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A NEW BARREMIAN (EARLY CRETACEOUS) ICHTHYOSAUR FROM WESTERN RUSSIA

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ABSTRACT—A new ophthalmosaurid ichthyosaur, *Sveltonectes insolitus*, gen. et sp. nov., is described from a sub-complete and three-dimensionally preserved specimen from the late Barremian of western Russia. This new taxon is supported by 11 cranial, dental, and postcranial autapomorphies, and is also characterized by features previously considered as autapomorphic for some other Ophthalmosauridae, such as a processus narialis on the prefrontal and relatively long hind fins with pre- and postaxial accessory digits. We conducted a new phylogenetic analysis of Thunnosauria, which supports a ‘*Stenopterygius*’ origin for Ophthalmosauridae. *Sveltonectes* is regarded as the sister taxon of *Aegirosaurus*, which shares a similar skull roof construction. Contrary to most other Cretaceous ichthyosaurs, *Sveltonectes* is characterized by delicate and sharply pointed teeth, confirming that the ophthalmosaurids were ecologically highly diversified during the Early Cretaceous.

INTRODUCTION

Ichthyosaurs were a successful group of marine reptiles ranging from the Olenekian (Early Triassic) to the Cenomanian (earliest Late Cretaceous; Bardet, 1992, 1994, 1995; Motani, 2005). Their Cretaceous record is limited, resulting in an apparent drastic diversity drop from the Jurassic to the Cretaceous (Bardet, 1994; Lingham-Soliar, 2003). During the Barremian, ichthyosaurs diversified with the appearance of the genus *Platypterygius*, firstly in South America and Australia (*Platypterygius sachicarum* [Paramo, 1997], *Platypterygius haultali*, [Fernández and Aguirre-Urreta, 2005], *Platypterygius* sp. [Choo, 1999; Kear, 2003]). This genus then reached a cosmopolitan distribution during the Aptian (Broili, 1907; Kear, 2003; V.F., pers. observ.). On the contrary, very few Barremian ichthyosaurs are known so far in the Northern Hemisphere. Here we describe a new, nearly complete, and three-dimensionally preserved late Barremian ichthyosaur from the Ul’yanovsk region in Russia. The specimen was first acquired by a German collector during the 1980s and then deposited in the collections of the Royal Belgian Institute of Natural Sciences (Brussels, Belgium). Small portions of the original matrix left in the skull, centra, neural arches, and phalanges were sampled for palynomorph analysis, in order to assess the authenticity and to reveal the age of the specimen. The Barremian strata of the same area (Ul’yanovsk region) have already yielded ichthyosaur remains, described by Bogolubow (1909) as ‘*Ichthyosaurus steleodon*. That taxon is an indeterminate ichthyosaur that is twice the size and more robust than the new taxon presented here.

Institutional Abbreviations—**CR2P**, Centre de recherche sur la paléobiodiversité et les paléoenvironnements, Paris, France; **IRSNB/RBINS**, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; **MHNH**, Muséum d’Histoire naturelle du Havre, Le Havre, France; **RGHP**, Réserve naturelle Géologique de Haute-Provence, France; **SNHM**, Staatliches Naturhis-

torisches Museum, Braunschweig, Germany; **UPMC**, Université Paris 6 Pierre et Marie Curie, Paris, France.

AGE

A dinoflagellate assemblage was extracted from the soft and calcareous marls using fluoric acid. Thirteen slides containing dinoflagellates were produced from the sampled matrix. These were analyzed at the CR2P laboratory (UPMC). The diversity of dinocysts is high, reaching a total of 35 taxa (Supplementary Data 1; available online at www.vertpaleo.org/jvp/JVPcontents.html). The co-occurrence of the species *Pseudoceratium pelliferum*, *Sirmiodinium grossii*, *Trichodinium speetonense*, *Batioladinium longicornutum*, and numerous *Cassiculosphaeridia magna* indicates a late Barremian age for the specimen. Indeed, *T. speetonense* (Fig. 1S, D) appears during the Barremian, and both *P. pelliferum* (Fig. 1S, B), *S. grossii* (Fig. 1S, C), *B. longicornutum* (Fig. 1S, E), and *C. magna* (Fig. 1S, A) disappear at the end of the Barremian (Costa and Davey, 1992; International Commission on Stratigraphy, 2006). *Phoberocysta neocomica* (Fig. 1S, F) is a long-ranging species (Berriasian–Aptian). The palynofacies of the matrix samples extracted from the rostrum, the orbit, the phalanges, the neural arches, and indeterminate bone remains are identical (Fig. 1S, G). Only one poorly preserved centrum that was slightly larger than the others was characterized by a different dinoflagellate assemblage, containing lots of black organic particles (Fig. 1S, H). This centrum probably originates from different sediments, although poorly preserved specimens of the upper Barremian marker *T. speetonense* have been recognized in the matrix surrounding it. Nevertheless, this centrum was removed from the specimen.

SYSTEMATIC PALEONTOLOGY

Order ICHTHYOSAURIA de Blainville, 1835
Family OPHTHALMOSAURIDAE Baur, 1887
SVELTONECTES INSOLITUS, gen. et sp. nov.
(Figs. 1–7)

*Corresponding author.

Etymology—From Greek ‘sveltos,’ agile or nimble, and ‘nektes,’ swimmer, to account for the small size, streamlined skull, and inferred powerful girdle musculature of this ichthyosaur, and from Latin ‘insolitus,’ unusual, to account for the numerous unusual features of this ichthyosaur, as well as its general bauplan and tooth morphology.

Diagnosis—Ophthalmosaurid characterized by the following autapomorphies: naris subdivided by extreme development of the descending process of the nasal; prootic perforated by a mediolateral foramen (reminiscent of Triassic ichthyosaurs such as *Mixosaurus*: Maisch et al., 2006); deep anteroventral fossa on the basioccipital; basipterygoid processes reduced to short rods; exoccipital with anterior pillar-like process; prominent, forked posterior process on the pterygoid; very small (tooth length index of 0.15), sharply pointed, and sometimes recurved teeth; acromion process of the scapula very prominent, rectangular, and lamellar dorsally; radiale, intermedium, and ulnare pentagonal with flat proximal surface and angular distal surface, allowing direct articulation of all (four) primary digits in a tightly packed polygonal fashion (reminiscent of *Ichthyosaurus*: McGowan and Motani, 2003); little or no contact between radius and intermedium, the intermedium being directly articulated with the ulna; presence of anterior and posterior accessory elements in the zeugopodial row of the hind fin. *Sveltonectes insolitus* is also characterized by a unique combination of characters presented in Supplementary Data 1.

Holotype—IRSNB R269, a nearly complete skeleton.

Locality and Horizon—Ul’yanovsk region, western Russia; upper Barremian, Lower Cretaceous.

DESCRIPTION

Skull

The skull is laterally compressed and lacks most of its right side. The left side is complete and articulated. A calcite-mineralized fault displaced the postorbital region of the skull dorsally by 3 cm (Fig. 1). Measurements and ratios can be found in Table 1.

Premaxilla—The premaxilla is slender and its height decreases abruptly 2 cm anterior to the external naris. Unlike in *Ophthalmosaurus icenicus* or *Brachypterygius* (Kirton, 1983), the premaxilla lacks a processus supranarialis. Posteriorly, the dorsal surface of the premaxilla becomes gutter-like and participates in the anteroventral border of the external naris. The fossa prae-maxillaris is continuous on its whole length, from the very tip of the rostrum to the level of the external naris. Anteriorly, this sulcus is so deep that the tip of the rostrum looks ‘X’-shaped in anterior view. In many other ophthalmosaurids (*Aegirosaurus*, *Ophthalmosaurus*, *Platypterygius*, *Brachypterygius*), the fossa prae-maxillaris ends anteriorly as a series of small, shallow foramina (Kirton, 1983; Bardet et al., 1997; Bardet and Fernández,

2000; Fischer et al., 2011; V.F., pers. observ.). The premaxilla articulates with the maxilla along a straight suture starting 52 mm posterior to the emergence of the nasal. The premaxilla-lacrimal external contact was probably broad because the maxilla is very low, but this region is poorly preserved.

Maxilla—The dentigerous maxilla is very low, triangular in shape in lateral view, and its anterior process is strongly reduced, barely extending anteriorly to the external naris, as in some European specimens of *Platypterygius* (Sirotti and Papazzoni, 2002; V.F., pers. observ.), *Aegirosaurus* (Bardet and Fernández, 2000), and *Plutoniosaurus bedengensis* (Efimov, 1997). Its lateral surface is slightly concave.

Nasal—The nasal contacts the premaxilla over a long and straight suture that bends ventrally 21 mm anterior to the external naris. A minute internasal foramen is present. As in *Platypterygius australis* and *Platypterygius hercynicus*, an elongate ridge borders the excavatio internasalis laterally (Kear, 2005; Fischer, in press). The posterior parts of both the internasal foramen and the excavatio internasalis are formed by the frontal, as in *P. hercynicus* (Fischer, in press). The nasal forms the anterodorsal and dorsal borders of the external naris. The ventral border of the nasal forms a protuberant hook-like descending process that nearly contacts the ventral floor of the external naris (Fig. 1).

Lacrimal—Unlike in *P. australis* and *Athabascasaurus*, the lacrimal participates in the posterior border of the external naris (Kear, 2005; Druckenmiller and Maxwell, 2010). Dorsally, the lacrimal contacts the prefrontal along a sinusoidal suture. The lacrimal forms a rounded bulge that contacts the orbit and is continuous with the supraorbital flange.

Prefrontal—The anterior portion of the prefrontal forms a transversely compressed processus naris between the nasal and the lacrimal, which contacts the external naris as in *Aegirosaurus* (Bardet and Fernández, 2000). A small prefrontal-external naris contact is also present in *O. icenicus* (Kirton, 1983). The whole posterior part of the prefrontal is dorsoventrally compressed and forms the anterior portion of the prominent supraorbital flange.

Frontal—The frontal participates in the anterior margin of the supratemporal fenestra (as in *P. australis* [Kear, 2005], *Aegirosaurus* [Bardet and Fernández, 2000], and *P. hercynicus* [Fischer, in press]), thus separating the parietal from the postfrontal. It also participates in the lateral and posterior margins of the internasal foramen and it encloses the ovoid parietal foramen, although not via a thickened ring as in *P. hercynicus* (Fischer, in press).

Postfrontal—The anterior portion of the postfrontal is ‘Y’-shaped and forms an anteromedial fan-shaped ramus that articulates with the frontal and the nasal, and an anterolateral ramus that contacts the prefrontal. The embayment between the anterior rami forms a wide and shallow groove posteriorly. Laterally, the postfrontal participates in the dorsal margin the orbit, forming the median part of the prominent supraorbital flange.

