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Endemism that never was? Australian swordfish-like pachycormiform in the Northern Hemisphere

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Abstract

Protosphyraena, a large swordfish-like pachycormiform fish that was globally distributed in the Cretaceous, remains poorly understood due to the fragmentary nature of most specimens. The stratigraphically oldest known records of this genus are dated as Albian in age and are currently represented by isolated teeth, pectoral fins and other fragments in the Northern Hemisphere, as well as partial skulls commonly referred to the endemic genus '*Australopachycormus*' in the Southern Hemisphere. The claim that the Australian protosphyraenine is endemic has been questioned by several authors for the last 20 years; however, direct comparison of protosphyraenines from the Northern and Southern Hemispheres remained impossible, due to the lack of anatomical overlap between coeval specimens. Here, we describe the first articulated skull of *Protosphyraena* discovered in the Albian of the Northern Hemisphere (Northern Caucasus) and survey the previously undescribed materials from the upper Albian of the UK, which allow for direct comparison between Albian protosphyraenines from geographically disparate parts of the world. New cranial materials are highly similar to both the type species, *Protosphyraena ferox* from the Cenomanian–Turonian of England and to the Australian '*Australopachycormus' hurleyi*. This strong similarity suggests that '*A.*' *hurleyi* is not simply a species of *Protosphyraena*, but is the closest species to *P. ferox* and its possible junior synonym. This discovery contradicts the assumed endemism of Australian protosphyraenines and the hypothesised provincialism of large marine vertebrates of the Northern and Southern Hemispheres in the Albian. Moreover, the material from the English Gault Formation potentially includes, in addition to *Protosphyraena*, some asthenocormine remains.

Key Words

Albian, Cretaceous, Pachycormiformes, palaeobiogeography, *Protosphyraena*, Protosphyraenidae

Introduction

Pachycormiformes are an extinct group of Mesozoic actinopterygian fishes that achieved a wide ecological diversity during the Jurassic and Cretaceous, including large pelagic predators and suspension feeders (Woodward 1895; Mainwaring 1978; Lambers 1992; Friedman et al. 2010; Friedman 2012a; Liston and Friedman 2012; Dobson 2019; Cooper et al. 2022; Kanarkina et al. 2026). Amongst them, *Protosphyraena* Leidy, 1857 represents the most derived macropredatory genus, characterised by an elongate rostrum and pectoral fins bearing a serrated leading edge (Loomis 1900; Hay 1903; Woodward 1908). *Protosphyraena* is best known from the Upper Cretaceous (e.g. Woodward 1895, 1908; Loomis 1900; Hay 1903; Diedrich 2001; Hayakawa 2003; Friedman

2012b; Amalfitano et al. 2017), whereas its origin and Early Cretaceous evolutionary history remain poorly understood (Kanarkina et al. 2025a).

Protosphyraena includes numerous species originating primarily from two regions: the United States and the United Kingdom. The North American species mainly derive from the Coniacian–Campanian (e.g. Hay 1903), whereas the English species come from the Cenomanian and Turonian (e.g. Woodward 1908; Friedman et al. 2016). The English material is highly fragmentary and known primarily from rostra. The only exception is *P. ferox*, for which other cranial elements have also been ascribed (e.g. Woodward 1908). However, because most materials from the English Cretaceous consist of isolated remains, *P. ferox* has often been used as a catch-all taxon for protosphyraenine material from these strata (Kanarkina et al. 2025a).

The presence of *Protosphyraena* in the Lower Cretaceous has been documented on the basis of fragmentary remains from the Albian of England (Woodward 1908; Dineley and Metcalf 1999), pectoral fins and some other postcranial fragments from Russia (Kanarkina et al. 2025a), as well as controversial records from Australia, initially described as an endemic pachycormiform taxon, *Australopachycormus hurleyi* Kear, 2007 (Kear 2007; Wretman and Kear 2013; Bartholomai 2015). Although many authors have suggested the synonymy of *Australopachycormus* and *Protosphyraena* (e.g. Friedman et al. 2013; Amalfitano et al. 2017; Dobson et al. 2021; Kanarkina et al. 2025a), some researchers consider *Australopachycormus* to be a valid endemic sister genus to *Protosphyraena* (e.g. Wretman and Kear 2013; Liston et al. 2019; Cooper et al. 2022; Maxwell et al. 2025; Cooper and Maxwell 2025). This latter opinion resulted in a hypothesis that Australia was the source region for longirostrine protosphyraenids (Wretman and Kear 2013; Cooper and Maxwell 2025). As noted by Wretman and Kear (2013: p. 7): '…based on its morphology and much greater age, the first billed pachycormiforms like *Australopachycormus* would appear to have evolved in Australia and subsequently spread out across the immense Tethys Ocean to populate the Northern Hemisphere'. However, this hypothesis is difficult to reconcile with the currently known evolutionary history of the group, as the putative Late Jurassic ancestor of *Protosphyraena*, *Orthocormus*, is at present known exclusively from Europe (e.g. Lambers 1992; Kanarkina et al. 2026).

Beyond the debate over the validity of *Australopachycormus*, the relationships amongst Albian protosphyraenids remain unclear, as direct morphological comparisons between Northern Hemisphere and Australian specimens are limited. Notably, diagnostic cranial material of Albian protosphyraenids is currently described only from Australia (Kear 2007; Bartholomai 2015), whereas the records from the Northern Hemisphere are based on isolated pectoral fins and teeth (Woodward 1908; Kanarkina et al. 2025a).

Here, we report a new occurrence of *Protosphyraena* in the Albian of the Republic of Dagestan, Russia. The new specimens are represented by the skull and two fragments of pectoral fins. Additionally, we describe the known pachycormiform remains from the Albian Gault Formation of England. These materials enable, for the first time, a direct comparison between European and Australian Albian protosphyraenids and address the question of endemicity of the Australian pachycormiforms, while also providing new evidence bearing on the biogeographic history of the group.

Geological context

The specimens described herein originate from the Albian grey clayey marls of the Khadzhalmakhi Formation in the Republic of Dagestan, Russia. The pectoral fins NChM-09 and NChM-10 were collected by O.K.K. from a locality near Gumramakhi Village, Akusha District, Dagestan, in the 2010s (Fig. 1C). The articulated specimen SGM-2169-1 was discovered in autumn 2025 by O.K.K. and J.A.B. near the Chindircero ski resort, Akusha District, Dagestan (Fig. 1D). Initially, only the anterior parts of the jaws were recovered; subsequent excavations resulted in the extraction of the remainder of the skull. Further extraction of the skeleton is possible but challenging and, thus, has been postponed.

The Albian and the Cretaceous, in general, of Dagestan has been studied by numerous researchers since the mid-twentieth century. Early work focused on macrofauna, including ammonites and bivalves, which formed the basis for the first zonal divisions of the deposits (e.g. Rengarten 1951; Glazunova 1953; Kudryavtsev 1960; Mordvilko 1962) [see also Baraboshkin et al. (1997)]. A foraminiferal zonation scheme for the region were as later proposed by Samyshkina (1983) [see also Isaeva (2023)]. Calcareous nannofossils have also been studied (Shcherbinina 2010).

The Khadzhalmakhi Formation, from which the specimens studied here were recovered, was named after the Village of Khadzhal-Makhi (Snezhko et al. 2011). Its thickness in the parastratotype reaches up to 102 m (Snezhko et al. 2011). The formation comprises alternating ash-grey carbonate clays, marls and limestones and also includes dark-coloured intervals enriched in organic matter (Fig. 1C, D). The organic-rich intervals have been correlated with the succession of global anoxic events (Oceanic Anoxic Events, OAEs) based on nannofossil data (Gavrilov et al. 2006; Shcherbinina 2010; Shcherbinina et al. 2011; Shcherbinina and Gavrilov 2015; Gavrilov et al. 2019; Fig. 1E).

These studies of nannofossil biostratigraphy are based on the Aimaki section, situated 30 km from the Akusha section, from which the specimens studied here were recovered (Fig. 1B). The Akusha outcrops were studied in detail by Baraboshkin et al. (1997), who proposed an ammonite biostratigraphic scheme close

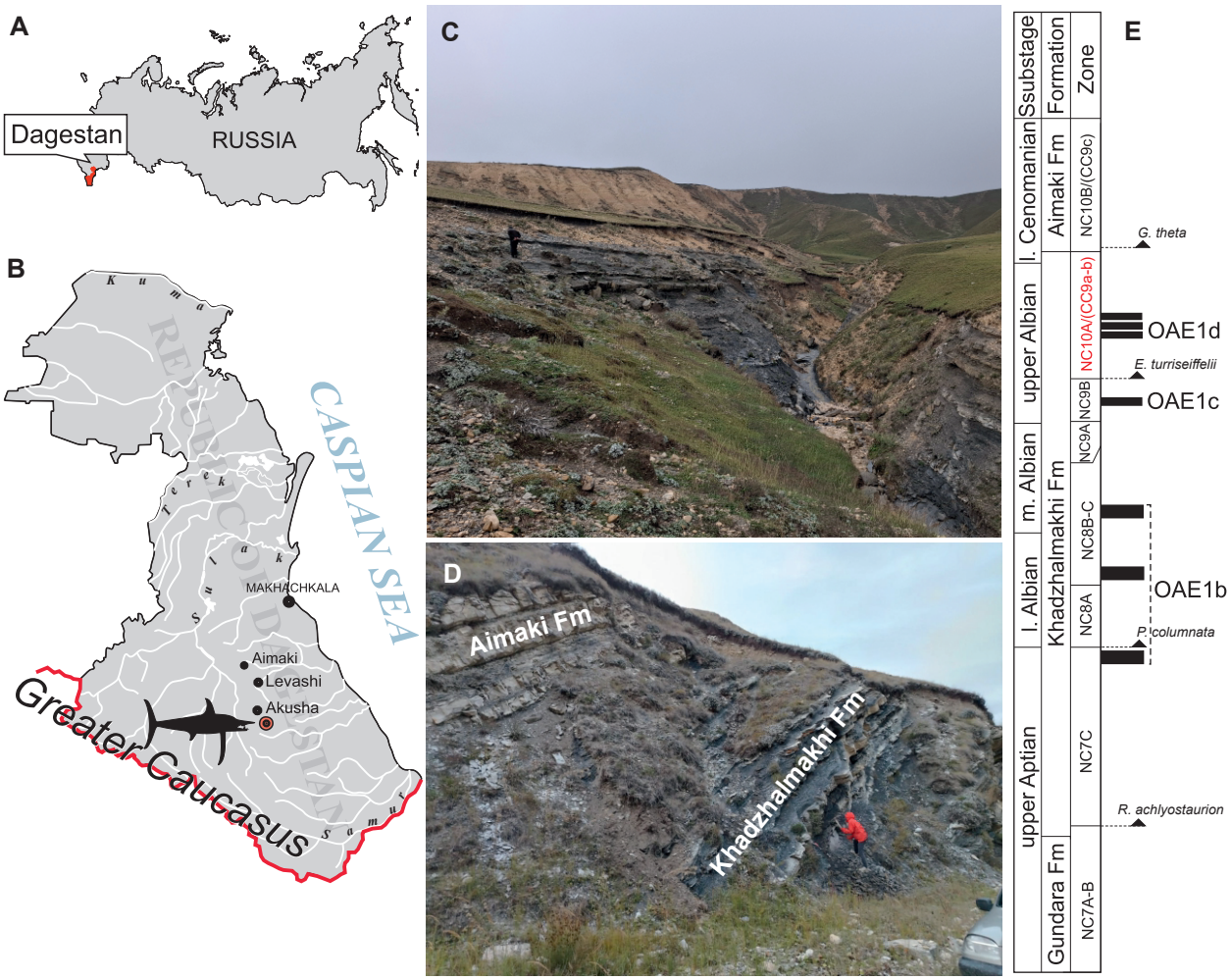

Figure 1. Spatiotemporal setting of the new *Protosphyraena* specimens from the Republic of Dagestan, Russia. **A.** Map of Russia showing the position of the Republic of Dagestan; **B.** Map showing the fossil localities; **C.** Field photograph of the Khadzhalmakhi Fm (Albian) at the site where the pectoral fins of *Protosphyraena* were discovered (Akusha section-1), O.K.K. for scale; **D.** Field photograph of the Khadzhalmakhi Fm (Albian) at the site where the skull of *Protosphyraena* was discovered (Akusha section-2), A.K. for scale; **E.** Stratigraphic scheme of the Khadzhalmakhi Fm, based on nannofossil data of Aimaki section after Shcherbinina (2010); Shcherbinina et al. (2011) and Gavrilov et al. (2019).

