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New data on the ichthyosaur *Platypterygius hercynicus* and its implications for the validity of the genus

VALENTIN FISCHER

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The description of a nearly complete skull from the late Albian of northwestern France reveals previously unknown anatomical features of *Platypterygius hercynicus*, and of European Cretaceous ichthyosaurs in general. These include a wide frontal forming the anteromedial border of the supratemporal fenestra, a parietal excluded from the parietal foramen, and the likely presence of a squamosal, inferred from a very large and deep facet on the quadratojugal. The absence of a squamosal has been considered as an autapomorphy of the genus *Platypterygius* for more than ten years and has been applied to all known species by default, but the described specimen casts doubt on this putative autapomorphy. Actually, it is shown that all characters that have been proposed previously as autapomorphic for the genus *Platypterygius* are either not found in all the species currently referred to this genus, or are also present in other Ophthalmosauridae. Consequently, the genus *Platypterygius* must be completely revised.

Key words: Ichthyosauria, Ophthalmosauridae, *Platypterygius hercynicus*, Cretaceous, Saint-Jouin, France.

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Introduction

The record of Early Cretaceous ichthyosaurs is particularly patchy and subcomplete specimens are rare. For a long time, all Cretaceous ichthyosaurs were grouped within the catch-all genus *Platypterygius* Huene, 1922 and new genera have been identified only recently (e.g., Maxwell and Caldwell 2006b; Fischer et al. 2009; Druckenmiller and Maxwell 2010). The cranial anatomy of *Platypterygius* was adequately described in two extra-Eurasian species (*Platypterygius americanus*, Romer 1968; *Platypterygius australis*, Kear 2005), and subsequently applied to the seven other valid species by default. European representatives of this genus are poorly known: the only specimen of *Platypterygius platydactylus* (the type species of the genus), a sub-complete skeleton from the upper Aptian of Germany, was destroyed during World War II and the holotype of *Platypterygius campylodon* is not diagnostic and presumably lost (McGowan and Motani 2003; personal observations). *Platypterygius hercynicus* (which was previously synonymised with *P. platydactylus* by McGowan and Motani 2003) from the upper Aptian of Germany was recently redescribed by Kolb and Sander (2009). However, their interpretation of the skull roof is questionable, as demonstrated below.

During the mid-1970s a large ichthyosaur skull was discovered in an upper Albian glauconitic sandstone at Saint-Jouin (Seine-Maritime department, northwestern France; Fig. 1) in three separate blocks by the amateur palaeontologist Jean-Pierre Debris, who donated the prepared specimen to the Muséum d'Histoire Naturelle du Havre (MHNH). The circumstances of the discovery and the geological setting were described in two papers by Debris (1977, 1978), but this author did not mention the presence of the ammonite *Callihoplites* gr. *strigosus* Spath 1927 in the same layer, which confirms the late Albian age (early *Callihoplites auritus* Subzone, *Mortoniceras inflatum* Zone; Wiedmann and Owen 2001) of the specimen. Buffetaut (1977) published a taphonomic analysis and a preliminary description of the specimen and referred it to *Platypterygius campylodon* on the basis of tooth morphology. Although the skull is crushed, a close examination shows that most bones are still present and articulated. The so-called Saint-Jouin ichthyosaur is one of the largest and most complete ichthyosaur skulls from the Cretaceous of Europe, and closely resembles SMSS "SGS", the holotype of *P. hercynicus* (Kuhn, 1946).

The aims of this paper are to (i) provide a detailed description of the cranial anatomy of the Saint-Jouin ichthyosaur, (ii) emend the diagnosis of the species *Platypterygius hercynicus* and clarify its skull roof anatomy, and (iii) evaluate the validity of the proposed diagnostic characters for the genus *Platypterygius*, as a first step towards a thorough re-evaluation of this genus.

Institutional abbreviations.—CAMSM, Sedgwick Museum of Earth Sciences, Cambridge University, Cambridge, UK; MHNH, Muséum d'Histoire Naturelle du Havre, Le Havre,

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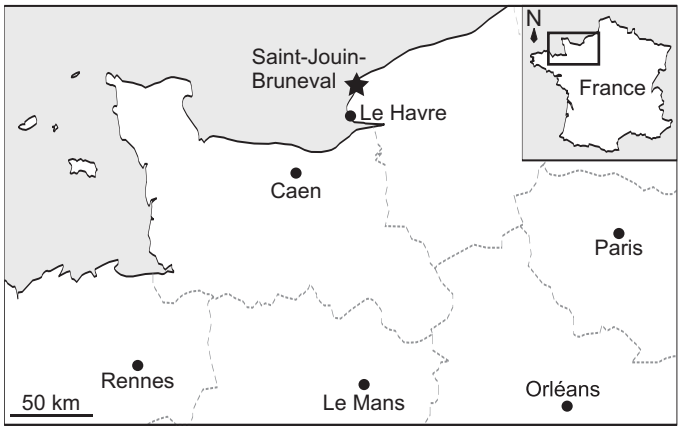


Fig. 1. Location of MHNH 2010.4 in Saint-Jouin, France.

France; NMB, Staadliches Naturhistorisches Museum Braunschweig, Braunschweig, Germany; SMSS, Städtisches Museum Schloss Salder, Salzgitter, Germany.

Systematic palaeontology

Ichthyosauria Blainville, 1835

Ophthalmosauridae Baur, 1887

Platypterygiinae Arkhangelsky, 2001, sensu Fischer et al. 2012

Genus *Platypterygius* Huene, 1922

Type species: *Platypterygius platydactylus* (Broili, 1907), upper Aptian of the Hannover area (Germany).

Platypterygius hercynicus Kuhn, 1946

Figs. 2–6.

Holotype: SMSS "SGS", a subcomplete skeleton comprising skull, shoulder girdle and axial skeleton.

Type locality: Salzgitter, Lower Saxony, Germany.

Type horizon: "neocomer Erzhorizont", Upper Aptian, Lower Cretaceous.

Referred material.—MHNH 2010.4, nearly complete skull from the early *Callihoplites auritus* Subzone (*Mortoniceras inflatum* Zone, late Albian, Early Cretaceous) of Saint-Jouin-Bruneval, Seine-Maritime department, north-west France. Coordinates: 49°38'42.96"N 0°09'11.21"E.

Emended diagnosis.—Platypterygiinae characterized by the following potentially unique features: long anterior ramus of nasal forming the dorsomedial surface of more than half of the rostrum; large naris with rounded dorsal margin; parietal foramen excluded from the parietal and surrounded posteriorly by a thickened process of the frontal.

