Re-appearance of hypercarnivore ichthyosaurs in the Cretaceous with differentiated dentition: revision of ‘Platypterygius’ sachicarum (Reptilia: Ichthyosauria, Ophthalmosauridae) from Colombia

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Early Cretaceous ichthyosaur diversity has markedly increased in recent years with the discovery of new taxa in the field and in museum collections. This has led to new characters, and a better understanding of taxonomically informative anatomy. Here, we re-describe the holotype of the ophthalmosaurid \textit{Platypterygius sachicarum} from the Barremian–Aptian of Colombia and place these data in a phylogenetic context. The validity of the species is supported by several new characters of the narial region, mandible and dentition. The dentition is unique among ichthyosaurs in that it presents several discrete tooth morphologies that range from piercing to cutting to crushing. In combination, these cranial specializations imply a large vertebrate diet and make this taxon the first Cretaceous hypercarnivorous ichthyosaur. Differences from the type species of \textit{Platypterygius}, \textit{P. platydactylus}, include a suite of characters associated with differing feeding ecologies and the complex external nares. The large number of character differences and revised phylogenetic relationships are used to remove the Colombian taxon from \textit{Platypterygius} and recognize it as a new genus, \textit{Kyhytysuka} sachicarum comb. nov. A revised set of taxonomic definitions are proposed for Ophthalmosauria to maintain stability at this important node. \textit{Kyhytysuka sachicarum} opens new questions regarding the diversity and paleobiogeography of Early Cretaceous ichthyosaurs from northern Gondwana and highlights the importance of individually assessing each ‘\textit{Platypterygius}’ species and, potentially, specimen to better understand the diversity of this broadly distributed taxon.

.http://zoobank.org/urn:lsid:zoobank.org:pub:E3FD55AF-2AD1-46CA-A49C-1FB4B102AB2C

\textbf{Keywords}: \textit{Platypterygius sachicarum}; Ophthalmosauridae; Early Cretaceous; South America; Colombia; Paja Formation

\section*{Introduction}

Barremian–Aptian outcrops of the Paja Formation of Villa de Leyva, Colombia, have yielded a stunning fossil record of a distinctive vertebrate fauna that fills a key gap in the fossil record of marine reptiles, spanning the Tithonian–Berriasian lagerstätten of Europe and Argentina, and the Albian of Australia and the North American Western Interior Seaway. Among the marine reptiles, ichthyosaurs are one of the most common groups hosted in multiple local collections, in contrast to other marine tetrapods such as thalattosuchians (Cortés et al. 2019), but also one of many groups that are in need of fundamental taxonomic descriptions and phylogenetic analysis.

The first report of an ichthyosaur from Colombia was a partial lower jaw with several teeth in situ, found close by the Quebrada Luni, Municipio de Piedras, Departamento del Tolima. It was tentatively assigned to Mixosauridae or Shastasauridae although its stratigraphical age, inferred based on Coniacian-aged mollusc samples associated with the specimen, made its assignment to either of these Triassic taxa dubious (Camacho-Hernández & De Porta 1963). The specimen was later considered as non-ichthyosaurian by McGowan (1972), and identified as a mosasaur by Bardet (1992). The specimen was reported to be hosted in the Museo Servicio Geológico Nacional, the current Colombian Geological Survey in Bogotá (SGC), but unfortunately, visits to the collection have confirmed that the specimen is lost. The first definitive ichthyosaur species from Colombia was \textit{Platypterygius sachicarum} Páramo-Fonseca, 1997, a spectacular skull preserved in three dimensions from Loma Pedro Luis, Villa de Leyva (Boyacá), found by a local, Jorge Cárdenas, in the 1970s and later described based mostly on the rostrum.
narial opening, jugal, postorbital and teeth (Páramo-Fonseca 1997). *Platypterygius sachicarum* was erected based on the following cranial characters (here translated from Spanish): “skull relatively small, robust rostrum, orbit markedly oval, no prenarial opening or ridge over the dorsal edge of the naris; jugal remarkably extended backwards [posteriorly], jugal widely extended towards the squamosal [supratemporal], slightly pronounced posterodorsal curvature of the jaw; small teeth, of thin roots, with no remarkable curvature of the lower ones, tightly spaced, showing a high density in their distribution” (Páramo-Fonseca 1997, p. 2). Most of these characters are distributed across thunnosaurian ichthyosaurs and not only within *Platypterygius*.

*Platypterygius sachicarum* itself was ignored for many years. The Ichthyosaurus handbook (McGowan & Motani 2003) did not consider *P. sachicarum* and for the first decade following publication the species was generally ignored and considered synonymous with *P. hautili* from the early Barremian of Argentina (Fernández & Aguirre-Urreta 2005). Although *P. sachicarum* has been included in some recent phylogenetic analyses (e.g. Moon 2019), the description of the holotype is inadequate and requires a reassessment in light of the proliferation of new taxa and diagnostic characters during the past 15 years.

As ichthyosaur systematics progressed over the past two decades, *P. sachicarum* became a problematic and uncertain taxon (Fischer 2016; Moon 2019). The discovery of a more complete specimen from the same formation allowed its diagnosis to be revised, integrating modern taxonomic criteria (Maxwell et al. 2019). A second specimen of *P. sachicarum* includes postcranial material (Maxwell et al. 2019), and partial left and right forefins of *Platypterygius* sp. have been published as well (Cortés & Páramo-Fonseca 2018). *Muiscasaurus catheti*, a second ophthalmosaurid from the Paja Formation, was diagnosed by its distinctive narial opening configuration and rostrum, postorbital region and tooth morphologies (Maxwell et al. 2016). Research on further material of the same formation is currently ongoing. Here, we provide a detailed re-description of the holotype of *P. sachicarum*, establish its validity as a unique taxon, evaluate its phylogenetic affinities against other ophthalmosaurids and address morphofunctional insights from the dental battery.

**Institutional abbreviations**

CIP, Centro de Investigaciones Paleontológicas, Villa de Leyva, Boyacá, Colombia; DON, Museo Geológico Nacional José Royo y Gómez, Colombian Geological Survey, Bogotá, Colombia; MHH, Museum Hauff Holzmaiden, Holzmaiden, Germany.

**Systematic palaeontology**

Order *Ichthyosauria* de Blainville, 1835
Infraorder *Ophthalmosauria* Motani, 1999

*Brachypterygiidae* fam. nov.

*Kyhytysuka* gen. nov.

(Figs 1–13)

1997 *Platypterygius sachicarum* Páramo-Fonseca: 4, fig. 2.

**Diagnosis.** As for the type and only species *Kyhytysuka sachicarum* comb. nov.

**Derivation of name.** The genus name is derived from the ancient language of the Muiscas people and culture, an ancestral indigenous group that inhabited the Altiplano Cundiboyacense in Colombia since the sixth century. The name is a combination of ‘*kyhyty*’ that is the verb ‘to cut with something sharp’ and ‘*suka*’ that is the particle of ‘the one that’. The combination *kyhytysuka* thus means ‘the one that cuts with something sharp’ to honour the ancient Muiscas culture and reference the unique dentition of this taxon. The phonetic transcription of the name is /ˈkʰihiˈsuka/ (see Saravia 2015, p. 15).

*Kyhytysuka sachicarum* comb. nov.

**Holotype.** DON-19671, a partial skull hosted in the palaeontological collection of the Museo Geológico Nacional José Royo y Gómez, Colombian Geological Survey (SGC).

**Emended diagnosis.** Mid-sized brachypterygiid with high degree of heterodonty; robust dentition with coarsely ridged enamel (13–14 ridges per 5 mm near base of crown); tooth roots quadrangular in cross-section; diagnosed by the following autapomorphies: surangular makes a greater total contribution than the angular to the lateral surface of the lower jaw; broad, squared descending process of nasal along posterior border of external naris; straight and posteriorly directed retroarticular process, and the following unique combination of characters: surangular foramen at midpoint of orbit (unlike *Brachypterygius*, *Capullisaurus* and *P. australis*); surangular with slightly greater contribution than the angular to the lateral surface of the retroarticular process (unlike in *Ophthalmosaurus*); posterior premaxillary fossa broad with shallow edge (as in *Brachypterygius, Capullisaurus* and *P. australis*); complete nasomaxillary pillar, subdividing posterior external naris (as in *Athabascasaurus, Arthropterygius thalassosotus, Simbirskiasaurus* and *P. australis*, but unlike *Brachypterygius* and *Capullisaurus*); nasal contribution
to nasomaxillary pillar stout, anteroposteriorly broad (as in *A. thalassonotus* and *P. australis*, but unlike most ophthalmosauromorphs); maxillary contribution to nasomaxillary pillar present to entire height of external naris (as in *Ahabascsaurus* but unlike *Simbirsksiasaurus*, *Arthropterygius* and *P. australis*); maxilla broadly expanding anterodorsally (as in *A. australis* but differing from *Ahabascsaurus*); broad lacrimal body width (unlike *Sveltonecetes*, *Aegirosaurus*, *Muiscasaurus* and *P. australis*); processus narialis of the prefrontal absent (unlike *Sveltonecetes* and *Aegirosaurus*); posterior margin of the jugal not excluded from the quadratojugal by the postorbital (unlike *Thalassodraco* and *Janusaurus*); anteroposteriorly wide postorbital portion of the jugal (unlike *Sveltonecetes* and *Aegirosaurus*); extensive lateral exposure of quadratojugal (unlike *P. hercynicus*, *Cryopterygius*, *Mollesaurus*, *Leninia*, *O. icenicus* and *B. natans*); basioccipital condyle much wider than high (unlike *P. platydactylus*); short and robust paroccipital process of the opisthotic (unlike *Acamptonectes*, *O. icenicus*, *Gengasaurus* and *B. natans*); relatively straight ventral margin of mandible (unlike *Nannopterygius* and *P. platydactylus*); low paracoronoideus process of surangular (unlike *Brachypterygius*); straight, posteriorly directed retroarticular process (unlike *P. platydactylus*, *Nannopterygius* and *Thalassodraco*); referred specimen preserving postcranium known by the following combination of characters: relatively short humerus bearing two distal facets for articulation with the radius and ulna; which are sub-equal to each other in size and sub-equal to the intermedium, radiale and ulnare in proximodistal length; intermedium pentagonal in outline supporting digit III; rectangular and dorsoventrally thicker than proximodistally long phalanges. Postcranial characters modified from Maxwell et al. (2019).

**Derivation of name.** Kyhytysuka sachicarum in the Muisca language means ‘the one that cuts with something sharp from Sáchica’. ‘Sáchica’ was used originally to name the specific epithet ‘sachicarum’, but it does not refer to a ‘Sáchicas’ indigenous community as originally conceived (Páramo-Fonseca 1997). Sáchica refers to a town nearby Villa de Leyva, but the holotype was found in Villa de Leyva and not in Sáchica.

**Referred specimen.** CIP-GA-01042014, a partial skull and associated postcranium hosted in the palaeontological collection of the Centro de Investigaciones Paleontológicas, Villa de Leyva, Boyacá, Colombia.

**Occurrence.** Loma Pedro Luis, 1.5 km northwest of Villa de Leyva, Barremian–Aptian Arcillolitas Abigarradas member (Páramo-Fonseca 1997, 2015). The type specimen was assigned an early Aptian age by Hampe (2005) although no stratigraphical constraint was provided; the referred specimen CIP-GA-01042014 comes from El Roble locality, Loma La Cabrera, ‘Finca Los Morros’ (5°39.923′N, 73°32.305′W), Villa de Leyva, Boyacá, Colombia, and it is uppermost Barremian in age (~125 Ma) (Maxwell et al. 2019) (Fig. 1).

### Description

#### Skull roof

**Skull.** The skull of the holotype DON-19671 is three-dimensionally preserved (Figs 2–4). The left lateral side is well preserved whereas the right side is more fragmentary and has been partially reconstructed. The skull is 940 mm in length, measured from the anterior tip of the premaxilla to the posterior end of the lower jaw. The antorbital length is 635 mm (Fig. 2). Measurements of the skull of DON-19671 are provided in Table 1.