to that of Western Europe. *Protosphyraena* specimens described herein originate from the terminal part of the Khadzhalmakhi Fm, the so-called 'fish-layer', corresponding to the uppermost Albian, *Stoliczkaia dispar* Ammonite Biozone (Baraboshkin et al. 1997; Fig. 1C, D) and nannofossil subzone NC10A (CC9a–b) (Shcherbinina 2010; Shcherbinina et al. 2011; Gavrilov et al. 2019). This suggests that the Dagestan *Protosphyraena* specimens are one nannofossil subzone younger than the Australian *Protosphyraena* (Kear 2007; Bartholomai 2015), which is derived from the Toolebuc Formation, corresponding to nannofossil subzone NC9B and containing the Toolebuc event [OAE1c] (e.g. Bralower et al. 1993).

The Khadzhalmakhi Fm is coeval with the Abrek Formation of the Central Caucasus (Snezhko et al. 2011), from which the first discovery of *Protosphyraena* in the Caucasus has been reported (Kanarkina et al. 2025a).

The English Albian pachycormiform specimens originate from the Gault Formation. The Gault Formation (Gault Group) spans the middle to upper Albian of the Lower Cretaceous (Wilkinson 2006) and corresponds to *Hoplites dentatus* (*lyelli* Subzone) – *Stoliczkaia dispar* (*perinflatum* Subzone) ammonite zones (Owen 1976, 2012; Owen and Mutterlose 2006; Wilkinson 2006). Most of the pachycormiform specimens come from Folkestone, East Kent, UK. Pectoral fins CAMSM B 33218 and NHMUK PV P 4511 and premaxilla NHMUK PV P 1796 are from the Barnwell suburb of Cambridge, Cambridgeshire, UK.

Material and methods

Specimen SGM-2169-1 (skull) was donated to the Vernadsky State Geological Museum of the Russian Academy of Sciences, Moscow, Russia. The specimen was prepared by sandblasting by A.K. Specimens NChM-09 and NChM-10 (pectoral fin fragments) are

housed at the Nizhneye Chugli Affiliate of the Kupa Museum of Palaeontology, Archaeology and Local Lore, Dagestan, Russia.

The specimens from the Gault Formation were studied in the collections of the Sedgwick Museum of Earth Sciences (Cambridge, UK) and the Natural History Museum (London, UK).

The phylogenetic nomenclature and beta-taxonomy of Pachycormiformes follow Kanarkina et al. (2026). We use the conservative hypodigm of *Protosphyraena ferox*, based on diagnostic cranial material referred to this species by Woodward (1908) and our subsequent revision (Kanarkina et al. 2025a) and personal observations (A.K. in NHMUK and CAMSM collections, Dec 2025).

Institutional abbreviations

CAMSM, Sedgwick Museum of Earth Sciences, Cambridge University, Cambridge, UK; **LACM**, Los Angeles County Museum, Los Angeles, California, USA; **NChM**, Nizhneye Chugli Museum of Archaeology and Palaeontology, Nizhnie Chugli, Levashinsky District, Dagestan, Russia; **NHMUK**, Natural History Museum, London, UK; **QMF**, Queensland Museum, Brisbane, Australia; **SGM**, Vernadsky State Geological Museum of the Russian Academy of Sciences, Moscow, Russia; **UPM**, Undory Palaeontological Museum, Undory, Ulyanovsk Region, Russia.

Description and comparisons

New specimens from the North Caucasus

Skull. The preserved portion of the skull SGM-2169-1 is approximately 37 cm in length. It includes most of the postrostral part, but lacks the rostrum, mandibular symphysis and most of the opercular region (Fig. 2). The external surface of most of the preserved elements is ornamented by reticulating rugae.

The rostrodermethmoid is not preserved, except for a fragment of its proximal part between the premaxillae (Figs 2, 3A: rd). The ventral surface of the element is distinctly convex. Dorsally, the rostrodermethmoid is buttressed by the median septum (Fig. 3A: rd) comparable to that in other protosphyraenines (e.g. *P. ferox* in Woodward (1908): pl. 31, fig. 1a). The dentigerous part of the rostrum is not preserved and, therefore, the orientation of the rostral teeth cannot be assessed.

The preserved fragment of the parasphenoid (Fig. 3B) is convex ventrally at the anterior portion and concave posteriorly. The ventral median surface of the parasphenoid is covered with small shagreen-like denticles (Fig. 3B). A similar parasphenoid morphology was described in American protosphyraenines by Loomis (1900).

The posterior portion of the neurocranium, comprising paired opisthotics, prootics, exoccipitals, fragmentary intercalar and dermopterotic, (?)pterosphenoid and basioccipital (Fig. 4), is preserved as a separate unit. The arrangement of these elements and their relationships closely resemble those of *Erisichthe nitida* (*Protosphyraena penetrans* in Loomis (1900)), the only Cretaceous protosphyraenid for which this region has been described in detail and the Jurassic protosphyraenid *Orthocormus* sp. (Rayner 1948).

The basioccipital is a large median element (Fig. 4: boc). In general, it is wedge-shaped, gradually tapering anteriorly, but slightly widening near its anterior extremity (posterior width 3.7 cm, narrowest width 2.6 cm). The posterior end of the bone is deeply concave and has an irregularly pitted surface (Fig. 4E, F: boc). On the ventral surface, close to the mid-line, there is a foramen (Fig. 4A, B: boc). The opisthotic (Fig. 4: oot) is a large (width 2.2 cm), paired, rectangular bone with rounded margins, bordered ventromedially by the basioccipital and anteriorly by the prootic. Posteriorly, it bears an opening for the vagus nerve (Fig. 4B: X) and, anteriorly, for the glossopharyngeal nerve (Fig. 4B: XI). Posterior to the opisthotic, a fragmentary intercalar is preserved (Fig. 4B: ic). The prootic is paired, bordered ventromedially by the basioccipital, comparable in size to the opisthotic (width not less than 2.3 cm), but is more square in shape. In its anterior part, it bears a foramen for the facial nerve (Fig. 4B: VII). Anterior to the basioccipital, a small rectangular bone, comparable in size to the opisthotic and prootic (width is about 2 cm), is preserved. By analogy with the skull anatomy of other protosphyraenids (Loomis 1900; Rayner 1948), this element may represent either a pterosphenoid or an orbitosphenoid, but its preservation makes identification difficult (Fig. 4B: ?ptsp). The paired exoccipitals (width 2.3 cm) are dorsally concave bones situated above the posterior part of the basioccipital and contacting each other medially, surrounding the foramen magnum (Fig. 4B: ex). Anterolateral to the left exoccipital, a fragmentary dermopterotic is preserved (Fig. 4B: dpt).

The premaxilla has a generally triangular outline (Fig. 2: pmx, 5A–D), but a complex three-dimensional shape: its ventral half is orientated vertically, whereas the dorsal half is strongly inclined medially and lies in a more horizontal plane (Fig. 5C). It bears an elongate posterior process for articulation with the maxilla (Fig. 5C, D: pmx). The length of the premaxilla is more than 9.2 cm (the anterior acute process is broken off), the height is 2.8 cm. The premaxilla is strongly thickened ventrally (thickness approximately 1.4 cm) due to a swollen longitudinal ridge on its medial surface (Figs 5B, 6A). The anterior process of the maxilla is located above this ridge (Fig. 5A, B). The premaxilla bears seven alveoli with six large blade-like teeth (maximum basal width of 8 mm) and at least four additional smaller teeth (maximum basal width of 1.5 mm) located more posteriorly (Fig. 2: pmx, 5A–D, 6A, B). The six large teeth are in functional position and