Platypterygius hercynicus is also characterized by the following unique combination of characters: presence of a large processus temporalis on the frontal (shared with *Aegirosaurus*, Bardet and Fernández 2000; *P. australis*, Kear 2005; *Sveltonectes insolitus*, Fischer et al. 2011b); presence of a squamosal (absent in *P. americanus*, Romer 1968; *P. australis*, Kear 2005); thick dental root with squared cross section (*Platypterygius* spp., Bardet 1990; *Undorosaurus*, Efimov 1999; *Maiaspondylus*, Maxwell and Caldwell 2006b; *Brachypterygius*, personal observation on CAMSM material); four distal facets on humerus for radius, ulna, and accessory zeugopodial elements (shared with one specimen of *P. australis*, Zammit 2010; Zammit et al. 2010); "longipinnate" forefin construction where the intermedium supports a single digit distally (shared with all *Platypterygius* spp. except *P. hautali*, Fernández and Aguirre-Urreta 2005; Maxwell and Kear 2010; *Caypullisaurus*, Fernández 2001; *Maiaspondylus*, Maxwell and Caldwell 2006b, and probably *Arthropterygius*, Maxwell 2010); presence of seven digits proximally, including two preaxial and one postaxial ones (shared with *Plutoniosaurus*, Efimov 1997); brick-like polygonal phalanges (shared with "*Platypterygius*" spp., McGowan 1972; *Caypullisaurus*, Fernández 1997; *Maiaspondylus*, Maxwell and Caldwell 2006b); femur with three distal facets including one for the astragalus (shared with *Maiaspondylus*, Druckenmiller and Maxwell 2010; Maxwell and Kear 2010).

Stratigraphic and geographic range.—Upper Aptian–upper Albian, Germany, France.

Description

Because the genus *Platypterygius* is clearly a catch-all taxon, the choice was made to compare MHNH 2010.4 and *Platypterygius hercynicus* with all well-known Ophthalmosauridae. The description and diagnoses are therefore not restricted to the different species of *Platypterygius*. MHNH 2010.4 is a large (ca. 1200 mm) skull roof with its associated partial rostrum. It is crushed but still articulated (Fig. 2).

Skull roof

Premaxilla (Fig. 2).—Both the proximal and distal portions of the premaxillae are missing. Anteriorly, the premaxillae form a robust rostrum with a semi-circular cross section. Laterally, a continuous fossa praemaxillaris vanishes posteriorly at the level of the lateral emergence of the maxilla. The irregular and rugose surface of the premaxilla has been interpreted as post-sedimentation damage by burrowing and encrusting organisms of the sea floor (Debris 1977; Buffetaut 1977). The dental groove is wide and deep. The lingual and labial walls have the same height, as in *Ophthalmosaurus* (Bardet et al. 1997) and *Aegirosaurus* (Fischer et al. 2011a). Shallow pseudo-alveoli can be observed on the medial surface of the labial wall.

Maxilla (Figs. 2, 3).—The anterior process of the maxilla has a moderately long lateral exposure. It extends beyond the level of the naris, farther than in *P. campylodon* (Kiprijanoff 1881; Capellini 1890), but does not reach the level of emergence of the nasal as in *Caypullisaurus* (Fernández 2007), *P. americanus* (Romer 1968), *P. bannovkensis* (Arkhangelsky 1998), or *P. australis* (Kear 2005), even though this character is

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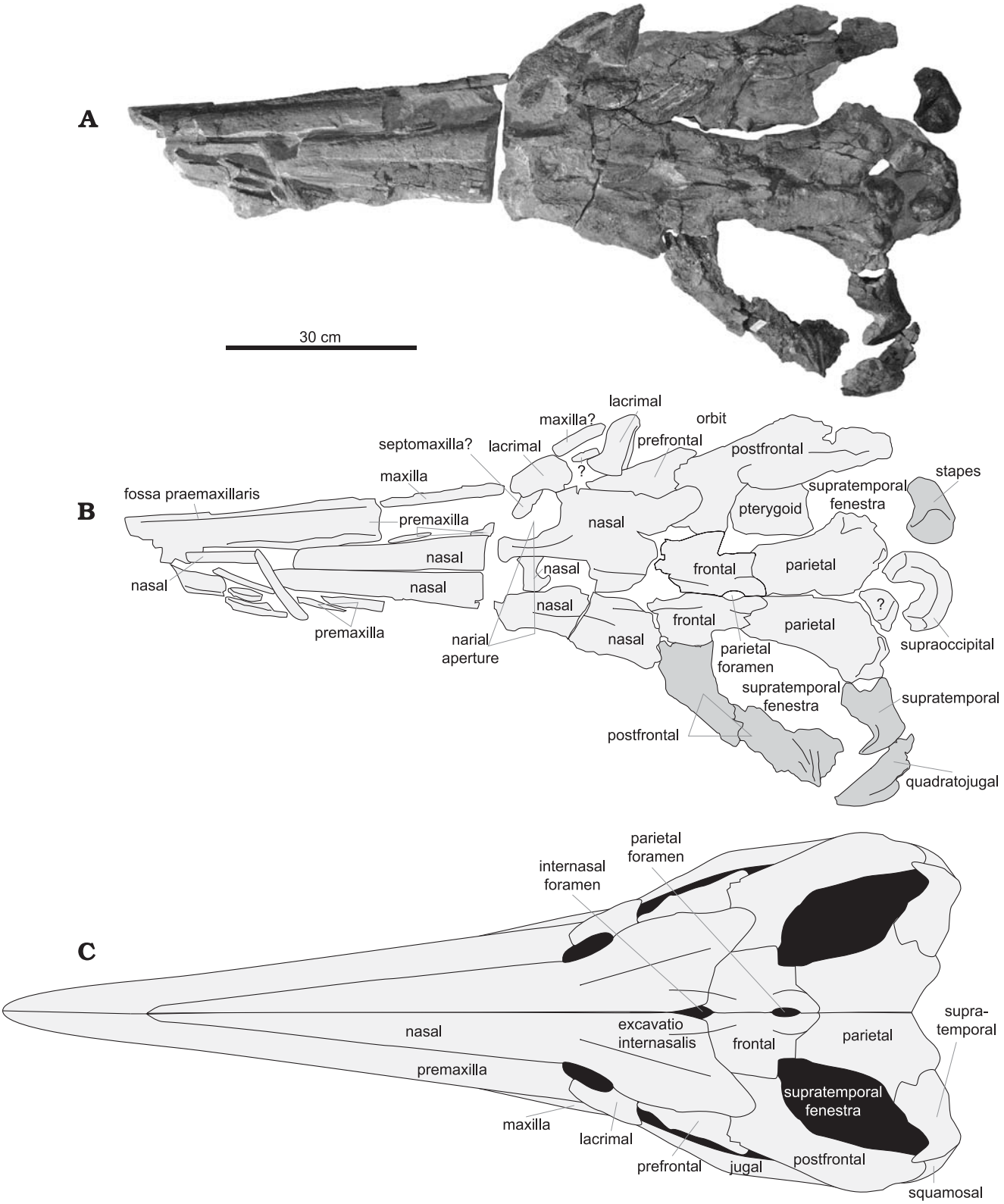