**Premaxilla.** The premaxilla is a robust bone relative to other ophthalmosauromorphs (minimum length is 490 mm and depth at midpoint is 50 mm). The left premaxilla is poorly preserved, with the anterior ramus missing anteriorly, the external surface missing posteriorly and the dorsal surface partially preserved. The right premaxilla is better preserved than the left; however, it also lacks the anterior half and dorsal surface. The description is based mostly on the right premaxilla. It is a slightly convex bone that constitutes the bulk of the rostrum, and bears a shallow alveolar groove extending towards its ventrolateral margin at the level of the premaxilla–maxilla contact. The groove is deepest at the premaxilla–maxilla contact and becomes shallower and wider as it continues anteriorly. The fossa premaxillaris (sensu Maisch 1998) is preserved on the right side, being shallow posteriorly and deeper and slightly narrower anteriorly (Supplemental material Fig. S1). Although the tip of the rostrum is not well preserved, the available external surface suggests the fossa premaxillaris extended anteriorly to the end. Due to poor preservation, the posterior contact of the premaxilla with the maxilla is not well defined, hence neither the processus supranarialis nor processus subnarialis can be assessed. However, posteroventrally, the premaxilla is overlapped by the nasal (preserved over the right side of the rostrum) (Fig. 3).

In transverse view across the anterior break, the alveolar borders of the premaxilla are robust and the lingual borders contact their counterpart. The labial and lingual borders of the premaxillary alveolar groove are of sub-equal width anteriorly, and the lingual border extends further ventrally (Fig. 4C). In cross-section, the labial border is falciform in shape, being roughly 36 mm
in height, with 10 mm of thickness ventrally and 5 mm dorsally. Compared to the labial border, the lingual border is remarkably convex, being 19 mm in height (Fig. 4C). The premaxilla bears alternating functionally mature and erupting replacement teeth along its length.

Maxilla. Only the anterior and posterior tips of the maxillae are missing (Fig. 2). The maxilla is overlapped anterodorsally by the premaxilla and posteriorly by the lacrimal in lateral view, and contacts the jugal posteriorly. As in most post-Triassic ichthyosaurs (Maisch & Matzke [2000] excepting Hauffiopteryx altera Maxwell & Cortés, 2020), a maxilla–prefrontal contact is absent. The deepest point of the maxilla is 50 mm in height. The maxilla is an elongate element (320 mm length) with a complex triangular shape in lateral view with delicate striations over its dorsolateral surface oriented anteroventrally. It extends over the postero lateral surface of the rostrum as in other ophthalmosaurids. A smooth lateral groove extends along the posterior two-thirds of the lower lateral surface of the maxilla. This groove is 10 mm wide anteriorly and 7 mm wide posteriorly. The alveolar groove of the maxilla bears at least 15 variably sized teeth that extend from the anterior end of the maxilla to a point ventral to the ascending process of the lacrimal. A transverse break shows the maxilla is ‘h’-shaped in cross-section with the large alveolar groove forming the ventral concavity. The lingual and labial boundaries of the alveolar groove are sub-equal in thickness and a thin palatal ramus is present anteriorly but absent posteriorly. The lateral surface is angled approximately 30° dorsomedially (Fig. 4).

The anterior and posterior rami of the maxilla are tapered and approximately 10 cm tall in lateral view. The anterodorsal margin of the maxilla is smooth laterally and forms a large narial fossa that bounds the anteroventral margins of the external narial openings. A complex ascending process is present on the maxilla that supports a naso-maxillary pillar that divides the external nares in two. The anterior ‘narial opening’ (the anterior foramen in the maxilla) is located 35 mm anterior to the external narial opening. The anterior narial opening is fusiform, being 25 mm long and 5 mm high. The ends of the anterior opening are pinched with anterior end tapering anterodorsally from a relatively rounded posterior margin. Although the extreme anterodorsal margin is poorly preserved, it appears that the foramen might have been bounded by the ventral edge of the nasals. The posterior narial opening is subcircular in shape and bounded by the maxilla, nasal and lacrimal. The maxilla bounds the anterior and ventral margins of the posterior narial opening whereas the nasal and lacrimal bound the dorsal and limited posteroventral margins, respectively.

The maxilla extends posteriorly beyond the lacrimal to form a small process ventral to the orbit. At this point, the maxilla expands as a lateral flange that is continuous with the ventrolateral edge of the lacrimal. The lateral surface of the maxillary posterior ramus extends the extensive narial fossa to the anteroventral edge of the orbit. The alveolar margin of the maxilla in this region is sharp, forming a thin separation between the jugal articulation and tooth row. A small remnant of the jugal is lodged within this facet above the second to fourth last preserved maxillary teeth. The maxillary alveolar walls are thick, similar to the alveolar width in the premaxilla (as in the dentary).

Lacrimal. The lacrimal of DON-19671 is a triradiate bone, and is longer than high in lateral view (minimally 74 mm × 40 mm) with a broad base contacting the maxilla. The lacrimal has three projections: an ascending process, a suborbital process and a subnarial process. The first two are crescent-shaped, and form the anteroventral rim of the orbit. The subnarial process, although broken anteriorly, forms a limited posteroventral margin of the posterior external narial opening (Fig. 2C). Although broken, the anterior extent of this process may have reached a level near the anterior margin of the posterior external nares as a pointed process to continue to a raised protuberance on the maxilla (Fig. 2C, D). The lacrimal has a small circumorbital region that is raised, smooth and rounded, creating a confluent surface between the orbital margin and the narial fossa. The posterior-most tip of the lacrimal overlaps the maxilla but is broken so any contact with the jugal is unknown. The lacrimal contacts the prefrontal posteroventrally, and the nasal anterodorsally. The lacrimal forms an interdigitating suture with the nasal.

Nasal. The left lateral nasal is incomplete anteriorly whereas the right nasal, which is used mainly for the description, is relatively complete. The nasal makes up approximately two-thirds of the dorsal length of the rostrum. The nasal is about ~50 cm in length up to the preserved anterior tip along the rostrum and about ~4 cm wide (right nasal). The presence of an internasal foramen (sensu Maisch & Matzke 2000) cannot be assessed. The lateral surface of the nasal is nearly vertical and the dorsal surface is slightly convex anteriorly and more squared in cross-section posteriorly. The nasal forms the arched dorsal margin of the external nares, forming a well-defined dorsal margin of the narial fossa. The narial fossa is sub-triangular in shape, unornamented, and broadly surrounds the external nares, which are depressed from the anterior edge of the anterior narial opening to the maxillary tooth row ventrally, and circumorbital area posteriorly (Supplemental material...
Fig. S2). An anterior descending process of the nasal forms the concave anterior margin of the external narial opening (narial process of the nasal). A lateral ‘wing’ of the nasal over the dorsal border of the naris is absent and thus presents a broad narial fossa. The nasal overlaps the lacrimal posteroventrally, maxilla anteroventrally, and frontal posterodorsally and is overlapped by the premaxilla anteriorly. The nasal contacts the prefrontal laterally and dorsally through an interdigitating curved suture. The nasal is not dorsoventrally deflected at the antorbital region and creates a robust dorsal rostrum extending to the skull roof. Posterodorsally, the nasal expands laterally to form an acute triangle with its counterpart. Its dorsal surface is remarkably flat.

**Jugal.** Although the anterior ramus of the jugal is poorly preserved, it appears to be dorsoventrally compressed. The presence of ridges on the posterior end of the maxilla suggests a broad, overlapping contact with the jugal was present. The jugal body is broad. The ascending process of the jugal is not fully exposed externally, but its contribution to the postorbital bar is approximately 40 mm in height. The dorsal surface of the jugal is wider posteriorly and becomes flattened towards its mid-point. The posterior jugal is overlapped by the postorbital and overlaps the anterior quadratojugal. The postorbital portion of the jugal is anteroposteriorly long.

**Prefrontal.** The prefrontal is a curved plate-like element, slightly projected dorsally and expanded laterally. The prefrontal forms the anterodorsal margin of the orbit. The anterior portion of the prefrontal is transversely broad and contacts the nasal anteriorly and lacrimal ventrally, but does not participate in the external nares (processus narialis of the prefrontal is absent). Posteriorly and ventrally, the prefrontal in lateral view forms a scarf suture with the lacrimal, with a thin descending process inside the anterior circumorbital area. The dorsal edge of the prefrontal contacts the frontal; it is uncertain whether this contact would have been exposed in external view. The posterior and dorsal edges of the prefrontal are not preserved.

**Frontal.** The right frontal is best preserved, although it is displaced from its anatomical position. It is narrow and saddle-shaped posteriorly over the orbits, becomes wider at the prefrontal contact, and narrows to a flattened point anteriorly that would have formed a broad wedge between the posteriorly diverging nasals. The robust contact between the frontal and the prefrontal is poorly preserved and it is unclear if this contact was overlapped externally by surrounding elements. The exposed dorsal surface of the frontal is smooth, but anteriorly bears a rugose texture and striae of varied size, which represent the suture with the overlying nasal.

The frontal bears two bony and equivalent sized projections roughly at the midpoint of its medial edge (arrow in Fig. 4F), representing the anterior and posterior edges of the parietal foramen. The parietal foramen is largely surrounded by the frontal in dorsal view; however, striations on the posterior-most frontal indicate that some parietal participation was present posteriorly (Fig. 4F). A broad, sagittal, dorsally facing fossa is present on the frontal anterior to the parietal foramen and extends to the nasal contact. A concave, finished surface is present on the posterodorsal margin, indicating a limited extension of the supratemporal fossa. The posterolateral edge of the frontal articulates with the parietal via an interdigitating suture (Fig. 4).

**Postfrontal.** The left postfrontal is poorly preserved and highly fragmented with no discernible diagnostic features. The right postfrontal is not preserved.

**Parietal.** The parietal is a broad, dorsoventrally thick and weakly dorsally convex element that forms a large part of the posterior skull roof. Although the left parietal seems to be in anatomical position, it is not as well preserved as the right one, which is used for the description. The anterior portion of the parietal is saddle-shaped with a remarkably rugose dorsal texturing near the posteromedial frontal contact. The frontal–parietal contact arches from a nearly transverse orientation at the midline to an anterior orientation anterolaterally. As the suture sweeps anteriorly, a long anterolateral prong of the parietal laterally contacts over half the length of the frontal. Laterally, the parietal is concave and forms the lateral braincase wall. A prong-like descending process extends from the anterolateral portion on the braincase wall. A sagittal eminence of the parietal is seemingly absent, although this feature can be difficult to evaluate in disarticulated material. The supratemporal process of the parietal is present, but the posterior half of the parietal is missing entirely.

**Supratemporal.** The supratemporal is a triradiate element forming the posterolateral corner of the skull roof. The dorsolateral surface of the supratemporal is highly textured. The anterior ramus is overlapped laterally by the posterodorsal edge of the postorbital. Posterolaterally, the supratemporal is oriented obliquely and bears a facet for articulation with a ventral element, probably the dorsal surface of the quadrate. The ventral ramus of the supratemporal is thick and wide, almost overlaps the dorsal flange of the pterygoid laterally, and seems to have a facet for articulation with this flange (Fig. 5A–D).
Figure 1. Locality information for *Kyhytysuka sachicarum* comb. nov. A, location of Colombia within South America; B, location of Villa de Leyva within the Departamento de Boyacá; C, satellite imagery map of Villa de Leyva and nearby areas; D, geological map of Villa de Leyva region showing the localities of the holotype DON-19761 and CIP-GA-01042014; E, local stratigraphical information, highlighting Paja Formation’s members: Arcillolitas Abigarradas (Aa), Arcillolitas con nódulos huecos (An), and Lutitas negras inferiores (Ln) (modified from Etayo-Serna 1968, 1979; Páramo-Fonseca et al. 2019). Imagery map obtained from Planet Team (2017).
Squamosal. The presence or absence of a squamosal cannot be determined with certainty, due to the fragmentary preservation of this region.

Postorbital. The postorbital is a broad and laterally compressed element forming the posterodorsal edge of the orbit. The anterior and posterior margins of the postorbital are slightly broken. It extends to the midpoint of the dorsal margin of the orbit and does not appear to contact the prefrontal, allowing a postfrontal contribution to the dorsal orbit between the prefrontal and postorbital. Posteriorly, it contacts the quadratojugal via a complex series of over- and underlapping flanges and has a broad posterodorsal contact with the supratemporal. The postorbital overlaps the dorsal edge of the jugal. The external surface of the postorbital is rugose, similar to the quadratojugal.