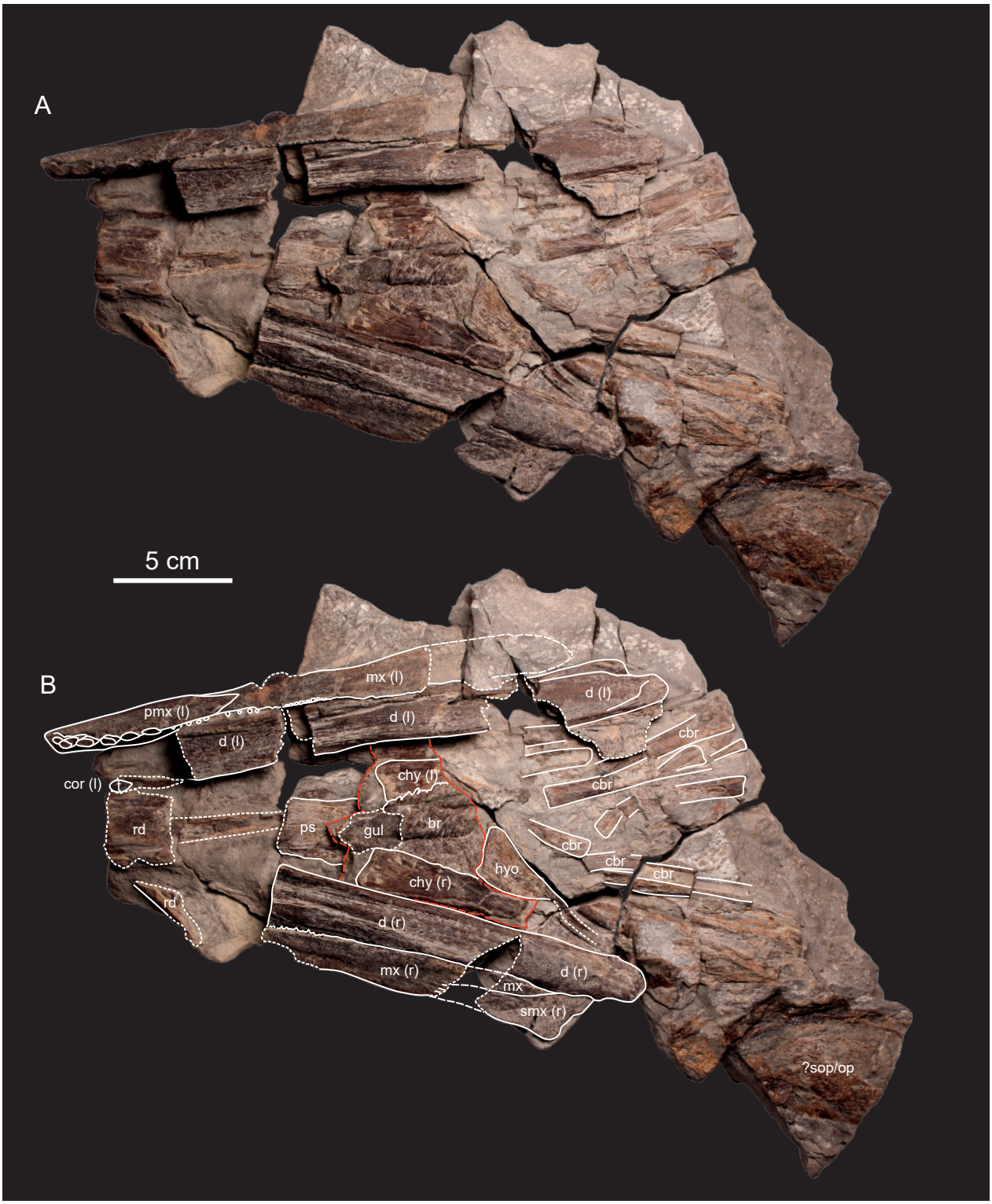

Figure 2. Skull of *Protosphyraena* (SGM-2169-1) from the Khadzhalmakhi Fm (Albian) of the Republic of Dagestan, Russia, general view, ventral surface. **A.** Photograph; **B.** Interpretative line drawing; **br** – branchiostegal rays; **cor** – coronoid; **cbr** – ceratobranchial; **chy** – ceratohyal; **d** – dentary; **gul** – gular plate; **hyo** – hyomandibula; **mx** – maxilla; **pmx** – premaxilla; **smx** –supramaxilla; **op** – operculum; **ps** – parasphenoid; **rd** – rostrodermethmoid; **sob** – suboperculum.

tightly packed, whereas the most posterior (seventh) alveolus is empty (Fig. 6A: 7). Replacement crypts are present on the inner side of the premaxilla adjacent to almost all large teeth (Fig. 6A: r.c.). The number of large premaxillary teeth corresponds to that of *P. hurleyi* (six teeth) and *P. ferox* (up to seven teeth; Woodward 1908), whereas North American species with preserved premaxillae typically possess four or five teeth/alveoli (Loomis 1900). In American protosphyraenines (Loomis 1900) and in some specimens referred to *P. ferox* by Woodward

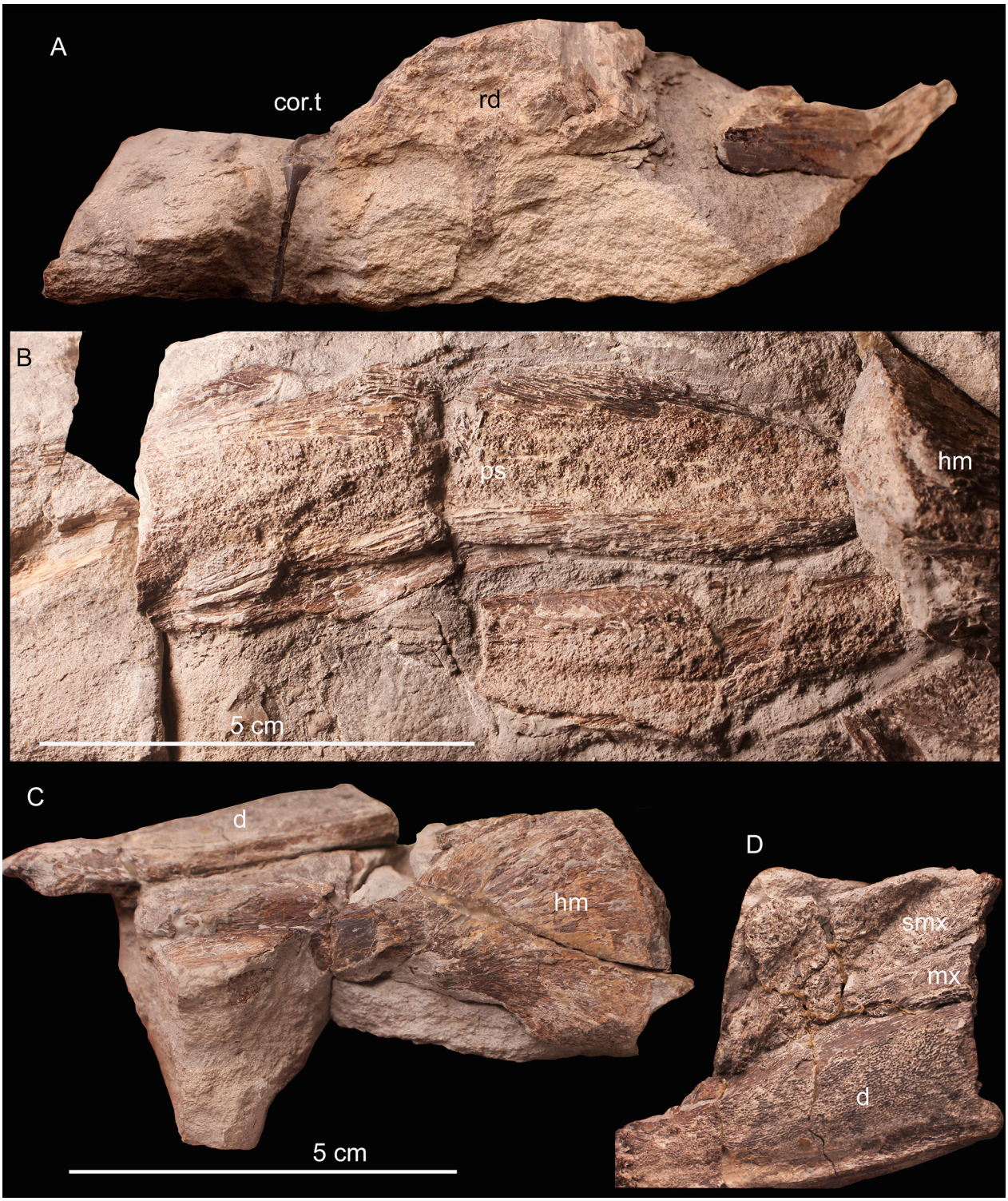

Figure 3. Skull of *Protosphyraena* (SGM-2169-1) from the Khadzhalmakhi Fm (Albian) of the Republic of Dagestan, Russia, additional magnified views. **A.** Anterior view; **B.** Central part without superimposed fragment (the fragment is outlined with a red line in Fig. 2); **C.** Reverse view of right dentary and hyomandibula; **D.** Posterior part of the right half of the jaw with supramaxilla preserved, reverse view; **cor.t** – coronoid tooth; **d** – dentary; **hyo** – hyomandibula; **mx** – maxilla; **pmx** – premaxilla; **smx** – supramaxilla; **ps** – parasphenoid; **rd** – rostrodermethmoid. A and B are the same scale.

(1908: pl. 31, fig. 2), only about half of the teeth are in their functional position, whereas the remaining alveoli are empty. In contrast, in *P. hurleyi* (Kear, 2007) and in some specimens referred to *P. ferox* (e.g. NHMUK PV P 3954 pers. obs; Woodward (1908: pl. 31, fig. 3)), as well as in SGM-2169-1, most of the premaxillary teeth are in their functional position. The taxonomic significance of the number of functional teeth on the premaxilla remains unclear; therefore, we merely report this observation here.

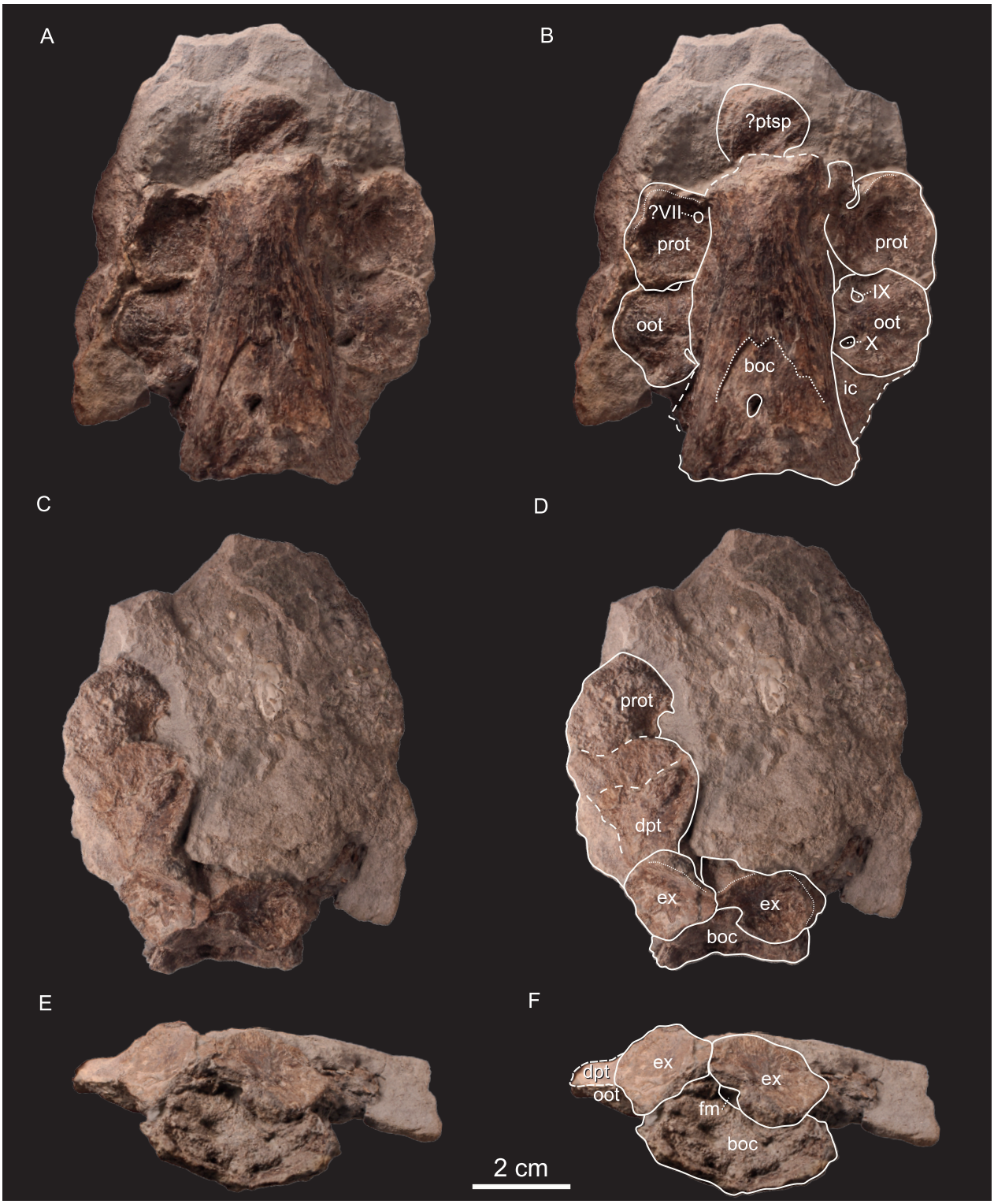

Figure 4. Basicranium of *Protosphyraena* (SGM-2169-1) from the Khadzhalmakhi Fm (Albian) of the Republic of Dagestan, Russia. **A.** Photograph; **B.** Interpretative line drawing; **boc** – basioccipital; **dpt** – dermopterotic; **ex** – exoccipital; **fm** – foramen magnum; **ic** – intercalar; **oot** – opisthotic; **prot** – prootic; **ptsp** – pterosphenoid; **VII** – foramen for facial nerve; **IX** – foramen for glossopharyngeal nerve; **X** – foramen for vagus nerve.

