C). Its sedimentation started in a continental environment at the beginning of the Cretaceous Period (during the so-called Wealden) thanks to an active subsidence, mainly controlled by intrastratal dissolution of deep evaporite beds in the Mississippian (Carboniferous) basement. This led to the creation of sinkholes, or natural pits, in various parts of the basin (Spagna 2010; Quinif & Licour 2012). When those natural pits reached the surface, after crossing all the overlying deposits, they acted as a trap and confined the sediment, fauna and flora present there at that moment. At Bernissart, the fossil remains were

found in a lacustrine clay, which was defined as the Sainte-Barbe Clays Formation (Cornet & Schmitz 1898; Cornet 1927). The age of this formation was recently determined based on palynologic data as late Late Barremian to earliest Aptian (Yans *et al.* 2006, 2012; Dejax *et al.* 2007). The environment at the top of the *Iguanodon* pit of Bernissart was formerly interpreted as lacustrine (Van den Broeck 1898) or lacustrine to swampy (Yans 2007; Schnyder *et al.* 2009; Spagna 2010; Spagna *et al.* 2012).

Fishes have so far been recovered in the *Iguanodon* sinkhole through the lateral tunnel, starting at the Sainte-Barbe mine shaft, at depth of –322 m (Fig. 1D). They were mainly found concentrated with chelonians and crocodiles in one or two bone beds (bone beds III and/or IVb) but also found isolated within dinosaur bone beds (I, II, IV and V) (Baele *et al.* 2012a). Unfortunately, the information on the exact provenance of these fossil fishes is lost because the specimens were mixed up before labelling when brought to the surface.

Material and methods

The specimens were prepared at the beginning of twentieth century and we have no record of the preparation protocol at this time, but it was most probably done mechanically. The general body outlines and the outlines of some of the skull bones are recognizable, but in most specimens the ossifications are damaged and poorly preserved, making recognition of the pattern of the skull bones difficult.

The phylogenetic analysis of the relationships of '*Lepidotes*' *bernissartensis* is based on the data matrix of Cavin *et al.* (2019), which itself is based on the data matrix of Sun & Ni (2017), ultimately based on that built by López-Arbarello (2012) and Cavin (2010), with multiple subsequent additions and corrections (analysis I). Based on new observations, some corrections of the scoring have been made (i.e. *Isanichthys palustris* for ch. 6(1), 35(0), 42(1) and 53(0); *I. lertboosi* for ch. 14(3), 20(0), 37(0), 71(1); *L. microrhis* for ch. 6(0), 53(0), 56(0)).

Recently, in a new analysis which aimed at resolving the phylogenetic relationships of a new basal ginglymodian, Xu *et al.* (2018) built a large new data matrix including characters of ginglymodians and halecomorphs. We also used this data matrix to run a phylogenetic analysis (analysis II).

Anatomical abbreviations. **a.f.hm**, articular facet of the hyomandibula; **Ang**, angular; **bpt**, basipterygoid process; **Cha**, anterior ceratohyal; **Chp**, posterior ceratohyal; **Cl**, cleithrum; **Co**, coronoid; **D**, dentary; **Dpl**,

dermopalatine; **Dplt**, dermopalatine tooth; **Dpt**, dermopterotic; **Dsp**, dermosphenotic; **Ecp**, ectopterygoid; **Es**, extrascapular; **Fr**, frontal; **gr**, groove; **Io**, infraorbital; **Iop**, interopercle; **(l)**, left; **msc**, mandibular sensory canal; **Op**, opercle; **Pa**, parietal; **Pcl**, postcleithrum; **Pmx**, premaxilla; **Pmxt**, premaxillary tooth; **Pop**, preopercle; **Psp**, parasphenoid; **Ptt**, posttemporal; **(r)**, right; **Scl**, supracleithrum; **So**, supraorbital; **Sob**, suborbital; **Sop**, subopercle; **t**, teeth; **Vo**, vomer.

Institutional abbreviation. IRSNB, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium.

Systematic palaeontology

Holostei Müller, 1844 (*sensu* Grande 2010)

Ginglymodi Cope, 1872 (*sensu* Grande 2010)

Lepisosteiformes Hay, 1929 (*sensu* López-Arbarello 2012)

Lepidotidae Owen, 1860

Scheenstia López-Arbarello & Sferco, 2011

Scheenstia bernissartensis (Traquair, 1911)
(Figs 2–4)

1911 *Lepidotus bernissartensis* Traquair in Traquair: 16, figs 4–7; pl. II, figs 1–6.

1911 *Lepidotus brevifulcratus* Traquair in Traquair: 23, fig. 8; pl. III, figs 1, 2.

1911 *Lepidotus arcuatus* Traquair in Traquair: 25, fig. 9.

Lectotype. IRSNB P 1205 (Fig. 2A), a head without lower jaw, with the pectoral girdle and the anterior part of the body.

Referred specimens. IRSNB P 9942, IRSNB P 9943, IRSNB P 9944, IRSNB P 9945, IRSNB vert 01680 – 00011, IRSNB P 1201 (*‘Lepidotus brevifulcratus’*), IRSNB P 1202 (*‘Lepidotus brevifulcratus’*), IRSNB P 1205, IRSNB P 1207, IRSNB P 1208, IRSNB P 1210, IRSNB P 1204 (*‘Lepidotus arcuatus’*).

Locality and horizon. Sainte-Barbe mine shaft, at a depth of –322 m, Sainte-Barbe Clays Formation, late Late Barremian to earliest Aptian.

Comparative emended diagnosis. Small- to medium-sized *Scheenstia* with a proportionally deeper body than *S. mantelli*; dorsal outline of the body more convex than *S. mantelli*, reminiscent of *S. zappi*; frontal tapering anteriorly, contrary to *S. laevis* and *S. zappi*; four or five suborbitals, vs eight in *S. mantelli*, six in *S. laevis* and *S. zappi*, and about 10 in *S. maximus*; dermal skull roof bones with weak ornamentation and with few small tubercles of ganoid, contrary to *S. laevis*; probably three pairs of extrascapulars as in *S. laevis*, vs four in *S.*

mantelli and more than three in *S. zappi*; 22 predorsal scale rows; dorsal fin composed of approximately four basal fulcræ, 11 fringing fulcræ and 12 rays; anal fin composed of approximately three basal fulcræ, more than seven fringing fulcræ and nine rays; caudal fin comprises around 5 dorsal and three ventral basal fulcræ, nine dorsal fringing fulcræ and a maximum of 20 rays.

Description

The central part of the frontals, dermopterotics, dermosphenotics, supraorbitals and some infraorbitals bears rare tubercles and grooves, with few small tubercles of ganoid. Other parts of the dermal bones are smooth.

Skull roof

The frontal is elongated, approximately 3.5–4 times longer than wide and 2.5 times longer than the parietal. The frontal slightly tapers anteriorly, has a notch at its anterior extremity at the level of the exit of the supraorbital sensory canal and has a concavity along its lateral margin at the level of the orbit (Figs 2G, H, 3D). Its medial margin is straight along its anterior half and forms a curve posteriorly (IRSNB 9943, IRSNB vert 01680–00011). The path of the supraorbital sensory canal is marked by a series of pores extending from the posterior limit of the lateral concavity (where it contacts the infraorbital sensory canal) and running parallel to the lateral margin of the bones. Posteriorly, two pores indicate the path of the temporal canal leading to the dermopterotic. The parietal is quadrangular, two times longer than wide (Fig. 3B). Both parietals are never completely visible together on the available material, but the medial margin of visible parietals is not on the midline of the skull, indicating that the two parietals are asymmetrical. The parietal bears a deep, T-shaped groove. The short bar of the T accommodated the anterior pit line and the long bar, which extends onto the dermopterotic, accommodated the middle pit line. Close to the anterolateral corner of the parietal, a large pore opens, extending posteriorly into a groove, which probably corresponds to the parietal extension of the supraorbital sensory canal. The dermopterotic visible in IRSNB P 1207 and IRSNB P 9943 (Fig. 2F, G, respectively) is roughly quadrilateral, with its longest margin along the parietal and the frontal, its shorter margin anteriorly contacting the dermosphenotic, and two equal margins contacting the suborbital and the preopercle laterally and the extrascapular posteriorly. Two pores along the anterolateral margin mark the path of the otic sensory canal, and a large pore located above the