Parietal—The ventral surface of the parietal is subdivided into two deeply concave portions separated by a transverse concavo-convex tentorial ridge (as in *Ophthalmosaurus*: Andrews, 1910). This complex surface probably represents dorsal folding of the brain surface (Andrews, 1910; Kear, 2005). Dorsolaterally, the bone plunges ventrolaterally, forming the medial margin of the supratemporal fenestra. Unlike in *P. australis* (Kear, 2005), the dorsal surface of the parietal is flat and there is no parietal ridge. The anterior margin of the parietal forms a crenate and oblique articulation with the frontal, similar to that of *Ophthalmosaurus* (Kirton, 1983), whereas that suture is transverse in *Platypterygius* (Kear, 2005; Kolb and Sander, 2009; V.F., pers. observ.). The elongated supratemporal process of the parietal and the medial ramus of the supratemporal articulate in a tongue-in-a-groove fashion. A posteromedian excavation on the parietal for the supraoccipital is present, although not as

TABLE 1. Measurements (in cm) and ratios of *Sveltonectes insolitus* (IRSNB R269).

Feature	Measurement	Ratio
Prenarial length	33	0.56
Snout depth	2.8	0.047
Jaw depth	3	0.051
Orbit length	13 (7.7*)	0.18†
Premaxillary length	30.2	0.51
Snout length	37.8	0.64
Jaw length	59	—

All ratios with respect to jaw length.

*Orbit height.

†Based on average of orbit length and height.

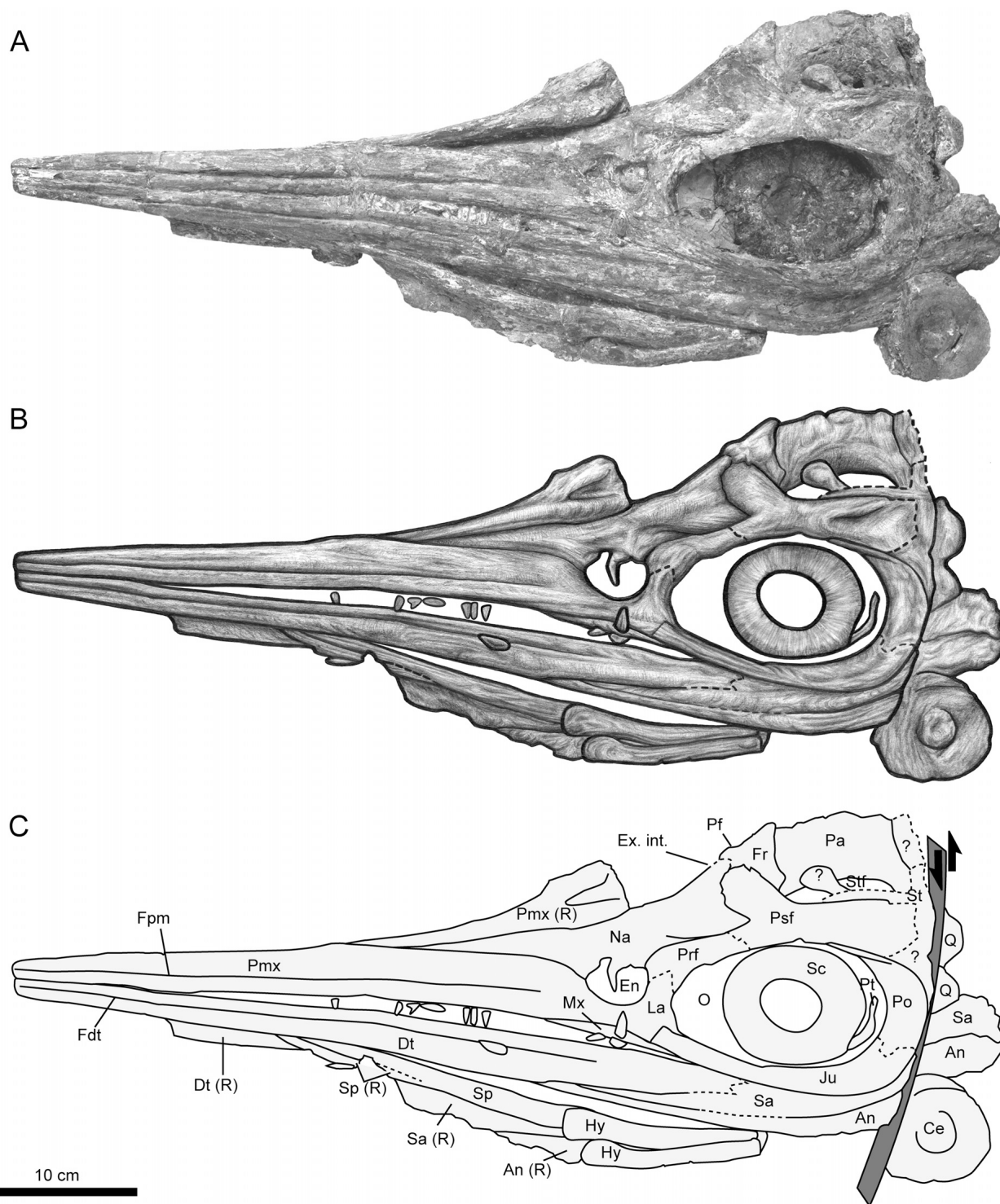


FIGURE 1. Skull of *Sveltonectes insolitus* (IRSNB R269) in lateral view. **A**, photograph; **B**, drawing; **C**, interpretive outline. The dark gray area in **C** represents the fault plane, and the arrows indicate the shear sense. **Abbreviations:** **An**, angular; **Ce**, centrum; **Dt**, dentary; **En**, external naris; **Ex. int.**, excavatio internasalis; **Fdt**, fossa dentalis; **Fpm**, fossa praemaxillaris; **Fr**, frontal; **Hy**, hyoid; **Ju**, jugal; **La**, Lacrimal; **Mx**, maxilla; **Na**, nasal; **O**, orbit; **Pa**, parietal; **Pmx**, premaxilla; **Pf**, parietal foramen; **Po**, postorbital; **Prf**, prefrontal; **Psf**, postfrontal; **Pt**, pterygoid; **Q**, quadrate; **Sa**, surangular; **Sc**, sclerotic ring; **Sp**, splenial; **St**, supratemporal; **Stf**, supratemporal fenestra.

deep as in *P. hercynicus* (Fischer, in press) and *Athabascasaurus* (Druckenmiller and Maxwell, 2010).

Postorbital—Dorsally, the postorbital is rod-like and slightly compressed dorsoventrally, with a teardrop-shaped cross-section. Ventrally, the postorbital is a thin and slightly concavo-convex

and forms an ‘S’-shaped suture with the jugal. The ventral part of the postorbital is undulating, as in *P. australis* (Kear, 2005).

Jugal—The anterior rod-like process of the jugal contacts the maxilla anteroventrally, and covers the lacrimal anteriorly and

anterodorsally as in many ophthalmosaurids (Druckenmiller and Maxwell, 2010).

Quadrate—The stout and crescentic quadrate closely resembles that of *O. icenicus* in having markedly expanded dorsal and ventral extremities (Andrews, 1910; Kirton, 1983). In dorsal view, two distinct lamellae form an angle of ca. 100°. The anterior pterygoid lamella is planoconcave and oblique anteromedially. Ventrally, the pterygoid lamella bends laterally to form the medial side of the articular condyle. The articular condyle is reduced anteriorly and saddle-shaped (unlike some European species of *Platypterygius* that have an extremely massive articular condyle: Kolb and Sander, 2009; V.F., pers. observ.). The anterior and dorsal edges of the pterygoid lamella bear deep, irregular central incisions, indicating the presence of cartilage in vivo. The stapedial facet is markedly concave and its ventral edge is raised, unlike in some species of *Platypterygius* (V.F., pers. observ.).

Sclerotic Ring—The left sclerotic ring is complete. It is composed of at least 10 articulated trapezoidal plates. Their external surfaces are textured by numerous radial striations. The sclerotic aperture is 43% the size of the sclerotic ring, and 12% the size of the orbit. This markedly differs from adult *Ophthalmosaurus*, the only thunnosaurian for which the sclerotic aperture reaches 20% the size of the orbit according to Fernández et al. (2005).

Pterygoid—The pterygoid lacks its anterior end. The anterior palatal ramus is twisted and dorsoventrally compressed, with a teardrop-shaped cross-section. The thicker posterior part of the pterygoid forms lateral, dorsal, and medial lamellae (Fig. 2G, H). The lateral lamella is the smallest, and it is slightly down-turned in the same plane as the dorsal lamella. The dorsal lamella is the thickest and the most prominent. It is oblique and faces dorsolaterally. Its medial surface is saddle-shaped and bears anteroventrally a deep rectangular incision receiving the basiptyergoid process of the parabasisphenoid. This region is pitted and rugose, especially posteriorly to the basiptyergoid facet, suggesting the presence of cartilage in life. The posterior edge of the dorsal lamella bears a large concave area that buttressed the shaft of the stapes. The pterygoid is unusual in forming a prominent posterior process with a kidney-shaped cross-section. These two lobes produce into acute bulges, giving the posterior process a forked end (Fig. 2G, H).

Parabasisphenoid—The basisphenoid is trapezoidal in lateral view and pentagonal in dorsal view (Fig. 2M, O). It is completely fused to the posterior end of the parasphenoid. The posterior surface of the basisphenoid is roughly circular and bears a deep incision that extends on the dorsal surface as a shallow groove. This feature is common amongst post-Triassic ichthyosaurs (e.g., McGowan, 1973; Kirton, 1983; McGowan and Motani, 2003; Kear, 2005; V.F., pers. observ.). The dorsal surface of the basisphenoid is kidney-shaped, unlike those of *P. australis* (hexagonal: Kear, 2005), *Brachypterygius* (squared: McGowan and Motani, 2003), and *O. icenicus* (rounded: Kirton, 1983). The basiptyergoid processes are reduced to short, right-angled, and dorsoventrally compressed rods (Fig. 2M–O). The carotid foramen is a deep furrow on the ventral side of the basisphenoid. It is set near the posterior end of the basisphenoid, whereas it is located in the centre of the ventral surface in most other ophthalmosaurids (Maxwell, 2010; V.F., pers. observ.). Elongated ridges border the carotid furrow laterally. Only the posterior end of the parasphenoid is preserved. It is an elongated rod with a triangular cross-section.

Basioccipital—The basioccipital is slightly compressed dorsoventrally. It bears a large, hemispherical condyle with an irregular surface. The dorsal surface of the basioccipital is flat (Fig. 2B), as in *Brachypterygius* (McGowan and Motani, 2003), *Arthropterygius* (Maxwell, 2010), and *P. australis* (Kear, 2005). The foramen magnum forms a median groove that separates the elliptical exoccipital facets. There is a deep median incision

on the anterior edge of the dorsal surface in the prolongation of the foramen magnum. This incision extends on the anterior surface and abuts in a deep ovoid anteroventral excavation (Fig. 2C). Dorsal to this pit, the median incision is bordered laterally by paired ovoid and rugose articular protuberances for the basisphenoid (Fig. 2C). The extracondylar area is extremely reduced (Fig. 2A, B), as in *Arthropterygius*, *Brachypterygius*, and *Platypterygius* (McGowan and Motani, 2003; Maxwell, 2010). Dorsally, the oblique stapedial facet contacts the elevated and flat-topped opisthotic facet.