The maxilla is an elongate, straight bone, slightly expanded in its posterior half and becoming lower anteriorly (Fig. 2: mx). The maximum height of the element is about 2.3 cm. Its dorsal margin is slightly thickened (thickness is about 0.9 cm), resulting in a wedge-shaped cross-section (Fig. 5F–I). It bears an elongate anteromedial process forming a tight, immovable articulation with the premaxilla internally (Fig. 5A, B, D: mx). A similar elongate process for the articulation with the premaxilla is observed in *P. hurleyi* (Kear 2007), *P. ferox* (Woodward 1908: pl. 31, fig. 4),

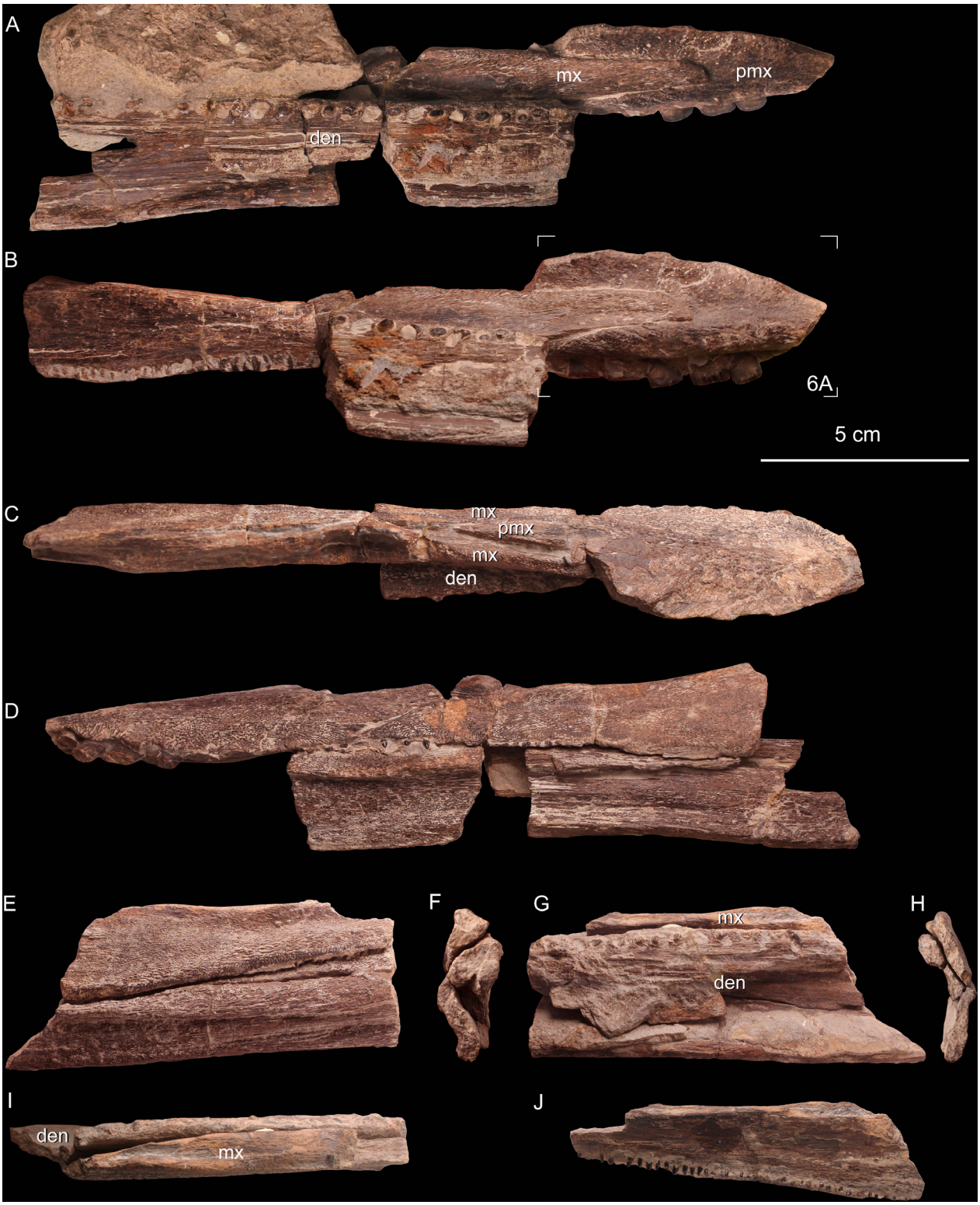

Figure 5. Jaws of *Protosphyraena* (SGM-2169-1) from the Khadzhalmakhi Fm (Albian) of the Republic of Dagestan, Russia. **A–D.** Right; **E–J.** Orthogonal views of left; **den** – dentary; **mx** – maxilla; **pmx** – premaxilla.

American protosphyraenines (Loomis 1900: taf. 19, figs 3, 6) and *Orthocormus* (Kanarkina et al. 2026).

The maxilla bears a single row of very small, blade-like teeth (Fig. 5A–C, J: mx). The largest teeth occur in the anterior part of the maxilla, reaching a maximum basal width of 1.5 mm and a height of up to 3 mm. In the posterior part of the maxilla, these teeth are extremely small and are clearly visible only from the internal side of the element (Fig. 5B, J: mx); externally, they appear absent (Fig. 5D, E: mx).

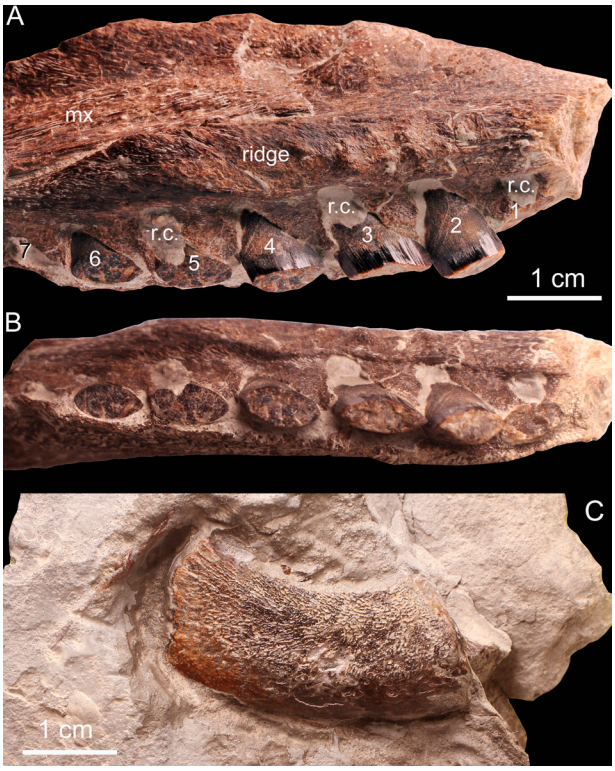

Figure 6. A, B. Magnified right premaxilla of *Protosphyraena* (SGM-2169-1): **A.** Oral view; **B.** Ventral view; **C.** Scleral ossicle (SGM-2169-1). **mx** – maxilla; **r.c.** – replacement crypts; **1-6** – large premaxillary teeth; **7** – seventh empty alveolus.

All species of *Protosphyraena* share a similar maxillary morphology, with teeth that are smaller than those on the premaxilla and dentary. The apparent disappearance of teeth in the posterior portion of the maxilla has also been observed in several species of *Protosphyraena*: *P. hurleyi* (Bartholomai 2015: fig. 3), *P. ferox* (Woodward 1908: pl. 31, fig. 5), *P. tenuis* (Loomis 1900: taf. 20, fig. 7), *P?. sequax* (Felix 1890, taf. 12) and *Protosphyraena?* cf. *sequax* (NHMUK P 10342, pers. obs.).

The fragmentary supramaxilla is observed on the posterodorsal edge of the right maxilla (Figs 2, 3D: smx). The length of the supramaxilla is more than 3.5 cm (not less than 1/5 of the length of the maxilla). It has a subtriangular outline with a concave posterior edge, although its current shape may be due to partial diagenetic deformation. A supramaxilla has not been described for other *Protosphyraena* species, but its presence has been suggested for *P. hurleyi* (Bartholomai 2015).

A fragment of one of the scleral ossicles is preserved on a separate block (Fig. 6C). The ossicle shows clearly defined ornamentation similar to that of other cranial elements and a smooth peripheral margin.

The hyoid arch includes a fragment of the right hyomandibula with an expanded dorsal (?) end (Figs 2, 3C: hyo) and anterior ceratohyals (Fig. 2: chy). Gill-arch remains are represented by bow-shaped ceratobranchials (Fig. 2: cbr).

The branchiostegal series comprises more than 14 preserved pairs of branchiostegal rays (Fig. 2: br) and a single small gular plate located anterior to them (Fig. 2: gul). A similar morphology for the region has been described for *Protosphyraena? sequax* (*Protosphyraena nitida* in Felix (1890)).

The dentary of SGM-2169-1 is elongate, straight and slender (dorsoventrally low) (Figs 2, 5: den). The preserved length of the left dentary is 19.5 cm (excluding the anterior portion); however, the placement of the coronoid tooth indicates that the complete bone would have measured at least 25 cm. The height of the dentary is not less than 3.2 cm. Thus, the dentary height to length ratio was approximately 0.125. Specimens of *P. ferox* (NHMUK PV P 3955; ratio is about 0.1) and *P. hurleyi* (Bartholomai 2015: fig. 3; ratio is about 0.125) show similar values, whereas the dentary of *Erisichthe nitida* (NHMUK PV P 10341) and *Protosphyraena*? cf. *sequax* (NHMUK PV P 10342) have a ratio of about 0.2.