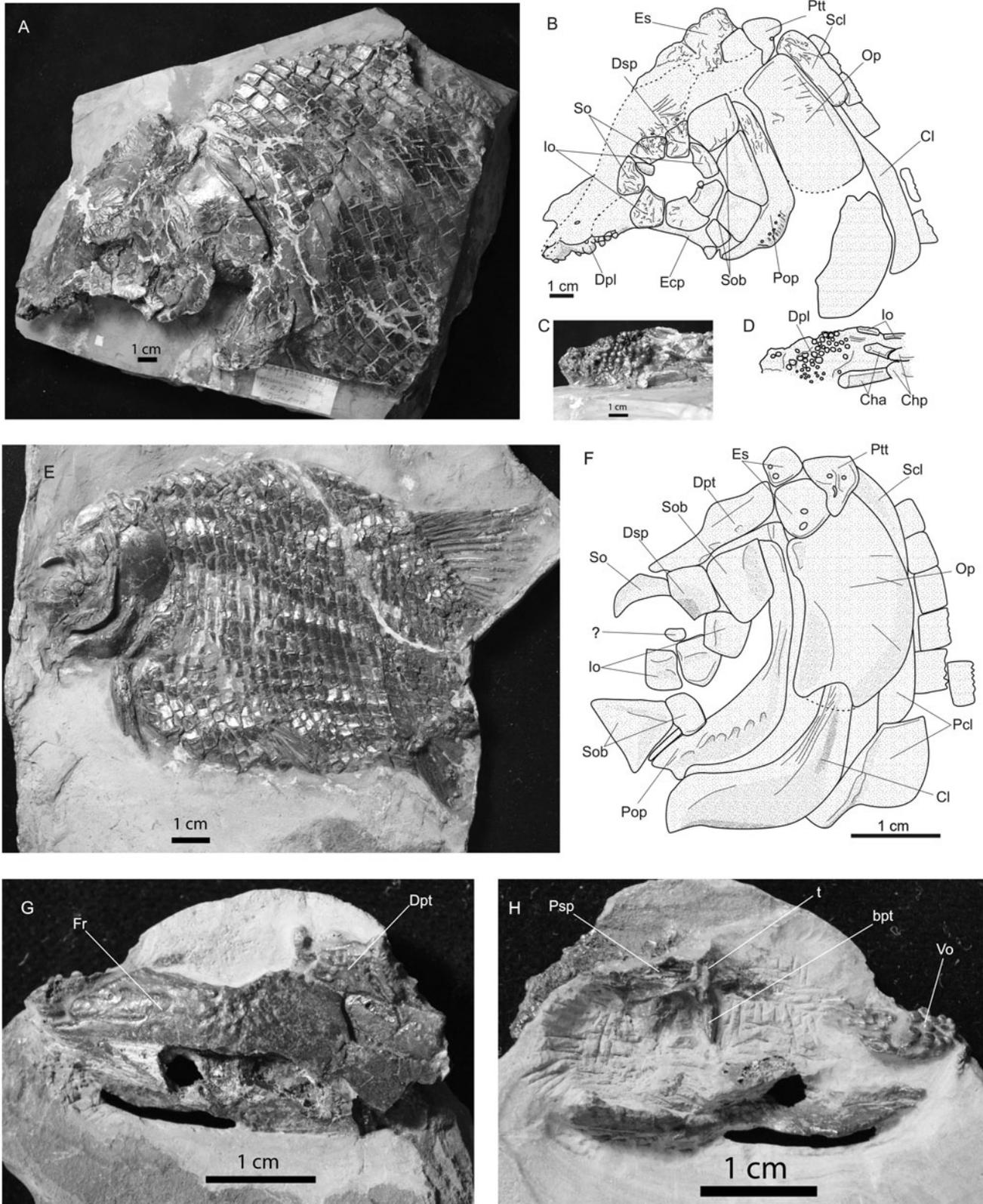


Figure 2. *Scheenstia bernissartensis*. **A–D**, IRSNB P 1205, lectotype, photograph of the specimen (**A**) and interpretative drawing of the skull (**B**); photograph (**C**) and interpretative drawing (**D**) of the palate in ventral view. **E, F**, IRSNB P 1207, photograph of the specimen (**E**) and interpretative drawing of the skull (**F**). **G, H**, IRSNB P 9943, photographs in dorsal (**G**) and ventral (**H**) view.

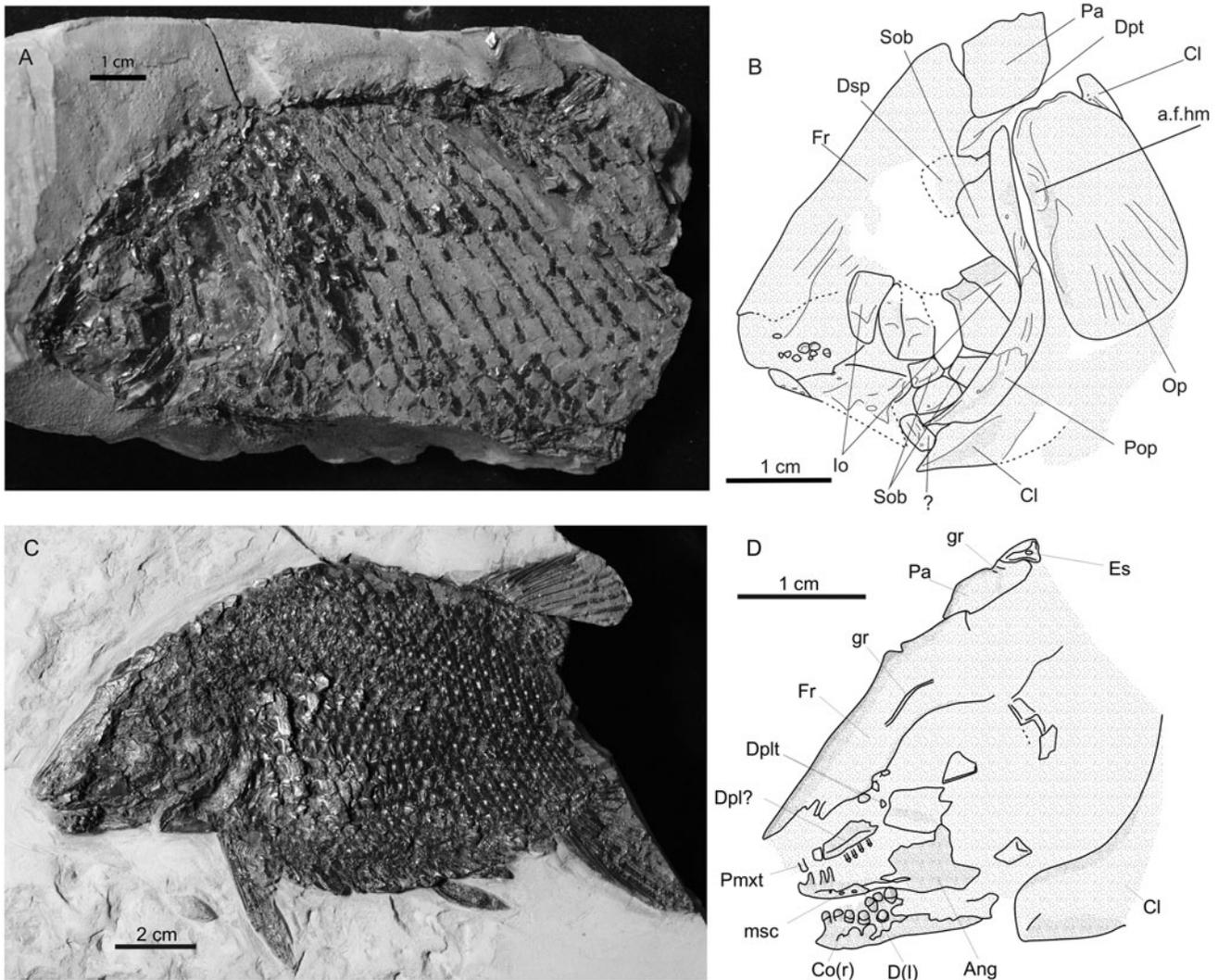


Figure 3. *Scheenstia bernissartensis*. **A, B**, IRSNB P 9944, photograph of the specimen (**A**) and interpretative drawing of the skull (**B**). **C, D**, IRSNB P 1208, photograph of the specimen (**C**) and interpretative drawing of the skull (**D**).

extremity of the preopercle indicates the exit for the connection with the preopercular sensory canal. The nasal is unknown.