Figure 2. Skull of Kyhytysuka sachicarum comb. nov., DON-19761. A, B, photo and interpretative illustration of the skull in left lateral view; C, D, close-up photo and interpretative illustration of the left narial region. Abbreviations: a, angular; aen, anterior external naris; ar, articular; d, dentary; en, external naris; f, frontal; f.de, fossa dentalis; f.sa, fossa surangularis; j, jugal; jf, jugal facet; m, maxilla; l, lacrimal; n, nasal; op, opisthotic; pf, postfrontal; pm, premaxilla; po, postorbital; prf, prefrontal; q, quadrate; qj, quadratojugal; sa, surangular; scr, sclerotic plate; sp, splenial; st, supratemporal. Scale bars: A, B = 10 cm; C = 5 cm.
Quadratojugal. The quadratojugal is a large flattened bone that forms the posterior cheek region. Despite being separated into two pieces by a crack, its extensive lateral surface exposure is obvious. The dorsal ramus of the quadratojugal largely overlaps the postorbital; the body is overlapped by the posterior jugal. The posterior quadratojugal covers much of the quadrate. The external surface of the dorsal quadratojugal bears striae originating obliquely from the postorbital, whereas the ventral part is smoother. The posterior region of the ventral ramus of the quadratojugal is saddle-shaped and bears a small peg-like processus quadratus that overhangs the quadrate condyle (Figs 2, 5E). Posterodorsolaterally, the quadratojugal seems to contact the ventral edge of the anterior ramus of the supratemporal.

Quadrate. The quadrate is a robust, hourglass-shaped element with broad condyles articulating dorsally with the supratemporal and ventrally with the articular and surangular. The body is formed by a laterally compressed posteromedial-facing pterygoid lamella and a robust posterolaterally oriented occipital lamella. A broad space is present between the dorsal surface of the occipital lamella and the ventral edge of the supratemporal. The dorsal condyle is transversely broad, nearly equal in width to the mandibular condyle. The dorsal surface of the quadrate is concave and may have supported a large cartilaginous pad to articulate within the concave space of the supratemporal, as inferred in other ichthyosaurs (McGowan 1972; Kear 2005), as well as a gap between the articular condyle and the articular, which were presumably covered with articular cartilages in life (Fig. 4F).

The pterygoid lamella is mostly concealed by the dorsal flange of the quadratojugal in medial view. This lamina is broad and articulates posteromedially with the quadratojugal and the quadrate. The columnar occipital lamella terminates ventrally as a large and rugose articular condyle. The articular condyle expands anteroposteriorly and transversely into an equally broad mandibular cotyle formed by the articular and surangular. A supratemporal groove runs along the medial edge of the occipital lamella (Fig. 5B, D). A well-defined, concave stapedial facet is present at the ventromedial base of the occipital lamella. The facet is dorsoventrally tall, ovate, and faces medially and slightly posteriorly. A discrete posterior raised edge would have partly covered the posterior surface of the stapes and makes the articulation face almost entirely medial. Dorsally, this ridge is sharp but expands to a thickened wall oriented ventrally. The wall curves medially to merge with the quadratojugal. The posterior ridge of the stapedial facet and tuberculum are separated from the articular

### Table 1. Skull measurements (mm) of *Kyhrytysuka sachicarum* comb. nov., DON-19671.

| Measurement                                                                 | mm     |
|----------------------------------------------------------------------------|--------|
| Orbit height                                                               | 130    |
| Orbit length                                                               | 170    |
| Lower jaw length                                                           | 940    |
| Length of the mandibular symphysis                                         | 515    |
| Dentary contribution to the symphysis                                       | 205    |
| Splenial contribution to the symphysis                                      | 310    |
| Length of antorbital rostrum (anterior edge of orbit to tip of premaxilla) | ~635   |
| Quadrate height                                                            | 93     |
| Width of quadrate articular condyle of the quadrate (base)                 | 50     |
| Width of quadrate articular condyle of the quadrate (top)                  | ~45    |
| Height of the articular                                                    | 47     |
| Length of the articular                                                    | 57     |
| Width of the articular                                                     | 23     |

| Teeth (left rostrum) – mm                                                   | Anterior | Mid-rostrum | Posterior |
|----------------------------------------------------------------------------|-----------|-------------|-----------|
| Total tooth height                                                         | 30–31     | 37–40       | 24–25     |
| Height of crown                                                            | 10–13     | 13–15       | 8–9       |
| Width of tooth root                                                         | 9–10      | 11–13       | 6–10      |
| Width at base of crown                                                     | 6–6.5     | 7–11        | 5–6       |

| Teeth (right rostrum) – mm                                                  | Anterior | Mid-rostrum | Posterior |
|----------------------------------------------------------------------------|-----------|-------------|-----------|
| Total tooth height                                                         | 31–32     | 32–35       | NA        |
| Height of crown                                                            | 9–10      | 8–9.5       | 11        |
| Width of tooth root                                                         | 11        | 12          | NA        |
| Width at base of crown                                                     | 7         | 6–8.5       | NA        |

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surface of the quadratojugal by a triangular, concave depression that forms a discrete separation between the facet and condyle. The mandibular condyle is sub-hemispherical in lateral aspect with a notably flatter ventral articular surface than the more strongly curved posterior surface. In posterior aspect, the condyle is squared. The articular surface is etched with reticulating grooves common on thick cartilage covered surfaces. A shallow surangular facet is present laterally. The articular surface is limited to only the ventral and posterior surface in lateral and medial aspects. However, where visible, the ventral surface is somewhat flatter than the sub-spherical posterior surface. Posteriorly, the articular surface extends up the entire posterior surface of the condyle. A discrete groove is present between the articulating surface and quadrate body on the dorsal and medial margins of the condyle (Fig. 5).

**Epiptrygoid.** No ossified epiptrygoid was observed in DON-19671.

**Vomers.** The palate is only visible from the right side from an approximately medial perspective and in cross-section across the two breaks in the snout (Fig. 4F). The paired vomers appear posteriorly, dorsal to the palatal shelves of the maxilla; only one is visible anteriorly.

**Palatine.** An elongate, plate-like palatine is preserved and is probably from the left side. The palatine expands dorsally, at the level of the external nares, but is broken without further information as to its contact with the vomer. The palatine–pterygoid contact is also not visible due to an overlying bone fragment.

**Pterygoid.** The left pterygoid is well preserved in medial view. The pterygoid is the most robust element of the palatal complex with a robust posterior quadrate ramus, a narrower body, and a broad palatal ramus anteriorly. Posterodorsally, the quadrate ramus of the pterygoid has a dorsal flange directed towards, but not anteriorly. Posterodorsally, the quadrate ramus of the pterygoid extends up the entire posterior surface of the condyle. A discrete groove is present between the articulating surface and quadrate body on the dorsal and medial margins of the condyle (Fig. 5).

**Basicranium**

Neither the basioccipital, parabasisphenoid, prootic, supraoccipital, nor stapes, can be identified in the holotype (DON-19671) of *K. sachicarum*. Several fragmentary bones are present in the region, but a confident anatomical attribution is not possible.

**Opisthotic.** The left opisthotic is preserved in anterior view. It is disarticulated and lies in the orbit, being best exposed on the medial portion of the orbit (Figs 2, 4F). The opisthotic bears a narrow notch, the horizontal canal.

**Exoccipital.** The left exoccipital is well preserved but displaced dorsally. It is a squat element expanded anteroposteriorly into a basioccipital facet. Anteriorly, the exoccipital is constricted at its mid-part and bears a relatively large notch interpreted as for the vagus nerve, based on the interpretations by Kear (2005) and Moon & Kirton (2016) and its relatively similar location and morphology. Ventromedial to this notch, the exoccipital bears three oval foramina that probably would have conveyed branches of the hypoglossal nerve (XII) interpreted based on its location following Moon & Kirton (2016, p. 41). The supraoccipital facet of the exoccipital is damaged. The basioccipital facet is broad and roughened.

**Hyolaryngeal skeleton.** The hyoid apparatus is not clearly preserved in the holotype DON-19671, although isolated and fragmentary remains may be present.

**Sclerotic plates.** The orbit is large and oval in outline. The external portion of the sclerotic ring is not preserved. Several sclerotic plates are preserved within the orbit but others can be found disarticulated over the braincase of the specimen. They are composed of two portions, a corneal portion that is flattened, shaping the sclerotic aperture, and a curved orbital portion forming the outer edge of the ring, which bears a minuscule flat and compressed margin. Twelve orbital plate portions of the sclerotic ring are preserved, which vary between 22 and 30 mm in width and interdigitate with each other (Fig. 4F). The inner surface of the plates bears millimetre-scale parallel radiating striations along the long axis of each plate (possibly for the attachment of Crampton’s muscle; Underwood 1970).

**Mandible**

**Dentary.** The dentary is broken anteriorly but the rest of its length is well preserved. The dentary forms the bulk of the lateral mandible and is the longest bone in the jaw. The dentary is 720 mm in preserved length and...
extends to the approximate midpoint of the orbit. The dentary houses at least 47 tooth positions in an alveolar groove that terminates near the level of the anterior boundary of the external narial fossa (Figs 4, 6). The dentary is elongated in lateral view and deepest dorsoventrally just anterior to the external nares. As it reaches the orbit, the dentary leaves the dorsal margin of the mandible to taper and terminate on the lateral surface of the orbit, the dentary leaves the dorsal margin of the ventrally just anterior to the external nares. As it reaches the dentary is elongated in lateral view and deepest dorsoventrally just anterior to the external nares. The groove that terminates near the level of the anterior dentary houses at least 47 tooth positions in an alveolar extends to the approximate midpoint of the orbit. The groove that terminates near the level of the anterior dentary houses at least 47 tooth positions in an alveolar.

A distinctive fossa dentalis (sensu Maisch 1998) is present on the lateral surface from the anterior region to nearly the level of the external nares. The fossa is remarkably deep at its mid-point (5 mm wide/4 mm deep), shallower at its extremes, and disappears on the posterior part of the dentary. The lateral surface dorsal to the fossa dentalis is relatively flat and vertical. The surface ventral to the fossa is convex and curves ventromedially to meet the splenial. The mandibular symphysis spans about 40% of the jaw. The anterior third is formed by the dentary and the remainder by the splenial. In cross-section, the dentary is remarkably robust. The lingual wall of the alveolar groove is nearly as thick as the labial wall of the alveolar groove (Fig. 4). In fact, each wall is as thick as the alveolar groove is wide in the visible cross sections.

**Splenial.** The splenial is a robust and laterally flattened element, externally exposed along the ventromedial lower jaw and occupies a considerable portion of the total length of the mandible (Fig. 3). The splenial plays a more extensive role in the mandibular symphysis than the dentary (roughly two-thirds of the length of the mandibular symphysis). The splenial forms much of the medial wall of the mandible. Posterior to the symphysis, the splenial forms the entire medial and ventral surface to about the level of the midpoint of the orbit. The splenial covers a large Meckelian groove bounded dorsally, laterally and ventrally by the dentary anteriorly and dorsally and laterally by the surangular and angular posteriorly (Fig. 4). The medial surface of the splenial posterior to the symphysis is slightly dorsoventrally convex. In cross-section, the splenial is overall ‘J’-shaped (Fig. 4). A pathology is present on the ventral surface at its midpoint and is associated with a slight thickening of the bone (Fig. 3C, D) (65 mm length \times 28 mm width of injured bone). Six deep depressions in this region are surrounded by, as noted by Pardo-Pérez et al. (2018, p. 22), “fibrous surface remodelling and possible abscesses derived from trauma and infection”.

**Coronoid.** The coronoid is not present in the holotype of *K. sachicarum*, as in most post-Triassic ichthyosaurs (Kear 2005).
orbit, the surangular expresses a flat dorsal surface that meets the lateral surface at a near 90° angle. A wide paracoronoal process is present behind the orbit but its dorsal extent is covered laterally and medially by other bones. The edge of the surangular bordering the mandibular cotyle is extended somewhat laterally, forming a small shelf, the Musculus adductor mandibulae externus (MAME) process (Kirton 1983; Fischer et al. 2012; Moon & Kirton 2016 p. 48), presumably for attachments of robust ligaments of the synovial capsule.