Exoccipital—The anterior process at the base of the exoccipital is strongly reduced in comparison to most ophthalmosaurids, such as *Mollesaurus*, *Ophthalmosaurus*, *Brachypterygius*, and *Platypterygius* (McGowan, 1976; Kirton, 1983; Fernández, 1999; Kear, 2005). The ventral surface is superficially heart-shaped. The shaft of the exoccipital is perforated by one large hypoglossal foramen, as in *Mollesaurus* (Fernández, 1999). A second hypoglossal foramen is possibly present, but seems strongly reduced (Fig. 2K). However, the number of foramina appears to be variable amongst ophthalmosaurids, as shown by Maisch (1997) for *Ophthalmosaurus*. Dorsally, a dorsoventrally oriented groove separates the supraoccipital head from a posterior pillar-shaped process (Fig. 2I, K), a unique condition in ichthyosaurs.

Prootic—The left prootic is roughly hexagonal in lateral view and laterally compressed. Its anterior lamella slightly bends laterally. Just below the midpoint, this lamella is perforated by a cylindrical, mediolateral foramen (Fig. 2E), bordered medioventrally by a curved ridge. This foramen probably housed facial nerve (cranial nerve VII) as in other reptiles, including the Triassic ichthyosaur *Mixosaurus* (Maisch et al., 2006). This is the first time that a prootic foramen is reported in post-Triassic ichthyosaurs. The posterior surface of the prootic is roughly triangular and bears a deep, triradiate impression of the anterior part of the otic capsule. The impression of the horizontal semicircular canal forms the widest branch and the impression of the anterior vertical semicircular canal forms the narrowest and shallowest branch. Unusually, the ventral part of the otic impression houses a single tear-shaped impression for the sacculus and/or utriculus. In other ophthalmosaurids, the ventral part of the otic impression is wide, with separated impressions for the sacculus, the utriculus, and the ampulla (e.g., Andrews, 1910; Kirton, 1983; Kear, 2005). The posterior surface is bordered ventrally by a large and rugose bulge and dorsally by a triangular and concave surface (Fig. 2E, F), which may be an articular facet or an attachment area for muscle or cartilage.

Mandible

Dentary—The dentary closely resembles the premaxilla. A deep, narrow, and continuous fossa dentalis extends along its lateral side and reaches the level of the anterior border of the orbit. Posteriorly, the fossa dentalis forms a broader but shallower sulcus that extends on to the surangular.

Splenial—Both splenials are incompletely preserved and partly disarticulated (Fig. 1). In ventral view, the anterior end of the splenials is situated 15 cm from the tip of the mandible.

Angular—The angular has a high, 'S'-shaped posterior end. As in all ophthalmosaurids (Maisch and Matzke, 2000b), the angular is markedly exposed laterally, although less than in *O. icenicus* (Kirton, 1983) and *Athabascasaurus* (Druckenmiller and Maxwell, 2010). Its lateral and medial surfaces are weakly concave.

Surangular—The surangular is superficially 'S'-shaped. Its lateral surface is concave in extension of the fossa dentalis. Unlike in other ophthalmosaurids (e.g., Kirton, 1983), the lateral surface of the surangular is flat and lacks a fossa surangularis.

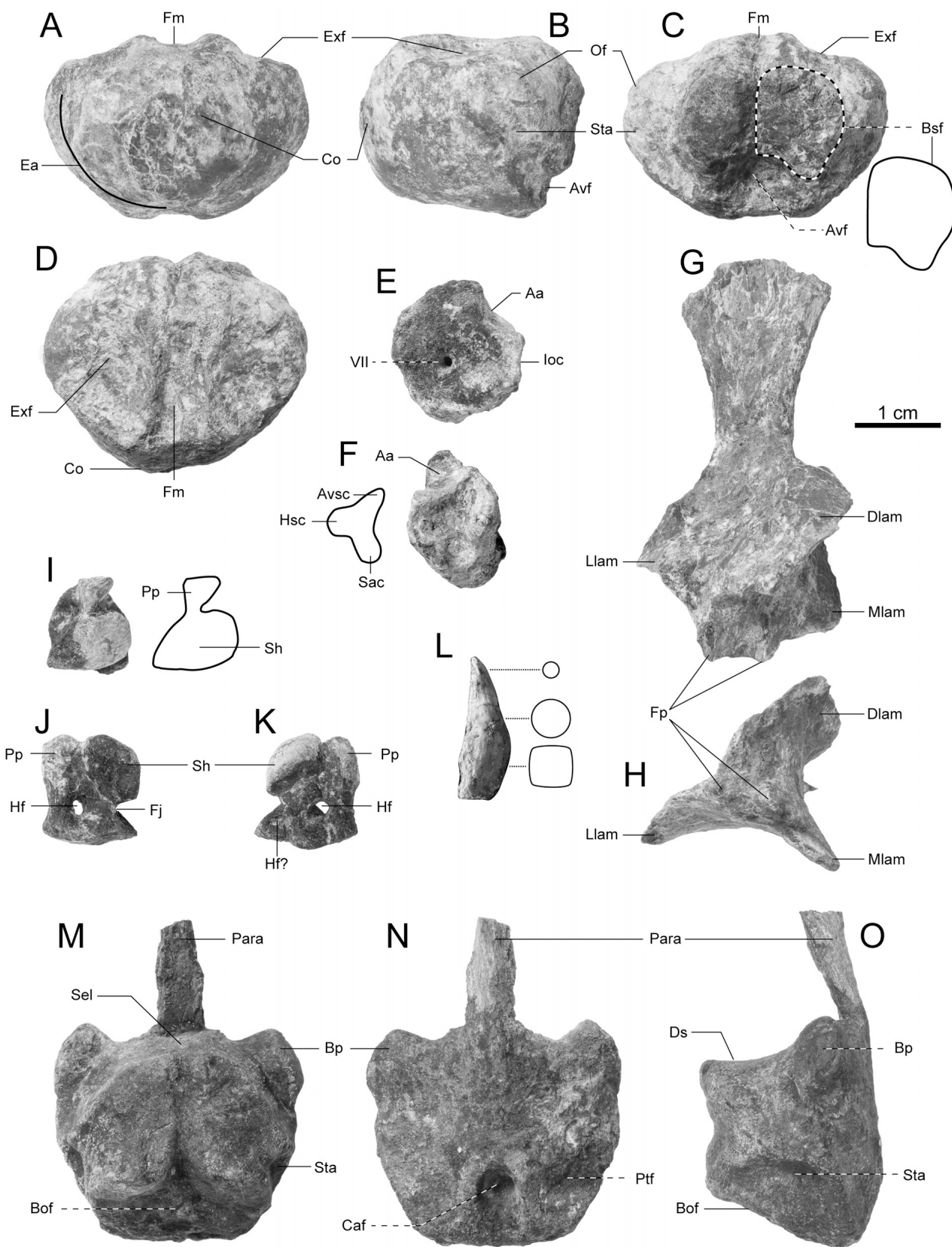


FIGURE 2. Basicranium, tooth, and palatal elements of *Sveltonectes insolitus* (IRSNB R269). **A**, basioccipital in posterior view; **B**, basioccipital in lateral view; **C**, basioccipital in anterior view and outline of the basisphenoid facet; **D**, basioccipital in dorsal view; **E**, left prootic in lateral view; **F**, left prootic in posterior view and outline of the impression of the otic capsule; **G**, left pterygoid in dorsal view; **H**, left pterygoid in posterior view; **I**, right exoccipital in dorsal view; **J**, right exoccipital in lateral view; **K**, right exoccipital in medial view; **L**, tooth and its cross-sections; **M**, basisphenoid in

Articular—Both articulars are disarticulated. The medial surface for the quadrate is saddle-shaped and it bears a small, dorsoventrally elongated bulge that possibly marks the insertion of a *M. adductor mandibulae internus pterygoideus posterior* (Kear, 2005). The ventrolateral surface is ovoid, concave, and slightly rugose. A prominent, flat-topped ridge separates these surfaces medially.

Hyoid—Both hyoids lie over the splenials and the right part of the mandible (Fig. 1A, C). They are rod-like and slightly curved. The anterior end is convex, smooth, and laterally compressed. Posteriorly, it becomes rounded in cross-section, the opposite condition of *P. australis* and *P. hercynicus* (Kear, 2005; Kolb and Sander, 2009).

Dentition

Thirty-four teeth are preserved. They are very small: the largest tooth measures 19 mm in total height and the relative tooth length index (TLI; sensu McGowan, 1976) is 0.11, which is about half that of typical toothed post-Liassic ichthyosaurs such as *Platypterygius* or *Brachypterygius*, but slightly larger than those of *Aegirosaurus* (Maisch and Matzke, 2000b; Fischer et al., 2011). About half of the teeth are recurved. All have a sharply pointed apex. The crown is circular in cross-section and restricted to the upper third of the tooth (Fig. 2L). The crown is ornamented by delicate longitudinal striations. The root progressively becomes squared in cross-section towards its base, as in *Brachypterygius*, *Platypterygius*, *Maiaspondylus*, and *Undorosaurus* (Bardet, 1990; Efimov, 1999; Maxwell and Caldwell, 2006b; V.F., pers. observ.) and bears subtle longitudinal striations.

Axial Skeleton

Centra—A discontinuous series of 76 centra is preserved. The different regions of the vertebral column are poorly defined in ichthyosaurs because the pectoral and pelvic girdles are not connected to the axial skeleton. For descriptive purposes only, it is commonly accepted that in Thunnosauria the cervical centra have diapophyses fused to the facet for the neural arch, the anterior dorsal centra have separated diapophyses and parapophyses on the upper half of the centrum, the posterior dorsal centra have separated diapophyses and parapophyses located in lower half of the centrum, the anterior caudal centra have a single, lateroventrally oriented apophysis, and that apical and postflexural centra are usually laterally compressed and bear chevron facets ventrally (McGowan and Motani, 2003; Kolb and Sander, 2009). According to these definitions, 22 cervical centra, six anterior dorsals, 11 posterior dorsals, 26 anterior caudals, two apicals, and 11 postflexurals are preserved in IRSNB R269. The atlas-axis is missing. All centra are strongly amphicoelous and similar in proportions (Fig. 3), resulting in a very poorly regionalized vertebral column, even less than that of *Ophthalmosaurus natans* (Massare et al., 2006). The nine anterior-most cervical centra are small and heart-shaped, with a prominent ventral keel. This ridge progressively disappears on posterior centra as the ventral surface of the centra becomes rounded. In the cervical region, the neural canal region is frequently slightly

concavo-convex in the transverse plane. This probably helped to straighten that part of the vertebral column. Thoracic and anterior caudal centra are rounded. The anterior surface of apical centra is bulged, resulting in a ball-and-socket articulation. The only complete apical centrum preserved accounts alone for 2.9° of the tail bend using McGowan's (1989) trapeze method. Apicals and postflexurals lack chevron facets. Postflexurals are dorsoventrally and anteroposteriorly elongated, although less than in *Platypterygius platydactylus* (Broili, 1907).

