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Behind the missing skull: A unique fin configuration redefines the Jurassic shark †*Palaeoscyllium formosum* Wagner, 1857 (Neoselachii, Galeomorphi)

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Abstract

The holotype of the type species †*Palaeoscyllium formosum* Wagner, 1857 from the Jurassic of Europe, lacking the cranial region, is herein carefully re-described and re-evaluated to clarify the taxonomic and nomenclatural status of this taxon. Post-cranial morphological characters identified through direct revision of the holotype are extensively compared with those of morphologically similar fossil and extant sharks, with particular emphasis on species-specific diagnostic traits. The results confirm the taxonomic validity and applicability of both the genus †*Palaeoscyllium* and its type species. The revaluation of the holotype reveals a distinctive fin configuration not documented in any known living or fossil shark to date. These findings further highlight the remarkable morphological disparity of Jurassic galeomorph sharks, indicating that some fin arrangements present in fossil taxa are absent among extant representatives of the same orders. The study also emphasizes that characters derived from the fossil dermal skeleton should be interpreted cautiously in systematic contexts due to their extensive variability and the potential influence of ecological factors on dermal structures. This study represents an additional step toward clarifying the diversity and evolutionary history of galeomorph sharks during the Jurassic, a crucial interval for their morphological diversification. Future studies reassessing other species and specimens currently referred to †*Palaeoscyllium*, also exploring additional dental and

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MA designed the study, performed investigations and comparisons, wrote and edited the draft of the manuscript and prepared figures; EVS photographed the holotype, performed comparisons and edited the draft of the manuscript; JK performed comparisons, edited the draft of the manuscript, and supervised all phases of the study; MA and JK ensured research funding. All authors read and approved the final version of the manuscript.

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skeletal characters, are highly desirable. Broader comparative investigations into fin position and configuration across extant and fossil galeomorph sharks are likewise required to better understand the structural variability and evolutionary significance of these life traits over a long temporal scale.

Keywords

Comparative morphology; fossil skeleton; Germany; Solnhofen; taxonomy; Tithonian

Introduction

Accurate taxonomic determinations and reassessments are fundamental for a wide range of scientific disciplines, such as palaeontology, biodiversity, and conservation (Schalk and Heijman 1997; Guerra-García et al. 2008; Mollen 2018; White et al. 2022; Amadori et al. 2025). However, the current decline in taxonomic expertise has led to increasingly outdated, inconsistent, or ambiguous species identifications (Guerra-García et al. 2008; Gippoliti 2020; Raposo et al. 2021; Wu et al. 2022; Löbl et al. 2023). Having a stable taxonomic framework is critical, especially in palaeontology, where fossil taxa often are described based on incomplete and fragmentary material, as well as limited diagnostic features (Hughes and Labandeira 1995; Cappetta 2012; Soul and Friedman 2015; Amadori et al. 2025). Morphological traits are mostly used to distinguish between closely related fossil taxa (morphospecies; Cappetta 2012; Underwood et al. 2015; Guinot et al. 2018; Amadori et al. 2025). Taxonomy is particularly crucial for better understanding the complex evolutionary history of neoselachian fishes (i.e. extant sharks, rays, skates, and their closest fossil relatives; see also Compagno 1977), supporting and anchoring the systematic framework necessary to identify, classify, and compare taxa in deep time (Underwood et al. 2015; Straube and Pollerspöck 2020; Amadori et al. 2025; Villalobos-Segura et al. 2025). Most taxonomic identifications for fossil neoselachians rely on dental features (tooth-based taxonomy) as isolated and associated teeth make up most of the shark fossil record, while complete articulated skeletons are comparably rare (e.g., Woodward 1889; Cappetta 2012; Underwood et al. 2015; Guinot et al. 2018; Stumpf et al. 2019; Türtscher et al. 2022; Amadori et al. 2025). The “monodontode dermal denticles” (*sensu* Maisey et al. 2019), often referred to as placoid scales (“Placoid-Schuppen” *sensu* Reif 1973; see also Cappetta 2012), are also very common in the neoselachian fossil record and occasionally used for taxonomic identification (e.g., Thies 1995; Leidner 1997; Thies and Leidner 2011; Rubin et al. 2025). However, the absence of a stable and widely approved framework based on tooth and denticle morphology of both living and fossil species hampers wider, effective use of isolated fossil material in neoselachian systematics (Johanson et al. 2008; Guinot et al. 2018; Mollen 2019; Türtscher et al. 2022; Appleby et al. 2024; Rubin et al. 2025; Villalobos-Segura et al. 2025). Articulated skeletal remains, conversely, have the potential to easily provide essential morphological and/or anatomical details that help to resolve long-standing taxonomic ambiguities, clarify relationships among taxa, and support a more robust phylogenetic framework (e.g., Jambura et al. 2023; Vullo et al. 2024; Villalobos-Segura et al. 2025; Stumpf et al. 2026). Shape and disposition of the fins across the body are also traditionally used to identify and define both extant and fossil neoselachian taxa (e.g.,