Cheek

The cheek is best preserved on IRSNB P 1205 (Fig. 2A, B), but information from other specimens is also considered. The circumorbital series is composed of a dermosphenotic, two supraorbitals (plus a small supplementary one at least in IRSNB P 1205), two infraorbitals posterior to the orbit (plus a small supplementary one at least in IRSNB P 1205), two infraorbitals along the anteroventral margin of the orbit and probably three infraorbitals anteriorly, without contact with the orbit (IRSNB vert 01680-00011). The dermosphenotic is trapezoidal and deeper

than long. Both supraorbitals are longer than deep, with their dorsal margin curved to fit the concavity of the frontal. In IRSNB P1 205, the anteroventral corner of the posterior supraorbital and the posteroventral corner of the anterior supraorbital are excavated, thus forming a space for a small supplementary supraorbital, deeper than long, that shows no contact with the skull roof. The dorsal posterior infraorbital is deeper than long, with a tapering dorsal extremity. The ventral posterior infraorbital is quadrangular, longer than deep, and bears a groove along its orbital margin marking the path of the infraorbital sensory canal. Wedged between the two posterior infraorbitals along the orbital margin is a small, rounded supplementary infraorbital. A similar pattern is observed in some specimens of *Thaichthys buddhabutrensis* (Cavin *et al.* 2013). Two other infraorbitals located along

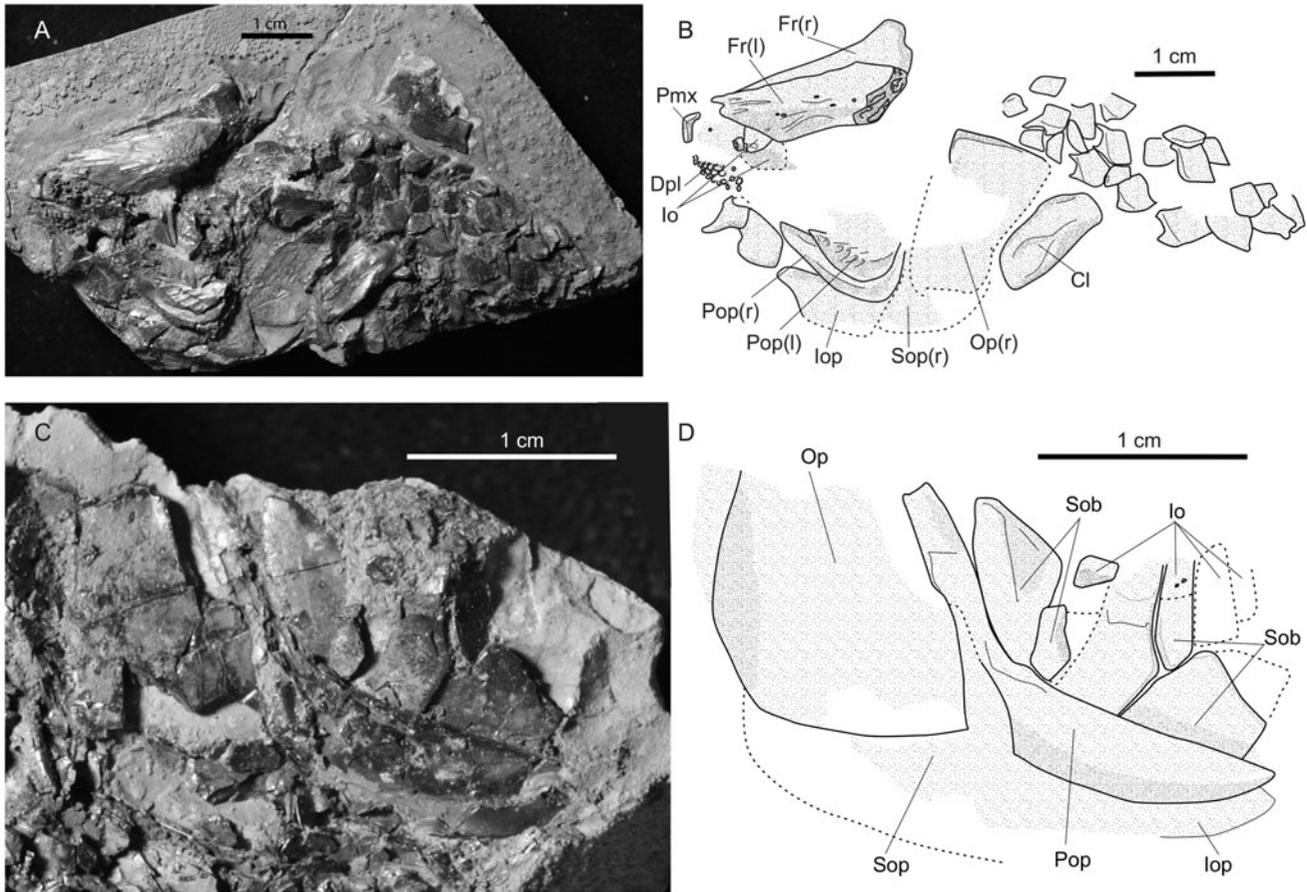


Figure 4. *Scheenstia bernissartensis*. **A, B**, IRSNB P 9942, photograph (**A**) and interpretative drawing (**B**) of the specimen. **C, D**, IRSNB P 9945, photograph (**C**) and interpretative drawing (**D**) of the specimen.

the ventral margin of the orbit are visible laterally as pentagonal ossifications bearing some traces of ornamentation. The anterior series of infraorbitals is preserved on a few specimens only. In IRSNB vert 01680-00011, one deep quadrangular infraorbital is preserved. It is preceded and followed by the traces of two other, approximately similar-shaped infraorbitals. This specimen shows fragments of bone anterior to the infraorbital series that probably correspond to the antorbital. In IRSNB P 1205, four suborbitals are aligned in a series between the infraorbital bones and the preopercle (Fig. 2A, B). The dorsal-most one is large and squarish. The one below is trapezoidal and deeper than long, and occupies most of the depth of the vertical limb of the preopercle. The following one below is squarish and contacts the preopercle, and the anteroventral-most one is smaller and quadrangular. In IRSNB P 1207, the latter suborbital is much larger and triangular in shape (Fig. 2E, F). In IRSNB P 9944, a small quadrangular suborbital is wedged between the fourth one and the ventral infraorbitals (Fig. 3A, B). It is unclear whether this suborbital was present but shifted in IRSNB P 1205, or if this situation corresponds to polymorphism

in this species. The cheek bones completely cover the suspensorium. One specimen (IRSNB P 9944, Fig. 3A, B) shows its cheek in medial view: five or six infraorbitals are located ventrally to the orbit (it is unclear whether there are more infraorbitals than in IRSNB P 1205 described above), and each one possesses a lamina that extends ventrally. In medial view, the two most posterior laminae extend ventroposteriorly and touch the preopercle, indicating that the ventral parts of these infraorbitals are likely located underneath the suborbitals visible in lateral view. Consequently, one or two suborbitals apparently rest above the hidden ventral expansions of the infraorbitals, thus constituting two superimposed layers of dermal bones in this part of the cheek. As far as we know, this pattern is unknown in other ginglymodians. We cannot exclude that this specimen (IRSNB P 9944) belongs to a taxon different from *S. bernissartensis*, for instance a Callipurbeckiidae (López-Arbarelo, pers. comm. 2019). However, because of the poor preservation of the material, we regard the pattern of the cheek bones with caution in this specimen pending its confirmation with better preserved material. We consider it more parsimonious to

include all the material in a single species, keeping in mind that the unusual mode of preservation of IRSNB P 9944, showing the medial side of the ossification, makes its interpretation problematic.

Jaws. Jaws are poorly preserved on the available material. In IRSNB P 9942, a fragment of the premaxilla is preserved showing part of the oral border with the lowest part of the nasal process, but we cannot see its development, or assess the possible presence of teeth (Fig. 4A, B). In IRSNB P 1205, the premaxillae with their teeth are certainly present, but their extent relative to other tooth-bearing bones of the palate is unclear (Fig. 2A, B). The maxilla is unknown. In IRSNB P 1208, the premaxilla is not preserved, but a tooth likely corresponding to this bone is preserved (Fig. 3C, D). It is pedicellate with a bulbous rounded cap. This specimen is also the only one which displays the lower jaw, with the left lower jaw partially visible in lateral view. The symphyseal region is low and the dentary bears three pedicellate teeth, but more were likely present. A few sensory pores of the mandibular canal are visible in this region. Posteriorly, the angular is partly preserved and forms part of a deep coronoid process. The right lower jaw is visible in medial view and shows the dentary extending posteriorly as a ventral process that almost reaches the posterior corner of the mandible. Eight crushing coronoid teeth, broader and stronger than the dentary teeth, form a patch on the lingual side of the anterior portion of the mandible.

Ventral region of the braincase and suspensorium

IRSNB P 9943 shows the dorsal part of the skull roof in dorsal view on one side of the slab, while the specimen was prepared on the other side of the slab to reveal part of the parasphenoid and the vomer (Fig. 2H). The parasphenoid bears elongated and pointed basipterygoid processes, and a small patch of teeth at the level of the basipterygoid processes. The vomer bears 11 teeth, and it is unclear whether the ossification is paired or unpaired. The oral edentulous margin of the ectopterygoid is visible on IRSNB P 1205 (Fig. 2A, B). But the more conspicuous elements are the dermopalatines, which bear a patch of strong crushing teeth (IRSNB P 1205, Fig. 2C, D). It seems, based on IRSNB P 1208, that the dermopalatine bears laterally a row of thinner pedicellate teeth (Fig. 3C, D).