The unusually high number of so-called cervical centra is interpreted as a retention of the neural facet-diapophysis contact up the middle thoracic region, and therefore does not indicate a particularly long neck. This condition is also found in "*Otschevia*" *alekseevi* (22 cervicals: Arkhangel'sky, 2001) and *Platypterygius americanus* (18 cervicals: Maxwell and Kear, 2010).

Neural Arches—Thirty-eight complete or partial neural arches are disarticulated. However, a series of eight neural arches can be identified as cervical, because their columnar pedicles perfectly articulate with the small and rounded facets on the dorsal surface of the cervical centra. The pedicles of the remaining neural arches are anteroposteriorly elongated. The emargination of the posterior edge of the neural spine is much deeper in the cervical region, each neural arch being tightly locked to the preceding one. The emargination becomes shallower or absent on posterior neural spines. As in *P. hercynicus*, pre- and postzygapophyses remain separated anteriorly in the cervical and anterior dorsal regions, and are usually completely fused in the posterior dorsal and anterior caudal regions (Kolb and Sander, 2009). They disappear in the postflexural region.

Ribs—Many rib fragments are preserved, but no rib is complete. Two shallow grooves run along the proximal portion of the ribs, resulting in an '8'-shaped cross-section. These grooves vanish distally and the ribs progressively acquire an oval and then a rounded cross-section.

Pectoral Girdle

Coracoid—The coracoid is massive, fan-shaped, and markedly saddle-shaped ventrally (Fig. 4E, F), unlike the oval and flattened coracoid of *Platypterygius* (Kolb and Sander, 2009; Zammit et al., 2010; V.F., pers. observ.). As in *P. australis*, the intercoracoidal facet is strongly thickened, rugose, and lenticular in medial view (Wade, 1984). Both coracoids perfectly articulate with each other, the intercoracoidal suture being sinusoidal dorsally. Unlike in *Ophthalmosaurus* (Appleby, 1956), the glenoid and the scapular facet are well demarcated, forming a 100° angle (Fig. 5E). The anterior and posterior margins of the coracoid are thin and convex. The anterior notch is deep and narrow.

Scapula—The scapula is laterally compressed and superficially 'S'-shaped, thus differing from the thick and rod-like scapular blade of some European specimens of *Platypterygius* (Kolb and Sander, 2009; V.F., pers. observ.), but similar to that of *P. americanus* (Nace, 1939). Its dorsal end is slightly expanded, dorsally bent, and concavo-convex, following the shape of the ribcage. Anteromedially, the scapula forms a prominent acromion process (Fig. 4A–C). Unlike in *Stenopterygius* (Johnson, 1979), the acromion process does not contact the coracoid. The acromion

← dorsal view; **N**, basisphenoid in ventral view; **O**, basisphenoid in lateral view. **Abbreviations:** **Aa**, area for articulation with unknown tissue; **Avf**, anteroventral fossa; **Avsc**, impression of the anterior vertebral semicircular canal; **Bof**, basioccipital facet; **Bp**, basiptyergoid process; **Bsf**, outline of the basisphenoid facet; **Caf**, carotid furrow; **Co**, condyle; **Dlam**, dorsal lamella; **Ds**, dorsum sellae; **Ea**, limit between the condylar and the extracondylar area; **Exf**, exoccipital facet; **Fj**, foramina jugularis; **Fm**, foramen magnum; **Fp**, forked process; **Hf**, hypoglossal foramen; **Hsc**, impression of the horizontal semicircular canal; **Ioc**, impression of the otic capsule; **Llam**, lateral lamella; **Mlam**, medial lamella; **Of**, opisthotic facet; **Para**, parasphenoid; **Pp**, posterior pillar process; **Ptf**, facet for medial lamella of the pterygoid; **Sac**, impression of the sacculus and/or the utriculus; **Sel**, sella turcica; **Sh**, supraoccipital head; **Sta**, stapedial facet; **VII**, facialis nerve (cranial nerve VII).

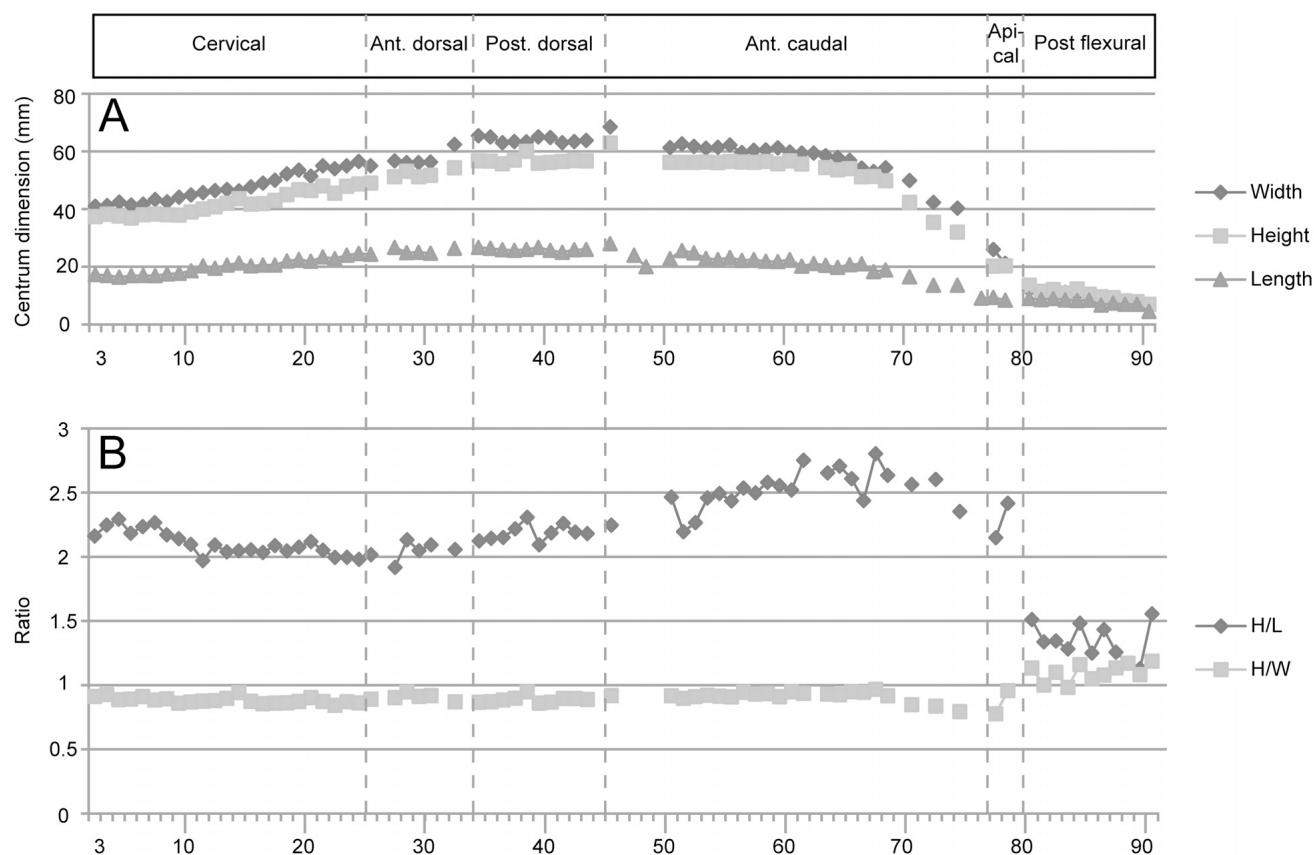


FIGURE 3. Vertebral dimensions of *Sveltonectes insolitus* (IRSNB R269). **A**, measurements; **B**, height/length and height/width ratios, showing the poor regionalization of the vertebral column of *S. insolitus*. The x-axis refers to the number of the centrum, not its actual position within the vertebral column. Each obvious gap in the vertebral column is represented by a single void.

is also clearly separated from the coracoid facet, unlike in most specimens of *Ophthalmosaurus* (Gilmore, 1905, 1906; Appleby, 1956; Kirton, 1983). The acromion process appears separated from the coracoid facet in *Caypullisaurus* (Fernández, 1997), although this region is poorly known in this taxon. Dorsolaterally, the acromion process forms a large, thin, 'S'-shaped, flange with a rectangular outline (Fig. 4A–C). The glenoid contribution of the scapula is reduced, as in *O. icenicus* (Andrews, 1910) and *P. americanus* (Nace, 1939, 1941).

Interclavicle—The anterior transverse bar of the interclavicle is slightly convex and its lateral extremities extend posterodorsally. They are separated at the midline by an oblique fracture, interpreted as a partially healed fracture, because it extends on the anterior part of the ventral surface of the interclavicle, but is absent on the dorsal (internal) surface. The posterior median stem is an elongated process with a 'U'-shaped cross-section. Its internal surface is markedly concave except at its base, where it has a rounded cross-section. The median stem forms numerous root-like ridges at its junction with the anterior transverse bar.

Forefin

Both forefins were found in articulation during excavation. However, about 26 displaced elements have also been unearthed, suggesting that the phalangeal count and/or the number of digits proposed here are underestimated.

Humerus—The humerus is robust, with a strongly expanded proximal half. The proximal head is slightly flattened, markedly rugose, and roughly rectangular in cross-section (Fig. 4G). Both

the narrow trochanter dorsalis and the wider deltopectoral crest are strongly developed (Fig. 4H, I), resembling those described in some specimens of *Platypterygius* (e.g., McGowan, 1972; Wade, 1990; McGowan and Motani, 2003; Kolb and Sander, 2009). Distally, the humerus has two deep and rugose distal facets for the radius and the ulna, and lacks any supplementary facets for anterior or posterior accessory elements, as in *Nannopterygius* and *Platypterygius campylodon* (Hulke, 1871; Kiprijanoff, 1881). The ulnar facet is the largest and is quadrangular in shape (Fig. 4J).

Zeugopodium—The zeugopodium is represented by both radii and one anterior extrazeugopodial element. The stout radius narrows anteriorly and distally. With the exception of its dorsal and ventral surfaces, it is rugose. Its proximal surface is convex, whereas the other surfaces are either flat or weakly concave. The right radius does not contact the intermedium, whereas the left radius and intermedium contact each other over a short distance (Fig. 5). The radius articulates anteriorly with two crescentic extrazeugopodial elements.