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Wagner 1857, 1862; Woodward 1889; Compagno 1977, 2001; Cappetta 2012; Ebert et al. 2021). Reviewing the taxonomy of fossil neoselachians using complete or partial skeletons, rather than relying solely on teeth, is thus crucial for a more accurate classification (Villalobos-Segura et al. 2025). In this perspective, the re-evaluation of type material, which serves as the standard for species definitions, is a priority (see also ICZN 1999). Despite significant advancements in recent years, the taxonomic identity and thus systematic relationships of many enigmatic Mesozoic elasmobranch fishes (i.e., neoselachians and their closest relatives; *sensu* Coates et al. 2018), such as †*Homalodontus* Mutter et al., 2008, †*Palidiplospinax* Klug & Kriwet, 2008, †*Palaeoscyllium* Wagner, 1857, and †*Phorcynis sensu auctorum*, remain ambiguous and require urgent revision (e.g., Pfeil 2021; Amadori et al. 2023, 2024; Jambura et al. 2023; Villalobos-Segura et al. 2024, 2025; Stumpf et al. 2026).

†*Palaeoscyllium* is a fossil selachimorph taxon commonly reported from the Middle Jurassic to the Early Cretaceous of Europe (Cappetta 2012; Stumpf et al. 2019; Villalobos-Segura et al. 2023). Since the establishment of the type species †*P. formosum* Wagner, 1857 based on a partial skeleton from the Tithonian of the Solnhofen Archipelago (Bavaria, southern Germany), various other specimens (both complete skeletons and isolated teeth) and new species have been assigned to †*Palaeoscyllium* for more than a century (see the Historical background section, below). The earliest occurrence of this genus consists of numerous isolated teeth from the Bathonian (Middle Jurassic) of central England assigned to †*P. tenuidens* Underwood & Ward, 2004, while a few teeth from the upper Albian of northeastern England assigned to †*P. reticularis* Underwood & Mitchell, 1999 represent its stratigraphically youngest record (see also Villalobos-Segura et al. 2023). However, the status of the species assigned to the genus †*Palaeoscyllium* requires careful re-evaluation (see also Stumpf et al. 2019). In particular, the holotype of †*P. formosum* (the type species) lacks both the neurocranium and splanchnocranium, as well as the jaws and dentition. This poses a significant challenge for the taxonomic stability of the entire genus. Consequently, a detailed study of the postcranial remains is essential to assess the diagnostic significance of the holotype. Identifying and fully understanding the morphologies observable in the original material of the type species is critical before identifying and comparing other specimens currently included in †*Palaeoscyllium* (see also ICZN 1999). Clarifying the status of †*P. formosum* using the morphological traits still preserved in its holotype will consequently help to avoid possible cascading misidentifications across related species and facilitate a subsequent stable definition for the whole genus.

In the present study, the holotype of †*P. formosum* is carefully re-described and re-evaluated to clarify the taxonomic and nomenclatural status of this species from the Jurassic of Europe. The re-defined post-cranial features based on the holotype revision are accurately and extensively compared with the morphologically closest fossil and extant sharks, also selecting species-specific characters to review the diagnosis of †*P. formosum*. According to the ICZN (1999: Glossary), the holotype of a species is the single specimen (name-bearing type) that provides the objective standard of reference (diagnostic features) for the application of the taxonomic name. The present reappraisal thus aims exclusively to identify unique and unambiguous characters for the type species (here, †*P. formosum*) and ensure the stability of its identity and usage for taxonomic purposes. Any further evaluation of other

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species (and specimens) included in the genus †*Palaeoscyllium* will be the focus of a future dedicated study.