Opercular series

The two arms of the preopercle form an open angle (IRSNB P 9945, Fig. 4C, D). The vertical limb is narrow, the bone broadens at the level of the posteroventral

corner and the horizontal limb is proportionally deep before tapering at its anterior extremity. Six large pores open along the horizontal arm (IRSNB P 1207, Fig. 2E, F), plus there is a large pore at the anterior extremity for the connection with the mandibular canal. The opercle is approximately twice as deep as long, roughly rectangular (Fig. 2A, B) although the posteroventral corner is poorly marked in some specimens (e.g. IRSNB P 1207, Fig. 2E, F). When rectangular, the longest part of the bone is located ventrally. The subopercle is poorly preserved on all specimens but it appears to have an elongated anterodorsal process (IRSNB P 9945, Fig. 4C, D).

Pectoral girdle

The posttemporal is large, roughly triangular with rounded angles and pierced by the lateral line. The anteroventral extremity formed a knob-like process (Fig. 2A, B). The supracleithrum is a large and roughly rectangular ossification, without a concave dorsal extremity. The cleithrum is also well developed, with a ventral limb forming a right angle with the vertical limb. Several denticulated ridges are present at the base of the vertical limb. At least two large postcleithra are present posterior to the cleithrum.

Post-cranial skeleton

No complete specimens are available, and the caudal part in particular is poorly known. The scales on the flanks are deeper than long and finely serrated along their posterior margin. There are 22 predorsal scale rows and the maximum number of scales in a row is 23, at the mid-level of the back. Other counts cannot be made because of the incomplete state of preservation of the specimens. The dorsal fin is composed of *c.* 4 basal fulcræ, 11 fringing fulcræ (IRSNB P 1202) and 12 rays (IRSNB P 1210), and the anal fin is composed of *c.* 3 basal fulcræ, more than seven fringing fulcræ (IRSNB P 1202) and nine rays (IRSNB P 1210). The caudal fin comprises approximately five dorsal and three ventral basal fulcræ (IRSNB P 1202), nine dorsal fringing fulcræ (indeterminate ventrally) and a maximum of 20 rays (IRSNB P 1210).

Discussion

Affinities

Traquair (1911) did not provide much information about the cranial anatomy of *Scheenstia bernissartensis*. We agree with his description of the skull bones (frontal,

opercle, supraorbitals, etc.) and of the upper and lower teeth, which are reminiscent of those of *S. mantelli*.

Traquair distinguished *Lepidotes brevifulcratus* from *L. bernissartensis* on the basis of postcranial characters, in particular the number, shape and orientation of the fulcræ of unpaired fins. However, IRSNB P 1201 and P 1202 (Traquair 1911, pl. III, figs 1 and 2, respectively) show the same number of basal and fringing fulcræ as a specimen of *S. bernissartensis*, and the difference in orientation and relative size is likely due to the general position of the dorsal fin, which is more posteriorly inclined in the specimens of *L. brevifulcratus*. Another difference from *S. bernissartensis* is the supposedly lower number of denticles on the posterior margin of the scales. But, as Traquair pointed out himself, the number and arrangement of these denticles are variable within a specimen and between specimens of *L. bernissartensis*, and we do not regard it as diagnostic.

Although Traquair did not provide specific characters for *L. arcuatus*, the description indicates that the main difference between this species and *S. bernissartensis* is the occurrence of a median dorsal row of prominent scales that becomes spiny posteriorly, but this feature is related to the mode of preservation. Consequently, we consider that a single species of ‘*Lepidotes*’ is present in the site of Bernissart that should be included in the genus *Scheenstia*, and that *S. bernissartensis*, *L. brevifulcratus* and *L. arcuatus* should be regarded as synonymous.

Traquair regarded *S. bernissartensis* and *S. mantelli* as closely related (“espèce voisines”, Traquair 1911, p. 61). Based on the description of *S. mantelli* by Woodward (1916) and on personal observation (LC, UD), *S. bernissartensis* differs by its smaller body size and smoother ornamentation (which are not reliable specific characters), by small meristic differences (either one or two rays in the dorsal and anal fins), and by body proportion (*S. bernissartensis* has a deeper body). Stronger diagnostic differences between the two species are the number of suborbitals (four or five in *S. bernissartensis* vs eight in *S. mantelli*), and the number of extrascapulars (four pairs in *S. mantelli* and an uncertain number in *S. bernissartensis*, but which was likely three based on what is preserved in IRSNB P 1205 and on the space available in IRSNB P 1207 – although, to be cautious, this character was not coded in the cladistic analysis). The structure of the scales (finely serrated along their posterior margin) is similar in the two species, and the number of predorsal scale rows and maximal number of scales in the longest row are the same or very close (respectively 22 and 23).

This discussion makes clear that *S. bernissartensis* is somehow related to *S. mantelli*. However, we performed

cladistic analyses in order to check whether the inclusion of this species would have an impact on the topology of the ginglymodian cladogram.

Phylogenetic analysis

Characters used in analyses I and II are distinguished in the following text by ‘ and ’’, respectively. In analysis I, we obtained 654 most parsimonious trees, with a large polytomy affecting *Scheenstia* spp., *Isanichthys* spp., *Lanxangichthys alticephalus*, *Camerichthys lunae* and the genus *Lepidotes*. This situation is unsatisfactory as the affected taxa are precisely those directly concerned by the present study. We experimentally pruned terminal taxa of lepidotids from the analysis to detect which one has the strongest impact on its resolution. The removal of *Lanxangichthys alticephalus*, a species known by a single isolated head (Cavin *et al.* 2019), generated a fully resolved topology of this clade. The new analysis I (Fig. 5, left) found 54 most parsimonious trees (tree length = 421; consistency index (CI) = 0.344; retention index (RI) = 0.6809). The general pattern is very similar to the pattern obtained by López-Arbarello *et al.* (2019) and Sun & Ni (2017), in particular with the recognition of the family Lepidotidae including *Isanichthys*, *Scheenstia*, *Camerichthys* and *Lepidotes*. The family was not recovered in Cavin *et al.* (2019), while López-Arbarello & Wencker (2016) recovered it, but without *Isanichthys*. In analysis I, the Lepidotidae node is supported by four synapomorphies (9’, 25’, 40’, 66’), among which *S. bernissartensis* shows the derived state for two. One is the presence of one row of suborbitals, which extends anteriorly below the orbit (ch. 40, state 1). Character state 1 is present in all terminal species of this clade except in *Isanichthys latifrons*, which has a mosaic of suborbitals. The other visible character state is a large interopercle, approximately as long as the ventral arm of the preopercle (ch. 66’, state 0), but its distribution is very homoplastic (consistency index (ci) = 0.167) among ginglymodians and poorly informative. Among Lepidotidae, the genus *Lepidotes*, including here *L. gigas* and *L. semiserratus*, is supported by four synapomorphies, which are all homoplastic within ginglymodians. Among the Lepidotidae, excluding *Lepidotes*, the basal-most species is *Scheenstia bernissartensis*, which shares four character states with more derived lepidotids. One of them visible in *S. bernissartensis* is unambiguous and uniquely derived: the first and last suborbitals are larger than the other suborbitals (ch. 42’, visible in IRSNB P 1207, Fig. 2F). Two other homoplastic and unambiguous synapomorphies supporting this clade are also visible in *S. bernissartensis*: the presence of a knob-like anteroventral process on the posttemporal (ch. 69’) and the presence of molariform

teeth on coronoids, pterygoids or vomers (ch. 93'). More derived than *S. bernissartensis* is *S. zappi*, the type species of the genus, which is the sister clade to the remaining lepidotids. This node is supported by two homoplastic character states absent in *S. bernissartensis*: the dermal bones of the skull are ornamented with tubercles and ridges (ch. 17', this character is possibly age-related) and the ventral border of infraorbital series flexes abruptly dorsally at the anterior margin of the orbit (ch. 27'). The remaining lepidotids comprise *Isanichthys* (with three species), sister to *Camerichthys*, plus three *Scheenstia* species (*S. maximus*, *S. laevis* and *S. mantelli*). Consequently, based on this topology, *Scheenstia* is not a monophyletic genus. It should be stressed, however, that the nodes in this part of the tree are weakly supported, as exemplified by the distribution of some characters. Among the four characters supporting the grouping of *Camerichthys* with the three *Scheenstia* species, for instance, two are unknown in *S. zappi* (ch. 4' and 49') and the other two are shared between *S. zappi* and at least one of the three other *Scheenstia* species (ch. 21' and 31'). *Camerichthys lunae* is a ginglymodian from the Tithonian–Berriasian beds of the Matute Formation, Spain, which was initially included in the Semionotiformes (Bermúdez-Rochas & Poyato-Ariza (2015) and is located close to *Scheenstia* in most recent analyses (López-Arbarello & Wencker 2016; Sun & Ni 2017; Cavin *et al.* 2019; López-Arbarello *et al.* 2019).