The anteriormost portions of both dentaries are not preserved. The posterior parts remain embedded in the matrix by their dorsomedial surfaces; however, the exposed portion of the left dentary (approximately half of its length) bears a single row of about 25 teeth (Fig. 5A: den). The teeth are oval in cross-section at the base (carinae are not developed in the preserved parts), orientated perpendicular to the oral margin and medium in size (maximum basal width = 3 mm)—larger than those on the maxilla, but markedly smaller than those on the premaxilla and coronoid. The inner surface of the dentary is covered with small shagreen-like denticles, comparable to those of the parasphenoid (Fig. 5A, B: den).

A similar dentary dentition with short, perpendicular teeth, as in SGM-2169-1, is also known in *P. hurleyi* (Bartholomai 2015: fig. 3), *P. ferox* (Woodward 1908: pl. 31, fig. 6) and *P?. sequax* (Felix 1890, taf. 12), whereas *P. tenuis* and *Erisichthe nitida* (Fig. 7A, B, J) are characterised by anteriorly-directed dentary teeth (Cope 1875; Loomis 1900). In contrast, *P?. sequax* is characterised by wide, flattened, teardrop-shaped teeth (Fig. 7D–F, I), while in *P. ferox*, *P. hurleyi* and SGM-2169-1, the teeth are smaller and display a more typical conical shape (Fig. 7G, H, K).

The absence of additional lateral (marginal) dentary teeth, as observed in specimen SGM-2169-1, is documented only in *P. hurleyi* (Bartholomai 2015: fig. 3) and *P. ferox* (Woodward 1908: pl. 31, fig. 6); other *Protosphyraena* species retain these teeth.

At the anterior part of the mandible, a fragment of the left coronoid with a single large tooth (Fig. 2: cor) is preserved. The tooth has well-developed carinae (Fig. 3: cor.t). It is likely that the coronoid originally carried two large teeth, which is a condition typical of all species of *Protosphyraena* and *Erisichthe* (Loomis 1900; Hay 1903; Kear 2007).

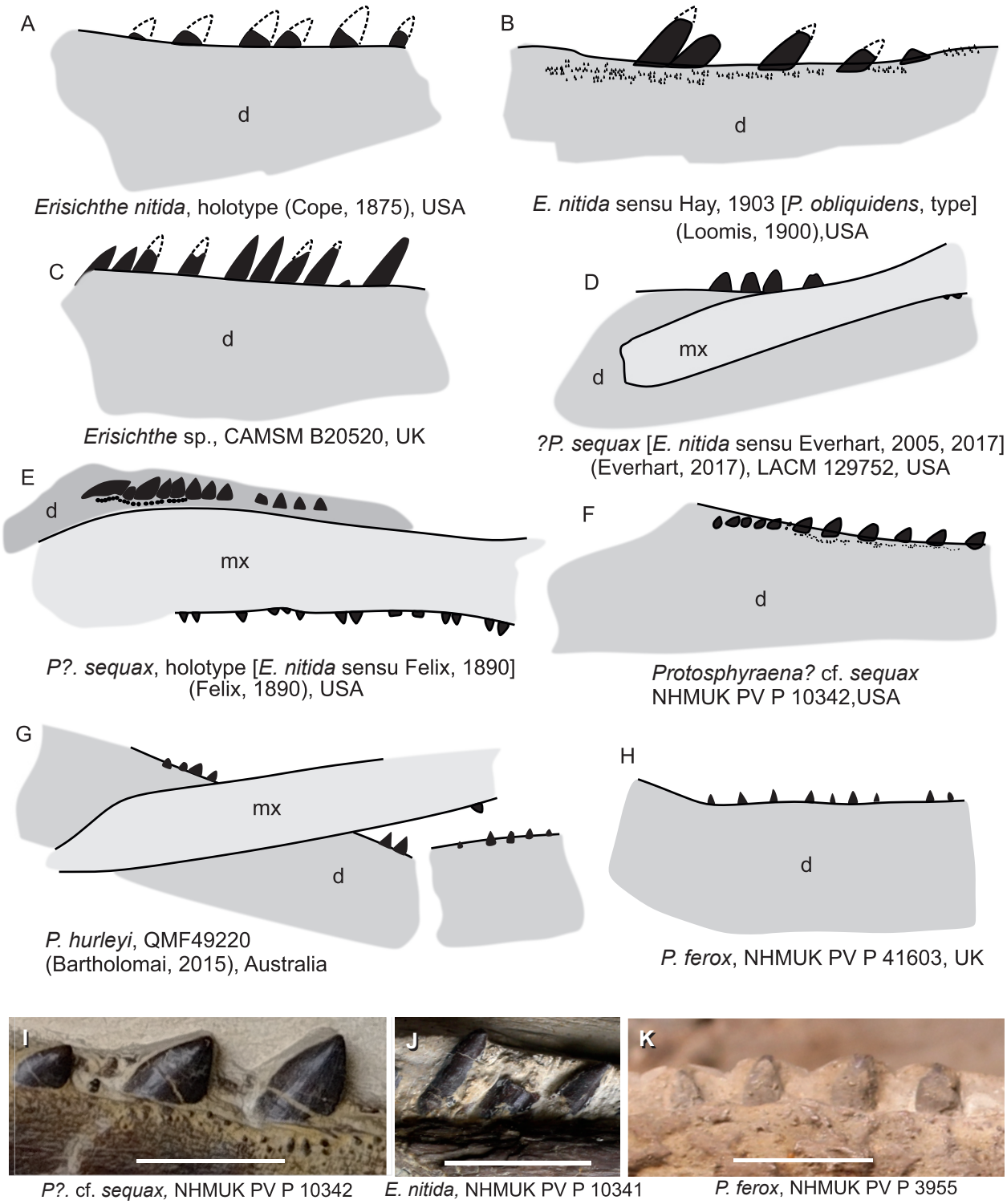

Figure 7. Comparison of the dentary dentition of the Cretaceous protosphyraenines. **A.** *Erisichthe nitida* Cope, 1872, holotype, Coniacian–Campanian, USA, redrawn from Cope (1875); **B.** *E. nitida* [*Protosphyraena obliquidens* Loomis, 1900 in Loomis (1900)], Coniacian–Campanian, USA, redrawn from Loomis (1900); **C.** *Erisichthe* sp., CAMSM B20520, Cenomanian–Turonian, UK; **D.** *?Protosphyraena sequax* [*E. nitida* sensu Everhart (2005, 2017)], LACM 129752, Upper Cretaceous, USA, redrawn from Everhart (2017); **E.** *P?. sequax* Hay, 1903 [*E. nitida* sensu Felix, 1890], holotype, Coniacian–Campanian, USA, redrawn from Felix (1890); **F.** *Protosphyraena?* cf. *sequax*, NHMUK PV P 10342, Coniacian–Campanian, USA; **G.** *Protosphyraena hurleyi* (Kear, 2007), QMF49220, Albian, Australia, redrawn from Bartholomai (2015); **H.** *Protosphyraena ferox* Leidy, 1857, NHMUK P 41603, Cenomanian–Turonian, UK; **I–E.** Dentary teeth: **I.** *Protosphyraena?* cf. *sequax*, NHMUK PV P 10342, Coniacian–Campanian, USA (F); **J.** *E. nitida*, NHMUK PV P 10341, Coniacian–Campanian, USA; **K** *P. ferox*, NHMUK PV P 3955, Cenomanian–Turonian, UK. **d** – dentary; **mx** – maxilla.

Pectoral fins. The fin fragments originate from approximately the same bed (same stratigraphic level) as SGM-2169-1, but from a different locality (see Geological context). Only the solid proximal parts of the fins, consisting of tightly arranged rays, are preserved (Fig. 8A–L). The external surface of the fin rays is smooth overall, but at the leading edge, it has a sandpaper-like ornamentation (Fig. 8L) similar to that of other Albian *Protosphyraena* specimens (cf. Fig. 8M, N), but unlike *Erisichthe* (see Kanarkina et al. (2026): fig. 9F1). The cross-section of the fins (Fig. 8C, K) is typical for *Protosphyraena* (compare with Kanarkina et al. (2025b): fig. 3). The fins had serrations along the leading edge (Fig. 8A, B), but the type of serration (*P. perniciosa* type/*P. tenuis* type) cannot be determined.

In the type material of *P. hurleyi*, the pectoral fin is poorly preserved (Kear 2007). However, isolated fins were later attributed to this species (Wretman and Kear 2013: fig. 3; and NHMUK PV P 73611 referred to this species by Friedman [2012b] and Liston et al. [2019]). Both of these specimens have serrations along the anterior edge, typical of *Protosphyraena*, not *Erisichthe* (see Kanarkina et al. (2026)). However, these fins have different types of serrations. The pectoral fin figured by Wretman and Kear (2013: fig. 3) has serrations that become more pronounced and frequent towards the distal end with triangular, somewhat proximally-inclined, tubercles (as in the North American *P. perniciosa* and *Protosphyraena* from the Albian of Karachay-Cherkessia [Kanarkina et al. 2025a]), while NHMUK PV P 73611 has serrations that become progressively lower and sparser towards the distal tip (as observed in the North American *Protosphyraena tenuis*). In the United States *Protosphyraena*, this difference in the serration pattern serves as the main feature distinguishing *P. perniciosa* and *P. tenuis* (e.g. Hay 1903), which suggests that there may be several species of *Protosphyraena* in the Albian of Australia as well. At the same time, there is an opinion that the difference in the morphology of the anterior edge may be attributed to an intraspecific variation (Hay 1903). However, it is impossible to verify, since nothing other than fins have been described for *P. perniciosa*. Protosphyraenine pectoral fin morphotypes from the Upper Chalk of England suggest the presence of several species differing in the shape and arrangement of serrations (Kanarkina et al. 2025a); thus, the presence of several protosphyraenines in the Albian of Australia or any other region would not be surprising.

In any case, the shape and orientation of the dentary teeth further indicate that SGM-2169-1 belongs to *Protosphyraena*, rather than *Erisichthe* (Fig. 7A–C). This, in turn, suggests that the *Protosphyraena* pectoral fins (NChM-09 and NChM-10) recovered from the same bed may belong to the same species as skull SGM-2169-1.

Specimens from the Albian Gault Formation

Protosphyraena from the Albian Gault Formation of England have so far only been mentioned in literature (Woodward 1908; Dineley and Metcalf 1999; Kanarkina et al. 2025a) without being described in detail. Although the known pachycormiform specimens from the Gault are too fragmentary for any adequate comparisons, we consider it worthwhile to describe and discuss them herein.

CAMSM B 33109 (Fig. 9B) is the best-preserved premaxilla from the Gault. It has a typical triangular outline with a tapered anterior end. The premaxilla bears at least seven large teeth with well-developed carinae. Four of these teeth are fully grown and in their functional position, while three, located in between, are in their early growth stages. In front of the first large forward-directed tooth there is a smaller, vertically-orientated tooth, similar to that of *P. ferox* (Woodward 1908: pl. xxi, fig. 2) and *P. hurleyi* (Kear 2007: fig. 1E). The first three large teeth are directed forward and the remaining four transition from vertical to backward orientation. The number of large premaxillary teeth corresponds to that of *P. ferox* (up to seven teeth; Woodward (1908)) and SGM-2169-1 [six teeth, but seven alveoli].