Historical background

Wagner (1857: 291) originally introduced the name †*Palaeoscyllium* by establishing the species †*P. formosum* Wagner, 1857 based on a single skeleton from the lower Tithonian (Upper Jurassic) of the Solnhofen area (Bavaria, southern Germany), but without information about its exact provenance. Wagner (1857) initially provided only a very brief description of the specimen (holotype), comparing it also with a few similar shark taxa, such as the orectolobiform *Ginglymostoma* Müller & Henle, 1837. Later, Wagner (1861: 12, pl. 5, fig. 2) provided the first drawings of the holotype (Fig. 1) and added a few more details to the original description (see also Wagner 1862: 289, pl. 2, fig. 2). In all these descriptions and illustrations of *P. formosum*, the head and teeth are missing. After the original establishment by Wagner (1857), von der Marck (1863) re-introduced the genus †'*Palaeoscyllium*' together with the species †'*P.*' *decheni* based on a single shark skeleton from the Campanian of Sendenhorst (northwestern Germany; see also Nomenclatural remarks in the Systematic Palaeontology section, below). Woodward (1889) established the species †*Palaeoscyllium minus* based on a complete skeleton from the Kimmeridgian of Eichstätt (southern Germany), which was subsequently reassigned to another problematic genus of fossil sharks, †*Phorcynis sensu auctorum* (see Cappetta 1987, 2012; Villalobos-Segura et al. 2023). Later, Cappetta (1987: 84) synonymized †*Palaeoscyllium* Wagner, 1857 with †*Corysodon* de Saint-Seine, 1949 from the Upper Jurassic of Cerin (France) based on similarities of the general morphologies of their skeletons and positions of the fins. However, several authors rejected the assumed synonymy between the two taxa, which are currently accepted as valid and separate from each other (e.g., Frickhinger 1991; Barthel et al. 1994; Thies 1995; Kriwet 1998; Thies and Candoni 1998; Leidner and Thies 1999; Underwood 2002; Kriwet and Klug 2004, 2015; Rees 2005; Sweetman and Underwood 2006; Thies et al. 2007; Thies and Leidner 2011; Cappetta 2012; Leuzinger et al. 2017; Stumpf et al. 2019; Batchelor and Duffin 2023; Villalobos-Segura et al. 2023). In addition to the holotype (partial postcranial skeleton) of †*Palaeoscyllium*, other more or less complete skeletons were assigned to this genus based on general morphological features (e.g., fin shape and size) and/or resemblance in the morphology of dermal denticles (Schweizer 1964; Frickhinger 1991; Barthel et al. 1994; Thies 1995; Leidner 1997; Kriwet and Klug 2004, 2015; Thies and Leidner 2011). Thies (1995: 469, fig. 5F) was the first to discuss the morphology of the dermal denticles of †*Palaeoscyllium*, mentioning only those obtained from the holotype and from other skeletons originally assigned to both †*P. formosum* and †*P. minus*. In the same publication, an additional isolated dermal denticle from the Kimmeridgian of Oker (northern Germany) was figured and assigned to †*Palaeoscyllium* sp. (Thies 1995: fig. 5F). An isolated dermal denticle from the Kimmeridgian of northeastern Spain was also assigned to †*Palaeoscyllium* sp. by Kriwet (1998: pl. 4, fig. 11). The dermal denticles of the holotype of †*P. formosum*, as well as from two other skeletons originally assigned to the same species, were later described and figured by Leidner (1997: pl. 37–42), Leidner and Thies (1999: fig. 2B) and Thies and Leidner (2011: pl. 46–51). Leidner and Thies (1999: 34) assigned an additional skeleton to †*P. formosum* based on the morphological similarity of the dermal denticles of the holotype and this new skeleton

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(see also Leidner 1997: pl. 41, fig. 1). Unlike the holotype, this previously unidentified, articulated specimen also preserves associated teeth (Leidner and Thies 1999: fig. 3F). Based on these, numerous isolated teeth were subsequently assigned to various species of †*Palaeoscyllium* (Mudroch 2001; Underwood 2002; Kriwet and Klug 2004; Rees 2005; Sweetman and Underwood 2006; Thies et al. 2007; Thies and Leidner 2011; Cappetta 2012; Leuzinger et al. 2017). Underwood (2002: 304) synonymized †*Palaeoscyllium formosum* Wagner, 1857 and †*Parasymbolus octevillensis* Candoni, 1993 and transferred the species †*P. reticularis* Underwood & Mitchell, 1999 from the Early Cretaceous to †*Palaeoscyllium*. Two other species of †*Palaeoscyllium*, †*P. tenuidens* Underwood & Ward, 2004 from the Middle Jurassic, and †*P. striatum* Underwood & Ward, 2008 from the Late Cretaceous, were established based on isolated teeth. Subsequently, Guinot et al. (2013: 69) established the new genus †*Sigmoscyllium* and included †*P. striatum* in it. More recently, almost complete articulated skeletons assigned to the genus †*Palaeoscyllium* were included in a study of another shark from the Upper Jurassic of the Solnhofen Archipelago (†*Bavariscyllium* Thies, 2005), highlighting the need for further in-depth studies to clarify the taxonomy and phylogenetic relationships of †*Palaeoscyllium* (see Stumpf et al. 2026).

Geological and geographical setting

The Solnhofen Archipelago, where the holotype specimen of †*Palaeoscyllium formosum* Wagner, 1857 originated, represented a complex lagoonal system located along the northwestern margin of the Tethys Ocean during the Late Jurassic (Villalobos-Segura et al. 2023). The exceptional fossil preservation within this setting (Konservat-Lagerstätten) is attributed to stagnant, hypersaline bottom-water conditions combined with rapid burial by episodic storm-induced sedimentation (Villalobos-Segura et al. 2023). The region's limestones encompass diverse depositional and stratigraphic contexts, but most historically collected fossils originate from deposits assigned to the early Tithonian Altmühltal Formation (Villalobos-Segura et al. 2023). Although the exact provenance of the holotype of †*P. formosum* remains unknown, it most likely was recovered from strata of the early Tithonian Altmühltal Formation.

Material and methods

Material

The holotype specimen (SNSB-BSPG AS I 1365) of †*Palaeoscyllium formosum* Wagner, 1857 from the lower Tithonian (Upper Jurassic) of the Solnhofen Archipelago in Bavaria (southern Germany) is part of the Häberlein Collection currently housed in the Bayrische Staatssammlung für Geologie und Paläontologie in Munich (southern Germany). The specimen consists of articulated post-cranial elements of a shark skeleton preserved on a slab of micritic lithographic limestone ("Lithographische Schiefer"; see Wagner 1857) characterized by extremely fine grains.