Basipodium—The radiale, the intermedium, and the ulnare are similar in size and pentagonal in shape, with a straight proximal surface (Fig. 5). Each element of the basipodium supports two digits distally, as in *Ichthyosaurus* and some specimens of *Ophthalmosaurus* (e.g., Kirton, 1983; McGowan and Motani, 2003), although none of these elements is diamond-shaped in IRSNB R269. The radiale articulates with the second crescentic preaxial element.

Digits—The manus is composed of four primary digits that directly articulate with the basipodium, one preaxial accessory digit, and one postaxial accessory digit. Elements of the primary

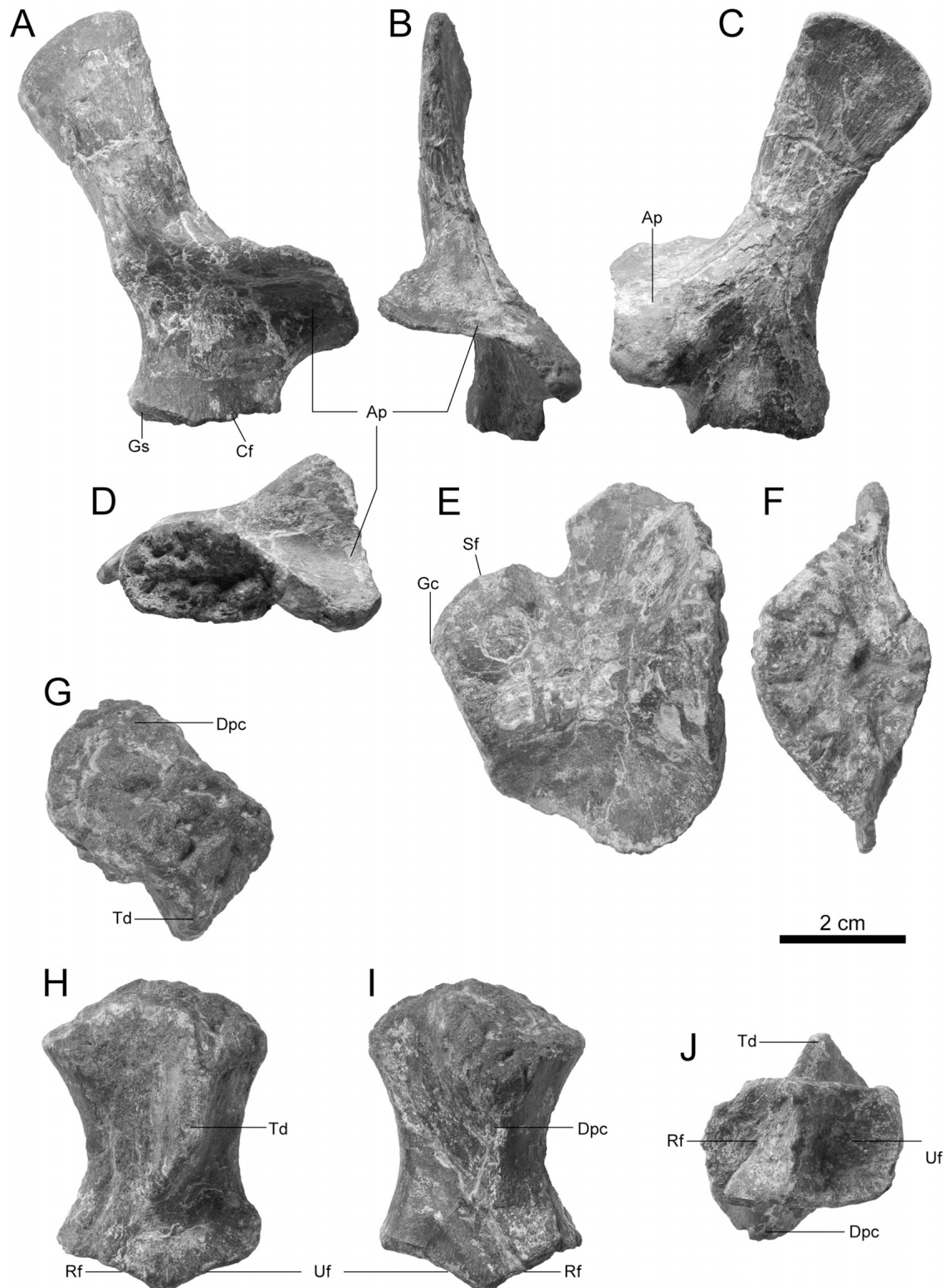


FIGURE 4. Anterior appendicular elements of *Sveltonectes insolitus* (IRSNB R269). **A**, right scapula in lateroventral view; **B**, right scapula in anterior view; **C**, right scapula in dorsomedial view; **D**, right scapula in proximal view; **E**, right coracoid in ventral view; **F**, right coracoid in medial view; **G**, left humerus in proximal view; **H**, left humerus in dorsal view; **I**, left humerus in ventral view; **J**, left humerus in distal view. **Abbreviations:** **Ap**, acromion process; **Cf**, coracoidal facet; **Dpc**, deltopectoral crest; **Gc**, glenoid contribution of the coracoid; **Gs**, glenoid contribution of the scapula; **Rf**, radial facet; **Sf**, scapular facet; **Td**, trochanter dorsalis; **Uf**, ulnar facet.

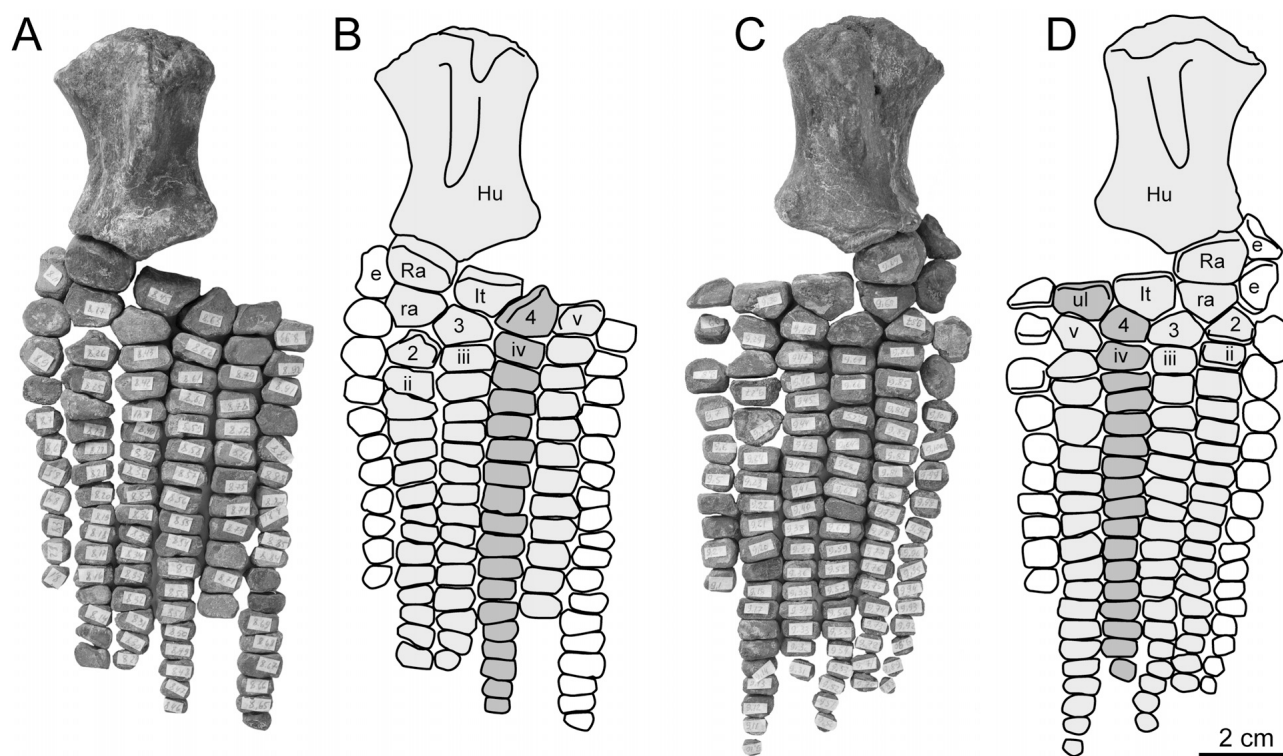


FIGURE 5. Forefins of *Sveltonectes insolitus* (IRSNB R269) in dorsal view. **A, B**, left forefin; **C, D**, right forefin. The primary axis of the fin is colored in dark gray and the accessory digits in white. **Abbreviations:** e, anterior accessory zeugopodial element; **Hu**, humerus; **It**, intermedium; **Ra**, radius; **ra**, radiale; **ul**, ulnare; **2–4**, distal carpals; **ii–v**, metacarpals.

digits are rectangular to polygonal in shape and form a tightly packed mosaic similar to that of *Platypterygius* (e.g., Broili, 1907; Wade, 1984). Like in *Platypterygius* (Maisch and Matzke, 2000b), most elements are dorsoventrally thicker than proximodistally wide. Distal elements of the primary digits and most pre- and postaxial accessory digit elements are rounded. The highest phalangeal count is 19. The very small size and rounded shape of most terminal phalanges suggest that the forefins, as preserved, are nearly complete.

Pelvic Girdle

Only one ischiopubis is preserved. Like in some other derived ophthalmosaurids (*Aegirosaurus*, *Caypullisaurus*, *Athabascasaurus*, and *P. australis*), it lacks an obturator foramen (Fig. 6E) (Bardet and Fernández, 2000; Druckenmiller and Maxwell, 2010; Zammit et al., 2010). It is rod-like with slightly expanded extremities. The shaft is teardrop-shaped in cross-section. Its distal end is strongly compressed laterally, whereas its proximal end forms a thickened and ovoid articular facet with rugose texture (Fig. 6F). This surface is truncated anteriorly by an anterolateral facet inclined anterolaterally.

Hind Fin

Femur—According to Maxwell (2010) and Maxwell and Kear (2010), we follow the orientation of the femur proposed by McGowan and Motani (2003) for *Ichthyosaurus* (contra the orientation proposed by Andrews [1910] and McGowan and Motani [2003] for *Ophthalmosaurus*). Both femora are preserved. The femur resembles the humerus in having an expanded proximal head and two distal facets. It is, however, about half the size of the humerus. In proximal view, the femur has a triangular outline (Fig. 6D). The femoral dorsal trochanter is oblique, high, and

narrow (Fig. 6A), and the thicker and not flat-topped ventral process lies close to the anterior border of the femur (Fig. 6B). Both these processes progressively decrease in height from mid-shaft. They are separated posteriorly by a sharp edge, which is the continuation of the right-angled corner of the femoral head, and anteriorly by a large and slightly concave triangular area. The two distal facets (for the tibia and the fibula) have the same size and are markedly concave (Fig. 6C).