NHMUK PV P 1796 (Fig. 9A) represents the anterior portion of a larger premaxilla, which differs in its proportions from CAMSM B 33109, being significantly higher and probably shorter. In overall shape, it resembles the premaxilla of more basal protosphyraenids, such as *Orthocormus* and *Erisichthe* (e.g. Loomis (1900): taf. XIX, figs 3, 6; Cooper et al. (2024): fig. 9F). There are three large carinate forward-directed teeth in the preserved anterior part and a smaller vertically orientated tooth in front.

Numerous isolated protosphyraenine teeth are known from the Gault (NHMUK PV OR 47225, 47231, P2298, P14, P5201; CAMSM B33107-8, B42770, B45479, B45480); however, in light of the recent revision of protosphyraenid genera (Kanarkina et al. 2026), their identification at genus level is not possible.

The rostrum CAMSM B 33104 (Fig. 9E) is elongated and circular in cross-section. Its dorsal surface is ornamented with reticulating ridges that are similar to the condition observed in *P. ferox*, *P. compressirostris*, *P. bentoniana* and *P. hurleyi* (Fig. 10) [*P. tenuirostris*, *P. tenuis* and *E. nitida* possess rostral ornamentation consisting mainly of longitudinal ridges; Woodward (1895, 1908); Loomis (1900)]. Its lateral surfaces possess a similar type of ornamentation, but longitudinally-orientated ridges are much more pronounced. It bears two small posteriorly-directed teeth, similar to *P. ferox*, *P. compressirostris*, *P. tenuirostris* (?one small tooth) and *P. hurleyi* (Woodward 1895; Woodward 1908; Kear 2007). The rostrodermethmoid has a median septum (compare with Fig. 3A). The rostrum appears more attenuated than that of *P. ferox* (cf. Fig. 10), resembling the referred rostrum of *P. hurleyi* (Wretman and Kear 2013) in this respect.

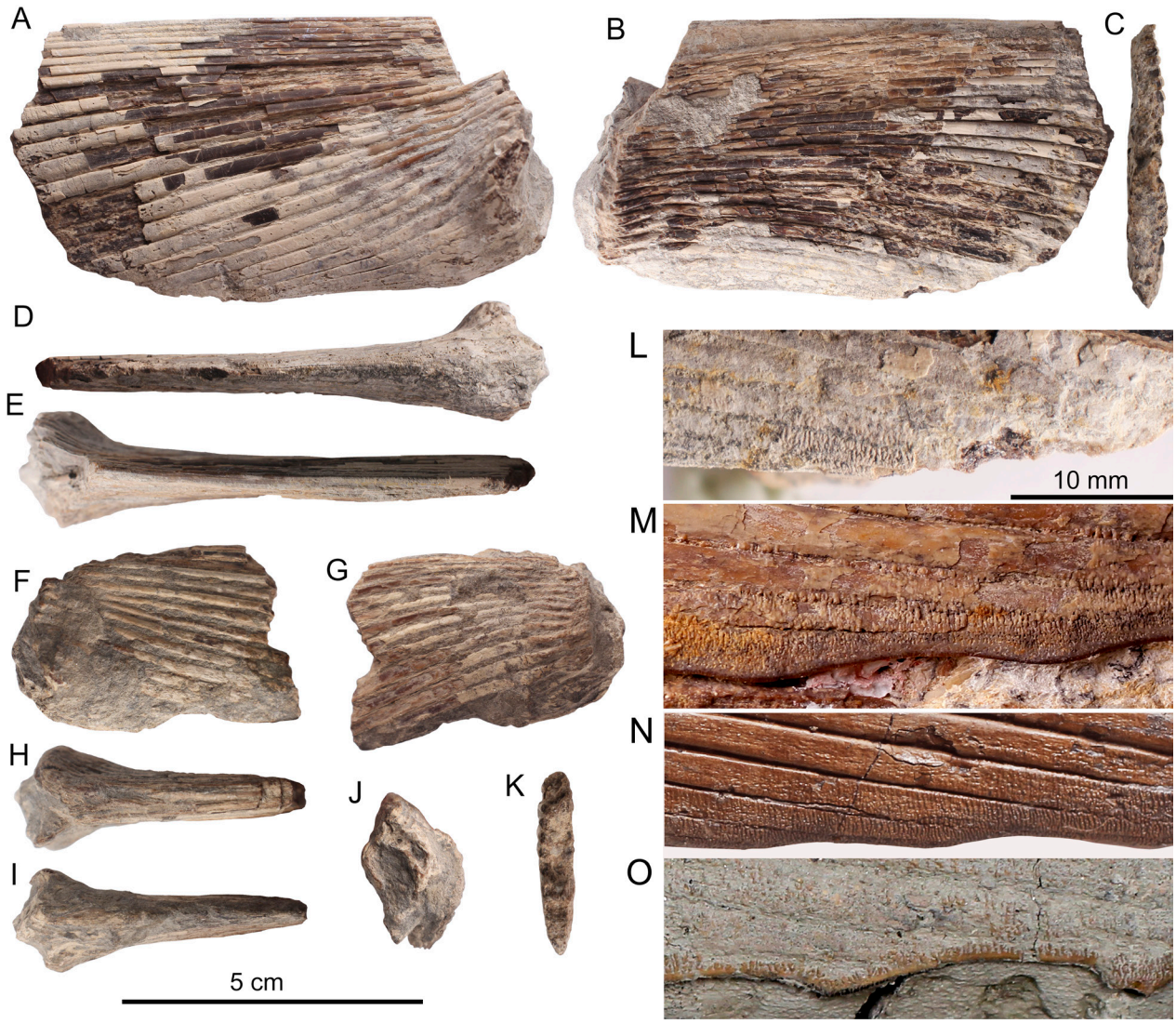

Figure 8. A–L. Pectoral fins of *Protosphyraena* from the Khadzhalmakhi Fm (Albian) of the Republic of Dagestan, Russia: **A–E, L.** Proximal portion of the right fin, NChM-09; **F–K.** Proximal portion of the left fin, NChM-10. Views: dorsal (A, G), ventral (B, F), anterior (D, I), posterior (E, H), proximal (J) and distal, cross-sectional (C, K); **L–M.** Comparison of pectoral fin ornamentation of the Albian *Protosphyraena* specimens; **L.** *Protosphyraena* from the Republic of Dagestan, Russia (NChM-09); **M.** *Protosphyraena* from Australia (NHMUK PV P 73611); **N.** *Protosphyraena* from the Republic of Karachay-Cherkessia, Russia (UPM 3264/1); **O.** *Protosphyraena* from the Gault Formation of Folkstone, UK (NHMUK PV OR 47192b).

In the Gault, two main types of pachycormoid hypural plates can be distinguished (Fig. 9C, D). The first type is rhomboid in outline (CAMSM uncatalogued, xiv.t.67; NHMUK PV P38) owing to a convex distal (posterior) margin (Fig. 9C). It is characterised by a large anterior process, a ventral incisure and poorly-developed ray impressions. This morphology is consistent with that of the Albian *Protosphyraena* from Karachay-Cherkessia (Kanarkina et al. 2025a: fig. 4I, J), *Protosphyraena* from the English Chalk figured by Woodward (1908: pl. XXXII, fig. 3) and some North American specimens (McClung 1908: pl. 13; Arratia and Lambers 1996: figs 9, 10).

The second type comprises kidney-shaped hypural plates (NHMUK PV OR 47191; PV OR 47296) with a concave distal margin (Fig. 9D). The ventral lobe is dorsoventrally lower and anteroposteriorly wider than the dorsal lobe. The anterior process is reduced and the ray impressions are pronounced. This morphology is similar to that of some specimens from the English Chalk referred to *Protosphyraena* by Woodward (1908: pl. XXXII, fig. 2), as well as to a specimen from the Niobrara Formation referred to as *Protosphyraena* cf. *P. tenuis* (Arratia and Lambers 1996: fig. 12E). However, we concur with Maxwell et al. (2025) that highly similar hypural plates of asthenocormines *Asthenocormus* and *Bonnerichthys* suggest that such a hypural plate type may belong not to *Protosphyraena*, but to an asthenocormine.

The pectoral fins from the Gault are fragmentary (Fig. 9F–H). Most specimens consist of portions of tightly packed rays with a poorly-preserved or broken-off leading edge (NHMUK PV OR 36171; PV OR 47192a, b; CAMSM B 33105, B 33106, B 45775). Only a few

Figure 9. *Protosphyraena* specimens from the Gault Fm, UK. **A, B.** Premaxillae: **A.** NHMUK PV P 1796; **B.** CAMSM B 33109; **C, D.** Hypural plates. **C.** CAMSM uncatalogued (xiv.t.67); **D.** NHMUK PV OR 47191; **E.** Rostrum CAMSM B 33104; **F, G.** Pectoral fins: **F.** NHMUK PV OR 47192b; **G.** NHMUK PV OR 47192a.

specimens preserve a serrated leading edge (NHMUK PV OR 35554, PV OR 47192a, b; Fig. 9F, G). The external surface of the fins is generally smooth, but the leading margin exhibits a sandpaper-like ornamentation, similar to that observed in other Albian *Protosphyraena* specimens (cf. Fig. 8L–N). Most fins have a serration morphology similar to *P. gibberula* or *Protosphyraena* from Karachay-Cherkessia (e.g. NHMUK PV OR 47192b, Fig. 9F; NHMUK PV OR 47192a, Fig. 9G; NHMUK PV OR 35554, erroneously noted as *Protosphyraena* cf. *P. spectabilis* in Kanarkina et al. (2025a): fig. 6N).

One of the fins from the Gault, historically catalogued as *Protosphyraena*, exhibits a markedly different morphology. The pectoral fin CAMSM B 33218 (Fig. 11A) also consists of tightly-packed rays and has a cross-sectional shape similar to *Protosphyraena* (Kanarkina et al. 2025b: fig. 3) and protosphyraenines in general (pers. obs. on *Orthocormus gushchinae* and *Paraorthocormus tenuirostris*). However, it lacks any serration and the external surface of its rays is distinctly grooved rather than smooth (Fig. 11A3), resembling the condition observed in *Erisichthe nitida*, *Orthocormus gushchinae* and

Figure 10. Rostrum of *Protosphyraena ferox* NHMUK PV P 5630 from the English Chalk, UK in ventral (top) and lateral (bottom; mirrored for consistency) views. Note pattern of external ornamentation and small, posteriorly inclined rostral teeth.

other basal protosphyraenids (Kanarkina et al. 2026). In contrast to *Protosphyraena*, *Erisichthe*, *Orthocormus* and *Paraorthocormus*, which are characterised by a variety of types of ornamentation along the leading edge (Kanarkina et al. 2026), CAMSM B 33218 lacks any distinct leading-edge ornamentation: the rays along the fin margin are grooved and perforated in the same manner as on the rest of the fin surface (Fig. 11A3, B4, B5). The leading edge of the fin is formed by a series of thin rays (significantly narrower than most of the rays) (Fig. 11B5). Some rays bifurcate in their distal part (Y-type of bifurcation, as in other pachycormiforms) (Fig. 11A2). A fin with an identical morphology to CAMSM B 33218 (Fig. 11B) is housed in the NHMUK (PV P 4511); however, its provenance is indicated as the Cambridge Greensand. Nevertheless, both fins have identical labels bearing the number 89, suggesting that they originate from the same collection (Enniskillen collection, according to NHMUK records). The similar nature of the preservation and sizes suggest that the fins might belong to the same individual. The pyrite covering the surface of both specimens is more consistent with a Gault Formation origin, because pyritisation is not characteristic of the Cambridge Greensand fossils.