Fig. 2. Ophthalmosaurid ichthyosaur *Platypterygius hercynicus* Kuhn, 1946, MHNH 2010.4, from the late Albian of Saint-Jouin-Bruneval, France. Skull roof anatomy. **A**. Photograph. **B**. Explanatory drawing. The bones found in connection are coloured in pale grey and the bone placed manually at their supposed position are coloured in dark grey. **C**. Reconstruction. This reconstruction is designed to provide an overview of the skull roof of MNHN 2010.4; please refer to the description and the other figures for anatomical comparison or character state scoring in phylogenetic analysis. The anterior ramus of the nasal is developed, forming the dorsomedial part of the rostrum over a very long distance. The nasal is also developed posterolaterally, overlapping the postfrontal extensively. The frontal participates to three cranial openings: the internasal foramen anteriorly, the pineal foramen posteromedially, and the supratemporal fenestra posterolaterally.

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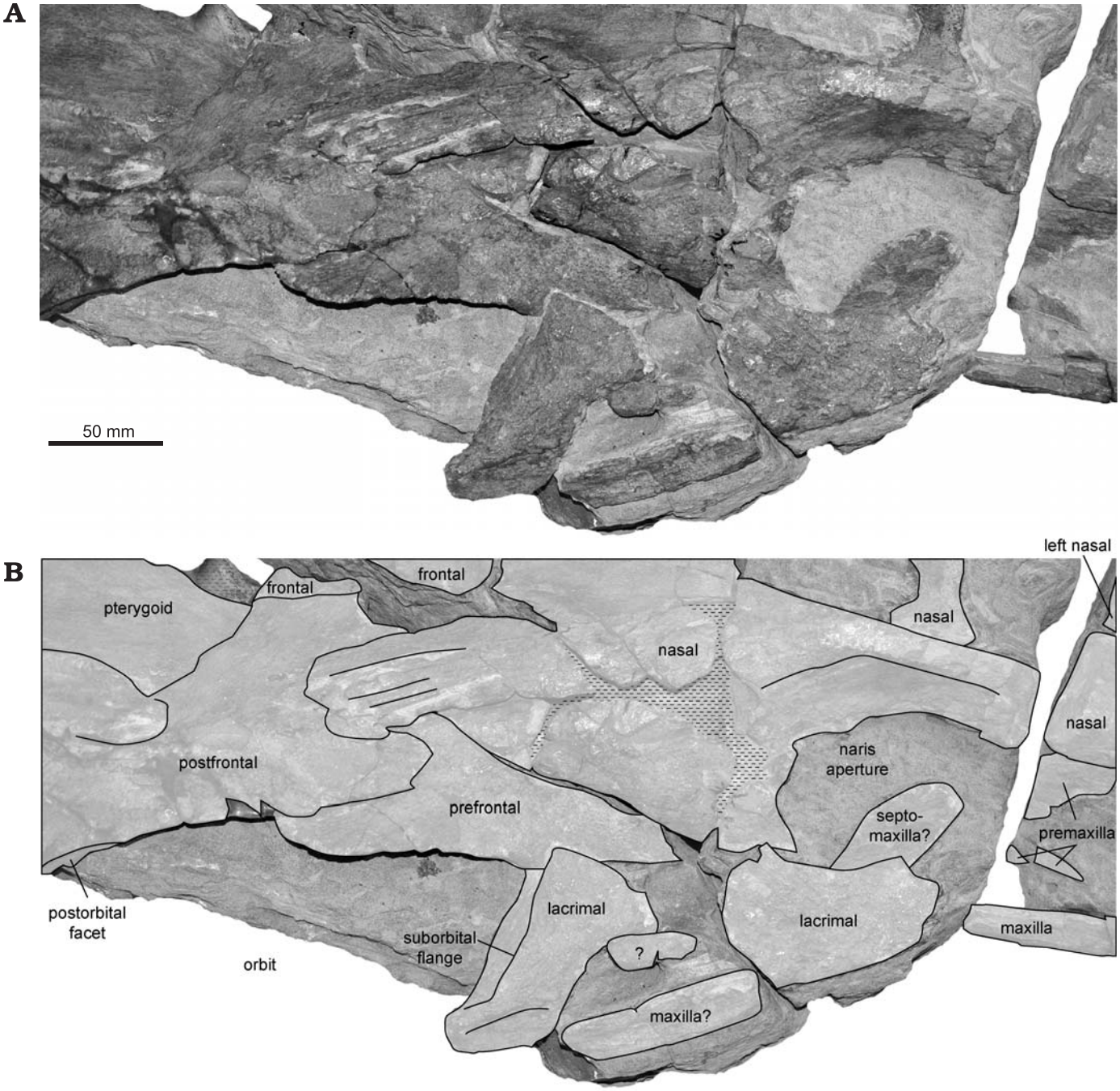


Fig. 3. Platypterygiine ophthalmosaurid *Platypterygius hercynicus* Kuhn, 1946, MHNH 2010.4, from the late Albian of Saint-Jouin-Bruneval, France. Detail of the orbital and narial regions. **A**. Photograph. **B**. Explanatory drawing. The lacrimal is broken in two and participates to the posterior and ventral borders of the bony naris aperture. The nasal is expanded posterolaterally, as in SMSS "SGS". A possible septomaxilla is present inside the naris, but its identification remains tentative. All bones are from the right side of the skull, except when stated otherwise by a (L).

mostly linked to the smaller anterodorsal exposure of the nasal in the latter two taxa. The rest of the maxilla is missing.