Methods

A Sony Alpha 7 M3KIT camera with a mounting 28–70 mm macro lens was used to take high-quality photos of the specimen SNSB-BSPG AS I 1365. The images of the fossils and illustrative drawings (both fossil and extant) were prepared using the software

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package Photoshop CS6 (v.25.0). The illustrative drawings depicting the variability in fin position among living sharks are based on selected species representative of each different fin arrangement (common and unusual) found within the various families of the group of interest (here, the superorder Galeomorphii). The red dotted lines in these comparative drawings, which highlight the relative positions of the fins in extant and fossil galeomorph sharks, were drawn at their starting and/or ending points, considering the fin total length as defined in Ebert et al. (2021). The fossil specimens considered for the morphological comparison with †*Palaeoscyllium formosum* Wagner, 1857 (see the Discussion section, below) were selected from the best-preserved holomorphic skeletons documented in the relevant literature and belonging to the galeomorph sharks (see also Suppl. material 1: table S1). Measurements of both the heterocercal angle (angle of upward bend of the vertebral axis) and the hypocercal angle (angle between the body axis and the line extending from the base to the tip of the ventral lobe) were taken to describe the orientation and direction of both lobes of the caudal fin, following Kim et al. (2013). Anatomical and odontological terminologies used in the present study follow Goto (2001), Cappetta (2012), and Kim et al. (2013). Fin morphology and topography follow Ebert et al. (2021), while the terminology for dermal denticles follows Rubin et al. (2025). The different fin configurations are compared here mainly on the basis of their relative position (location described in relation to the other fins) rather than their absolute placement along the body.

Institutional abbreviations

Institutional acronyms and abbreviations follow Sabaj (2020): CM, Carnegie Museum of Natural History, Pittsburgh, USA; JME SOS, Jura-Museum Eichstätt, Germany (SOS indicates specimens from the Solnhofen area); NHMUK PV P, Natural History Museum in London, UK (PV, paleovertebrate collections); MHNL, Musée des Confluences, Lyon, France; SNSB-BSPG AS, Bayerische Staatssammlung für Paläontologie und Geologie (Bavarian State Collection for Paleontology and Geology), München, Germany (SNSB, Staatliche Naturwissenschaftliche Sammlungen Bayerns; AS, “Alte Sammlung”, used for specimens that entered the collection before 1944 and whose original numbers could not be reconstructed); SMNK-PAL, Staatliches Museum für Naturkunde Karlsruhe, Germany (PAL, fossils).

Systematic Paleontology

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Superorder Galeomorphii Compagno, 1973

Order Incertae Sedis

Family Incertae Sedis

Genus †*Palaeoscyllium* Wagner, 1857

Type species: †*Palaeoscyllium formosum* Wagner, 1857.

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Diagnosis: Same as for the type species due to mono-typy according to ICZN (1999: art. 67 and 68.3).

Remarks: Wagner introduced †*Palaeoscyllium formosum* Wagner, 1857 with a brief and concise description, but which clearly refers to the holotype figured subsequently (Wagner 1861, 1862). A first general description for the genus was provided only later by the same author (see Wagner 1861, 1862), providing characters that were intended for identifying the genus. The identification of additional unique characters for †*Palaeoscyllium*, including possible tooth features, is here deferred pending the evaluation of other skeletal specimens to be included in the genus (Amadori et al. in prep.). We tentatively consider four holomorphic specimens (CM 4780 [labelled as †"*Phorcynis catulina*"], SMNK-PAL 44950, SNSB-BSPG AS I 589a-b, and JME SOS 7885 [labelled as †"*Macrourogaleus hassei*"]) that all were recovered from the Upper Jurassic lithographic limestones of the Solnhofen Archipelago as possible members of †*Palaeoscyllium*, but with species status uncertain, pending further evaluations.

†*Palaeoscyllium formosum* Wagner, 1857

Figs 1, 2

Holotype: The specimen SNSB-BSPG AS I 1365 (see Fig. 2) from the Upper Jurassic of the Solnhofen Archipelago in southern Germany, preserving only the postcranial skeleton but completely lacking the head (both cranium and dentition are missing). The holotype was originally described by Wagner (1857: 291) and subsequently figured by him (see Wagner 1861: pl. 5, fig. 2; Wagner 1862: pl. 2, fig. 2; see also Fig. 1).

Referred specimens: Only the holotype (SNSB-BSPG AS I 1365).

Nomenclatural remarks: Wagner (1857: 291) undoubtedly established the type species †*Palaeoscyllium formosum* in accordance with the requirements reported in the ICZN (1999: art. 12) and, consequently, it must be considered as 'available' (i.e., exist for the purposes of zoological nomenclature; see also Notton et al. 2011). Furthermore, the name-bearing type material of the species (holotype, catalogue number: SNSB-BSPG AS I 1365) provides a set of species-specific characters (see also the Amended diagnosis section, below). This set of unambiguous morphological features represents an "objective standard of reference", making the name both valid and applicable for taxonomic purposes (see ICZN 1999: art. 61; see also Notton et al. 2011). According to the ICZN (1999: art. 42.3, 43, 67), the name-bearing type of a genus (or subgenus) is its nominal taxon, called its "type species" (see also ICZN 1999: Glossary), and its application is determined with reference to such nominal species. Therefore, the validity here confirmed for the type species †*P. formosum* also applies to the genus name †*Palaeoscyllium*.