**Prearticular.** Only the left prearticular is preserved and is inserted into a deep medial facet on the dorsomedial surface of the angular (Figs 4F, 5). Posteriorly, the prearticular is strap-shaped, contributing the posteromedial edge of the glenoid fossa and extending posteriorly to the end of the retroarticular process. This configuration places the prearticular between the articular and angular on the medial wall of the retroarticular process. Anteriorly, the prearticular expands dorsally as a plate-like bone but its extent is unknown due to the displaced right pterygoid concealing this region.

**Articular.** The articular is rounded and lateromedially compressed. Laterally, the articular inserts into a posteromedial surangular groove, and anteriorly, the articular bears a shallow concave facet for articulation with the quadrate. The medial surface of the articular is smoothly concave whereas the dorsal surface is slightly saddle-shaped. A large, medial foramen is present at the mid-length of the retroarticular process (Figs 4F, 5); such a foramen is not known from other ichthyosaurs, and may be pathological.

**Dentition.** The teeth are held in a deep and continuous groove in the premaxilla, maxilla and dentary. The alveolar groove is approximately 14 mm wide on average. The anterior extent of the dentition is unknown; however, the maxillary groove terminates roughly 20 mm from the anterior edge of the orbit. The dentary groove terminates at approximately the level of the anterior margin of the narial fossa. The anterior section of the break in this region (Fig. 4C) preserves a shallow alveolar groove with a tooth resting, slightly displaced, within it. The posterior section of this break preserves no teeth but a slight alveolar depression that may have housed a smaller tooth. Two dentary teeth are preserved a little further posteriorly at the level of the posterior external nares, suggesting the posterior dentary teeth are housed on this shallow alveolar table, rather than a discrete groove. However, it is clear that the dentary dentition terminates anterior to the maxillary dentition, with perhaps seven reduced maxillary teeth unopposed by dentary teeth.

All fully erupted teeth have exposed roots apical to the edge of the tooth-bearing bones. The exposed portions of the roots are about as long as the crowns but wider. The crowns are lightly recurved lingually and posteriorly and the roots are slightly recurved in the same direction. This orientation may be due to some taphonomic displacement, but it is not displaced enough to be certain. In most cases, the teeth have coarsely striated enamel and a robust crown with no cutting edges. The striations occur at a density of approximately 13–14 per 5 mm along the labial surface of the anterior to middle dentition. Teeth are smaller anteriorly (30 mm total height, 12 mm crown height, 9 mm root width, 5 mm width crown) and largest in the mid-rostrum (35–37 mm total height, 14 mm crown height, 10–12 mm root width, 6–7 mm crown width) and smallest posteriorly (24 mm total height, 9 mm crown height, 7 mm root width, 6 mm crown width). The crown is conical, oval to rounded in cross-section. The crown striations are formed by a complex chain of multiple vertically organized submillimetre-scale spheres (Fig. 7). There is apical wear on the crowns of some teeth (Fig. 7A) and dental pathologies (e.g. potential sign of dental caries) (Fig. 6B, C). The base of the enamel layer is well defined. The tooth roots are quadrangular in cross-section. A ring of acellular cementum 4–7 mm height is present, separating the enamel crown from the root cellular cementum of the teeth. This ring is smooth and thin and lacks grooves. The osteocementum is highly vascularized and thick.

The teeth in the right dentary are better preserved than those in the right premaxilla and maxilla, which apart from the anterior premaxillary teeth, are either displaced or missing. The right dentary is more damaged than the left but the preserved dentition matches well the patterns seen in the left dentary. A nearly complete dentition is preserved in the left premaxilla, maxilla and dentary. The dentition has a remarkable degree of variation throughout the jaw. Zahnreihe (sensu Woerdeman 1919 and Edmund 1960) appear to be present in some regions of the dentition. The wave-like process of alternating tooth replacement appears well defined in the anterior and posterior regions of the dentition, but not in the middle. The dentition of DON-19671 is expressed bimodally as either fully erupted and functional teeth and or smaller teeth that would have been neither erupted nor functional (Figs 2, 6). There are no clear cases of any intermediate teeth. The anterior three preserved premaxillary teeth are more elongate than the other teeth and spaced near each other with a small gap between each tooth root. An obvious alternating functional–non-functional series of teeth is present in the anterior premaxillary dentition and the anterior maxillary dentition. The dentary dentition alternates in a similar
Phylogenetic analysis

To investigate the phylogenetic position of *K. sachicarum* within Ophthalmosauridae, we used the dataset from Campos et al. (2020), incorporating the character and taxon scoring changes of Fernández et al. (2021). We added 18 more characters to a data matrix generated with Mesquite v. 3.61 (Madison & Madissen 2019). We also included the recently described *Acuetzpalin carranzae*, *Nannopterygius saveljevensis* and *Thalassodraco etschesi* (Barrientos-Lara & Alvarado-Ortega 2020; Jacobs & Martill 2020; Zverkov & Jacobs 2021). To examine the phylogenetic relationships of the genus *Platypterygius*, we included *Platypterygius platydactylus* and *Platypterygius americanus* in our analysis, scored based on the available literature and personal observation (*P. americanus*, EM). We also corrected the character scoring for *K. sachicarum* based on personal observation of the holotype and referred material (see Supplemental material for character list and for character–taxon matrix). *Muiscasaurus catheti* was scored solely based on the holotype material. A list of Barremian–Aptian ophthalmosaurid ichthyosaur taxa known to date is included as a reference that were also included in the analysis (Table 2).

Our phylogenetic analysis is based on 34 OTUs and 88 characters, with all characters unordered and unweighted. TNT v. 1.5 (Goloboff et al. 2008; Goloboff & Catalano 2016) was used with *Temnodontosaurus* sp. as the outgroup. The analysis was run by a New Technology search set to 5000 random addition sequences employing sectorial and tree fusing search parameters. Such a deep search was required because fewer replicates led to searches becoming stuck on heuristic islands of suboptimal trees (Maddison 1991). The tree search of the analysis recovered four most-parsimonious trees (MPT) with a length (TL) of 300, a consistency index (CI) of 0.340 and a retention index (RI) of 0.535. These trees yielded a strict consensus tree with a polytomy of *Nannopterygius*, *Keilhauia*, *Cryopterygius*, *Leninia*, *Athabascasaurus*, *Platypterygius platydactylus*, *Mollesaurus*, *Undorosaurus*, *Maiaspondylus*, and the remaining clades described below. IterPCR (implemented in TNT) (Pol & Escapa 2009) identified *Keilhauia* and *Maiaspondylus* as unstable taxa and they were deleted from the analysis. The same analysis was re-run with the remaining 32 taxa and recovered two MPTs with a length of 292, a CI of 0.349 and a RI of 0.554. The topology is congruent with the 34 taxon results above but resolves the intermediate node. The tree has low bootstrap and Bremer support (Fig. 8). *Gengasaurus nicosiai* and *Leninia stellans* were omitted to test if these fragmentary taxa influence the tree topology. The search produced 15 MPTs with a length of 285, a consistency index of 0.358 and a retention index of 0.570. Only the basal nodes of the strict consensus were resolved but Ophthalmosauria was collapsed to a
polytomy, suggesting that important characters for phylogenetic resolution are present in these incomplete taxa. Omitting one or a combination of these three taxa yielded similar consensus results.

**Tooth shape analysis**

Tooth shape and positions were measured to explore if quantitative aspects of the dentition align with the qualitative zones described below. The dentition of the left upper jaw ramus is well enough preserved to measure tooth shape variation along the jaw (Table 3). Measurements of each tooth position were made from the midpoint of the mandibular condyle to the tip of each functional tooth. Although the orientation of some teeth may be slightly taphonomically altered, the relative positioning was unaltered. Tooth positions were measured to the nearest millimetre to account for the minimal
taphonomic distortions and tooth dimensions were measured to the nearest 0.5 mm to account for potential taphonomic and preparation artefacts, although minimal distortions were observed. Tooth diameters were measured at the root contact to their alveolar walls and the missing portions of the labial alveolar walls of the posterior premaxilla were estimated using the preserved walls in the anterior and posterior dentition and opposite side when measuring teeth in that region. Total tooth heights were measured from the labial alveolar margin to the crown tip.

Discussion

The phylogenetic definition of Ophthalmosaurus

The taxonomy of Ophthalmosaurus has a complex history. Seeley (1874) introduced *Ophthalmosaurus*
icenicus with a partial pectoral skeleton and forelimb. Marsh (1879) introduced *Sauranodon natans* from a skull and partial skeleton and coined the higher taxonomic groups Sauranodonta and Sauranodontidae. Marsh was soon forced to emend the preoccupied name *Sauranodon* to *Baptanodon* (Marsh 1880). In 1887 Baur coined several taxonomic names to include *Ophthalmosaurus* and *Baptanodon*. Baur (1887a) originally named Baptanodontidae to include *Baptanodon*. In a broader taxonomic report of Sauropsida, Baur changed the name to Baptanodontia (Sauranodontia) (Baur 1887b). A German text published the same year

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**Figure 6.** Dentition of *Kyhytysuka sachicarum* comb. nov., DON-19761. **A,** showing dental zones (*z*); **B,** close-up photos of the five dental zones (*zI* to *zV*); **C,** enhanced view of premaxillary tooth in Zone II showing pathological erosion on lateral surface of root. Scale bar: A = 10 cm.

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**Figure 7.** **A,** digitally isolated tooth of *Kyhytysuka sachicarum* comb. nov., DON-19761; **B,** illustrating the major tooth regions; **C,** close-up photo of a tooth showing the enamel with microspheres; **D,** **E,** photo and cutaway diagram illustrating the internal tooth structure in cross-section in relation to external surface. Scale bar = 1 cm.
Table 2. List of Barremian–Aptian ophthalmosaurid ichthyosaur taxa known to date.

| Taxon                          | Holotype   | Geographical range                      | Formation and age                          | Reference                          |
|-------------------------------|------------|-----------------------------------------|--------------------------------------------|------------------------------------|
| *Platypterygius hauthali*     | MLP 79-I-30-1 | Santa Cruz Province, Argentina; Tyndall Glacier, Torres del Paine National Park, Chile | Rio Belgrano Fm., Barremian; Zapata Fm., Valanginian–Hauterivian | Pardo-Pereyra et al. 2012; Fernández & Aguirre-Urreta 2005; Stinnesbeck et al. 2014 |
| *Simbirskiasaurus birjukovi* | YKM 65119  | Volga River, Ulyanovsk Region, Russia   | Simbirskites Clay Fm., lower Barremian    | Fischer et al. 2014a               |
| *Sveltonectes insolitus*      | IRSNB R269 | Ulyanovsk Region, Russia                | Formation not available in the literature, upper Barremian | Fischer et al. 2011               |
| *Muiacasaurus catheti*        | CIP-FCG-CBP-74 | Sáchica, Boyacá, Colombia             | Paja Fm., Barremian–Aptian                | Maxwell et al. 2016               |
| *Kyhytysuka sachicarum* comb. nov. | DON-1967  | Villa de Leyva, Boyacá, Colombia       | Paja Fm., Barremian–Aptian                | Prámo-Fonseca 1997; Maxwell et al. 2019; this study |
| *Leninia stellans*            | YKM 65931  | Kriushi locality, Ulyanovsk Region, Russia | lower Aptian                             | Fischer et al. 2014b              |
| *Platypterygius platydactylus*| BSPG, destroyed during World War II | Ricklinger Moor, Lower Saxony, Germany | lower Aptian                             | Broili 1907                        |
| *Platypterygius hercynicus*   | SMSS ‘SGS’ | Lower Saxony, Germany; Normandy, France | upper Aptian–upper Albian                | Kolb & Sander 2009; Fischer 2012  |
| *Platypterygius australis*    | MV P12989 (neotype) | North Central Queensland, Australia | Toolebuc Fm., Albian                    | Kear 2005; Zammit 2011          |