Nasal (Figs. 2–4).—In dorsal exposure, the anterior part of the nasal forms an elongate and narrow medial spine, contrasting with the shorter triangular nasal of *P. bannovkensis* and *P. australis* (Arkhangelsky 1998; Kear 2005). The nasal widens mediolaterally posterior to the external naris to form a fan-shaped posterodorsal ramus for articulation with the frontal, the prefrontal and the postfrontal. This ramus has a long posterolateral process that overlaps the postfrontal extensively, as in SMSS "SGS" (Kolb and Sander 2009) and *P. australis* (Kear 2005). The posterior ramus of the nasal also forms an oblique, wide and low bony ridge at midline, which encloses the anterolateral part of excavatio internasalis. In cross section, this bony ridge gives the dorsal surface of the nasal a markedly angled profile. Excavatio internasalis is lacriform and formed by the nasal and the frontal. The dorsal

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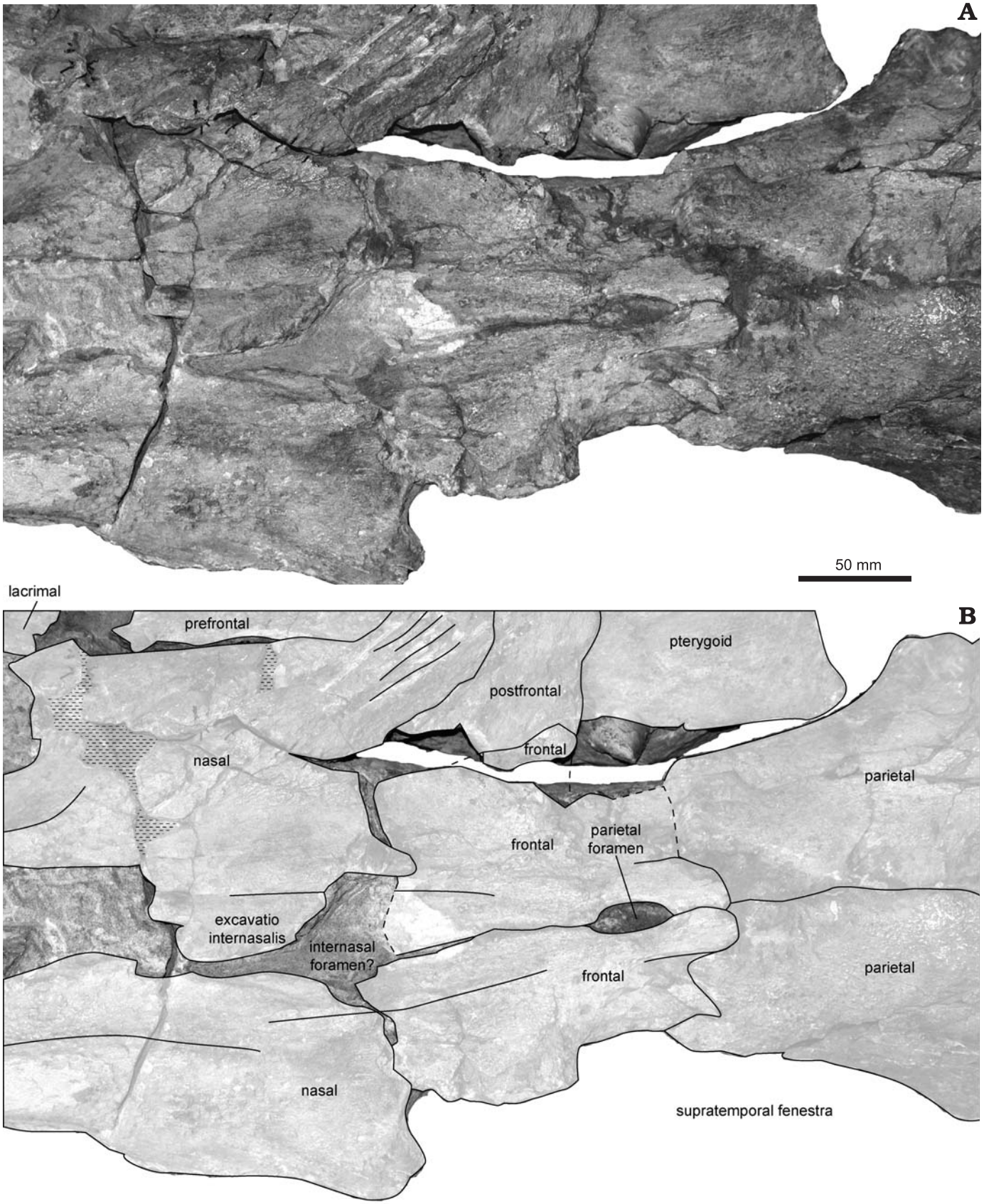


Fig. 4. Platypterygiine ophthalmosaurid *Platypterygius hercynicus* Kuhn, 1946, MHNH 2010.4, from the late Albian of Saint-Jouin-Bruneval, France. Detail of the fronto-parietal region. **A**. Photograph. **B**. Explanatory drawing. The frontal forms a thickened posteromedial process that fully encloses the parietal foramen and separates it from the parietal.

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margin of the naris is rounded, contrasting with the condition in *Aegirosaurus* (Bardet and Fernández 2000), *Ophthalmosaurus* (Kirton 1983), and *P. americanus* (Romer 1968), where a ventral process of the nasal gives the naris a kidney shape.

Prefrontal (Figs. 2, 3).—The prefrontal is markedly expanded posterodorsally. It forms a prominent supraorbital flange with a concave dorsal surface. Anteroventrally, the prefrontal forms a thin lacrimal ramus that buttresses the nasal extensively. The shape of the nasal, forming the entire posterodorsal margin of the naris suggests the absence of processus narialis of the prefrontal, contrasting with the condition described in *Aegirosaurus* (Bardet and Fernández 2000; personal observation).

Lacrimal (Figs. 2, 3).—The lacrimal is broken in two, but remains in partial articulation with both the prefrontal and the nasal. Anterodorsally, the lacrimal forms the posteroventral margin of the external naris and contacts the nasal in a crenate suture. This condition differs from *Athabascasaurus* and *P. australis*, where the lacrimal does not participate in the external narial border (Kear 2005; Druckenmiller and Maxwell 2010). The posterior surface of the lacrimal is concave and forms a narrow suborbital flange. The shape of the anterior edge of the lacrimal suggest the naris was large, unlike in *P. australis* (Kear 2005) or *P. bannovkensis* (Arkhangelsky 1998).

Frontal (Figs. 2, 4).—The frontal of MHNH 2010.4 is extensively exposed dorsally. Anterodorsally and medially, the frontal is depressed and forms the posterior part of the internasal foramen and the posteromedial part of excavatio internasalis. Laterally, the frontal participates in the anteromedial border of the supratemporal fenestra (as in *P. australis*, Kear 2005 and *Aegirosaurus*, Bardet and Fernández 2000); a short trapezoidal temporalis process contacts the anteromedial temporalis ramus of the postfrontal. The temporalis process is formed by a rod-like posterior edge and a thinner anterior lamella. The posterolateral suture with the parietal is damaged, but it is clear that the frontal forms a thick posteromedial bony ridge that fully encloses the raised ovoid parietal (or "pineal") foramen, which is unique in Ophthalmosauridae.