After the original establishment by Wagner (1857), von der Marck (1863: 67, pl. 8, figs 6–9) erroneously re-introduced the genus †'*Palaeoscyllium*' with a different type species, †'*P.*' *decheni* (see also Cappetta 2012: 290). However, Marck's genus name is preoccupied by †*Palaeoscyllium* Wagner, 1857 (see ICZN 1999: art. 23; see also Cappetta 2012). According

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to the “Principle of Homonymy” (see ICZN 1999: art. 52), the name of each taxon must be unique. †*Palaeoscyllium* von der Marck, 1863 is thus a junior homonym of †*Palaeoscyllium* Wagner, 1857 and, although available, must not be used as a valid name for taxonomic purposes (see ICZN 1999: Glossary and “Principle 5” of the Introduction). Consequently, the species †‘*P.*’ *decheni*, together with the material assigned to it (see Bertling 2018: fig. 44.5), should be moved to a different genus (see also Cappetta 2012: 289). Müller (1989: text-fig. 12, pl 15, fig. 1) moved †‘*P.*’ *decheni* to the genus †*Paratriakis* Herman, 1977 based on morphological similarities between the teeth associated to the skeleton (holotype) of †‘*Palaeoscyllium*’ *decheni* and those used by Herman (1977: pl. 12, figs 5, 6) to establish the taxon †*Paratriakis bettrechiensis* (type species of †*Paratriakis*) and those assigned to †*Palaeotriakis curtirostris* Davis, 1887 (ex †*Paratriakis curtirostris*).

Amended diagnosis (after Wagner 1862: 289; asterisks indicate species-specific characters): A fusiform shark with short, rounded, triangular paired and unpaired fins. The pectoral fin is anterior to the dorsal fin and well separated from the pelvic fin. The pelvic fin originates approximately at the midpoint of the dorsal fin with a straight anterior margin and wide base*. Both dorsal fins have a convex anterior margin, but they slightly differ in proportions, with the second dorsal fin being narrower and higher than the first one. The anal fin originates posterior to the anterior margin of the second dorsal fin and is well separated from the caudal fin*. The anal fin is wide with a straight anterior margin that is longer than the posterior one. The caudal fin is markedly heterocercal with a shallow, angular posterior notch that separates the upper lobe from the lower one*. The lower lobe is triangular and well developed, but shorter than the upper one. The radial elements of the pelvic and dorsal fins are slender and not reaching the distal margins. The vertebrae are fully mineralized. The caudal vertebrae have short epichordal radials and hypochordal processes. Dermal denticles (placoid scales) have a small base, short peduncle, and inclined crown. Denticle morphology varies from arrow-shaped with ridges to oval without ornamentations, depending on the position across the body. Pointed arrow-shaped denticles characterize the head region and the dorsal fins. Pelvic and caudal fins have rounded arrow-shaped denticles. The anal fin is characterized by oval denticles, which are the only ones lacking ridges.

Locality, horizon, and age: The type specimen, SNSB-BSPG AS I 1365, comes most likely from the *Hybonoticeras hybonotum* zone of the lower Tithonian of the Upper Jurassic (compare Schweigert 2015) of the Solnhofen area Archipelago in Bavaria (southern Germany; see also Villalobos-Segura et al. 2023). The specimen most likely was recovered from one of the stone quarries in the vicinity of the village of Solnhofen.

Re-description of the holotype: SNSB-BSPG AS I 1365 (Fig. 2) is an incompletely articulated skeleton embedded in a limestone slab in lateral view. The post-cranial outline and a few skeletal remains are clearly recognizable, while all skeletal and soft body elements of the head are missing. Its general body shape is elongated and fusiform, tapering posteriorly. Only one of each paired fin (pectoral and pelvic) is preserved (see Fig. 2A). Although the proximal portion of the pectoral fin (Fig. 2B, p1f) is not visible (not fully preserved or covered by matrix), its distal potion is wide and rounded. The latter is placed anteriorly to the first dorsal fin. The pelvic and both dorsal fins are triangular with round

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apices (Fig. 2A). The pelvic fin (Fig. 2B, p2f) originates in line with the midpoint of the dorsal fin and the distance between the pectoral and pelvic fins is around 78 mm. The complete outline of the pelvic fin has a wide base and a straight anterior margin. Both dorsal fins are similar in shape with an anterior margin slightly curved (Fig. 2A). The first dorsal fin (Fig. 2B, d1f; length: 63 mm; height: 36 mm) is wider than the second one (Fig. 2B, d2f; length = 48 mm; height = 36 mm). The anal fin (Fig. 2B, af) originates at the midpoint of the second dorsal fin and is well separated from the caudal fin. The anal fin is asymmetric with a wide base (length = 44 mm) and a straight anterior margin (42 mm) that is longer than the posterior one (23 mm). The caudal fin (Fig. 2B, caf) is short and asymmetrical with the upper lobe longer than the lower one, which is triangular, and the vertebral column continues into the upper lobe (heterocercal). The two caudal lobes are wide and divided by a shallow, angular posterior notch (Fig. 2B, pn) forming an obtuse angle of about 146°. The heterocercal angle of the caudal fin is ca. 23°, while the hypocercal angle is ca. 40°. Although the upper postventral margin of the upper caudal lobe is slightly damaged in some areas, it has a regular outline with no obvious discontinuities running from the posterior notch to the posterior tip (Fig. 2B, pt). The posterior tip is large and rounded.