Figure 8. A, constrained tree, showing the phylogenetic position of *Kyhytysuka sachicarum* comb. nov. within Ophthalmosauria. Nodes were manually positioned to roughly equal minimum branch lengths about known occurrences. The tree search of the analysis recovered four most-parsimonious trees (MPT) with a length (TL) of 300, a consistency index (CI) of 0.340 and a retention index (RI) of 0.535. Bremer support values are shown above the branches. The only node recovered more than 50% of the time with a 2000 bootstrap replicates was the ingroup node. B, diagram showing the node-stem triplet, modified from Sereno 1999. C, map showing most closely related Barremian–Aptian species (purple star), and Colombian taxa (red star).
Figure 9. A, potential buccal connective tissue in *Kyhytysuka sachicarum* comb. nov., DON-19761, soft tissue preservation in the buccal region associated with B, a specimen of *Stenopterygius* from Holzmaden (MHH 432). Scale bar = 5 cm.
discussing ichthyosaur limbs revised Baptanodontidae to include *Ophthalmosaurus* and *Baptanodon* but also used the term *Ophthalmosaurus* (sic) in a figure caption (Baur 1887c). Baur (1887a, c) diagnosed this clade as having a radius, ulna and third bone articulating to the distal humerus and teeth rudimentary or absent. His use of two names implies he intended this clade to include the then known genera *Ophthalmosaurus* and *Baptanodon*. Although later finds discovered these taxa to have complete dentitions, the distal humeral articulations stood. Until recently, *Baptanodon* has generally been considered a junior synonym of *Ophthalmosaurus* (for a review, see McGowan & Motani 2003); *Ophthalmosaurusidae* held priority. In Andrews’s monograph of *O. icenicus*, he maintained the family name and presented an updated diagnosis of the family as: “Specialized ichthyosaurs in which the orbit is extremely large and the dentition is reduced in the adult to a number of small teeth, which are loosely set in the anterior of the jaws only. The humerus articulates distally with three bones and the fore-paddle is much larger than the posterior which is greatly reduced. The pubes and ischium are fused together”, with a distribution of “Middle and Upper Jurassic of Europe and North America with doubtful representatives in the Upper Greensand of England” (Andrews 1910, p. 2). Appleby (1956, p. 444) later amended the description of the dentition as “Teeth present along the whole length of the jaw but loosely attached. Teeth smaller anteriorly than posteriorly”.

Motani (1999) presented the first phylogenetic definition of the same clade but elevated it to Ophthalmosaurusia. He proposed a node-based definition as the last common ancestor of *Brachypterygius extremus* and *Ophthalmosaurus icenicus* and all its descendants (Motani 1999). Motani updated the diagnosis of the clade as having a reduced extracondylar area of the basioccipital, angular largely exposed laterally, reaching as anteriorly as the surangular, and an extra-zeugopodial element anterior to radius associated with an accessory anterior digit (Motani 1999). Several authors have followed the use of Ophthalmosaurusia (e.g. Fernández 2001; Fernández et al. 2005; Maxwell & Caldwell 2006).

Fischer et al. (2012) modified the definition of Ophthalmosaurusidae but maintained a node-based definition as the last common ancestor of *Arthropterygius chrisorum* and *O. icenicus* plus all its descendants. They revised the definition only to maintain the ‘crucial’ diagnostic characters historically associated with the clade. They recovered *A. chrisorum* sister to the traditional ophthalmosaurians and the majority of diagnostic characters for the traditional Ophthalmosaurusidae dropped one node stemward. This definition presents some confusion because Ophthalmosaurusia (sensu Motani 1999) now becomes a clade nested within Ophthalmosauridae. Moon (2019) later redefined Ophthalmosaurusidae as a stem-based definition as all taxa more closely related to *Ophthalmosaurus icenicus* and *Platypterygius hercynicus* than to *Stenopterygius aalenensis* and *Chacaicosaurus cayi*. He presented a diagnosis for the clade that only included a plate-like dorsal humeral ridge and an acute angle at the anterodistal humerus, to accommodate an anterior accessory element. The change in one of the ingroup anchor taxa to *Platypterygius hercynicus* was made to harmonize to two recently erected subfamilies within the clade. Arkhangelsky (2001) proposed the subfamily Platypterygiinae, and Fischer et al. (2012) provided a definition and diagnosis for it and Ophthalmosaurinae. Ophthalmosaurinae was given a stem-based definition as all taxa more closely related to *Ophthalmosaurus icenicus* than to *Platypterygius hercynicus* and Platypterygiinae also a stem-based definition as all taxa more related to *Platypterygius hercynicus* than to *Ophthalmosaurus icenicus*.

However, the monophyly of *Platypterygius* and even *Ophthalmosaurus* have been challenged when some phylogenetic resolutions of ophthalmosaurids have been achieved, including analyses by Fischer et al. (2012) and several others (Moon 2019 and references therein). The issues with *Ophthalmosaurus* are easily solved as *O. icenicus* has priority for the genus. However, the choice of *P. hercynicus* as an anchor taxon is unfortunate and more difficult to solve.

The type species of the genus, *P. platydactylus*, was described in 1907 from the Aptian of northern Germany, and the description is insufficient by modern standards. However, the holotype and only referred specimen was destroyed during WWII, preventing restudy. No subsequent referred material exists for *P. platydactylus* and the only available data of the type specimen consist mostly of an original description and drawings in Broili (1907). The genus became a catch-all for Early Cretaceous ichthyosaurs, and acquired a range of 35 million years. *Platypterygius* now constitutes a complex and problematic genus lacking a robust phylogenetic definition (Fischer 2016), but for which the type specimen no longer exists. The unstable and highly variable *Platypterygius* has gathered a continuous set of problems in the topologies when coded at the species-level (Moon 2019). Although the taxonomic validity of *Platypterygius* as a genus remains unclear, some attempts have been made to address this problem (e.g. Zammit 2011; Fischer 2012, 2016; Ji et al. 2016; Moon 2019), inviting a critical and separate re-evaluation based on morphology rather than historical (and
Table 3. Left premaxillary and maxillary tooth measurements (mm) used in Figure 11.

| Position | l (mm) | Diameter crown (mm) | Diameter implantation (mm) | Height crown (mm) | Height implantation (mm) | Tooth shape crown | Tooth shape total | Comments |
|----------|--------|---------------------|----------------------------|------------------|--------------------------|------------------|------------------|----------|
| pm2      | 853    | 5.5                 | NA                         | 14               | 26                       | 2.55             | NA               | Slightly displaced |
| pm3      | 845    | 6                   | 8.5                        | 15               | 26                       | 2.50             | 3.06             | Functional |
| pm4      | 835    | 6                   | 8.5                        | 12               | 20                       | 2.00             | 2.35             | Functional |
| pm5      | 831    | NA                  | NA                         | NA               | NA                       | NA               | NA               | Non-functional |
| pm6      | 816    | 5                   | 8.5                        | 11               | 18                       | 2.20             | 2.12             | Functional |
| pm7      | 807    | NA                  | NA                         | NA               | NA                       | NA               | NA               | Non-functional |
| pm8      | 787    | 5                   | 10                         | 11.5             | 18.5                     | 2.30             | 1.85             | Functional |
| pm9      | 783    | NA                  | NA                         | NA               | NA                       | NA               | NA               | Non-functional |
| pm10     | 762    | 6.5                 | 10.5                       | 11.5             | 18.5                     | 1.77             | 1.76             | Functional |
| pm11     | 759    | NA                  | NA                         | NA               | NA                       | NA               | NA               | Non-functional |
| pm12     | 742    | 8.5                 | 10.5                       | 11.5             | 18                       | 1.35             | 1.71             | Functional |
| pm13     | 737    | NA                  | NA                         | NA               | NA                       | NA               | NA               | Non-functional |
| pm14     | 706    | 9                   | 10.5                       | 14               | 22                       | 1.56             | 2.10             | Functional |
| pm15     | 701    | NA                  | NA                         | NA               | NA                       | NA               | NA               | Crown broken |
| pm16     | 677    | 7.5                 | 11                         | 13.5             | 22                       | 1.80             | 2.00             | Functional |
| pm17     | 680    | NA                  | NA                         | NA               | NA                       | NA               | NA               | – |
| pm18     | 658    | 7                   | 10.5                       | 12               | 22                       | 1.71             | 2.10             | – |
| pm19     | 648    | 6                   | 9                          | 10               | 22.5                     | 1.67             | 2.50             | – |
| pm20     | 635    | 8.5                 | 11.5                       | 10.5             | 22                       | 1.24             | 1.91             | – |
| pm21     | 634    | 7                   | NA                         | 11.5             | NA                       | 1.64             | NA               | Not fully erupted |
| pm22     | 614    | 8                   | 11                         | 11.5             | 23.5                     | 1.44             | 2.14             | – |
| pm23     | 613    | 7                   | NA                         | 10               | NA                       | 1.43             | NA               | Very displaced, not fully erupted |
| pm24     | 580    | 8                   | NA                         | 10               | NA                       | 1.25             | NA               | Slightly displaced |
| pm25     | 576    | 7                   | NA                         | 10.5             | NA                       | 1.50             | NA               | – |
| pm26     | 556    | 7                   | 9.5                        | 10               | 21                       | 1.43             | 2.21             | – |
| pm27     | 548    | 7                   | 9                          | 9.5              | 17.5                     | 1.36             | 1.94             | – |
| pm28     | 538    | 7.5                 | 9                          | 10               | 18                       | 1.33             | 2.00             | – |
| pm29     | 528    | 9                   | 11.5                       | 10.5             | 17.5                     | 1.17             | 1.52             | – |
| pm30     | 522    | 8.5                 | NA                         | 11               | NA                       | 1.29             | NA               | Not fully erupted |
| pm31     | 508    | 8.5                 | 10.5                       | 10               | 15.5                     | 1.18             | 1.48             | – |
| pm32     | 497    | NA                  | NA                         | NA               | NA                       | NA               | NA               | Tip broken |
| pm33     | 485    | 6.5                 | 8.5                        | 10               | 13                       | 1.54             | 1.53             | – |
| m1       | 476    | 9                   | 11                         | 11.5             | 16                       | 1.28             | 1.45             | First tooth with preserved lateral m, but likely still inset into pm |
| m2       | 464    | NA                  | NA                         | NA               | NA                       | NA               | NA               | Not fully erupted |
| m3       | 448    | 8.5                 | 9.5                        | 10               | 15.5                     | 1.18             | 1.63             | – |
| m4       | 443    | NA                  | NA                         | NA               | NA                       | NA               | NA               | Not fully erupted |
| m5       | 428    | 8                   | 9                          | 10               | 15.5                     | 1.25             | 1.72             | – |
| m6       | 423    | NA                  | NA                         | NA               | NA                       | NA               | NA               | Not fully erupted |
| m7       | 403    | 6                   | 9                          | 7.5              | 12.5                     | 1.25             | 1.39             | – |
| m8       | NA     | NA                  | NA                         | NA               | NA                       | NA               | NA               | Series of several missing teeth |
| m9       | NA     | NA                  | NA                         | NA               | NA                       | NA               | NA               | Series of several missing teeth | (Continued) |
Revision of ‘Platypterygius’ sachicarum

Table 3. (Continued).

| Position | l (mm) | Diameter crown (mm) | Diameter implantation (mm) | Height crown (mm) | Height implantation (mm) | Tooth shape crown (mm) | Tooth shape total (mm) | Comments |
|----------|--------|---------------------|-----------------------------|------------------|-------------------------|-----------------------|-----------------------|----------|
| m10      | NA     | NA                  | NA                          | NA               | NA                      | NA                    | NA                    | –        |
| m11      | NA     | NA                  | NA                          | NA               | NA                      | NA                    | NA                    | –        |
| m12      | 311    | 8.5                 | 9.5                         | 8                | 14                      | 0.94                  | 1.47                  | –        |
| m13      | 300    | 4.5                 | 6.5                         | 5.5              | 8.5                     | 1.22                  | 1.31                  | –        |
| m14      | 296    | 6.5                 | 7.5                         | 8.5              | 16                     | 1.31                  | 2.13                  | –        |
| m15      | 286    | 5                   | 6                           | 5.5              | 10.5                    | 1.10                  | 1.75                  | –        |
| m16      | 278    | 8                   | 8.5                         | 9                | 13.5                    | 1.13                  | 1.59                  | –        |
| m17      | 269    | 5                   | 5.5                         | 5.5              | 9                      | 1.10                  | 1.64                  | –        |
| m18      | 262    | 7                   | 8                           | 5                | 8                      | 0.71                  | 1.00                  | –        |

temporal) criteria (Fischer 2016). Previous studies (e.g. Fischer et al. 2016) have shown the non-monophyly of species referred to Platypterygius (Fischer 2016), but retained the name for convenient classification (Bardet et al. 2016). Remarkably, the genus was still used to name the subfamily Platypterygiinae but with Platypterygius hercynicus as the anchor taxon. The questionable validity of the namesake of this clade and using a taxon potentially distantly related to P. platydactylus to anchor the clade definition makes this taxonomic definition problematic. Because of the inaccessible nature of P. platydactylus for any future research, we recommend removing the genus Platypterygius from any phylogenetic definition.