Postfrontal (Figs. 2–4).—Post-mortem deformation of the skull resulted in dorsoventral compression of both postfrontals. A thickened ridge extends obliquely along its ventral side. Anteriorly, this ridge strengthens the supraorbital flange. The sutural facet for the prefrontal is marked by a series of parallel grooves and ridges. An elongate posterior process reaches the posterior margin of the skull roof and forms the entire lateral edge of the supratemporal fenestra, unlike in other Ophthalmosauridae, in which the postfrontal is reduced and buttressed by an elongate anterolateral process of the supratemporal (e.g., Andrews 1910; Bardet and Fernández 2000; Kear 2005). However, the posterior half of the postfrontal is covered dorsally by numerous parallel ridges, which indicate that this elongate posterior process was partially overlapped by other bones, probably the anterior ramus of the supratemporal and the dorsal ramus of the postorbital. As in *Aegirosaurus* and *P. australis* (Bardet and Fernández 2000; Kear 2005), the postfrontal and the parietal do not contact anterodorsally because of the extension of the temporalis process of the frontal.

Orbit (Figs. 2, 3).—The Saint-Jouin ichthyosaur (MHNH 2010.4) possesses large orbits, unlike other specimens currently referred to *Platypterygius*, which have an orbital ratio (diameter of the orbit divided by mandible length) < 0.15 (McGowan 1972). Both the mandible and orbital lengths are unknown in MHNH 2010.4, but the distance from the orbital margin of the lacrimal (when replaced in contact with its anterior part) to the postorbital facet of the postfrontal is 245.5 mm. This distance usually represents about three-fourths of the total orbit length (personal observation); a gross estimate of the orbital diameter would thus give a value of ca. 327 mm. Therefore, a 0.15 orbital ratio implies a skull length of 2182 mm for the Saint-Jouin ichthyosaur, suggesting than one metre is missing, which is completely unrealistic. Although the orbital ratio of MHNH 2010.4 cannot be accurately estimated, it was in any case markedly higher than 0.15.

Parietal (Fig. 2).—As already mentioned, the parietal is excluded from the parietal foramen and from the postfrontal by the frontal. There is no parietal ridge and the medial part of the dorsal surface is perfectly flat, unlike in *P. australis* where a parietal ridge is present (Kear 2005). Posteriorly, the parietal is thickened and forms a short and very robust supratemporal process. A deep, wide, and rugose groove extends along the posterolateral surface of this process and articulates with the supratemporal. In dorsal view, the posterior edge of the parietal forms a marked medial notch that encloses the dorsal part of the supraoccipital (Kear 2005); this notch appears absent in *P. australis* (Kear 2005: fig. 1) but it is present and much deeper in *Athabascasaurus* (Druckenmiller and Maxwell 2010).

Supratemporal (Fig. 2).—The supratemporal lacks its ventral and medial extremities, and therefore appears much smaller than that of SMSS "SGS". Its medial portion is very robust, markedly concavo-convex, and it separates the thick anteromedial ramus that articulates with the parietal from the thinner posterior occipital lamella. Although the ventral part of the supratemporal is poorly preserved, there is evidence of protruding processes medioventrally. Laterally, the supratemporal is constricted at mid-length and expands anterolaterally as a transversely compressed lateral ramus. The posterolateral end of the supratemporal fenestra is consequently acute, as in *Athabascasaurus* (Druckenmiller and Maxwell 2010).

Quadratojugal (Figs. 2, 5).—The quadratojugal is roughly diamond-shaped and tapers anterodorsally. It is not reduced in length as in *O. icenicus* (Kirton 1983). Its posterior margin is robust and saddle-shaped and forms an acute angle with the ventral margin, resembling the morphology encountered in *Aegirosaurus* (Bardet and Fernández 2000) and *Caypulli-*

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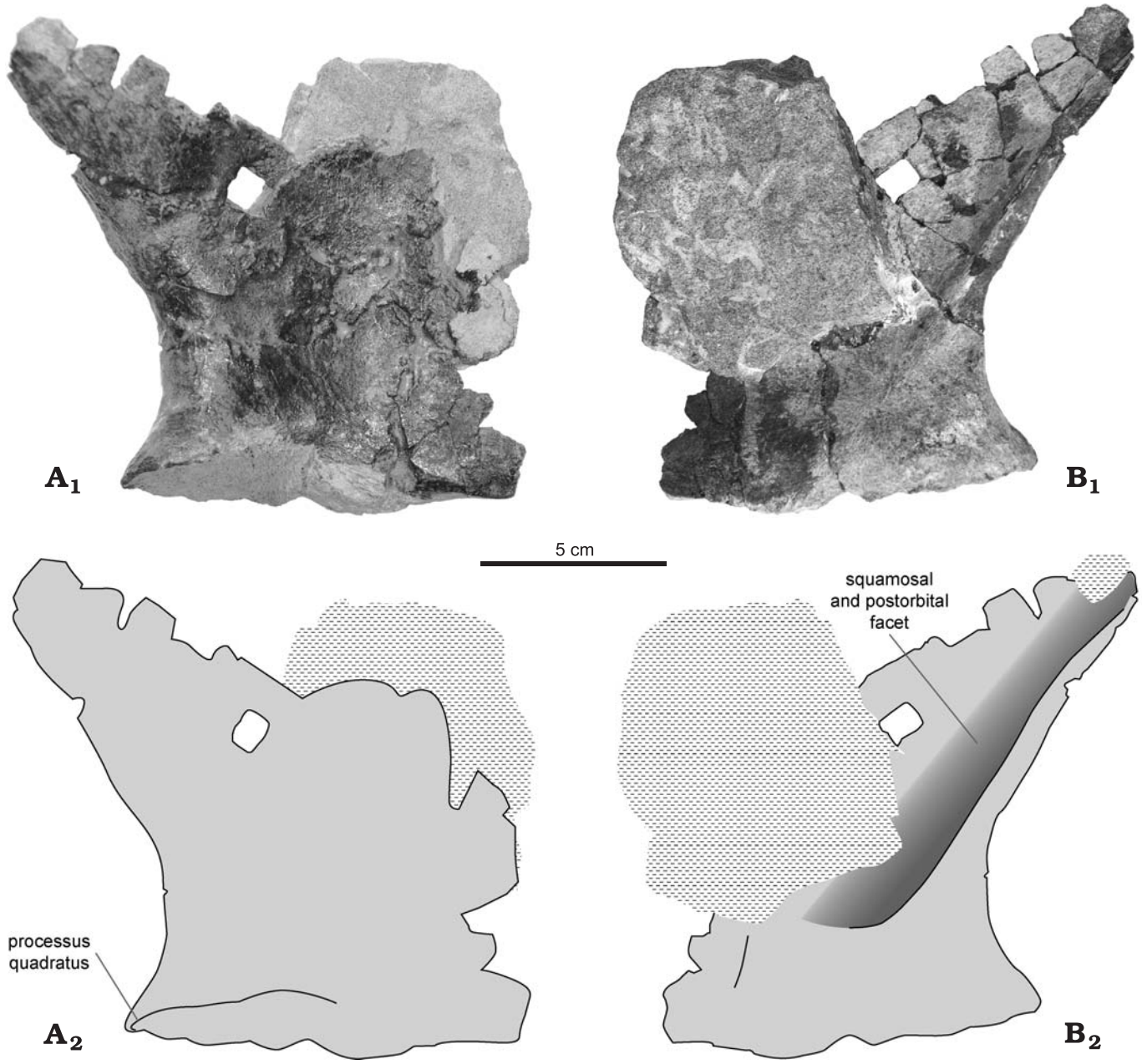