Concerning the skeletal elements of SNSB-BSPG AS I 1365 (Fig. 2A, B), all structures of the neurocranium and splanchnocranium are not preserved, while some post-cranial cartilaginous remains are recognizable. Those include most of the vertebral column and portions of basal and radial elements of the pelvic, dorsal, anal, and caudal fins. Overall, traces of at least 98 fully mineralized vertebrae are clearly observable (Fig. 2B, vc). The anterior-most vertebrae are missing, while those at the level of the first dorsal and caudal fins are poorly preserved. The pectoral and pelvic girdles, as well as the skeletal elements of the pectoral and pelvic fins, are not preserved. Although partially covered in skin, some basal and radial elements of the pelvic fin are clearly recognizable. For the unpaired fins, only the radials (Fig. 2B, rd) are preserved. In the proximal region of the caudal fin, hypochordal processes (Fig. 2B, hcp) are recognizable directly ventral to the vertebrae, while short epichordal radials (Fig. 2B, ecr) are barely visible only towards the tail end. All radial elements are slender and limited to the proximal region of the fins; no segmentation is observed, possibly because of their poor state of preservation. In addition, patches of skin are recognizable on the tip and external margins of the fins (see Fig. 2B).

Different morphologies are recognizable in the twenty-three dermal denticles detached from different regions of SNSB-BSPG AS I 1365 (Fig. 2C, D), which can be grouped into three different morphotypes (here named α, β, and γ). All denticles of SNSB-BSPG AS I 1365 (Fig. 2C, D) have a single plane of symmetry (antero-posterior) and a short peduncle, which is wider than its height and connected to the crown in the centre with a posterior obtuse angle (see Fig. 2C, D). The crown is larger than the base protruding over it all around. Morphotype α (Fig. 2D) has an arrow-shaped crown with a rounded, anterior margin and a single-vertex posterior side; the marginal micro-texture is smooth on all sides. The anterior edge is scalloped with three bulges (one central, two lateral) separated by two deep notches. The vertex consists of a rounded cusp protruding posteriorly from the denticle crown. Two slender, straight ridges start at the anterior margin of each bulge and converge towards the posterior vertex. Often, each ridge running along the central bulge is further paired in double ridges that can fuse posteriorly. Double ridges rarely occur on the lateral bulges. All ridges

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are equally marked and well defined, while the rest of the crown surface is relatively smooth, without a recognizable secondary texture. Morphotype β (Fig. 2D) is almost identical to the previous morphotype but differs in having less distinct notches between the three bulges, ridges mostly limited to the anterior area of the crown, and a more rounded posterior vertex (no well-developed cusp). Morphotype γ (Fig. 2D) has an oval crown with no bulges or notches (smooth anterior margin) and a very wide, rounded posterior edge (no cusp); the ridges are absent. In morphotypes α and β, the ridges do not always reach the posterior margin of the denticle crown in some of them because they are markedly abraded.

Discussion

Authorships and further details of all taxa mentioned in the present Discussion chapter are reported in Suppl. material 1: table S2.

Morphology of the holotype of †*Palaeoscyllium formosum*

In general, the state of preservation of the specimen chosen as type material (skeleton SNSB-BSPG AS I 1365; Fig. 2A, B) for †*Palaeoscyllium formosum* by Wagner (1857) is quite poor (see also Thies and Candoni 1998; Cappetta 2012; Villalobos-Segura et al. 2023). After the original, brief establishment, Wagner (1861: 12) provided a better description of the holotype and mentioned for the first time the lack of teeth, arch elements, and some vertebrae (see also Wagner 1862: 289). There are some inconsistencies, however, between the original and subsequent descriptions. Different from what was claimed in the first descriptions of †*P. formosum*, the “entire body outline” (“der ganze Körperumris”; see Wagner 1857: p. 291) of the shark is not recognizable in the holotype SNSB-BSPG AS I 1365 (see Wagner 1861, 1862). Indeed, there is no evidence that the “elongated blunt-tipped shape” (“gestreckte stumpfspizige Form”; see Wagner 1857: p. 291) of the imprint observable on the anterior side of the slab (Fig. 2A) actually reflects the real outline and proportions of the shark’s head. Consequently, the total length of 1.5 feet (≈ 457 mm) reported by Wagner (1857, 1861, 1862) for the type specimen should be considered no more than an approximate estimate. Contrary to what was reported initially by Wagner (1857), the vertebral column is actually incomplete due to a calcite formation that destroyed its anterior-most portion (see also Wagner, 1861, 1862). However, the complete mineralisation of the vertebral centra indicates that †*P. formosum* undoubtedly is a neoselachian.