Based on analysis I, *S. bernissartensis* differs only slightly from other species of the genus and notably from *S. mantelli* as mentioned above, which is ecologically and stratigraphically a closely related species. Most differences between these species concern characters that might be size-dependent, such as the relative position of the lower jaw articulation (ch. 14'), the ornamentation of the dermal bone (ch. 17') and the relative size of the basal fulcræ (ch. 75'). Other characters unlikely related to size, but difficult in some way to code, are the shape of the ectopterygoid (ch. 11'), the shape of the antorbital portion of the frontal (ch. 22'), the shape of the ventral border of the infraorbital series at the anterior margin of the orbit (ch. 27'), the shape of the infraorbital at the posterior border of the orbit (ch. 34') and the relative sizes of the dermopterotic and parietal (ch. 85'). Another potential difference between *S. mantelli* and *S. bernissartensis* is the arrangement of some of the infraorbitals, which in the latter species extend ventrally underneath the suborbitals. But the disposition of this feature is unknown in most of the species included in the analyses, and consequently was not scored in the analyses. Although *Scheenstia* does not appear to be monophyletic in analysis I, we do not

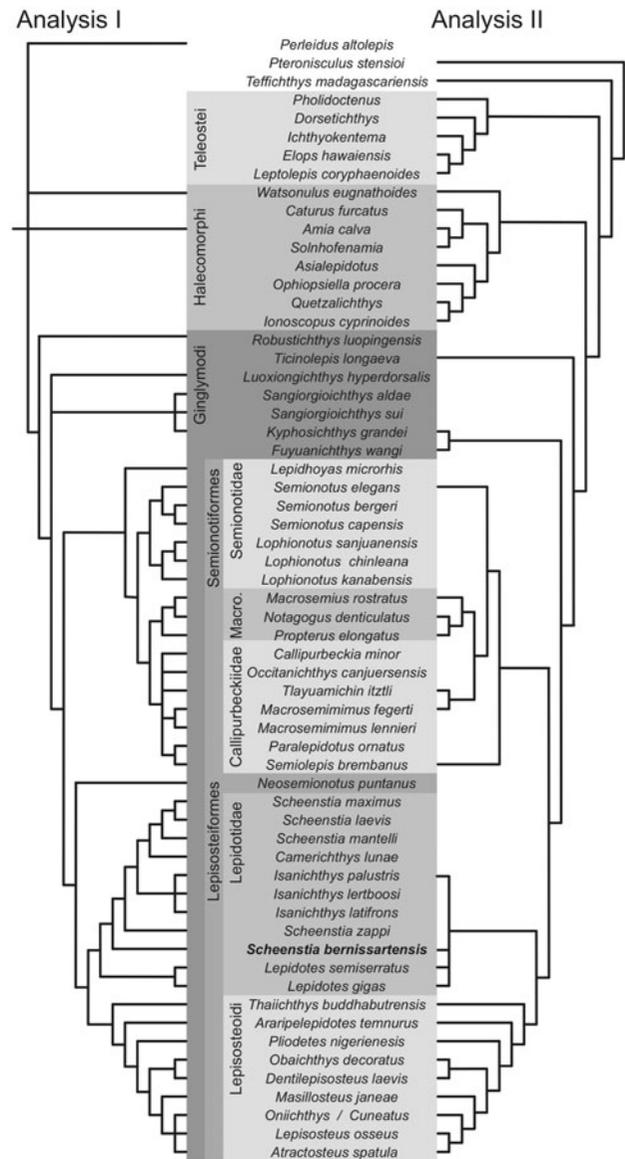


Figure 5. Left: analysis I, strict consensus tree of 54 most parsimonious trees (tree length = 421; CI = 0.344; RI = 0.6809); right: analysis II, strict consensus tree of five most parsimonious trees (tree length = 474; CI = 0.4873; RI = 0.7477). **Abbreviation: Macro.**, Macrosemiidae.

propose to change the generic names of the *Scheenstia* species, other than the type species *S. zappi*, pending new analyses to confirm the pattern obtained here. In particular, it will be important to decipher the relationships between *Camerichthys lunae* and the *Scheenstia* spp. because the sister clade of *Camerichthys* is not always the same according to different studies. *Camerichthys* is sister to the clade ([*S. maximus* *S. laevis*] *S. mantelli*) in the present analysis, to *S. zappi* in López-Arbarello *et al.* (2019), and to a clade including four *Scheenstia* species in López-Arbarello & Wencker

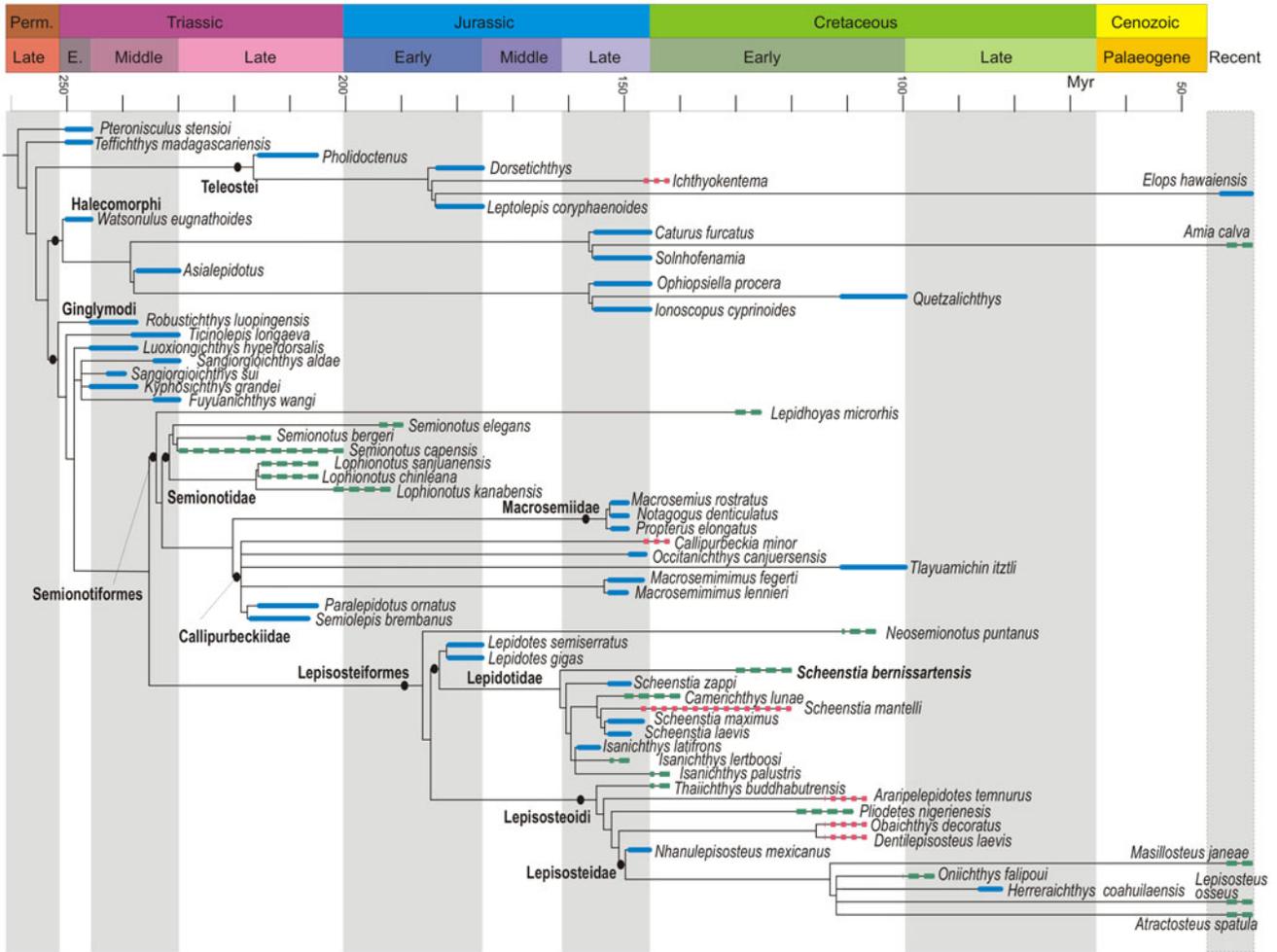


Figure 6. Time-scaled tree of the neopterygian crown group, with a focus on the ginglymodians based on analyses I and II, plus the insertion of two terminal taxa (*Herreraichthys* and *Nhanulepisosteus*) based on other phylogenetic analyses. Continuous blue range, marine occurrences; long-dotted green ranges, freshwater occurrences; short-dotted red ranges, occurrences from mixed (brackish) environments.