Fig. 5. Platypterygiine ophthalmosaurid *Platypterygius hercynicus* Kuhn, 1946, MHNH 2010.4, from the late Albian of Saint-Jouin-Bruneval, France. Left quadratojugal in medial (**A**) and lateral (**B**) views. Photographs (A_1, B_1), explantatory drawings (A_2, B_2). The quadratojugal possess an extensive lateral facet for the missing postorbital and squamosal, and a large processus quadratus.

saurus (Fernández 2007), but contrasting with the obtuse angle observed in *Ophthalmosaurus* (Kirton 1983), *Athabascasaurus* (Druckenmiller and Maxwell 2010), *P. australis* (Kear 2005) or *P. americanus* (Romer 1968). Ventrally, the quadratojugal is comma-shaped. The anterior part of the ventral side is flat and textured by narrow bony ridges and furrows. The posterior part forms a very large, oval, oblique, and slightly concave processus quadratus that is not separated from the body of the quadratojugal, unlike in *Ophthalmosaurus* (Kirton 1983) or *P. australis* (Kear 2005), in which a distinct process forms the posterior end of processus quadratus. The medial surface is concave and bears a small rugose area in its centre whereas the lateral surface bears an extensive and deep articular facet that continues posterodorsally. This depression is 15.5 mm deep and occupies most of the lateral surface with the exception of the ventral part and the very posterior edge. The position and extent of this facet do not match the morphology of the postorbital in thunnosaurian ichthyosaurs (e.g., Appleby 1961; Romer 1968; Maisch and Matzke 2000a). While the postorbital always overlaps the quadratojugal, the posterior lamella of the postorbital is thin and does not extend to the posterior end of the skull, except in the very large-eyed taxon *Ophthalmosaurus,* whose quadratojugal is extremely reduced in antero-

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posterior length (Kirton 1983). In Ophthalmosauridae that lack a squamosal (*P. americanus* and *P. australis*), the quadratojugal shows extensive lateral exposure (see Romer 1968; Kear 2005). The size and shape of the facet on the lateral surface of the quadratojugal of MHNH 2010.4 suggest the presence of a squamosal in *P. hercynicus*, as in most other Ophthalmosauridae (see for example *Aegirosaurus*, which seems to have a very similar quadratojugal exposure despite its very large orbits [Bardet and Fernández 2000]).

Palatal complex

Numerous fragments of palatal elements are preserved, but it is impossible to identify them accurately. One of them, displaced into the right supratemporal fenestra, is interpreted as the median portion of the right pterygoid (Figs. 2–4). Another similar but isolated element possesses markedly concave lateral and medial margins giving rise to pointed processes. This might suggest the presence of a processus postpalatinalis pterygoidei in *P. hercynicus*, but this interpretation is highly tentative.

Septomaxilla (Figs. 2, 3).—An oval bony plate protruding into the right naris is tentatively interpreted as a septomaxilla, bearing close resemblance with that described by Sollas (1916) and Appleby (1961) in *Ichthyosaurus*. Romer (1968) also mentioned the presence of a septomaxilla in *P. americanus*, but on the dorsal edge of the naris.

Basicranium

Supraoccipital (Fig. 2).—The anterior and ventral surfaces of the supraoccipital are exposed. As in *P. australis* (Kear 2005) and *O. natans* (Appleby 1956), it is U-shaped, and forms a significant part of foramen magnum. Its anterodorsal margin is slightly concave for articulation with the parietal and the exoccipital facets are broad and rectangular.

Stapes (Fig. 2).—The right stapes is incomplete. It is similar to that of *P. platydactylus* and *P. australis* (Broili 1907; Kear 2005) in being stout and robust, with a straight posterior margin and a concave anterior margin, contrasting with the straight anterior edge of the stapes in *O. icenicus* (Kirton 1983). Both the proximal and distal heads are expanded. The ventral surface is poorly preserved, but a bulge-like hyoid process is present, as in *P. platydactylus* (Broili 1907) and *O. icenicus* (Kirton 1983).

Mandible

Surangular.—The distal end of the right surangular is complete. A concave ventral facet for the angular extends along its whole length. The lateral extend of this facet becomes higher and sinusoidal posteriorly. At its posterior end, this facet is bordered dorsally by a series of parallel ridges. The dorsal surface of the surangular forms three successive bulges: a wide and rounded coronoid process, a small but prominent dorsomedial insertion area for M. adductor mandibulae externus (M.a.m.e.), and a thin lamella bordering the medial side of the angular. Laterally to the insertion area for M.a.m.e., a flattened shelf separates the coronoid process from the posterodorsal lamella. Medially, the surangular forms wide and slightly concave facets for angular, prearticular and articular. The prearticular facet and the glenoid fossa are textured by shallow bony ridges and furrows.

Angular.—Anteriorly, the angular is semi-oval in cross section. Two grooves bordered by lamellae extend along its dorsal surface, giving it an inverted "3"-shaped dorsal surface, as in *O. icenicus* (Kirton 1983) and *P. campylodon* (Kiprijanoff 1881). The narrower lateral groove articulates with the ventral edge of the surangular and the medial one forms the ventral border of the Meckelian groove. The shape of the angular dramatically changes posteriorly: the dorsal grooves vanish rapidly, the height of the medial wall decreases whereas the lateral wall becomes a high and internally striated lamella.

Dentition

Although seven teeth are preserved, only one is complete. They are relatively small (66.4 mm) compared to the > 1200 mm skull. The conical crown is relatively small (15.5 mm) and textured by numerous longitudinal ridges. As in some specimens of *P. campylodon* (Kiprijanoff 1881; personal observation), these ridges have a coarse surface, whereas the grooves in between are smooth. The two preserved apices are smoothened and truncated by wear. Basally, a prominent acellular cementum ring separates the crown from the slightly striated root (see Maxwell et al. 2011for a detailed study of the histology of the teeth of *Playptergyius*). The root has a square cross section, as in "*Platypterygius*" spp. (Bardet 1990), *Undorosaurus* (Efimov 1999), *Brachypterygius* (personal observation on CAMSM material), and *Maiaspondylus* (Maxwell and Caldwell 2006b) and tapers basally.