In an attempt to stabilize the phylogenetic definitions of ophthalmosaurians, we propose a node-stem-triplet approach (Sereno 1999) (Fig. 8B), which allows for addition, deletion, or local changes of taxa to be better placed across the phylogeny (Sereno 1999). Ophthalmosauridae was originally used to group Ophthalmosaurus and Baptanodon (Baur 1887a; Appleby 1956) diagnosed the clade with specific references to ichthyosaurs with extremely large orbits. The next oldest named ophthalmosaur currently recognized as a valid taxon is Brachypterygius extremus (Boulenger 1904, amended by von Huene 1922). While most authors (e.g. Moon & Kirton 2018) consider Brachypterygius extremus, the holotype of which is an isolated forelimb, a senior synonym of Grendelius mor-dax following McGowan (1997), an alternative view holds that the two species are distinct (Zverkov et al. 2015). In either case, both OTUs cluster within Platypterygiinae (Jacobs & Martill 2020).

In keeping with this historical taxonomy, we propose a revision of ophthalmosaurs to maintain taxonomic stability with reference to historical definitions and accessible, valid taxa that are generally recovered relatively deep in their respective lineages. We retain a node-based Ophthalmosaura as defined by Motani (1999) as the last common ancestor of Ophthalmosaurus icenicus and Brachypterygius extremus and all its descendants. The name and definition are retained to maintain priority in the taxonomy of this node. Ophthalmosauridae is defined with a stem-based definition as all taxa more closely related to Ophthalmosaurus icenicus than to Brachypterygius extremus. This taxonomic definition best comprises the intention of the original usage of this family name by Baur (1887a), Andrews (1910), and Appleby (1956). The taxa these authors included in this family are recovered here and the diagnosis by Appleby for this family was the relatively large orbits present in the clade. Brachypterygiidae is a new stem-based definition as all taxa more closely related to Brachypterygius extremus than to Ophthalmosaurus icenicus. This new family respects the oldest valid taxon in this clade. The abundant and well-preserved specimens of O. icenicus and B. extremus are important to serve as accessible anchors for this node-stem-triplet (Moon & Kirton 2016, 2018). This taxonomy will accommodate both future rearrangements within ophthalmosaurs and the inevitable revisions to the several ‘Platypterygius’ species not sister to P. platydactylus.

Ophthalmosaura Motani, 1999

Definition. The last common ancestor of Ophthalmosaurus icenicus and Brachypterygius extremus and all its descendants (node-based).

Diagnosis. Well-defined base of the enamel layer on teeth, nasal contribution to nasomaxillary pillar forming a short projection, and an incipient divided external nares.

Remarks. The previous oldest ophthalmosaur occurrence, a forefin from the Aalenian–Bajocian boundary showing a preaxial element articulating with the humerus (Fernández 2003), now would be situated basal to this node based presence of this character in the basally positioned taxa Nanopterygius and Thalassodraco.

Characters that resolve as stemward symplesiomorphies of Ophthalmosaura may be useful to describe the origins...
of this diverse clade. Several of these were traditionally used as ophthalmosaurian diagnoses, but they are recovered here as stemward synapomorphies with our proposed taxonomy. These are: reduced processus supranarialis of the premaxilla (only present in Thalassodraco and Nannopterygius), absence of premaxilla–lacrimal contact ventral to the external naris (also absent in A. bitumineus), presence of processus narialis of the prefrontal (also in N. saveljevensis and T. etchesi), reduced extracondylar area of basioccipital (also in A. bitumineus and N. saveljevensis), basioccipital peg absent (also in N. saveljevensis and C. cayi), angular lateral exposure under orbit (also in N. saveljevensis), plate-like dorsal ridge on humerus (also in N. saveljevensis, and apparently absent in T. etchesi), posteriorly deflected ulnar facet present (also in N. saveljevensis and T. etchesi), ischium–pubis fusion in adults present with no obturator foramen (also in A. bitumineus). Chacaicosaurus cayi, from the Bajocian of Argentina, is recovered as the sister taxon of Ophthalmosauria. In the holotype, only one forefin is preserved, in which the distal half of the humerus is lost (Fernández 1994, figs 3f, 5d; Gasparini & Fernández 2005), and a plate-like dorsal ridge appears to be absent. With Nannopterygius outside Ophthalmosauria, it brings the plate-like dorsal humeral ridge more phylogenetically proximal than the node, challenging this classic ophthalmosaurid synapomorphy.

Ophthalmosauridae Baur, 1887a

Definition. All taxa more closely related to Ophthalmosaurus icenicus than to Brachypterygius extremus (stem-based).

Diagnosis. Relatively large orbits (relative orbital ratio >0.1 to <0.25), elongated and slender paroccipital
Remarks. Although all well-preserved ophthalmosaurid forefins preserve at least one preaxial and one postaxial supernumerary digit, it should be noted that this character was previously considered to be a synapomorphy of Ophthalmosauria.

Brachypterygiidae fam. nov.

Definition. All taxa more closely related to Brachypterygius extremus than to Ophthalmosaurus icenicus.

Diagnosis. Tooth roots tightly appressed and quadrangular in cross-section in adults. This combination of morphologies presumably strengthens tooth implantation, and may also be attributed to space constraints in the dental groove resulting from having proportionately bigger teeth than other forms (e.g. Ophthalmosaurus).

Remarks. Potential synapomorphies of the group may include a maxillary contribution to the nasomaxillary pillar, broad anterior margin of the jugal, supra-temporal-postorbital contact, absence of a squamosal, fluke centra as wide as high (also in Stenopterygius quadriscissus).
Phylogenetic results

The resolved topology recovered a well-supported Ophthalmosauria diverging into three subclades (Fig. 8), but that excludes several taxa previously considered ophthalmosaurs (Thalassodraco, Nannopterygius and Athabascsaurus). The recently described taxon Thalassodraco etchesi was recovered outside Ophthalmosauria in our analysis, contrary to its original phylogenetic placement (Jacobs & Martill 2020). The recovery of Thalassodraco outside Ophthalmosauria requires closer scrutiny. Nannopterygius saveljevensis was recovered as the sister taxon of Athabascsaurus bitumineus and Ophthalmosauria; Athabascsaurus bitumineus was recovered as the sister taxon to Ophthalmosauria. This was the most unexpected result, as this taxon is usually recovered within ‘Platypterygiinae’ (Fischer et al. 2016; Zverkov & Jacobs 2021). This anomalous placement is supported by the following characters: premaxilla–lacrimal contact ventral to the external naris, presence of maxillary contribution to nasomaxillary pillar, slender and gracile stapedial shaft in adults, and ischium–pubis fusion in adults present with no obturator foramen. Ophthalmosauria is supported by a well-defined base of the enamel layer on the tooth crown, a short projection of the nasal contribution to nasomaxillary pillar, an incipient divided external nares, lateral contribution of angular approximately one-third under the orbit, and the presence of preaxial accessory digits on the forefin. This latter character is likely an artefact of preservation rather than a true synapomorphy, as a preaxial forelimb element is preserved in both T. etchesi and N. saveljevensis, although in both cases the distal forelimb is too fragmentary to assess the presence of a digit (Jacobs & Martill 2020; Zverkov & Jacobs 2021).

Ophthalmosauria is divided into the clades recovered in part in some previous analyses. A clade including Acamptonectes, Ophthalmosaurus icenius, Gengasaurus and Baptanodon natans is supported by an elongated and slender paroccipital process of the opisthotic. Its sister clade is composed of all other ophthalmosaurs, which in turn is divided into three clades. Its basal clade, composed by Palvannia hoybergeti, Janusaurus lundi, A. thalassonotus and A. chrisorum becomes a polytomy when including Miucasaurus catheti in the analysis (Fig. 8), although the inclusion of this taxon does not change the topology of other branches. The second clade includes the type species of Platypterygius, P. platydactylus, as sister taxa to Leninia, Undorosaurus gorodischensis and Mollesaurus. Sister to this clade is a third major clade that includes K. sachicarum and the remaining derived ophthalmosaurs, including all other ‘Platypterygius’ species.

The inclusion of Platypterygius platydactylus and P. americanus did not reduce the resolution of the topology. Previous analyses have generally recovered a poorly resolved Ophthalmosauria when these two taxa were included (e.g. Ji et al. 2016; Maxwell et al. 2019; Moon 2019), but the combination of adding new narial characters, including the type species of Platypterygius and its seemingly related P. americanus, and excluding poorly preserved taxa in the analysis improved the phylogenetic resolution and highlighted the non-monophyly of the genus Platypterygius. Forcing a monophyletic Platypterygius requires a minimum of nine extra steps. Of all Platypterygius species, only P. hercynicus and P. australis are nested together as sister taxa with Caypullisaurus, K. sachicarum, Simbirskiasaurus, P. americanus and Brachypterygius as successive sister taxa. The type species, P. platydactylus, and P. americanus and K. sachicarum have been previously recovered as paraphyletic (e.g. Fernández & Campos 2015; Fischer et al. 2016; Jacobs & Martill 2020; Zverkov & Jacobs 2021, but different from Maxwell et al. 2019). The position of K. sachicarum was resolved within a broader clade (Brachypterygiidae) composed of other ophthalmosaur species including the coeval European Sveltonectes insolitus and Simbirskiasaurus birjukovi, and the Colombian Miucasaurus catheti (Fig. 8C).

Phylogenetic discussion

There have been several attempts to clarify the phylogenetic relationships of ophthalmosaurs in recent years (Roberts et al. 2014; Fernández & Campos 2015; Fischer 2016; Ji et al. 2016; Maxwell et al. 2016, 2019; Moon 2019; Zverkov & Jacobs 2021), opening questions about the unstable nature of topologies. However, new material has added useful data that may provide resolution to unresolved topologies (e.g. Maxwell et al. 2016, 2019; Campos et al. 2020; this study). Our strict consensus is consistent with previous studies in recovering a paraphyletic status of the genus Platypterygius, and most earliest Cretaceous taxa closely nested, again with notable exceptions (Athabascsaurus, Acamptonectes). However, this analysis differs from other contributions in retrieving four relatively large clades composed of (1) Ophthalmosauridae; (2) a clade encompassing Palvannia, Janusaurus, Miucasaurus and Arthropterygius; (3) a clade including Platypterygius platydactylus and Undorosaurus; and (4) a clade including Brachypterygius and Kyhytysuka. A close relationship between P. platydactylus and taxa from relatively
high latitudes, and the recovery of *N. saveljevensis* not as sister tax on of *Arthropterygius* species but outside of Ophthalmosauria, also differ from previous analyses.

Two novel evolutionary patterns emerge from the time-calibrated tree (Fig. 8). Nodes were manually positioned to roughly equal minimum branch lengths about

Figure 12. Complete skeletal drawing of *Kyhytysuka sachicarum* comb. nov. based on the holotype skull DON-19671, and postcranial material of the referred specimen CIP-GA-01042014 with relatively similar skull proportions. White colour indicating preserved bones, and grey colour indicating reconstructed elements. Scale bar = 50 cm.