Given the plesiomorphic morphology of CAMSM B 33218 and NHMUK PV P 4511, it is reasonable to suggest that these specimens belong either to a more basal protosphyraenid genus than *Erisichthe* and *Protosphyraena* or to some derived asthenocormine, such as *Rhinconichthys* (but not *Bonnerichthys*; see Kanarkina et al. (2025b)). Early Y-type ray bifurcation and a lack of leading-edge ornamentation tend to support the latter option.

In summary, based on isolated remains, several pachycormiform taxa are recognised in the Gault. One of the premaxillae from the Gault is very similar to those of *P. ferox* [and SGM-2169-1]. The hypural plates are represented by two main morphotypes of Cretaceous pachycormiforms, indicating at least two taxa, with some specimens being similar to the hypural of the Albian *Protosphyraena* from the Caucasus (Kanarkina et al. 2025a) and others, kidney-shaped, either representing a different protosphyraenine taxon or some asthenocormine. The only known rostrum from the Gault closely resembles that of *P. ferox*, although it appears more slender with less pronounced ornamentation.

Most pachycormiform fins from the Gault exhibit a morphology similar to the Cenomanian-Turonian *P. gibberula* or the Albian *Protosphyraena* from Karachay-Cherkessia (Kanarkina et al. 2025a); however, their fragmentary preservation precludes detailed comparisons. Additionally, there was a further undetermined pachycormiform taxon (potentially an asthenocormine) in the Gault, currently known only from two fragmentary fins.

These observations do not allow a confident species-level assignment of the *Protosphyraena* material from the Gault, but suggest the co-existence of several pachycormiform taxa in the late Albian of Western Europe, one of which was similar to *P. ferox* and *P. hurleyi*.

Discussion

The preceding morphological description of the SGM-2169-1 skull clearly indicates its assignment to protosphyraenines, based on: presence of a rostrum; ornamentation of the cranial bones with reticulating rugae; relative position and shape of the neurocranial elements; triangular outline of premaxilla with tapered anterior end; maxilla with straight oral margin and an elongate anteromedial process forming an immovable articulation with the premaxilla; extremely small maxillary teeth that are not exposed externally in the posterior half of the element; relative sizes of teeth of the premaxilla/dentary/maxilla with enlarged blade-like teeth on the premaxilla and coronoid, with well-developed carinae.

Comparison of the Dagestan specimen with other Cretaceous protosphyraenines, shows that it shares jaw structural features with the type species *P. ferox* and the Australian *P. hurleyi* (Fig. 12), namely: (1) high dentary

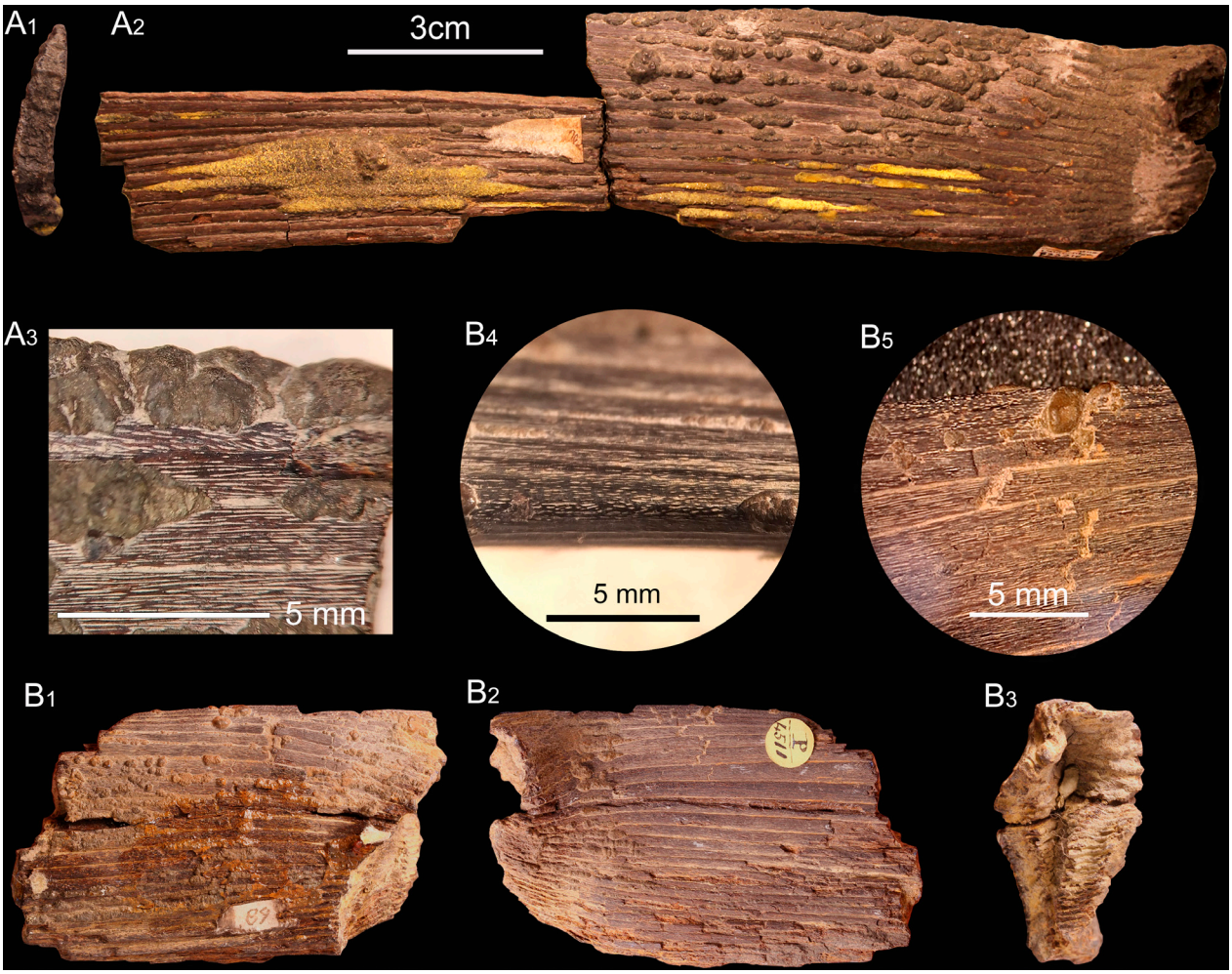

Figure 11. Pectoral fins of Pachycormiformes indet. from the Gault Fm of Cambridge, UK. **A.** CAMSM B 33218; **B.** NHMUK PV P 4511. Views: dorsal (A2, B2), ventral (B1), proximal (B3) and distal, cross-sectional (A1). A3, additional magnified view of A2. B4, B5, additional magnified views of B.

length-to-height ratio, corresponding to an elongated skull; dentary with (2) moderately small and (3) perpendicular teeth [also perpendicular but larger in *P?. sequax*]; (4) absence of additional lateral (marginal) dentary teeth (denticles); and (5) six large premaxillary teeth [in a functional position]. However, the referral of the new specimen from Caucasus to *P. ferox* or *P. hurleyi* is complicated. The only autapomorphy proposed by Kear (2007) for his genus *Australopachycormus* and species *A. hurleyi* (= *P. hurleyi*), was the rostrodermethmoid teeth directed obliquely backwards. The inconsistency of this character has been discussed previously (Kanarkina et al. 2025a), as it is also present in several *Protosphyraena* species, including the type species *P. ferox* (Fig. 10). In addition, Kear (2007) proposed a combination of five characters. Three of these—tapered rostrum, inflated coronoid plate and dentary with procumbent anterior teeth—are shared with *Protosphyraena* (Kear 2007) and more basal protosphyraenines *Erisichthe*, *Orthocormus* and *Paraorthocormus* (e.g. Friedman 2012a; Kanarkina et al. 2026), whereas the remaining two require further commentary. According to Kear (2007), *Australopachycormus* shares the presence of one row of teeth on the dentary only with *Pachycormus*, but the same condition is also observed in *Protosphyraena ferox* (Figs 7H, K, 12) [and SGM-2169-1]. Another character indicated by Kear (2007) is the absence of the frontoparietal boss that *Australopachycormus* shares with *Sauropsis* and *Euthynotus* [according to Kear (2007)]. The structure of this region in *Protosphyraena* is poorly known, but a frontoparietal boss does not appear to be present in American protosphyraenines either (Loomis 1900: pl. xix). Moreover, this character is rather vaguely defined, expressed differently among pachycormiforms and, in fact, requires additional study and discussion.

Thus, at present, the differences between *Australopachycormus* and *Protosphyraena* remain unclear. Furthermore, given the identical backward orientation of the rostrodermethmoid teeth, the similar rostral ornamentation, the overall similarity in jaw morphology and skull proportions (see above), it is difficult to find any perceptible distinctions between *Australopachycormus hurleyi* (= *P. hurleyi*) and the type species, *Protosphyraena ferox.* Phylogenetic analysis