Although the position of the pectoral fin cannot be determined with precision in †*P. formosum* due to its poor preservation, it is clearly placed far more anterior than all other fins (Fig. 2A, B). Any more precise interpretation concerning the shape, size, and position of the pectoral fin of †*P. formosum* (see Wagner 1857, 1862) remains speculative and unreliable. Since the first description by Wagner (1857), the position of the pelvic fin originating at the midpoint of the first dorsal fin has been recognised as a distinctive feature of †*P. formosum* (see also Wagner 1862). In all other neoselachians with two dorsal fins and one anal fin (galeomorphs), the pelvic fins insert either further anteriorly or much more posteriorly along the body (see the Comparative body morphology section, below). Conversely, the alignment of the anal fin with the midpoint of the second dorsal fin, considered by Wagner (1857) also as distinctive, is a feature shared by several

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galeomorph sharks (e.g., *Carcharias, Ginglymostoma*, and *Mustelus*; see Ebert et al. 2021). The difference in size of the dorsal fins of †*P. formosum* was a subject of debate in the past (e.g., Thies and Candoni 1998; Kriwet and Klug 2004; Cappetta 2012). The state of preservation and curvature seen in the holotype (Fig. 2A, B) might have complicated preliminary comparisons in the past. This has probably resulted in conflicting opinions, with some authors advocating for a very similar size of both fins (e.g., Cappetta 2012: 280), while others suggested that the second dorsal fin was smaller than the first one (e.g., Thies and Candoni 1998: 225; Kriwet and Klug 2004: 88). Although the size difference between the two fins is not great, the accurate measurement performed in this study reveals that the base of the first dorsal fin is truly wider than the one of the second dorsal fin, while their height is approximately the same. Although partially over-looked in the original descriptions, the separation between the anal and caudal fins in †*P. formosum* is a crucial feature for comparative purposes (see also the Comparative body morphology section, below). The presence or absence of the subterminal notch cannot be confirmed due to the poor preservation of the terminal portion of the upper caudal lobe (see Fig. 2A; see also Wagner 1862).

More than a century after the original description of the holotype of †*P. formosum*, Leidner (1997: pls. 37, 38) figured for the first time dermal denticles extracted from various regions of the holotype (see Fig. 2C; see also Thies and Leidner 2011: 77, pl. 46). The classification of the different denticle features into three morphotypes proposed in the present study (see above) is consistent with the brief discussion of their morphologies previously provided by Leidner (1997: 17). Morphotype α characterizes denticles extracted from the head region, the dorsal fins, and lateral areas close to the pectoral and pelvic fins (see Fig. 2C). The denticle detached from the second dorsal fin likely has its posterior cusp broken (Fig. 2C, ? α). Denticles with morphotype β were isolated from the pelvic fin and the ventral area immediately posterior to it and from the caudal fin (see Fig. 2C). The ridges of dermal denticles detached from the pelvic fin are abraded (see also Leidner 1997). The only denticle recognized as morphotype γ was isolated from the anal fin (see Fig. 2C); no abrasion has been observed on it (see also Leidner 1997). Morphotype α (arrow-shaped with pointed cusp and deep notches) mostly characterizes the anterior and dorsal regions of the skeleton SNSB-BSPG AS I 1365, while morphotypes β and γ were collected only from more ventral and caudal areas.

Comparative body morphology

The poor state of preservation of the holotype of †*Palaeoscyllium formosum* (Fig. 2A, B) and the absence of the cranial region complicates the identification of unambiguous characters and, consequently, the rigorous taxonomic determination of this taxon. However, the shape and position of all fins included in the present comparison (pelvic, both dorsal, anal, and caudal) are clearly recognizable in the articulated skeleton of †*P. formosum* (see Fig. 2A). In particular, the body configuration (here intended as the arrangement of the different components across the body) and shape of †*P. formosum* (here intended as only the post-cranial region) reveal important morphological features when carefully compared with those of other extant and fossil galeomorph sharks (carcharhiniforms, heterodontiforms, lamniforms, and orectolobiforms). Among neoselachians (*sensu* Compagno 1977), the

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latter resemble †*P. formosum* in having a similar general shape and same number of fins (see Ebert et al. 2021). Conversely, squalomorph sharks (echinorhiniforms, hexanchiforms, pristiophoriforms, squaliforms, and squatiniforms) are excluded from the present comparison as they lack one of the two dorsal fins or the anal fin, unlike †*P. formosum* (Fig. 2; see also Ebert et al. 2021). Concerning fossil taxa, the present morphological comparisons between different body shapes and fin configurations mainly target species known from well-preserved, articulated skeletons. This reduces misinterpretations due to possible taphonomic alterations of the fossil material considered, which can never be excluded *a priori* (Lyman 1994). In the following, the fin placement of †*P. formosum* is compared with other extant and extinct galemorph sharks to establish similarities and dissimilarities.