Figure 13. 3D life reconstruction of *Kyhytysuka sachicarum* comb. nov. Illustration by DC.
known occurrences. The details discussed below are not dependent upon these node estimations but on the presence of two hitherto unrecognized radiations. Although most ophthalmosaurs are Late Jurassic in age, there appear to be two radiations hitherto unnoticed. The first is a small radiation of the Palvienia–Arthropterygius clade before the Tithonian. This small clade appears constrained to the Late Jurassic but may have survived well into the Early Cretaceous as the lineage to Muiscasaurus. The second is a Tithonian radiation of derived Brachypterygiidae. The clade is composed of ‘Platypterygius’ americanus, Simbirskaiaurus, Kyhytysuka, Caypullisaurus, ‘Platypterygius’ australis and ‘Platypterygius’ hercynicus. Although Caypullisaurus appears in the Tithonian and crosses the Jurassic–Cretaceous boundary (Fernández 2007), the remainder of the clade is restricted to the Early Cretaceous, indicating long ghost lineages.

Comparison to P. platydactylus and the paralogy of Platypterygius. Platypterygius platydactylus shares with Kyhytysuka sachicarum (DON-19761) some aspects of the morphology of the angular. In both, the angular comprises approximately one-third of the lateral surface of the mandible under the orbit and more than half of the lateral surface of the retroarticular process. These traits are present in most other ophthalmosaurids. Some notable differences can be identified between the specimens. The ventral margin of the mandible under the orbit is broadly sinusoidal in P. platydactylus compared to a relatively straight mandible of DON-19761. The paracoronal process is very reduced in both taxa, but forms a distinct low dorsal projection in DON-19761. Also, the shape of the retroarticular process is curved dorsally with a paddle-like profile in P. platydactylus, whereas it is straight and posteriorly directed in DON-19761. It should be noted that the posterior-most portion of the angular in P. platydactylus seems to be projected far posterior compared to the posterior extent of the articular (Broili 1907, plate XII). This posterior extension of the angular is not present in K. sachicarum, but is observed in P. americanus (Romer, 1968). The contribution of the quadrate to the quadrate foramen of P. platydactylus seems to be greater than that in DON-19671, but this cannot be confirmed. The quadrate condyle is approximately as tall as wide in P. platydactylus but wider than high in DON-19761.

Although several of the above characters have high homoplasy within Ophthalmosauria, as noted previously forcing a monophyletic Platypterygius requires a minimum of nine extra steps and is unlikely given the relatively lower support for most clades within the tree.

The paraphyletic genus, traditionally considered a wastebasket taxon, constitutes a relevant argument against continuing keeping K. sachicarum within the genus. The anatomical differences between K. sachicarum and P. platydactylus and the distant phylogenetic relationships recovered here are used to defend the erection of the new genus. Furthermore, recent phylogenetic analyses (e.g. Fischer et al. 2016) and the one presented here recover no other Platypterygius species sister to P. platydactylus. The non-monophyly of the genus will necessitate erecting a new genus or several genera for these other ‘Platypterygius’ species, including the well-preserved ‘P.’ hercynicus. Thus, the subfamily name and definition of Platypterygius should be revised.

Comparison to other ‘Platypterygius’, Pervushovisaurus campylodon and Simbirskaiaurus. Kyhytysuka sachicarum shares a robust rostrum, a relatively small orbit, forelimb structure and tooth enamel ornamentation with several other species formerly included in ‘Platypterygius’ (Páramo-Fonsca 1997; Maxwell et al. 2019). However, the holotype DON-19761 differs from these in the pronounced size difference in crown height and acuteness along the jaw, narial morphology, a robust lower jaw with the surangular contributing more than the angular to the lateral surface, and shallow fossa surangularis on the mandible (Maxwell et al. 2019).

‘Platypterygius’ hauthali, known from fragmentary forefins and vertebral centra from the Barremian of Argentina (von Huene 1922; Fernández & Aguirre-Urreta 2005) and numerous articulated specimens from the Valanginian-Hauterivian of southern Chile (Pardo-Pérez et al. 2012; Stinnesbeck et al. 2014), is diagnosed by a humerus with a small facet for the extrazugopodial element anterior to the radius, and a hexagonal intermedium in articulation with two digits distally (Fernández & Aguirre-Urreta 2005). ‘Platypterygius’ hauthali differs from K. sachicarum in the shape of the intermedium (pentagonal in K. sachicarum) and digits supported by the intermedium (digit III in K. sachicarum), and in zeugopodial row/proximal carpals relative size (Stinnesbeck et al. 2014; Maxwell et al. 2019). Since cranial material of P. hauthali is undescribed to date, detailed comparison between these two coeval species is not possible.

The narial opening of K. sachicarum is similar to that in ‘P.’ australis. In ‘P.’ australis, the anterior maxilla forms a notch, ventrally enclosing a small anterior narial opening, as in K. sachicarum (Kear 2005). The maxilla contacts the nasal between the anterior and posterior narial openings via a broad contact, also as in K. sachicarum. However, the two taxa differ in that the lacrimal is excluded from the narial opening in lateral view by
an ascending process of the maxilla in ‘P.’ australis but the lacrimal forms the posterior border of the narial opening in *K. sachicarum*, and there is a small foramen posterodorsal to the posterior narial opening (= supranarial foramen of the nasal; Zverkov & Efimov 2019) in ‘P.’ australis but not in *K. sachicarum* (Kear 2005). Moreover, the prearticular underlies the entire length of the articular in medial view in *K. sachicarum*, whereas in ‘P.’ australis the prearticular does not (Kear 2005).

In *K. sachicarum*, the quadrate process of the quadratojugal is short but in ‘P.’ australis it is elongated, a feature that has the potential to become an autapomorphy of ‘P.’ australis (Kear 2005).

‘Platypterygius’ hercynicus from the upper Aptian of Germany–Albian of France shares multiple cranial features with *K. sachicarum*. However, the parietal–frontal suture differs between ‘P.’ hercynicus and DON-19761: the frontal articulates with the parietal posteriorly in ‘P.’ hercynicus (Fischer 2012), whereas it articulates postero-laterally in *K. sachicarum* (Fig. 4F). Moreover, the frontals in *K. sachicarum* taper anteriorly, whereas those of *P. hercynicus* form a broad transverse suture with the nasals, and the occipital lamella of the quadrate is better developed in *K. sachicarum*, dorsally enclosing the quadrate foramen (Fischer 2012). Additional differences are present in the postcranium: the humerus of ‘P.’ hercynicus is broad distally, articulating with four elements in the epipodial row (Kolb & Sander 2009), whereas that of *K. sachicarum* is distally much narrower.

‘Platypterygius’ americanus differs in enamel ornamentation which is extremely lightly faceted enamel compared to that in *K. sachicarum*. The distal humerus bears a facet for a postaxial element in ‘P.’ americanus (Maxwell & Kear 2010); such a facet is absent in *K. sachicarum*.

*Pervushovisaurus campylodon* is diagnosed by its slight overbite, less densely ridged enamel, and acellular cementum with shallow apicobasal ridges and furrows (Fischer 2016). *Kyhytsuka sachicarum* lacks an overbite, and has denser apicobasal enamel ridges on the tooth crown, although variability in the latter character has not been explored in ichthyosaurs so its significance is unclear.

*Simbirksiasaurus birjukovi* from the lower Barremian of the Ulyanovsk area, Russia shares several characters with *K. sachicarum*, but differs mostly in the shape of the narial opening area (Fischer et al. 2014a). *Simbirksiasaurus birjukovi* bears both an anterior and posterior narial opening, as does *K. sachicarum*. However, the shape, direction and arrangement of the bones participating in the nares are different in the two taxa. In *S. birjukovi*, a narrower nasomaxillary pillar of the maxilla separates the anterior and posterior nares than in *K. sachicarum*. The posterior nares of *S. birjukovi* bear an anteroposterior constricted dorsal extension; the posterior opening is round in *K. sachicarum*. The anterior naris of *S. birjukovi* is oval in shape and antero-posteriorly oriented (Fischer et al. 2014a). In *K. sachicarum*, the anterior naris is fusiform in shape and anterodorsally–posterovertrally angled (Fig. 2C). The premaxillary fossa is broader and shallower in *K. sachicarum* than in *S. birjukovi* (Fischer et al. 2014a).

**Comparison to CIP-GA-01042014.** CIP-GA-01042014 is the second known specimen of *K. sachicarum* and the only specimen of this species including postcranial material (Maxwell et al. 2019). CIP-GA-01042014 shares with *K. sachicarum* the densely ridged tooth enamel, tooth shape, robust jaws, shallow surangular fossa on the mandible, surangular contribution relative to the angular on the lateral surface of the lower jaw, and a relatively small orbit (Maxwell et al. 2019). All these features diagnose *K. sachicarum* and CIP-GA-01042014 to the exclusion of all currently known ichthyosaurian material from the Paja Formation, both described and undescribed (Maxwell et al. 2016, 2019; Páramo et al. 2021). However, there are some differences between CIP-GA-01042014 and the holotype DON-19671. The cheek region in CIP-GA-01042014, although moderately well preserved, seems to be antero-posteriorly narrower relative to the orbit (approximately one third the width of the orbit) compared to the broad cheek region in DON-19671 (half the width of the orbit). The parietal–frontal suture in CIP-GA01042014 is ‘v’-shaped whereas it is sloping and deflected in DON-19671 (Fig. 4F). Due to the lack of preserved material in each specimen, no comparisons can be made between postcranial material and braincase.

**Comparison to other ophthalmosaurids.** Morphologically, *K. sachicarum* is consistent with Ophthalmosauria based on the large lateral exposure of the angular, reaching as far anteriorly as the surangular, and a descending process of the nasal on the dorsal border of the nares (Ji et al. 2016). *Kyhytsuka sachicarum* is consistent with Brachypterygiidae based on the quadrangular tooth roots in cross-section. The lower jaw structure is unique to *K. sachicarum* among ophthalmosaurians. The surangular makes a greater contribution than the angular to the lateral surface of the lower jaw. *Capullisaurus bonapartei* from the Tithonian–Berriasian of the Vaca Muerta Formation, Argentina, shares the robust rostrum and the oval shape and large size of the orbits with *K. sachicarum* (orbital ratio 0.16 and 0.20, respectively) (Fernández 1997, 2007); the long anterior exposure of the maxilla in lateral view, and the large lateral exposure of the
is relatively short in *L. stellans* orbit in *tra*. The surangular has less lateral exposure under the laterally broadened to contact the upper temporal fenestra of *K. sachicarum*. In *L. stellans*, the surangular bears a hook shape (Fernández et al. 1997, 2007). In *L. stellans*, the surangular and angular are excluded from lateral view posterior to the mandibular symphysis (Maxwell et al. 2016); in addition, the retroarticular process in *M. cathetii* is dorsally curved and the jaw is more gracile.

**Feeding ecology**

**Tooth shape analysis.** The total tooth height of functional teeth varies threefold, from 26 mm to 8 mm. Surprisingly, the height of the crowns ranges only twofold, from only 12 mm to 5 mm with most crowns about 10 mm high. Much of the variation in tooth height is the product of longer roots rather than longer crowns.

Overall tooth and crown shape vary as well. The anterior-most teeth are pointed with minimal wear and more posterior teeth are blunt with apical wear. However, across this spectrum, we can identify five relatively discrete dental zones using a combination of tooth dimensions and qualitative morphologies (Figs 6, 12). The anterior-most premaxillary teeth (Dental Zone I) are relatively slender and packed to form a terminal rosette of teeth. Probably the first tooth is missing, suggesting this rosette was composed of three teeth. Following the terminology and methods of Massare (1987), the anterior two teeth have shapes of 2.5 (crown) and 3.0 (total tooth). Their pointed, unworn apices and slender shape would be categorized as Pierce II guild. These teeth occlude lingual to the opposing dentary teeth, creating a differentiated tooth region probably used for catching small fish and softer prey. Probably only the anterior-most tooth is missing from the specimen, suggesting this zone would have been composed of pm1–3 (premaxillary teeth 1–3).

The subsequent 10 premaxillary teeth and their opposing dentary teeth (Dental Zone II) present an in phase series of alternating functional and unerupted replacement teeth. These teeth also occlude on the lingual surface of the opposing dentary teeth and share the pointed apices of the anterior-most teeth. Their tooth shape ranges from 1.5 to 2.0 (for both the total tooth and crown) but are over 5 mm shorter (total tooth height and crown) than the anterior dentition. This dental zone also has a relatively high contribution of the crown to overall tooth height (> 60%).