Distal Hind Fin—Despite the slight disarticulation of the proximal rows of both hind fins, most elements of the zeugo- and basipodium can be identified (Fig. 7). Unlike in most other thunnosaurians, the hind fin is not reduced: five digits, containing up to 12 elements, are present. Only the closely related *Aegirosaurus* possess a comparable phalangeal count (Fernández, 2007). As in *P. australis* (Zammit et al., 2010), an anterior accessory element is present (Fig. 7A, C). However, *Sveltonectes* is unique in having four elements in the zeugopodial row of the hind fin. The anterior accessory element is pentagonal and the posterior accessory element is wedge-shaped. There are three primary digits, one preaxial accessory digit, and one postaxial accessory digit. Elements of the primary digits are brick-like, similar to those of the forefin and become rounder distally. Accessory digit elements are rounded in shape.

PHYLOGENETIC ANALYSIS

Methodology

We conducted a new phylogenetic analysis of Thunnosauria (the last common ancestor of *Stenopterygius quadriscissus* and *Ichthyosaurus communis* plus all its descendants: Motani, 1999) based on 15 taxa and 50 characters (see Appendix 1 for the character list and Appendix 2 for the character matrix). Thirty-three characters are modified from literature (Godefroit,

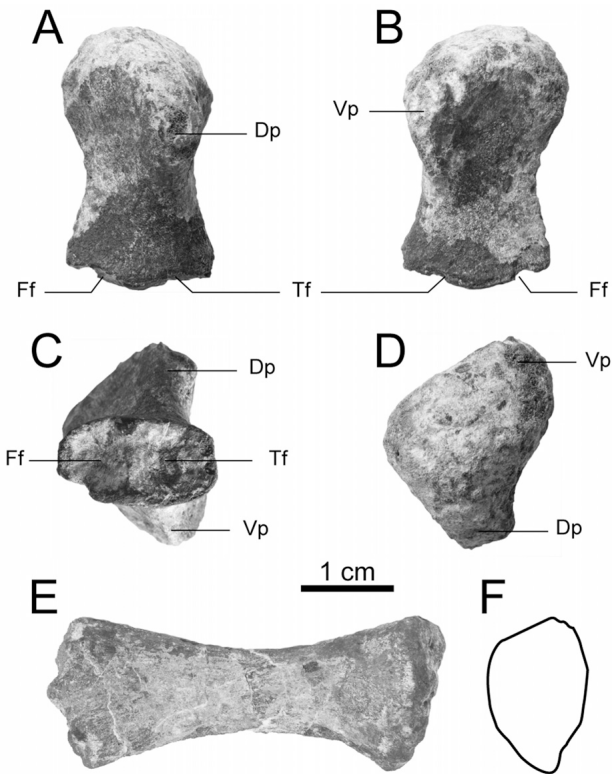


FIGURE 6. Posterior appendicular elements of *Sveltonectes insolitus* (IRSNB R269). **A**, right femur in dorsal view; **B**, right femur in ventral view; **C**, right femur in distal view; **D**, right femur in proximal view; **E**, ?left ischiopubis in ?lateral view; **F**, outline of the acetabular end of the ischiopubis. **Abbreviations:** Dp, dorsal process; Ff, fibular facet; Tf, tibial facet; Vp, ventral process.

1993; Motani, 1999; Maisch and Matzke, 2000b; Sander, 2000; Fernández, 2007; Maxwell, 2010) and 17 characters are new. Characters were coded from the literature and personal observations for *Temnodontosaurus* (IRSNB R122 and IRSNB R123), *Stenopterygius* (IRSNB R124 and IRSNB R125), *Aegirosaurus* (RGHP LA 1), *P. hercynicus* (MHNH 2010.4 and a cast of the holotype held at the SNHM), and *Sveltonectes* (IRSNB R269). Characters were not weighted and, except for characters 19, 38, and 44, were not ordered.

All currently valid thunnosaurian genera are included in the data matrix, except *Nannopterygius* and *Undorosaurus*, which are too incompletely described. The genus *Chacaicosaurus* is used for the first time in a phylogenetic analysis. Because the monophyly of *Ophthalmosaurus* and *Platypterygius* has never been convincingly demonstrated, we coded the best-known ingroup species *O. icenicus*, *P. australis*, and *P. hercynicus* in the analysis. *Temnodontosaurus*, regarded by Motani (1999) as the sister taxon for Thunnosauria, is the outgroup of this analysis. The character states were coded from the species *Temnodontosaurus platyodon* and *Temnodontosaurus trigonodon*, because other species are badly defined and of doubtful generic assignment. Exact algorithms of TNT v1.1 (2010, original version: Goloboff et al., 2003) were used to analyze the character matrix (Appendix 2) and calculate the Bremer support and bootstrap values.

Results

Two most parsimonious trees were recovered from the analysis. The strict consensus tree (Fig. 8) has a length of 100 steps, a consistency index (CI) of 54 and a retention index (RI) of 60. These coefficients reflect a high degree of homoplasy, as already suggested in a previous analysis of ophthalmosaurid ichthyosaurs (Maxwell, 2010). The Bremer support is similarly low, being 1 at each node, except for the clade Thunnosauria (4+) and Ophthalmosauridae (3). Similarly, only the clades Thunnosauria and Ophthalmosauridae have bootstrap values above 50 (100 and 64, respectively). The clade Ophthalmosauridae as defined by Motani (1999) (the last common ancestor of *Brachypterygius extremus* and *O. icenicus* plus all its descendants) would not include *Arthropterygius*. Because this taxon shares crucial characters with

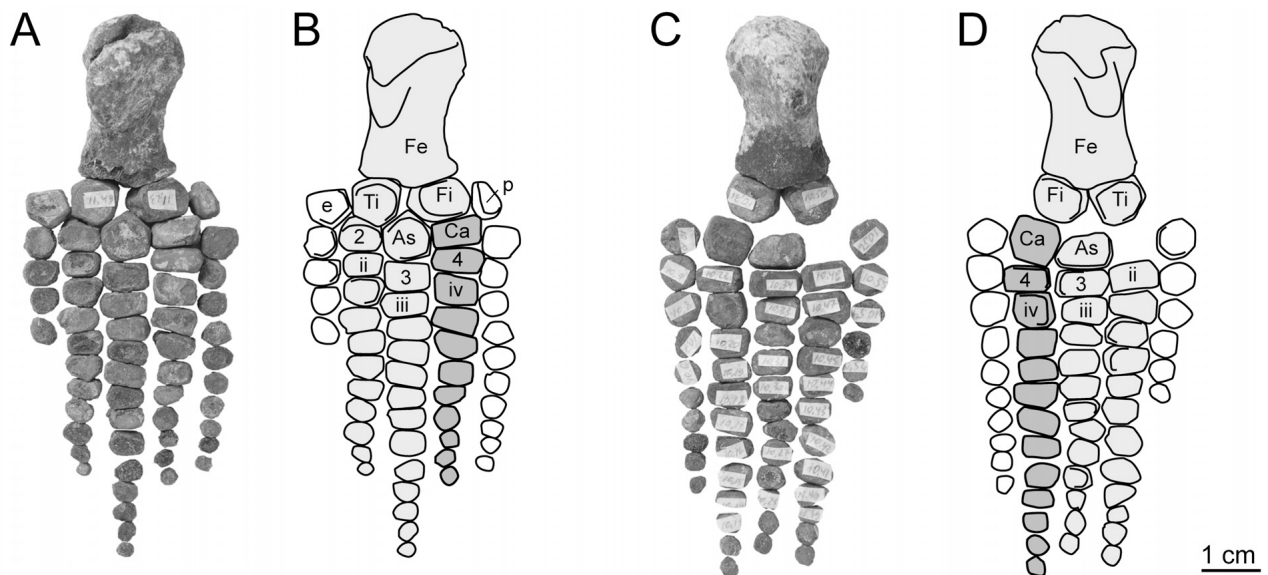


FIGURE 7. Hind fins of *Sveltonectes insolitus* (IRSNB R269) in dorsal view. **A**, **B**, left hind fin; **C**, **D**, right hind fin. The primary axis of the fin is colored in dark gray and the accessory digits in white. **Abbreviations:** As, astragalus; Ca, calcaneum; e, anterior accessory zeugopodial element; Fe, femur; Fi, fibula; p, posterior accessory zeugopodial element; Ti, tibia; 2–4, distal tarsals. ii–iv, metatarsals.

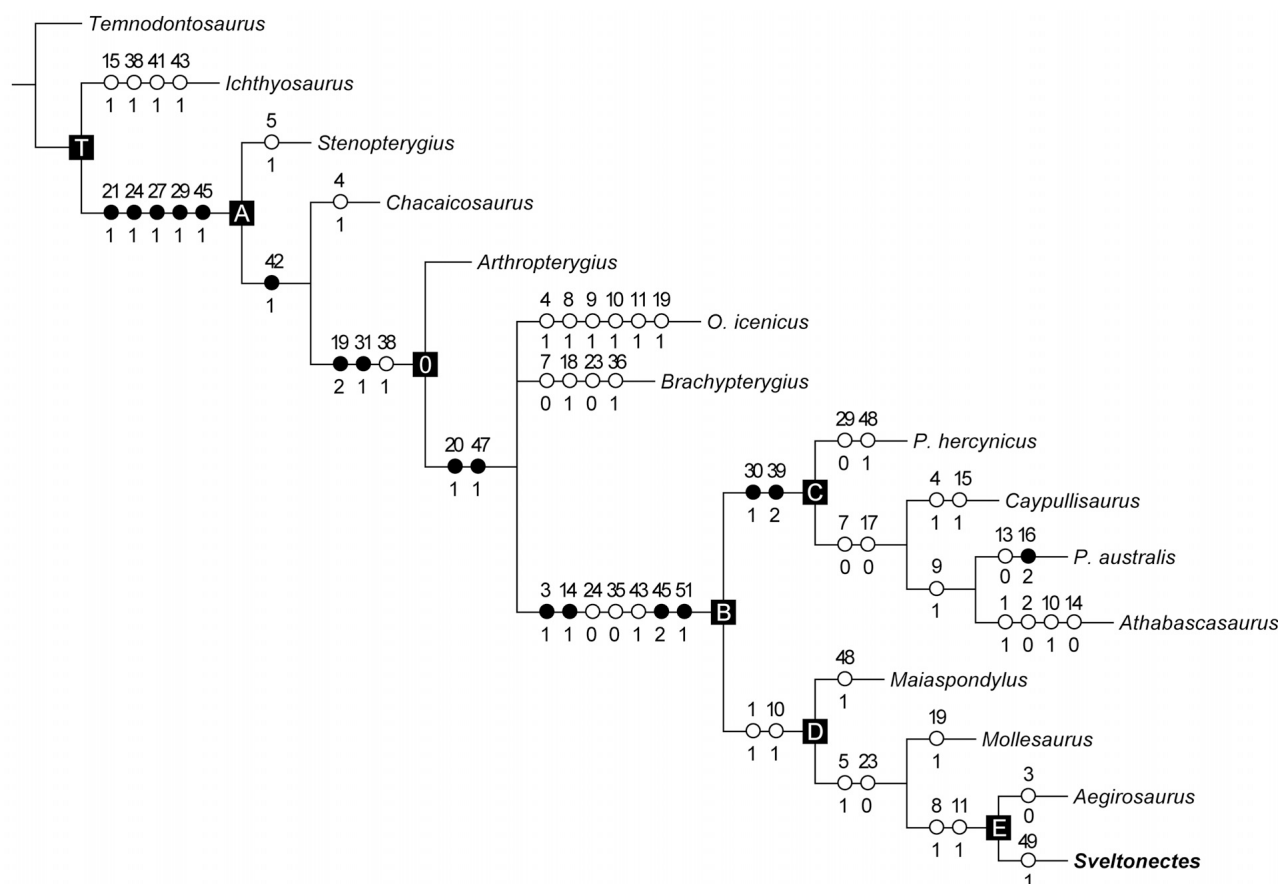


FIGURE 8. Strict consensus of the two most parsimonious trees indicating the phylogenetic position of *Sveltonectes* amongst Thunnosauria in unambiguous optimization. Black circles represent non-homoplasious synapomorphies, open circles homoplasious synapomorphies, and numbers above and below circles represent character number and character state, respectively. **Abbreviations:** T, Thunnosauria; O, Ophthalmosauridae.