Discussion

Identification.—Characters commonly encountered in specimens referred to as *Platypterygius* (e.g., Bardet 1990; McGowan and Motani 2003; Maxwell et al. 2011; personal observation) can be observed in MNHN 2010.4, including square-shaped dental roots, an acellular cementum ring between the root and the crown, coarsely ridged enamel, an elongate maxilla, a U-shaped supraoccipital and an hyoid process on the stapes, even though this combination of features is not diagnostic for every species of the genus (see below). The thick (in dorso-ventral height) and straight snout of MHNH 2010.4 and the likely presence of a squamosal differs from extra-Eurasian species of *Platypterygius*, *P. americanus*, *P. australis*, and *P. sachicarum*, characterized by slender and slightly down-turned snouts and the absence of a squamosal, their quadratojugal being markedly exposed laterally (Romer 1968; Wade 1984, 1990; Paramo 1997; Kear 2005). Among Eurasian species, MNHN 2010.4 does not correspond to *P. campylodon* because the maxilla is moderately elongated, extending anteriorly beyond the external naris and the nasals are long and wide (Kiprijanoff 1881). The cranial anatomy of the problematic species *P. platydactylus*, the type and only specimen of which was destroyed

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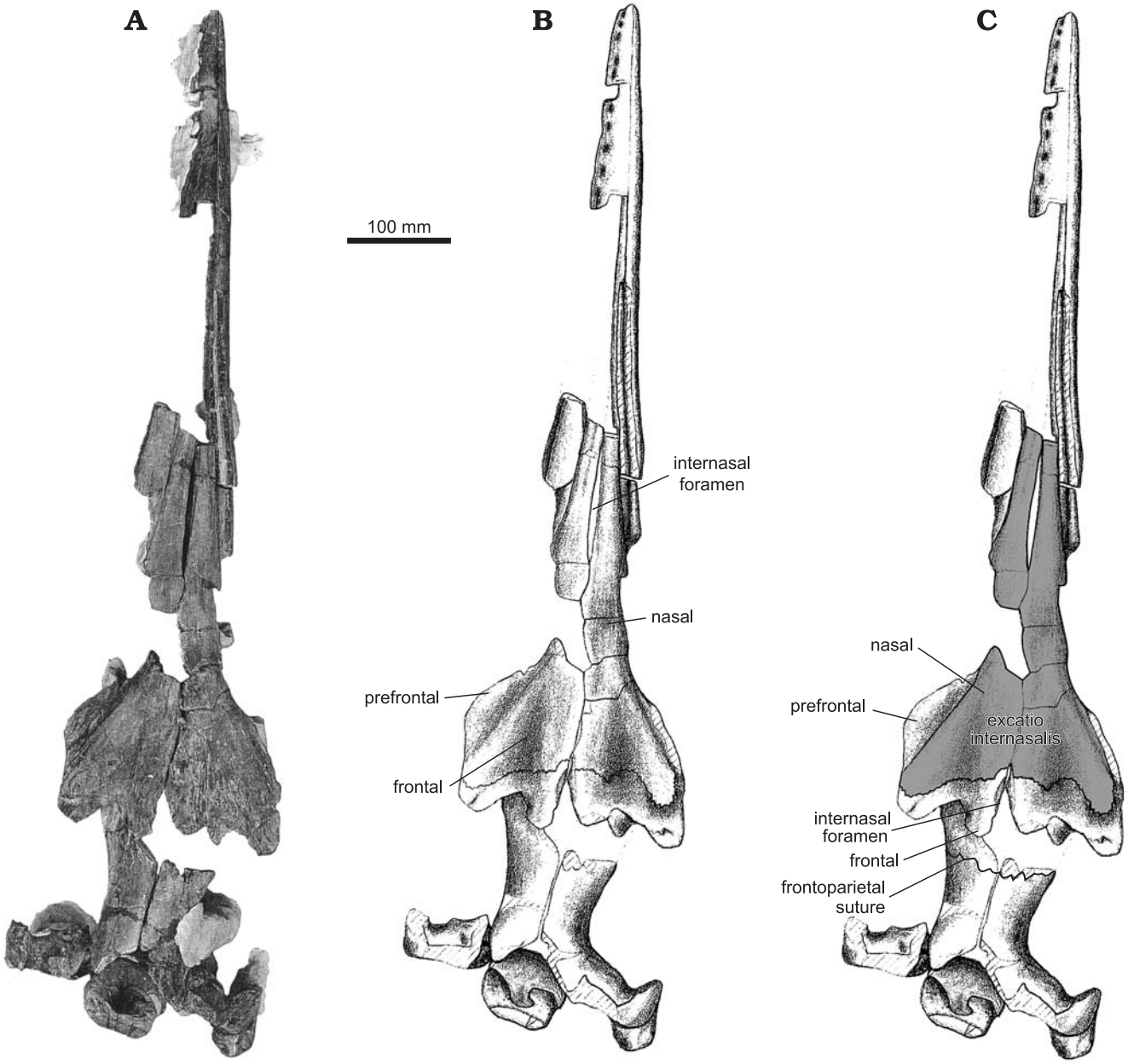


Fig. 6. Platypterygiine ophthalmosaurid *Platypterygius hercynicus* Kuhn, 1946, SMSS "SGS", holotype, from the late Aptian of Salzgitter, Germany. Skull roof of the type-specimen in dorsal view. **A**. Photograph. **B**. Interpretative drawing by Kolb and Sander (2009). **C**. Reinterpretation based on the nasal morphology of MHNH 2010.4 and on a cast of SMSS "SGS". As in MHNH 2010.4 (see Fig. 2), the nasal is markedly elongated anteriorly and wide posteriorly, overlapping the postfrontal extensively. The nasal is coloured grey. The foramen situated at the nasal-frontal suture is interpreted as the internasal foramen, and the holotype lacks the parietal foramen and most of the frontal. Illustrations borrowed from Kolb and Sander (2009) and used with the permission of both authors.

during WWII (McGowan and Motani 2003), is basically unknown. Although its snout appears as robust as in MNHN 2010.4, the only bone that can be directly compared is the stapes. Both MNHN 2010.4 and *P. platydactylus* possess an hyoid process on the stapes (as also does *O. icenicus*, Kirton 1983), but it is much more strongly developed in *P. platydactylus* (Broili 1907) than in MNHN 2010.4. The Saint-Jouin specimen closely resembles the holotype of *P. hercynicus* from the late Aptian of the Harzvorland area (Lower Saxony, Germany) (Kuhn 1946; Kolb and Sander 2009), in sharing the following unique combination of characters: nasal with long and narrow anterior process, forming the dorsomedial surface of more than half of the rostrum, nasal with developed posterolateral process overlapping the postfrontal extensively (after reassessment of the type specimen, see below), U-shaped supraoccipital, notched posterior edge of the parietals, teeth with a well-defined enamel base and a large acellular cementum ring between the crown and the root.