(2016), Sun & Ni (2017) and Cavin *et al.* (2019). Addressing this issue is beyond the scope of this article.

Analysis II (Fig. 5, right) found five most parsimonious trees (tree length = 474; CI = 0.4873; RI = 0.7477) with a topology of relationships of the species common between the two matrices very congruent and fully resolved, with the exception of a polytomy including all Lepidotidae. In this analysis the Lepidotidae comprise two species of *Lepidotes* (*L. gigas* and *L. semiserratus*), *Isanichthys palustris* and *S. bernissartensis* only, the other Lepidotidae of analysis I having not been scored. In analysis II, the Lepidotidae is supported by four homoplastic synapomorphies, among which three are visible in *S. bernissartensis*: absence of contact relationships of infraorbital bone at posteroventral corner of orbit with preopercle (ch. 51'', state 0), four or more suborbitals (ch. 67'', state 2) and suborbital bones extend anteriorly below the orbit (ch. 69'', state 1).

Evolutionary history of ginglymodians

Figure 6 is a time-scaled tree based on analyses I and II produced here, to which we added *Herreraichthys coahuilaensis* from Santonian marine deposits, and *Nhanulepisosteus mexicanus* from Late Jurassic marine deposits, both from Mexico (Alvarado-Ortega *et al.* 2016; Brito *et al.* 2017). We placed both taxa in our phylogeny on the basis of phylogenetic analyses available in Alvarado-Ortega *et al.* (2016), i.e. *Herreraichthys* as a Lepisosteini, and in Brito *et al.* (2017), i.e. *Nhanulepisosteus* as the basal-most Lepisosteidae.

The general pattern of the evolutionary history of ginglymodians indicates that the first diversification within the clade occurred in a marine environment during the Early–Middle Triassic, with most of the fossils found in the Middle Triassic. Representatives of this diversification occurred mostly along the northern margin of the

Tethys, i.e. South China and Europe. After this diversification, two clades split, i.e. the Semionotiformes and the Lepisosteiformes. Among Semionotiformes, the Semionotidae (*Semionotus* and *Lophionotus*) radiated in freshwater in Europe and North Africa during the Late Triassic and the Early Jurassic (with the production of species flocks for the *S. elegans* group; McCune 1996). The Macrosemiidae and the Callipurbeckiidae diversified in marine environments during the Late Triassic up to the late Early Cretaceous, except a single species, *Callipurbeckia minor*, found in the Purbeck facies. The recent revision of the genus *Eosemionotus* by López-Arbarello *et al.* (2019) indicates that marine macrosemiids had already radiated in European marine environments during the Middle Triassic (not shown in Fig. 6). The Lepisosteiformes show a first diversification with the Lepidotidae, firstly with marine forms in the Early Jurassic (*Lepidotes*) and then in marine, brackish and freshwater environments. The pattern is still unclear because we observed a mix of species from various environments in Europe (four *Scheenstia* species and *Camerichthys*) and from freshwater environments in Southeast Asia (two species of *Isanichthys*). The remaining Lepisosteiformes, the Lepisosteoidi, diversified in fresh waters of Asia (*Thaichthys*) and fresh and brackish waters of Western Gondwana (*Araripelepidotes*, *Pliodetes*, Obaichthyidae). Surprisingly, the oldest and basal-most Lepisosteidae occurred in a marine environment (*Nhanulepisosteus*), while most representatives occurred in freshwater environments, with the exception of *Herreraichthys*.

In this scheme, some taxa are difficult to integrate. This is the case for *Lepidohyas* and *Neosemionotus*. The former is resolved as a basal Semionotiformes (Cavin *et al.* 2019; present study) or as a basal Lepisosteiformes (Cavin 2010), and the latter is similarly resolved as a basal Lepisosteiformes (Cavin 2010; Sun & Ni 2017; present study) or as a basal Semionotiformes (Cavin *et al.* 2019; López-Arbarello *et al.* 2019). Interestingly, Lins de Paiva & Gallo (2018) found these two taxa to form a clade with *Quasimodichthys* and *Hoyasotes*, two genera that are not included in the present analysis. In Lins de Paiva and Gallo's study, however, the Lepidotidae are not recovered: *Scheenstia* spp. and *Lepidotes* spp. are found in a pectinated position at the base of the Lepisosteiformes. López-Arbarello *et al.* (2019) found *Neosemionotus* to be closely related to *Lophionotus*, forming a clade of freshwater taxa. These phylogenetically labile genera (*Quasimodichthys*, *Neosemionotus*, *Hoyasotes*, *Lepidohyas*) indicate how fragile the phylogenetic relationships are at the base of the Semionotiformes and Lepisosteiformes clades, although the composition of

the more derived taxa in these clades is regularly recovered in most recent analyses.

Conclusions

The new description of the ginglymodian from Bernissart allows its inclusion in the genus *Scheenstia*. No significant differences among the three species originally recognized at this site are observed here, and a single species, *S. bernissartensis*, is retained. As already noted by Traquair in 1911, *S. bernissartensis* shows similarities to *S. mantelli*, although the two species are not directly related in the cladistic analysis. The relationships among the four *Scheenstia* species, *Camerichthys* and *Isanichthys* (and *Lanxangichthys*, which is not included in the present study) should still be confirmed. *Scheenstia mantelli* is the commonest species of this clade, and is the species with the most similar palaeoecology and stratigraphical range to *S. bernissartensis*. It was recognized in the British Upper Purbeck (Berriasian?) and in the Wealden Group (Berriasian to Aptian), in the Obnerkirchen Member of the Germanic Wealden (Late Berriasian) (Hornung *et al.* 2012) and in the Berriasian of Cherves-de-Cognac, France (Pouech *et al.* 2015). Thus, this species was distributed over a large part of Europe during the first part of the Early Cretaceous, and it is not surprising that a related species is present in the Barremian–Aptian in Belgium.

The phylogeny of the ginglymodians is becoming progressively more complete and better resolved. Bones of contention concern the relationships of the taxa at the base of otherwise well-defined clades, i.e. the basal-most ginglymodians, the basal-most Semionotiformes and the basal-most Lepisosteiformes. The Lepidotidae is a family regularly found in recent analyses. However, the composition of the clade and its intra-relationships are weakly supported. The task of resolving this issue should be conducted by describing and re-describing the existing taxa, but also by better defining the characters used in the cladistic analyses.

The ginglymodians form a large clade of ray-finned fishes present during the whole Mesozoic, with a single clade extending through the Cenozoic up to the Recent (the Lepisosteidae). Within the Lepisosteiformes a general shift from marine towards freshwater environments is observed during the evolution of several clades (ginglymodians as a whole, lepidotids, lepisosteiforms). A similar trend, i.e. shifts of habitats from marine to freshwater environments, was observed in various actinopterygian clades during the Late Jurassic–Paleocene time interval (Guinot & Cavin 2018). In the

ginglymodians, however, this general trend suffers exceptions, with the marine *Nhanulepisosteus* and *Herreraichthys* among the brackish and freshwater Lepisosteids.

Acknowledgements

We gratefully acknowledge A. Folie and C. Cousin (IRSNB) for granting access to the collections. T. Hubin (IRSNB) provided the photographs. This article is a contribution to the project BR/143/A3/ColdCase funded by the Belgian Science Policy. UD was supported by a Research Fellowship Grant 2015 from the French Embassy of Thailand and by the Mahasarakham University Development Fund 2015. We thank an anonymous reviewer and Adriana López-Arbarello (München) for their detailed and constructive comments and suggestions, and G.-H. Xu (Beijing) for providing data about character scoring.

Supplemental material

Supplemental material for this article can be accessed here: <https://doi.org/10.1080/14772019.2019.1634649>.