ophthalmosaurids such as the reduced extracondylar area of the basioccipital, a well-developed anterior accessory element and associated digit and a plate-like dorsal trochanter of the humerus (Maxwell, 2010), we propose here to redefine Ophthalmosauridae as comprising the last common ancestor of *Arthropterygius chrisorum* and *O. icenicus* plus all its descendants. The characters (char.) discussed below are non-homoplasious unless stated otherwise.

The analysis supports a *Stenopterygius* origin for the Ophthalmosauridae: this clade ('A') is supported by five unambiguous synapomorphies: a massive stapedial head matching that of the opisthotic in size (char. 21), anterior caudals with high height/length ratio (char. 24, reversed in clade 'B'), no chevron facets in the apical region (char. 27), a well-expressed acromion process (char. 28), and the presence of an ischiopubis (char. 44). Thick proximal elements in the paddles (char. 42) characterizes Ophthalmosauridae + *Chacaicosaurus*. Ophthalmosauridae is united by three unambiguous synapomorphies: the reduction of the extracondylar area of the basioccipital (char. 19), the presence of a plate-like dorsal trochanter (char. 30), and an unnotched anterior facet on elements of the leading edge of the fins (char. 38; homoplasious). The presence of an anterior accessory element articulating with the humerus (char. 34) also characterizes Ophthalmosauridae, but only in accelerated optimization. Ophthalmosauridae without *Arthropterygius* are characterized by the loss of the basioccipital peg (char. 20) and the presence of well-developed dorsal and ventral trochanters on the femur (char. 46). Advanced ophthalmosaurids ('B') are united by seven unambiguous autapomorphies: a quadrangular

root section (char. 3), the presence of a processus temporalis on the frontal (char. 14, reversed in *Athabascasaurus*), anterior caudals with low height/length ratio (char. 24, homoplasious), no posterior deflection of the ulnar facet on humerus (char. 34, homoplasious), tightly packed rectangular phalanges (char. 42, homoplasious), the loss of the obturator foramen in the ischiopubis (char. 44), and the presence of postaxial accessory digits on the hind fin (char. 50). Advanced ophthalmosaurids are divided in two clades, a 'platypterygiine' clade ('C') and a 'sveltonectine' clade ('D'). Clade 'C' is supported by two autapomorphies: the absence of an anteromedial process on the coracoid (char. 29) and at least two postaxial accessory digits on the forefin (char. 38). However, the analysis failed to recover a monophyletic *Platypterygius* clade, suggesting that the genus *Platypterygius*, as currently defined, is invalid. Clade 'D' is supported by two autapomorphies: the absence of crown striations (char. 1, homoplasious) and the absence of a processus supranarialis of the premaxilla (char. 10, homoplasious). *Sveltonectes* is united with *Aegirosaurus* (clade 'E') by the presence of a descending process in the external naris (char. 8; homoplasious) and the presence of a processus narialis on the prefrontal (char. 11, homoplasious).

DISCUSSION

Maturity

Johnson (1977) established four criteria of the forefin to assess the osteological maturity of the Early Jurassic genus *Stenopterygius*. The texture of the left humeral shaft, like fine

sandpaper, and the flattened articular head of the humerus suggest that IRSNB R269 was not completely ossified when it died. Conversely, the phalanges are fully ossified and tightly packed, which indicates osteological maturity (Johnson, 1977). Fernández et al. (2005) proposed another criterion based on the relative size of the sclerotic ring: in parvipelvian ichthyosaurs, the aperture of the sclerotic ring usually equals 20% of the total surface of the orbit in juveniles, but this ratio decreases with age. Exceptions to this rule are the supposed deep divers *Eurhinosaurus* and *Ophthalmosaurus*, whose sclerotic ring aperture remains around 20% of the orbit size in adults (Fernández et al., 2005). In IRSNB R269, the sclerotic ring aperture represents 12% of the orbit size. Kear (2005) noted that the complete fusion between the parasphenoid and the basisphenoid is a potential indicator of osteological maturity in *P. australis*. The fusion of these bones is complete on IRSNB R269. Finally, the muscle attachment areas on the pectoral girdle are well developed, which also indicates osteological maturity in secondarily aquatic marine reptiles (Maxwell and Kear, 2010). Consequently, this specimen is considered as an adult.

Ecological Diversity of Early Cretaceous Ichthyosaurs

On the basis of tooth morphology, Massare (1987, 1997) defined feeding guilds amongst marine reptiles. However, most of the ichthyosaurs used in Massare's analysis were Early Jurassic in age, coming from the well known Hettangian–Sinemurian and Toarcian anoxic shales of Europe. The incorporation of Late Jurassic to 'middle' Cretaceous ichthyosaurs in that canvas proved to be problematic because of the appearance of intermediate or mosaic-like dental morphologies in taxa whose diet cannot be constrained by gastric contents or bromalites (Fischer et al., 2011). Furthermore, some ichthyosaurs, which were identified as belonging to the 'Grasp: smash' guild and supposedly fed on lightly armored cephalopods, were probably far more opportunistic than hypothesized by Massare: the preserved gut of a specimen of *P. australis* from the Albian of Australia contained the remains of birds, fishes, cephalopods, and small turtles (Kear et al., 2003). The ecological diversity of Cretaceous ichthyosaurs is therefore largely unknown. *Sveltonectes* is characterized by very small (tooth size ratio = 1.16; see Appendix 1, character 5), delicate, and sharply pointed teeth that contrast with those of most other Late Jurassic to Early Cretaceous ichthyosaurs, which possess large and robust teeth with a blunt apex (*Brachypterygius*, *Platypterygius*; Massare, 1987) and are grouped within the 'Grasp: smash' guild. Whereas the tooth morphology of *Sveltonectes* cannot be directly assigned to any of the guilds defined by Massare, it suggests the presence of a 'pierce'-oriented guild among Cretaceous ichthyosaurs, intermediate between the 'Pierce I' and 'Pierce II/General' guilds. Indeed, Massare (1987:122) indicated that a "slender shape, moderate size and a pointed apex" are general dental features effective at piercing small, soft prey. The slender snout and absence of visible tooth wear is also reminiscent of members of the Pierce I guild such as Leptonectidae, although the snout and orbital ratios of *Sveltonectes* are smaller than in leptonectids. The dental morphology of *Sveltonectes* would indicate a diet of small, delicate, and fleshy prey such as aulopiform or clupeiform fishes and soft cephalopods.

Studies on the locomotion of advanced ichthyosaurs indicate that the limbs were most likely used in stabilizing the body and maneuvering (McGowan, 1991; Buchholtz, 2001). The hind fins of *Sveltonectes* are long (about two-thirds the size of the forefins) and wide (presence of one preaxial and one postaxial accessory digits) by ophthalmosaurid standards, and the very prominent muscle attachment areas on the scapula, the coracoid, the humerus, and the femur suggest strong, functional limbs that could have given this taxon greater maneuvering capabilities,

which is in agreement with the diet deduced from the dental morphology. The vertebral column of *Sveltonectes* is also poorly regionalized (Fig. 4A, B), which suggests lower sustained swimming speed in favor of increased maneuverability (Massare et al., 2006). New specimens belonging to a new ophthalmosaurid taxon briefly discussed by Fischer et al. (2009) indicate that a 'pierce' guild was still occupied by ichthyosaurs during the late Albian. Interestingly, small 'pierce' and large 'smash' ichthyosaurs are commonly associated in Lower Cretaceous formations of Europe (Aptian–Albian of southeastern France: Fischer et al., 2009; Albian of England: V.F., pers. observ.) and Russia (Barremian of the Ul'yanovsk region where *Sveltonectes* is associated with '*Ichthyosaurus*' *steleodon*). This suggests that ichthyosaurs had a much more significant hold over the Early Cretaceous marine trophic webs than previously supposed (e.g., Bardet, 1992).

CONCLUSIONS

Sveltonectes insolitus is a new and highly derived ophthalmosaurid ichthyosaur from the late Barremian of western Russia. This taxon significantly increases the morphological and ecological diversity of Early Cretaceous ichthyosaurs, by colonizing a 'pierce'-oriented feeding guild with a possible diet of small, fleshy, and swift prey. Its complex osteology, combining numerous unique features and characters previously considered as autapomorphic for other taxa, confirms that the radiation of Ophthalmosauridae was rather complex, with considerable homoplasy involved, as already suggested by Maxwell (2010). This radiation took place during the Middle–Late Jurassic from a *Stenopterygius*-like ancestor.