Skull roof of Platypterygius hercynicus.—The study of MNHN 2010.4 and the examination of a cast of SMSS "SGS" housed at the NMB suggest that Kolb and Sander (2009) mis-

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interpreted the internasal and parietal foramina in the holotype of *P. hercynicus*. In all post-Liassic ichthyosaurs (Maisch and Matzke 2000a), the internasal foramen, when present, is set in a dorsomedial depression, named excavatio internasalis, between the external naris and the orbit. This depressed area is bordered by oblique ridges along the nasal and sometimes along the frontal, when this bone is widely exposed dorsally (e.g., Kear 2005). On the contrary, Kolb and Sander (2009) interpreted a post-mortem aperture situated in the anterior half of the nasal as the internasal foramen, and the next posterior foramen, situated at the level of the anterior edge of the orbit as the parietal foramen. They interpreted the very wide bone anterior to the latter foramen as the frontal. According to this interpretation the frontal would be excluded from their "pineal" foramen, which would be surrounded by the postfrontal instead, a unique condition in thunnosaurian ichthyosaurs. Furthermore, this interpretation suggests an extensive lateral contact of the prefrontal and the frontal, which is also unlikely. A very small dorsolateral prefrontal-frontal contact has been recognized recently in *Ichthyosaurus* and *Stenopterygius* "*longifrons*" (= *S. triscissus* according to Maisch 2008) (Motani 2005), but via a very narrow mediolateral passage between the nasal and the postfrontal. Because the internasal and parietal foramina can be very close in some taxa (Fischer et al. 2011b), the "pineal" (parietal) foramen of Kolb and Sander (2009) is actually the internasal foramen and the parietal foramen is missing in SMSS "SGS" (Fig. 6). The "frontal" of Kolb and Sander (2009) is actually the posterior end of the nasal, which is closely similar to that of MHNH 2010.4. Furthermore, the fronto-parietal suture is actually present on the holotype of *P. hercynicus* and similar in shape and position to that of MHNH 2010.4 (Fig. 6), confirming the frontal participation to the supratemporal fenestra in *P. hercynicus*. Following this interpretation, the skull roof of *P. hercynicus* is consistent with the condition observed in other thunnosaurian ichthyosaurs (e.g., Appleby 1961; Maisch and Matzke 2000a; McGowan and Motani 2003), with a long lateral contact between the prefrontal and nasal and a postfrontal excluded from the parietal foramen. Some of the characters included in the differential diagnosis of *P. hercynicus* by Kolb and Sander (2009) are therefore based on an incorrect interpretation of the skull roof and, according to the new interpretation proposed here, the Saint-Jouin ichthyosaur can be confidently referred to *P. hercynicus*. The presence of rare features in MHNH 2010.4, such as a large processus temporalis of the frontal and the exclusion of the parietal from the parietal foramen, indicates a large morphological disparity in the forms currently referred to *Platypterygius*.

Maisch and Matzke (2000a) regarded the absence of a squamosal as an autapomorphic feature for *Platypterygius* among Ophthalmosauridae, but Maisch and colleagues (Maisch and Matzke 2000b; Maisch et al. 2008) and Motani (1999) showed that the loss of the squamosal may be intraspecifically variable in *Ichthyosaurus communis*, the only other ichthyosaur in which this ossification is supposedly missing. Furthermore, the loss of the squamosal was only observed in *P. australis* (Kear 2005) and *P. americanus* (Romer 1968), and was subsequently applied by default to the whole genus, because of the lack of complete skulls in the other species tentatively referred to as *Platypterygius*. The likely presence of a squamosal in *P. hercynicus* has important taxonomic implications that will be discussed below.

The validity of the genus Platypterygius.—McGowan (1972), considered *Platypterygius* as the only valid genus of Cretaceous ichthyosaurs, with a worldwide distribution and an impressive time span (Hauterivian–Cenomanian, 40.3 Myr). The Cretaceous record of ichthyosaurs was subsequently regarded as sparse and not very diversified (e.g., McGowan 1972; Bardet 1989, 1994, 1995; Sander 2000). Recently, several new ophthalmosaurid genera have been described (e.g., Maxwell and Caldwell 2006b; Druckenmiller and Maxwell 2010), and some share characters that were previously considered as autapomorphic for *Platypterygius*, showing that the radiation of Ophthalmosauridae was far more complex than previously supposed, involving many homoplasies (Maxwell 2010; Fischer et al. 2011b, 2012). Moreover, detailed descriptions of the anatomy of Australian and North American species of *Platypterygius* (*P. australis* and *P. americanus*; Kear 2005; Maxwell and Kear 2010; Zammit et al. 2010) have unveiled a large morphological disparity among the members of this genus. *Platypterygius* appears to be a catch-all genus that has served as a repository for all Cretaceous material, worldwide, as already suggested by Maxwell and Caldwell (2006a).

As a first step towards a thorough revision of the genus, I listed all the characters that have been proposed to be diagnostic for *Platypterygius* and its junior synonym *Myopterygius* in the literature since the erection of these genera by Huene (1922) (see Supplementary Online Material at http://app.pan.pl/SOM/app57-Fischer_SOM.pdf). All 74 characters listed are shared by other genera or fail to encompass all species of *Platypterygius*, or both. Consequently, the genus *Platypterygius*, as defined in previous studies, lacks autapomorphies. It is even difficult to propose an accurate differential diagnosis for this genus because the radiation of Ophthalmosauridae is characterized by many homoplasies (Maxwell 2010; Fischer et al. 2011b), and because *Platypterygius* displays wide interspecific variation. A large-scale phylogenetic analysis at the species level is currently being developed in order to clarify the relationships of the species currently referred to as *Platypterygius*.

Geographic and stratigraphic range.—Salzgitter (Germany), Saint-Jouin-Bruneval (France), Upper Aptian–upper Albian, Lower Cretaceous.

Conclusions

The Saint-Jouin ichthyosaur (MHNH 2010.4) is one of the first nearly complete European *Platypterygius* skulls described so far. This specimen expands the stratigraphic range of *Platypterygius hercynicus* up to the late Albian and clari-

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fies its skull roof anatomy. Features that were previously regarded as rare, such as the presence of a large processus temporalis on the frontal, appear to be actually widespread among Ophthalmosauridae (*Aegirosaurus*; Bardet and Fernández 2000; *P. australis*; Kear 2005; *P. hercynicus*; this work; a new ophthalmosaurid from Russia; Fischer et al. 2011b). A review of characters that have been proposed to be diagnostic for *Platypterygius* since Huene (1922) shows that none of them is autapomorphic, and that this genus is in a serious need of revision.

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