ORCID

Lionel Cavin  <http://orcid.org/0000-0001-9666-5864>

References

- Alvarado-Ortega, J., Brito, P. M., Porrás-Múzquiz, H. G. & Mújica-Monroy, I. H. 2016. A Late Cretaceous marine long snout 'pejelagarto' fish (Lepisosteidae, Lepisosteini) from Múzquiz, Coahuila, northeastern Mexico. *Cretaceous Research*, **57**, 19–28.
- Baele, J.-M., Godefroit, P., Spagna, P. & Dupuis, C. 2012a. Geological model and cyclic mass mortality scenarios for the Lower Cretaceous Bernissart *Iguanodon* Bonebeds. Pp. 155–171 in P. Godefroit (ed.) *Bernissart dinosaurs and early Cretaceous terrestrial ecosystems*. Indiana University Press, Bloomington and Indianapolis.
- Baele, J.-M., Godefroit, P., Spagna, P. & Dupuis, C. 2012b. A short introduction to the geology of the Mons Basin and the *Iguanodon* sinkhole, Belgium. Pp. 35–42 in P. Godefroit (ed.) *Bernissart dinosaurs and Early Cretaceous terrestrial ecosystems*. Indiana University Press, Bloomington and Indianapolis.
- Bermúdez-Rochas, D. D. & Poyato-Ariza, F. J. 2015. A new semionotiform actinopterygian fish from the Mesozoic of Spain and its phylogenetic implications. *Journal of Systematic Palaeontology*, **13**, 265–285.
- Bruto, P. M., Alvarado-Ortega, J. & Meunier, F. J. 2017. Earliest known lepisosteoid extends the range of anatomically modern gars to the Late Jurassic. *Scientific Reports*, **7**, 17830.
- Cavin, L. 2010. Diversity of Mesozoic semionotiform fishes and the origin of gars (Lepisosteidae). *Naturwissenschaften*, **97**, 1035–1040.
- Cavin, L. & Brito, P. M. 2001. A new Lepisosteidae (Actinopterygii: Ginglymodi) from the Cretaceous of the Kem Kem beds, southern Morocco. *Bulletin de la Société géologique de France*, **172**, 141–150.
- Cavin, L. & Suteethorn, V. 2006. A new Semionotiform (Actinopterygii, Neopterygii) from Upper Jurassic–Lower Cretaceous deposits of North-East Thailand, with comments on the relationships of Semionotiforms. *Palaeontology*, **49**, 339–353.
- Cavin, L., Deesri, U. & Suteethorn, V. 2013. Osteology and relationships of *Thaichthys* nov. gen.: a Ginglymodi from the Late Jurassic–Early Cretaceous of Thailand. *Palaeontology*, **56**, 183–208.
- Cavin, L., Deesri, U., Veran, M., Khentavong, B., Jintasakul, P., Chanthasit, P. & Allain, R. 2019. A new Lepisosteiformes (Actinopterygii: Ginglymodi) from the Early Cretaceous of Laos and Thailand, SE Asia. *Journal of Systematic Palaeontology*, **17**, 393–407.
- Cope, E. D. 1872. Observations on the systematic relations of the fishes. *Proceedings of the American Association for the Advancement of Science*, **20**, 317–343.
- Cornet, J. 1927. L'époque wealdienne dans le Hainaut. *Bulletin de la Société belge de Géologie, Paléontologie et Hydrologie*, **50**, 89–104.
- Cornet, J. & Schmitz, G. 1898. Note sur les puits naturels du terrain houiller du Hainaut et le gisement des iguanodons de Bernissart. *Bulletin de la Société belge de Géologie, Paléontologie et Hydrologie*, **12**, 196–206, 301–318.
- Deesri, U., Jintasakul, P. & Cavin, L. 2016. A new Ginglymodi (Actinopterygii, Holostei) from the Late Jurassic–Early Cretaceous of Thailand, with comments on the early diversification of Lepisosteiformes in Southeast Asia. *Journal of Vertebrate Paleontology*, **36**, e1225747. doi.org/10.1080/02724634.2016.1225747
- Deesri, U., Lauprasert, K., Suteethorn, V., Wongso, K. & Cavin, L. 2014. A new species of the ginglymodian fish *Isanichthys* from the Late Jurassic Phu Kradung Formation, northeastern Thailand. *Acta Palaeontologica Polonica*, **59**, 313–331.
- Dejax, J., Pons, D. & Yans, J. 2007. Palynology of the dinosaur-bearing Wealden facies in the natural pit of Bernissart (Belgium). *Review of Palaeobotany and Palynology*, **144**, 25–38.
- Delmer, A. & Van Wichelen, P. 1980. Répertoire des puits naturels connus en terrain houiller du Hainaut. *Professional Paper, Publication du Service Géologique de Belgique*, **172**, 1–79.
- Forey, P. L., López-Arbarello, A. & MacLeod, N. 2011. A new species of *Lepidotes* (Actinopterygii: Semionotiformes) from the Cenomanian (Upper Cretaceous) of Morocco. *Palaeontologia Electronica*, **14**, 1–12.
- Gallo, V. & Brito, P. M. 2004. An overview of Brazilian semionotids. Pp. 253–264 in G. Arratia & A. Tintori (eds) *Systematics, paleoenvironments and biodiversity*. Verlag Dr. Friedrich Pfeil, Munich.

- Gaudant, J.** 1966. Sur la nécessité d'une subdivision du genre *Anaethalio* White (Poisson Téléostéen). *Comptes rendus sommaire Société géologique France*, **8**, 308–310.
- Gibson, S. Z.** 2013. A new hump-backed ginglymodian fish (Neopterygii, Semionotiformes) from the Upper Triassic Chinle Formation of southeastern Utah. *Journal of Vertebrate Paleontology*, **33**, 1037–1050.
- Godefroit, P., Yans, J., Bultynck, P. & Godefroit, P.** 2012. Bernissart and the Iguanodons: historical perspective and new investigations. Pp. 1–20 in P. Godefroit (ed.) *Bernissart dinosaurs and Early Cretaceous terrestrial ecosystems*. Indiana University Press, Bloomington and Indianapolis.
- Grande, L.** 2010. An empirical synthetic pattern study of gars (Lepisosteiformes) and closely related species, based mostly on skeletal anatomy. The resurrection of Holostei. *American Society of Ichthyologists and Herpetologists, Special Publication 6, supplementary issue of Copeia 10, 2a*, 1–871.
- Grande, L. & Bemis, W. E.** 1998. A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. *Journal of Vertebrate Paleontology*, **18**, 1–696.
- Guinot, G. & Cavin, L.** 2018. Body size evolution and habitat colonization across 100 million years (Late Jurassic–Paleocene) of the actinopterygian evolutionary history. *Fish and Fisheries*, **19**, 577–597.
- Hay, O. P.** 1929. Second bibliography and catalogue of the fossil Vertebrata of North America. *Publication of the Carnegie Institute of Washington*, **390**, 1–2003.
- Hornung, J. J., Böhme, A., van der Lubbe, T., Reich, M. & Richter, A.** 2012. Vertebrate tracksites in the Obernkirchen Sandstone (late Berriasian, Early Cretaceous) of northwest Germany – their stratigraphical, palaeogeographical, palaeoecological, and historical context. *Paläontologische Zeitschrift*, **86**, 231–267.
- Lins de Paiva, H. C. & Gallo, V.** 2018. *Quasimodichthys* gen. nov. (Neopterygii: Semionotiformes): a morphological and ontogenetic study. *Journal of South American Earth Sciences*, **88**, 132–143.
- López-Arbarello, A.** 2008. Revision of *Semionotus bergeri* Agassiz, 1838 (Upper Triassic, Germany), with comments on the taxonomic status of *Semionotus* (Actinopterygii, Semionotiformes). *Paläontologische Zeitschrift*, **82**, 40–54.
- López-Arbarello, A.** 2012. Phylogenetic interrelationships of ginglymodian fishes (Actinopterygii: Neopterygii). *PLoS ONE*, **7**(7), e39370. doi:10.1371/journal.pone.0039370
- López-Arbarello, A. & Alvarado-Ortega, J.** 2011. New semionotiform (Neopterygii) from the Tlayúa Quarry (Early Cretaceous, Albian), Mexico. *Zootaxa*, **2749**, 1–24.
- López-Arbarello, A. & Codorniu, L.** 2007. Semionotids (Neopterygii, Semionotiformes) from the Lower Cretaceous Lagarcito Formation, San Luis Province, Argentina. *Journal of Vertebrate Paleontology*, **27**, 811–826.
- López-Arbarello, A. & Sferco, E.** 2011. New semionotiform (Actinopterygii: Neopterygii) from the Late Jurassic of southern Germany. *Journal of Systematic Palaeontology*, **9**, 197–215.
- López-Arbarello, A. & Wencker, L. C.** 2016. New callipurbeckiid genus (Ginglymodi: Semionotiformes) from the Tithonian (Late Jurassic) of Canjuers, France. *Paläontologische Zeitschrift*, **90**, 543–560.
- López-Arbarello, A., Bürgin, T., Furrer, H., Stockar, R.** 2019. Taxonomy and phylogeny of *Eosemionotus* Stolley, 1920 (Neopterygii: Ginglymodi) from the Middle Triassic of Europe. *Palaeontologia Electronica*, **22**, 1–64. DOI: 10.26879/904
- López-Arbarello, A., Sun, Z.-Y., Sferco, E., Tintori, A., Xu, G.-H., Sun, Y.-L., Wu, F.-X. & Jiang, D.-Y.** 2011. New species of *Sangiorgioichthys* Tintori and Lombardo, 2007 (Neopterygii, Semionotiformes) from the Anisian of Luoping (Yunnan Province, South China). *Zootaxa*, **2749**, 25–39.
- McCune, A. R.** 1996. Biogeographic and stratigraphic evidence for rapid speciation in semionotid fishes. *Paleobiology*, **22**, 34–48.
- Müller, J.** 1844. Über den Bau und die Grenzen der Ganoiden und über das natürliche System der Fische. *Bericht Akademie der Wissenschaften Berlin*, **1844**, 416–422.
- Olive, S., Taverne, L. & López-Arbarello, A.** 2019. A new genus of coccolepidid actinopterygian from the Cretaceous *Iguanodon*-bearing locality of Bernissart, Belgium. *Cretaceous Research*, **95**, 318–335.
- Olive, S., Taverne, L., Cavin, L. & Deesri, U.** 2017. Systematic revision of the Cretaceous actinopterygian fauna from Bernissart, Belgium. *Research & Knowledge*, **3**, 43–46.
- Owen, R.** 1860. *Palaeontology, or, a systematic summary of extinct animals and their geological relations*. A. and C. Black, Edinburgh, 494 pp.
- Pouech, J., Mazin, J.-M., Cavin, L. & Poyato-Ariza, F. J.** 2015. A Berriasian actinopterygian fauna from Cherves-de-Cognac, France: biodiversity and palaeoenvironmental implications. *Cretaceous Research*, **55**, 32–43.
- Poyato-Ariza, F. J. & Wenz, S.** 2004. The new pycnodontid fish genus *Turbomesodon*, and a revision of *Macromesodon* based on new material from the Lower Cretaceous of Las Hoyas, Cuenca, Spain. Pp. 341–378 in G. Arratia & A. Tintori (eds) *Systematics, paleoenvironments and biodiversity*. Verlag Dr. Friedrich Pfeil, Munich.
- Quinif, Y. & Licour, L.** 2012. The karstic phenomenon of the *Iguanodon* Sinkhole and the geomorphological situation of the Mons Basin during the Early Cretaceous. Pp. 51–61 in P. Godefroit (ed.) *Bernissart dinosaurs and Early Cretaceous terrestrial ecosystems*. Indiana University Press, Bloomington and Indianapolis.
- Schnyder, J., Dejax, J., Keppens, E., Tu, T. T. N., Spagna, P., Boulila, S., Galbrun, B., Riboulleau, A., Tshibangu, J.-P. & Yans, J.** 2009. An Early Cretaceous lacustrine record: organic matter and organic carbon isotopes at Bernissart (Mons Basin, Belgium). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **281**, 79–91.
- Spagna, P.** 2010. *Les faciès wealdiens du Bassin de Mons (Belgique): paléoenvironnements, géodynamique et valorisation industrielle*. Unpublished PhD thesis, Faculté Polytechnique de l'UMons, Mons, 138 pp.
- Spagna, P., Yans, J., Schnyder, J. & Dupuis, C.** 2012. The paleoenvironment of the Bernissart iguanodons: sedimentological analysis of the Lower Cretaceous Wealden facies in the Bernissart area. Pp. 87–96 in P. Godefroit (ed.) *Bernissart dinosaurs and Early Cretaceous terrestrial ecosystems*. Indiana University Press, Bloomington and Indianapolis.
- Sun, Z. & Ni, P.** 2017. Revision of *Kyphosichthys grandei* Xu & Wu, 2012 from the Middle Triassic of Yunnan