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- mentary specimens and that still maintains an ecological significance (basioccipital width is well correlated to skull width/‘gullet size’ in ichthyosaurs [$R^2 = 0.88$; V.F., unpubl. data]). *Sveltonectes* and *Mollesaurus* have very reduced TSR (1.16 and ≈ 1.12 , respectively), whereas other ichthyosaurs such as *Brachypterygius* and *Platypterygius* have much larger teeth (TSR in between 2.96 and 4.88).
- (6) Processus postpalatinis pterygoidei: absent (0); present (1). (Maisch and Matzke, 2000b:character 38).
- (7) *Maxilla anterior process: extending anteriorly as far as nasal or further anteriorly (0); reduced (1).
- (8) Descending process of the nasal on the dorsal border of the nares: absent (0); present (1). (Fernández, 2007:character 2).
- (9) *Processus narialis of the maxilla in lateral view: absent (0); present (1). This character replaces Fernández’s (2007:375) character 0 “premaxilla-lacrimar contact below the external nares,” which had 3 states: ‘no,’ ‘narrow,’ and ‘broad.’ The distinction between latter two is subjective.
- (10) Processus supranarialis of the premaxilla: present (0); absent (1) (Maisch and Matzke, 2000b:character 10).
- (11) *Processus narialis of prefrontal: absent (0); present (1).
- (12) Anterior margin of the jugal: tapering, running between lacrimar and maxilla (0); broad and fan-like, covering large area of maxilla ventrolaterally (1) (Druckenmiller and Maxwell, 2010:character 6).
- (13) Sagittal eminence: present (0); absent (1) (Fernández, 2007:character 5, inverted codings).
- (14) *Processus temporalis of the frontal: absent (0); present (1). Motani (1999) introduced a character related to the contact between the nasal and the parietal lateral to the frontal, in dorsal view. That contact is present in some *Temnodontosaurus* specimens and in *Stenopterygius*. However, the absence of this contact might have different origins, either by a medial process of the postfrontal, like in *Ichthyosaurus*, or by a lateral process of the frontal, like in *P. australis*, *Aegirosaurus*, and *Sveltonectes*, or both, like in *Ophihalmosaurus* (McGowan, 1973; Kirton, 1983; Bardet and Fernández, 2000; Kear, 2005; Kolb and Sander, 2009). Thus, this character state is obtained by different processes, and does not carry any phylogenetic signal. Consequently, a new character is proposed here, based on the presence or absence of a clearly developed processus temporalis of the frontal, forming the anteromedial edge of the supratemporal fenestra.
- (15) Supratemporal-postorbital contact: absent (0); present (1) (Sander, 2000:character 27).
- (16) *Squamosal shape: triangular (0); squared (1); squamosal absent (2). Maisch and Matzke (2000a) showed some specimens of *Ichthyosaurus* retained a squamosal.
- (17) Quadratojugal exposure: extensive (0); small, largely covered by squamosal and postorbital (1) (modified from Maisch and Matzke, 2000b:character 30).
- (18) *Basipterygoid processes: short, giving basisphenoid a square outline in dorsal view (0); markedly expanded laterally, being wing-like, giving basisphenoid a marked pentagonal shape in dorsal view (1).
- (19) Extracondylar area of basioccipital: wide (0); reduced but still present ventrally and laterally (1); extremely reduced, being nonexistent at least ventrally (2) (Fernández, 2007:character 10, modified).
- (20) Basioccipital peg: present (0); absent (1) (Motani, 1999:character 29, modified).
- (21) Stapes proximal head: slender, much smaller than opisthotic proximal head (0); massive, as large or larger than opisthotic (1) (Sander, 2000:character 34, modified). *Stenopterygius* is the only Liassic ichthyosaur to display the derived state (e.g., Fraas, 1891:table 2 II [*S. quadriscissus* according to

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APPENDIX 1. Description of characters used in phylogenetic analysis. Characters are polarized with respect to *Temnodontosaurus* as the outgroup. New characters are indicated by an asterisk (*).

Skull

- (1) Crown striation: presence of deep longitudinal ridges (0); crown enamel subtly ridged or smooth (1) (Druckenmiller and Maxwell, 2010:character 25).
- (2) *Base of enamel layer: poorly defined, invisible (0); well defined, precise (1).
- (3) *Root cross-section: rounded (0); quadrangular (1).
- (4) Complete, well-developed dentition retained in adults (0); adult completely or nearly edentulous (1) (Maisch and Matzke, 2000b:character 4).
- (5) Tooth size relative to basioccipital width: large (≥ 3) (0); small (≤ 1.5) (1). Derived from character 39 of Motani (1999). The tooth size relative to basioccipital width (Tooth size ratio [TSR] = $10 \times$ largest crown height/basioccipital width) is a new ratio that is easy to obtain even in frag-

Maisch, 2008:233]; Owen, 1840 [*S. triscissus* according to Maisch, 2008:237]; Dechaseaux, 1954 [*S. triscissus* according to Maisch, 2008; M. Maisch, pers. comm., 2010]).

- (22) Angular lateral exposure: much smaller than surangular exposure (0); extensive (1) (Motani, 1999:character 32, inverted coding).

Axial Skeleton

- (23) 'Cervical' centra (diapophysis-neural arch facet contact) extend up to middle dorsal region (0); anterior dorsal region (1) (Sander, 2000:character 66, modified).
 (24) Posterior dorsal/anterior caudal centra: 3.5 times or less as high as long (0); four times or more as high as long (1) (Maxwell, 2010:character 15, inverted codings).
 (25) Tail fin centra: strongly laterally compressed (0); as wide as high (1) (Maxwell, 2010: character 16).
 (26) Neural spines of atlas-axis: completely overlapping, may be fused (0); functionally separate, never fused (1) (Druckenmiller and Maxwell, 2010:character 26).
 (27) Chevrons in apical region: present (0); lost (1) (Sander, 2000:character 72).

Shoulder Girdle

- (28) *Prominent acromion process of scapula: absent (0); present (1).
 (29) *Anteromedial process of coracoid: present (0); absent (1).

Forefin

- (30) Plate-like dorsal ridge on humerus: absent (0); present (1) (Motani, 1999:character 56).
 (31) *Protruding, strongly developed deltopectoral crest on humerus, matching in height the trochanter dorsalis, and bordered by concave areas: absent (0); present (1). This character may tentatively be coded as derived for *Caypullisaurus* based on the single fully prepared humerus figured in Fernández (1998:fig. 2), which shows strongly developed trochanters.
 (32) Humerus distal and proximal ends in dorsal view (thus regardless of the size of the dorsal and ventral processes): distal end wider than proximal end (0); nearly equal or proximal end slightly wider than distal end (1) (Motani, 1999:character 55, modified).
 (33) Humerus anterodistal facet for accessory zeugopodial element anterior to radius: absent (0); present (1) (Godefroit, 1993:character 10, modified).
 (34) *Posteriorly deflected ulnar facet: absent (0); present (1).
 (35) Humerus/intermedium contact: absent (0); present (1) (Fernández, 2007:character 15).
 (36) Manual pisiform: absent (0); present (1) (Motani, 1999:character 67, inverted codings).
 (37) Notching of anterior facet of leading edge elements of forefin in adults: present (0); absent (1) (Motani, 1999:characters 59 and 65, modified). Motani's (1999) characters 59 and 65 were clearly linked to each other in our data matrix, and have therefore been combined in the present analysis.

- (38) Posterior enlargement of forefin: number of postaxial accessory 'complete' digits: none (0); one (1), two or more (2). (Maisch and Matzke, 2000b:character 89, modified).

- (39) Preaxial accessory digits on forefin: absent (0); present (1) (Maisch and Matzke, 2000b:character 91). Since the reappraisal of the forefin of *Caypullisaurus* (Fernández, 2001), there is no current evidence of two well-developed preaxial digits in this taxa: Fernández (2007) mentioned that the anterior extrazeugopodial element supports two digits, but one of them is the 'radiale' digit (II). At the current state of knowledge, the presence of two preaxial digits remains a valid autapomorphy of *Platypterygius* (Maxwell and Caldwell, 2006a; V.F., pers. observ.).

- (40) *Longipinnate or latipinnate forefin construction: one (0); two (1) digit(s) directly supported by the intermedium.

- (41) Zeugo- to autopodial elements flattened and plate-like (0); strongly thickened (1) (Maisch and Matzke, 2000b:character 94). According to Maisch and Matzke (2000a), no Liassic ichthyosaur exhibits the derived state. However, this is not restricted to Ophthalmosauridae, because *Chacaicosaurus cayi* presents clearly thickened phalanges as well (Fernández, 1994). This reinforces the status of *Chacaicosaurus* as an intermediate form between *Stenopterygius* and Ophthalmosauridae (see Maisch and Matzke, 2000a).

- (42) Tightly packed rectangular phalanges: absent, phalanges are mostly rounded (0); present (1) (Maisch and Matzke, 2000b:character 102, modified).

- (43) *Digital bifurcation: absent (0); frequently occurs in digit IV (1).

Pelvic Girdle

- (44) Ischium-pubis fusion in adults: absent or present only proximally (0); present with an obturator foramen (1); present with no obturator foramen (Mazin, 1982:character 13, modified).
 (45) Ischium or ischiopubis shape: plate-like, flattened (0); rod-like (1) (Motani, 1999:character 87, modified).

Hind Fin

- (46) *Prominent, ridge-like dorsal and ventral processes demarcated from the head of the femur and extending up to mid-shaft: absent (0); present (1).
 (47) Astragalus/femoral contact: absent (0); present (1) (Maxwell, 2010:character 33).
 (48) *Femur anterodistal facet for accessory zeugopodial element anterior to tibia: absent (0); present (1). This character replaces character 32 of Maxwell (2010:411), "Number of articular facets on distal femur," because these facets are not homologous (compare Kolb and Sander, 2009; Maxwell and Kear, 2010; Zammit et al., 2010).
 (49) Tibia peripheral shaft in adults: notched (0); straight (1) (Motani, 1999:character 92, modified).
 (50) *Postaxial accessory digit: absent (0); present (1).

APPENDIX 2. Character-taxon matrix used for phylogenetic analysis of Thunnosauria, with *Temnodontosaurus* as the outgroup. **Abbreviations:** **A**, polymorphism for states 0 and 1; **B**, polymorphism for states 0 and 2.

Taxon	10	20	30	40	50
<i>Temnodontosaurus</i>	0000000000	0000000000	0000000000	0000000000	0000000000
<i>Ichthyosaurus</i>	000000100A	00001B1000	0010000000	01000A1A01	0110100010
<i>Stenopterygius</i>	A00A1110A0	0000001000	10111-1100	00000A0000	00111-0000
<i>O. icenicus</i>	0101011111	1110001011	1111011101	0111011111	1001110010
<i>Chacaicosaurus</i>	---1---0--	-----00	-----0	--0-010000	100-----
<i>Brachypterygius</i>	01000-0-00	-1-----121	-10---1-1	1101111111	100-----
<i>Arthropterygius</i>	-----	-----020	1-11-1-01	01110-1-0	-----00---
<i>Mollesaurus</i>	----1-00-	0---11-11	1-00-----	-----	-----
<i>Caypullisaurus</i>	---10-0A00	0---110---	-110---111	1110011210	1102-10-11
<i>Aegirosaurus</i>	A0001-1101	11-1001---	-1-----1	-100111111	-1021-0011
<i>P. australis</i>	0110000010	0101020121	1110111111	1110011210	1102010111
<i>P. hercynicus</i>	01100-100-	01110A1-2-	1---1-1011	1110011210	110-1101-
<i>Maiaspondylus</i>	11100-1-01	-1-----0--	--10-----1	-10011-1-0	-10---10--
<i>Athabascasaurus</i>	10-00-0011	-110010-2-	11-0-1----	-----	---201----
<i>Sveltonectes</i>	10101-1101	1111---021	11000-1101	11000-1111	1102-10111