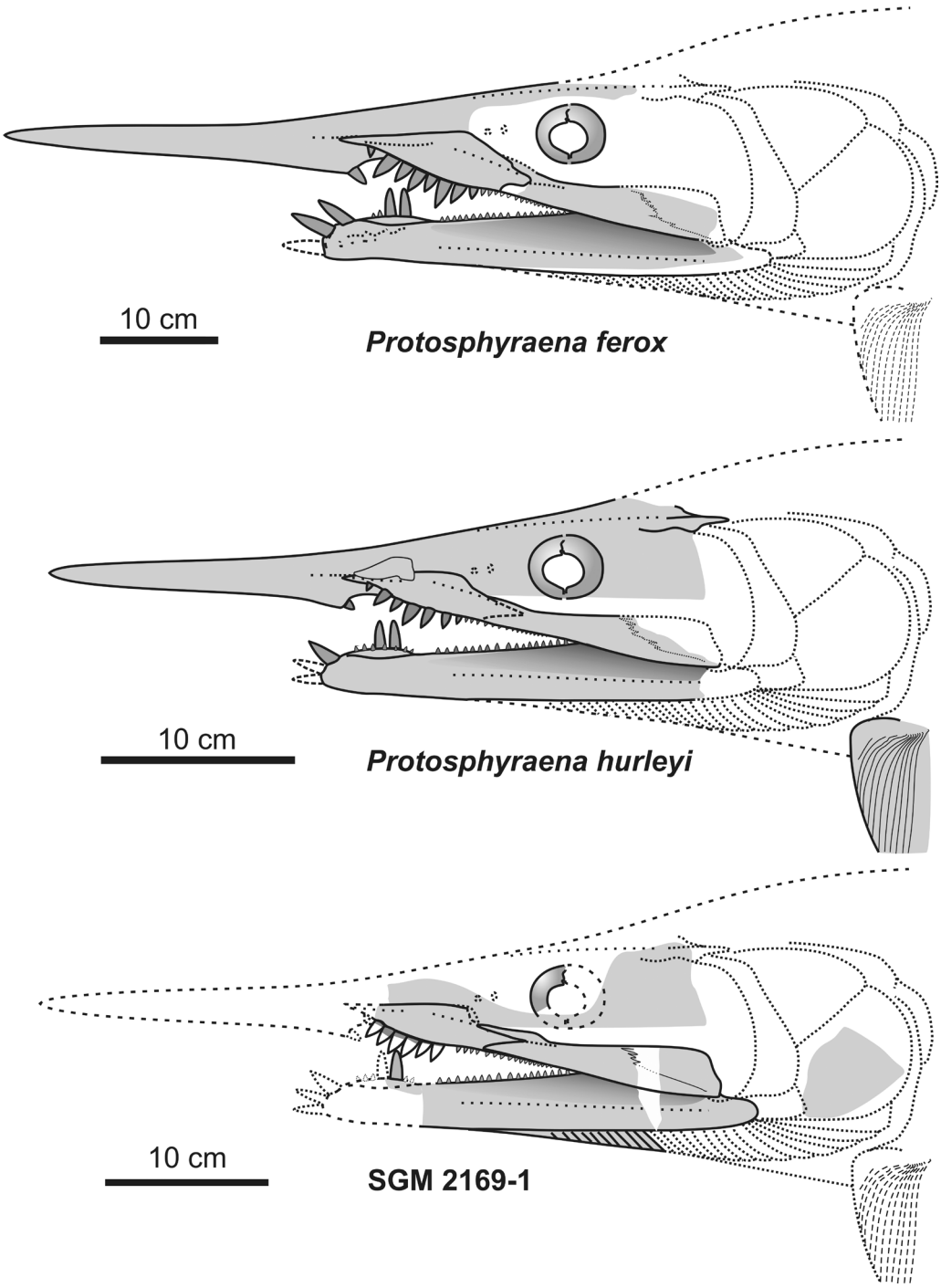

Figure 12. *Protosphyraena* skulls in left lateral view (grey shading indicates the currently known parts of the skeleton). **A.** *P. ferox*, based on NHMUK PV P 6529 associated rostrum and mandible depicted by Woodward (1908); NHMUK PV OR 39438 dentary syntype depicted by Woodward (1908); NHMUK PV OR 49012 premaxilla syntype depicted by Woodward (1908); NHMUK PV P 5634 premaxilla depicted by Woodward (1908); NHMUK PV P 3954 premaxilla (with most teeth preserved), NHMUK PV P 5651 (skull roof and posterior part of premaxilla); NHMUK PV P 3955 (mandible and scleral ring) + NHMUK PV P 3956 rostrum of the same individual (mandible depicted by Woodward [1908]); **B.** *P. hurleyi*, based on Kear (2007); Wretman and Kear (2013) and Bartholomai (2015); **C.** SGM-2169-1.

also supports the close relationship of *P. hurleyi* and *P. ferox* (Kanarkina et al. 2026: fig. 10). Kanarkina et al. (2025a) suggested that differences in coronoid dentition might separate these taxa: Woodward (1908) noted that *P. ferox* lacks small teeth in the posterior portion of the coronoid, whereas Kear (2007) indicated that *Australopachycormus* possesses small coronoid teeth in both the anterior and posterior parts of the element. However, examination of the coronoid in NHMUK PV OR 39438, which belongs to the type series of *P. ferox*, reveals the presence of small partially resorbed alveoli in the posterior region of the bone, suggesting that teeth

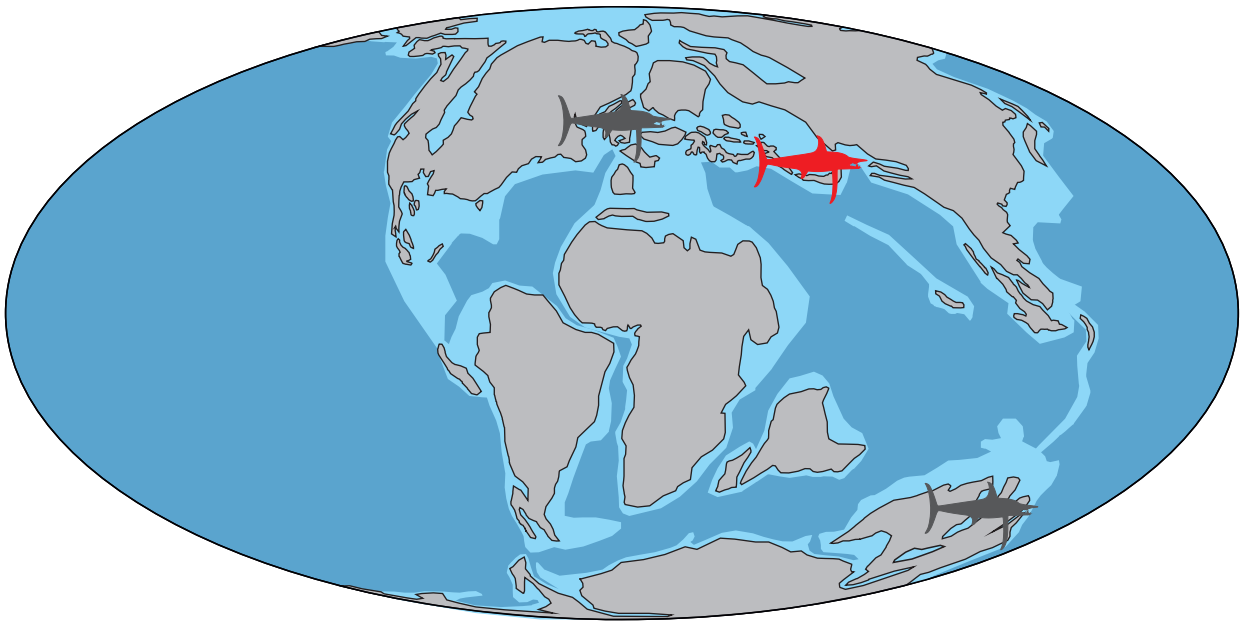

Figure 13. Palaeobiogeographical distribution of *Protosphyraena* in the Albian. Map modified from Scotese (2014), with epicontinental sea outlines partially changed after Blakey (deeptimemaps.com).

were also present there, as in *Australopachycormus* (= *P. hurleyi*). However, the discussed specimens of *P. ferox* are nearly twice as large as known specimens of *P. hurleyi* (Fig. 12) and the SGM-2169-1 specimen. Therefore, the difference in the number of small coronoid teeth may be related to ontogeny. At the same time, SGM-2169-1 is very close in size to one of the *P. hurleyi* specimens (QMF49220), for which Bartholomai (2015) provided the measurements of individual bones (e.g. length of premaxilla 8.76 cm in QMF49220 and 9.2 cm in SGM-2169-1; maximum depth of maxilla 2.06 cm in QMF49220 and 2.3 cm in SGM-2169-1).

The taxonomic conclusions are further complicated by the fragmentary nature of *Protosphyraena* material from the English Chalk, within which several protosphyraenine taxa are clearly present (fins of *P. gibberula*, *P. spectabilis*, *Protosphyraena* cf. *tenuis* and *Erisichthe* cf. *nitida* [see Kanarkina et al. (2025a)]; mandibles of *P. ferox* type [Fig. 7H, K] and of *Erisichthe* type [Fig. 7C]). Nevertheless, historically, most isolated protosphyraenine remains from the English Chalk have been attributed to *P. ferox* by default, which clearly requires revision. The occurrence of different fin morphologies of *Protosphyraena* in the Albian of Australia (see above) adds further complexity to this issue.

Thus, the only clear differences between *P. ferox* and *P. hurleyi* at present appear to be geographic and stratigraphic occurrence: *P. ferox* is known from the Cenomanian–Turonian of Europe (England and European Russia; Kanarkina et al. (2025a)), whereas *P. hurleyi* is recorded from the upper Albian of Australia (Kear 2007). Therefore, at the present state of knowledge, these two species may be regarded as potential synonyms, probably representing an anagenetic lineage. If both *P. ferox* and *P. hurleyi* are considered valid, a confident species-level identification of the SGM-2169-1 skull becomes unwarranted.

Given that the skull morphology of *Protosphyraena* from the Albian of Dagestan agrees with that of *P. hurleyi* from the Albian of Australia, the assumption of endemism of Australian Cretaceous pachycormiforms, which has persisted for nearly 20 years, seems unfounded. We therefore suggest that, already in the Albian, *Protosphyraena* was widespread not only at the generic, but also at the species level. This is not unexpected, given that, during the Albian, both the Caucasus and the Australian Eromanga Sea were connected with the Tethys Ocean (Fig. 13).

The observations on protosphyraenine material from the Gault Formation, including the premaxilla that is highly similar to those of *P. ferox*, *P. hurleyi* and SGM-2169-1, some hypural plates similar to the hypural of the Albian *Protosphyraena* from Karachay-Cherkessia in the Caucasus (Kanarkina et al. 2025a) and the strong similarity between the pectoral fins of the Karachay-Cherkessia specimens and the fins from the Gault (see section ‘Specimens from the English Gault’) further suggests a globally distributed Albian species of *Protosphyraena*. The only known rostrum from the Gault closely resembles that of the stratigraphically younger *P. ferox*, although it appears more slender and with less pronounced ornamentation, potentially indicating the condition present in the Australian *P. hurleyi* (Wretman and Kear 2013). Unfortunately, at this stage of the study, it is still impossible to reliably associate cranial material with pectoral fins for any of the aforementioned species. It is, however, worth noting that the study of undescribed materials in the Australian Kronosaurus Korner Museum (Richmond, Queensland), might finally help unravel this tangled knot of fragmented and non-overlapping *Protosphyraena* specimens.

Conclusions

The skull SGM-2169-1 and pectoral fins NChM-09 and NChM-10 from the Albian of Dagestan, Russia, can be confidently assigned to *Protosphyraena*. As the skull morphology of *Protosphyraena* from the Albian of Dagestan is identical to that of Albian specimens from Australia and Albian–Cenomanian specimens from the UK, the previous assumption of endemism of Australian protosphyraenines during the Albian is no longer tenable. We therefore suggest that *Protosphyraena* had achieved a wide geographic distribution by the Albian, not only at the genus, but also potentially at the species level. Examination of the material from the Gault Formation (upper Albian) of the UK provides additional support for our interpretation. Moreover, some of the specimens from the Gault Formation recorded in museum collections as *Protosphyraena* (some hypurals and pectoral fins lacking serration and ornamentation of the leading edge), may in fact represent the remains of one or more pachycormids.

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