- Province, South China: implications for phylogenetic interrelationships of ginglymodian fishes. *Journal of Systematic Palaeontology*, **16**, 67–85.
- Taverne, L.** 1981. Ostéologie et position systématique d'*Aethalionopsis robustus* (Pisces, Teleostei) du Crétacé inférieur de Bernissart (Belgique) et considérations sur les affinités des Gonorynchiformes. *Bulletin de l'Académie Royale de Belgique, Classes des Sciences*, **67**, 958–982.
- Taverne, L.** 1982. Sur *Pattersonella formosa* (Traquair, R. H., 1911) et *Nybelinoides brevis* (Traquair, R. H., 1911): Téléostéens Salmoniformes Argentinoïdes du Wealdien inférieur de Bernissart, Belgique, précédemment attribués au genre *Leptolepis* Agassiz, L., 1832. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **54**, 1–27.
- Taverne, L.** 1999. Ostéologie et position systématique d'*Arratiaelops vectensis* gen. nov., téléostéen élopiforme du Wealdien (Crétacé inférieur) d'Angleterre et de Belgique. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **69**, 77–96.
- Tintori, A. & Lombardo, C.** 2007. A new early Semionotidae (Semionotiformes, Actinopterygii) from the Upper Ladinian of Monte San Giorgio area (Southern Switzerland and Northern Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, **113**, 369–381.
- Traquair, R. H.** 1911. Les poissons wealdiens de Bernissart. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, **6**, 1–65.
- Van den Broeck, E.** 1898. Les coupes du gisement de Bernissart. Caractères et dispositions sédimentaires de l'argile ossifère du Cran aux Iguanodons. *Bulletin de la Société belge de Géologie, Paléontologie et Hydrologie*, **12**, 216–243.
- Wen, W., Zhang, Q.-Y., Hu, S.-X., Zhou, C.-Y., Xie, T., Huang, J.-Y., Chen, Z. Q. & Benton, M. J.** 2011. A new basal actinopterygian fish from the Anisian (Middle Triassic) of Luoping, Yunnan Province, southwest China. *Acta Palaeontologica Polonica*, **57**, 149–160.
- Wenz, S.** 1999. *Pliodetes nigeriensis*, gen. nov. et sp. nov., a new semionotid fish from the Lower Cretaceous of Gadoufaoua (Niger Republic): phylogenetic comments. Pp. 107–120 in G. Arratia & H.-P. Schultze (eds) *Mesozoic fishes 2 – systematics and fossil record*. Verlag Dr. Friedrich Pfeil, Munich.
- Wenz, S.** 2003. Les *Lepidotes* (Actinopterygii, Semionotiformes) du Crétacé inférieur (Barrémien) de Las Hoyas (Province de Cuenca, Espagne). *Geodiversitas*, **25**, 481–499.
- Wenz, S. & Brito, P. M.** 1992. Première découverte de Lepisosteidae (Pisces, Actinopterygii) dans le Crétacé inférieur de la Chapada do Araripe (N-E du Brésil). Conséquence sur la phylogénie des Ginglymodi. *Comptes rendus de l'Académie des Sciences, Paris*, **314**, 1519–1525.
- Wenz, S. & Brito, P. M.** 1996. New data about the lepisosteids and semionotids from the Early Cretaceous of Chapada do Araripe (NE Brazil): phylogenetic implications. Pp. 153–165 in G. Viohl & G. Arratia (eds) *Mesozoic fishes – systematics and paleoecology*. Verlag Dr. Friedrich Pfeil, Munich.
- Woodward, A. S.** 1916. The fossil fishes of the English Wealden and Purbeck formations. Part 1. *Monograph of the Palaeontographical Society*, **69**, 1–48.
- Xu, G. H. & Wu, F.** 2011. A deep-bodied ginglymodian fish from the Middle Triassic of eastern Yunnan Province, China, and the phylogeny of lower neopterygians. *Chinese Science Bulletin*, **57**, 111–118.
- Xu, G. H., Ma, X. Y. & Ren, Y.** 2018. *Fuyuanichthys wangi* gen. et sp. nov. from the Middle Triassic (Ladinian) of China highlights the early diversification of ginglymodian fishes. *PeerJ*, **6**, e6054. doi.org/10.7717/peerj.6054
- Yans, J.** 2007. Lithostratigraphie, minéralogie et diagenèse des sédiments à faciès wealdien du Bassin de Mons (Belgique). *Mémoires de la Classe des sciences, Académie royale de Belgique*, **9**, 1–179.
- Yans, J., Dejax, J. & Schnyder, J.** 2012. On the age of the Bernissart iguanodons. Pp. 79–84 in P. Godefroit (ed.) *Bernissart dinosaurs and Early Cretaceous terrestrial ecosystems*. Indiana University Press, Bloomington and Indianapolis.
- Yans, J., Dejax, J., Pons, D., Taverne, L. & Bultynck, P.** 2006. The iguanodons of Bernissart are middle Barremian to early Aptian in age. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **76**, 91–95.

Associate Editor: Zerina Johanson