Dental Zone III is composed of larger teeth in the posterior premaxilla and anterior maxilla that are packed

*quadratojugal. Yet, *K. sachicarum* is distinct from *C. bonapartei* in that the former bears both anterior and posterior external nares whereas the latter bears an undivided narial opening (Fernández 1997, 2007). Furthermore, in *C. bonapartei*, the maxilla is excluded from the ventral edge of external nares by the premaxilla–lacrimal contact (Fernández 2007), but in *K. sachicarum*, the maxilla forms the ventral edge of the posterior external nares. Although the nasal of both taxa has a descending process on the dorsal edge of the external nares, it is relatively large in *K. sachicarum* compared to that of *C. bonapartei* (Fernández 1997, 2007). The humerus of *C. bonapartei* has a relatively large distal facet for articulation with a preaxial element (Fernández 1997, 2007), whereas the preaxial facet is small or absent in *K. sachicarum*.

*Leninia stellans*, from the early Aptian of western Russia, bears an anteromedial process of the supratemporal articulating anteriorly with the parietal and narrow frontals (Fischer et al. 2014b); the anteromedial process is relatively short in *K. sachicarum* and the frontals are laterally broadened to contact the upper temporal fenestra. The surangular has less lateral exposure under the orbit in *L. stellans* than in *K. sachicarum*. In *L. stellans*, the prefrontal has an angled suture with the nasal and the lacrimal (Fischer et al. 2014b). In *K. sachicarum*, the contact with the lacrimal and nasal is interdigitating.

*Sveltonectes insolitus* from the late Barremian of western Russia differs from *K. sachicarum* in tooth morphology. In *Sveltonectes*, the tooth crown enamel is poorly defined at its base and bears delicate longitudinal striations (Fischer et al. 2011), whereas in *K. sachicarum* the crown striations are deep longitudinal ridges and the base of the enamel layer is well defined. *Sveltonectes insolitus* also differs from *K. sachicarum* in the arrangement of the nasomaxillary pillar. The nasal of *Sveltonectes* bears a thin and long descending process with a hook shape (Fischer et al. 2011). In *K. sachicarum*, the anterior descending process is flatter and broader compared to that in *Sveltonectes*. The prefrontal in *Sveltonectes* participates in the external nares, separating the nasal and lacrimal (Fischer et al. 2011). In *K. sachicarum*, the prefrontal is excluded from the external nares by a broad contact between the nasal and lacrimal. Additionally, the distance between the orbit and narial opening is at least three times narrower in *Sveltonectes* compared to *K. sachicarum*, in which that distance, represented by the width of the lacrimal, is significantly broad.

*Athabascasaurus* from the lower Albian of Alberta, Canada, has frontals excluded from the temporal fenestrae (Druckenmiller & Maxwell 2010). In *K. sachicarum*, the frontal has a significant contribution to the upper temporal fenestra (UTF).
together forming a near-continuous saw-tooth ridge that occludes on the labial surface of the dentary teeth. All the teeth are fully erupted and oppose smaller dentary teeth. The roots of these teeth are more elongate, even taking into account the missing labial portions of those bones; the crowns of these teeth comprise only about 50% of the height of the tooth. Crown shapes are slightly less than 1.5 and total tooth shapes are slightly more than 1.5. Crowns are blunted and the enamel organized into vertical columns of spheres. The compacted arrangement and large tooth sizes in this zone are unique among ichthyosaurs. In general, ichthyosaurs have regular, interlocking dentition with obvious inter-dental spaces to receive the opposing tooth. However, the continuous tooth edge in Zone III of K. sachicarum presents a robust cutting edge to meet the dentary teeth that occlude lingual to the upper teeth. We speculate this region was specialized for shearing prey, similar to the specialized dentition of some carnivoran mammals.

Dental Zone IV comprises the remaining maxillary teeth, which diminish in size and form an alternating set of erupted and emerging teeth. The crown comprises nearly 60% of the total tooth height. Dental Zone V, the most posterior Zone, is composed of a set of small, tightly packed robust teeth with the shortest crown heights and lowest tooth shapes (<1.0 total tooth).

Estimates of relative stress were calculated throughout the upper dentition using the methods presented by Cohen et al. (2020a, b). We standardized tooth stress to the stress of the anterior-most preserved tooth with complete measurements (pm3), rather than the median-scaled residual stress used by Cohen and colleagues (2020a, b) simply to graph the changes of relative stress starting from the anterior-most tooth. The ranges of relative stress follow a relatively linear pattern throughout most of Dental Zones I–IV. In spite of the differences in tooth size, shape, and intra-tooth morphology, the estimated stresses do not follow the interpreted dental zone boundaries. The evenly distributed estimated stresses suggest the tooth zone differences are mitigating dramatic differences in stresses throughout the dentition. Dental Zone V yields the highest estimated relative stresses despite the smallest tooth sizes due to their proximity to the jaw joint. This relative stress and relatively blunt tooth shape implies their function is dedicated toward crushing (the shape index (<1) is within the crush guild of Massare [1987]).

Parvipelvian ichthyosaurs, in general, are characterized by relatively homodont dentition. The departure observed in K. sachicarum is not described in any other ophthalmosauroid and highlights a unique zonation of dentition. Although the dentition is anatomically heterodont, the estimated relative stresses suggest functional homodonty over dental zones I–IV (Cohen et al. 2020a). We caution, though, that the estimates of relative stress are calculated for each tooth independent of each other and do not take into account the effects of adjacent teeth. Doing so would require more complex equations and would likely yield reduced stresses over zone III as this region has tightly packed, large teeth that would have formed a continuous cutting edge. More significant might be the altering replacement pattern, which could have served to dissipate stress. The dental variation described here also cautions the use of isolated teeth to infer ecologies of ichthyosaurs. For example, Fischer (2016) inferred a generalist feeding guild for K. sachicarum based on measurements from teeth in Zone III.

Lower jaw connective soft tissue. Connective soft tissue preservation associated with ichthyosaurian postcrania are relatively well documented (Lingham-Soliar 2001; Plet et al. 2017; Lindgren et al. 2018); however, connective tissue remains associated with the skull are rarely described or discussed (but see Lingham-Soliar 1999). The potential presence of connective tissue structures lying over the left lower jaw of DON-19671 correspond to those observed in a specimen of Stenopterygius quadriscissus from Holzmaden (MHH 432) (Fig. 9). The elements in DON-19671 are oriented parallel to each other, and are packed along the medial surface of the left lower jaw. Posteriorly, they cluster and form a flat and oblong arrangement; a similar configuration is present in the Holzmaden specimen. In addition, small discoidal structures are present in both specimens, displaying a complex web of structures, which apparently are very common in some formations, and might be diagenetic (i.e. abiotic) in origin (Alexander & Frey 2010).

Although the elements look like fragments of bone, they might be pathologically mineralized soft tissue, or plant remains with carbonate replacement as indicated by Páramo-Fonseca (1997) and Noé & Gómez-Pérez (2020), or even teleost fish bones (e.g. lepidotrichia). If indeed connective tissue, this may be partially decayed skin, muscle fascia, or supporting cutaneous ligaments from the throat region (Fig. 9). Their poor preservation does not allow further speculation on identification pending further analysis.

Diet and feeding. The large body size, robust skull, putative gular soft tissues, and unique heterodont dentition of K. sachicarum can be used to propose its feeding ecology. Most ophthalmosaurs, with the exception of P. hercynicus and P. platydactylus, bear an ear-shaped quadrate formed from a well-developed occipital lamella. The quadrate of P. platydactylus is almost
identical in shape to that of *P. hercynicus* with a slightly better developed occipital lamella and remarkably pronounced quadrate foramen, with an overall ‘J’-shape (see Kolb & Sander 2009, fig. 6; Broili 1907, pl. 13.1). The quadrate in DON-19761 is similar in shape to the quadrate of these two taxa. However, the stapedial facet of DON-19761 is robust with a strongly concave articular surface to receive the stapes. In *Ophthalmosaurus* (Moon & Kirton 2016), the quadrate stapedial facet is oriented posteriorly but is not excavated to reinforce the articulation with the stapes. Typically, the stapedial facet is poorly defined. Miedema & Maxwell (2019) show that even through ontogeny in *Stenopterygius*, there is little change to the contact facet. The robust stapedial facet of DON-19761 reinforces the connection between the quadrate and the braincase, potentially related to increased bite forces.

The extreme restriction of the quadrate condylar cartilage medially and laterally with the full posterior extension could be related to the gape of DON-19761. The reduced medial-lateral cartilage in DON-19761 suggests a very tight jaw joint with no lateral motion (as expected based on jaw architecture). The long symphysis also would limit any transverse or torqueing motion. The posterior surface of the quadrate condyle covered by cartilage could be used to provide an estimated maximum gape. Rotating the articular cotyle against the condyle until the cartilaginous margins meet yields a jaw opening angle of approximately 70–75° (Fig. 10). Although this angle seems extreme, the proportionately enormous prey item preserved as gut contents in *Guizhouichthyosaurus* (Jiang et al. 2020) implies that some ichthyosaurs were capable of consuming remarkably large prey. Moreover, in addition to reinforcement of the quadrate-stapedial contact, the shape of the quadrate mandibular condyle implies a strong bite force. In posterior aspect, the condyle is squared, presenting a robust contact surface. In lateral aspect, the ventral surface of the condyle is more flattened than the more convex posterior surface. This anatomy implies the mandibular joint is relatively mobile at wide gape angles but at low gape angles, the joint would be more constrained in the relatively flatter articulation that may have functioned to assist in resisting jaw opening.

The heterodont dentition of *K. sachicarum* implies it was capable of piercing and grasping with its anterior dentition (Dental Zones I and II), shearing large prey (Dental Zone III), grasping smaller portions of prey (Dental Zone IV), and crushing smaller portions of moderately soft prey (Dental Zone V). These dental specializations and large gape (Fig. 10) imply this ichthyosaur was adapted for capturing and consuming large vertebrate prey. We speculate that the possible presence of ligament-like connective tissues in the floor of the oral cavity were perhaps used to support gular expansion when swallowing large prey. The relatively small orbits and linear jaw line suggest a relatively shallow water ecology (Stubbs & Benton 2016), especially in contrast to the deeper water ecologies hypothesized for the large-eyed ophthalmosaurids (Motani et al. 1999; Motani 2009) (Figs 11–13).

Furthermore, the skull of *K. sachicarum* is strengthened along its long axis with a hypertrophied premaxilla-nasal-frontal bar and a massive and heavily reinforced symphysis. All ichthyosaurs have an elongate symphysis, but it can be very delicately built, consisting only of the dentary. The large splenial contribution is seen in other distantly related megapredatory ichthyosaurs (e.g. *Temnodontosauras*) and may function to resist torque. These suggest the skull was braced for large anteriorly loaded forces. Together, these morphologies support a ‘hypercarnivorous’ lifestyle. Predator–prey interactions in fossil marine reptiles can be assessed from direct evidence i.e. gastric contents (Böttcher 1989; Jiang et al. 2020), or by using morphological and ecological data (Figs 11–13). We attribute *K. sachicarum* to be a high trophic level, relatively shallow water, large vertebrate predator.

**Conclusions**

The re-description of the holotype of ‘*Platypterygius* sachicarum’ DON-19671 provides valuable information to improve the taxonomy of Cretaceous ophthalmosaurians and offers insights into the validity of the genus *Platypterygius*. Our study indicates that DON-19671 is a valid unique ophthalmosaurian taxon supported by morphological and phylogenetic data but phylogenetically removed from *Platypterygius platydictus*, thus merit- ing generic reassignment. *Khytysuka sachicarum*, along with *Muicasaurus*, represent the two ichthyosaur taxa known from the Lower Cretaceous Paja Formation of Colombia but are nested within separate, previously unrecognized radiations. Examination of the holotype and comparative material re-evaluate dental morphologies and function, creating questions regarding skull biomechanics of these upper trophic level predators. Our phylogenetic analyses indicate that *K. sachicarum* is part of a broad radiation of ophthalmosaurians, closely related to European and South American species. The presence of a pathology in the splenial and soft tissue over the lower jaw of the holotype show the potential of calcareous concretions of the Paja Formation to yield interesting preservation of delicate structures. The hypercarnivorous ecology of this Early Cretaceous
ophthalmosaurian signifies a reappearance of this feeding ecology not present in ichthyosaurs since the Early Jurassic.

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