Carcharhiniforms: Extant carcharhiniform sharks have pelvic fins placed much further posteriorly than †*Palaeoscyllium formosum* except for most members of the living families Pentanchidae and Scyliorhinidae (Fig. 3A–N). Both the latter indeed have a body configuration that is commonly observed in some groups of orectolobiform sharks (e.g., orectolobids, parascylliids, brachaelurids, and hemiscylliids; see also Ebert et al. 2021). The pentanchid sharks *Bythaelurus bachi, B. giddingsi, B. naylori, Cephalurus cephalus, Parmaturus albipenis* and *P. angelae* are the few noteworthy exceptions having the anterior margin of the pelvic fins aligned with or slightly posterior to that of the first dorsal fin (Fig. 3C–E). However, the origin of the anal fin is anterior to the second dorsal fin in these pentanchids, unlike in †*P. formosum* (see also Ebert et al. 2021). The pentanchid *Pentanchus profundicolus* is the only known galeomorph shark having a single dorsal fin, which clearly separates it from †*P. formosum* (see Ebert et al. 2021).

Among fossil carcharhiniforms, the caudal fin of †*Paratriakis decheni* (ex †'*Palaeoscyllium*' *decheni*) is very different in shape from that of †*P. formosum* without separation between caudal lobes (no posterior sulcus) and a poorly developed lower lobe (compare Bertling 2018: fig. 44.5). Unfortunately, the poor preservation of the skeletons assigned to †*Paratriakis decheni* and †*P. curtirostris* does not allow for any further, reliable comparison (see Cappetta 1980: pl. 24, fig. 1; Frickhinger 1991: text-fig. on p. 187). Both †*Scyliorhinus angustus* (ex †'*Thyellina angusta*'; Fig. 3O) and †*S. elongatus* (Fig. 3P) differ significantly from †*Palaeoscyllium formosum* in having pelvic and anal fins that originate anterior to the first and second dorsal fins, respectively (see also Wagner 1861, 1862). The minor morphological similarities between †*P. formosum* and †*Corysodon cirinensis* (Fig. 3A, Q) have been the subject of much debate since Cappetta (1987) proposed the alleged synonymy of the two taxa (see Thies and Candoni 1998; Leidner and Thies 1999; Kriwet and Klug 2004; Cappetta 2012; Villalobos-Segura et al. 2023). Various morphological features that are potentially useful for separating †*P. formosum* and †*Corysodon cirinensis* were highlighted over the years (e.g., Thies and Candoni 1998; Kriwet and Klug 2004). The size of the fins in relation to the body length mentioned by Thies and Candoni (1998) should not be considered a reliable morphological trait, as the body length of †*P. formosum* cannot be accurately determined because the head region is completely missing (see above). The position of the pelvic and anal fins in relation to the two dorsal fins is nearly identical in †*P. formosum* and †*C. cirinensis*, thus not providing any significant distinction between

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the two taxa (Fig. 3A, Q). The size difference of the dorsal fins is another aspect often mentioned in the literature for separating †*P. formosum* and †*C. cirinensis* (e.g., Thies and Candoni 1998; Kriwet and Klug 2004; Cappetta 2012). De Saint-Seine (1949: 14) provided the measurement of the bases of the dorsal fins for the holotype of †*C. cirinensis* with the second dorsal fin (52 mm) being slightly wider than the first one (50 mm), unlike in †*P. formosum* in which the condition is reversed (see above). In addition, the clear separation of the anal and caudal fins in †*P. formosum* is an even more distinctive characteristic separating it unambiguously from †*C. cirinensis*, in which both are placed very closely to each other (see also Thies and Candoni 1998; Kriwet and Klug 2004). In both †*Eogaleus bolcensis* (Fig. 3R) and †*Galeorhinus cuvieri* (Fig. 3S), the pelvic fin is placed much more posteriorly than the first dorsal fin and a very deep posterior sulcus is clearly recognizable, differently from the body configuration in †*P. formosum*. The same differences are also observable in the fossil skeleton (Fig. 3T) tentatively assigned to the family Carcharhinidae by Frickhinger (1991).

Heterodontiforms: Extant heterodontiform sharks, which include only the genus *Heterodontus* (family Heterodontidae) have the pelvic fins placed posteriorly to the first dorsal fin, different from †*Palaeoscyllium formosum* (Fig. 4A–C). In addition, *Heterodontus* have spines supporting both dorsal fins anteriorly (Ebert et al. 2021). The species *H. quoyi* has a slightly more forward position of the pelvic fin, but also an anal fin very close to the caudal fin, unlike the condition in †*P. formosum* (Fig. 4D).

Various well-preserved fossil skeletons are currently assigned to three heterodontiform species: †*Paracestracion danieli*, †*P. falcifer*, and †*Heterodontus zitteli* (see Villalobos-Segura et al. 2023). Differently from †*Palaeoscyllium formosum*, the pectoral and pelvic fins as well as the two dorsal fins are placed close to each other in †*Paracestracion danieli* and †*P. falcifer* (Fig. 4E, F). The fin arrangement across the fossil skeletons of †*Heterodontus* sp. and †*H. zitteli* (Fig. 4G, H) is instead closer to that of †*Palaeoscyllium formosum*. The different fin configuration between †*Paracestracion* and *Heterodontus* (both fossil and extant) was mentioned already by Kriwet (2008: 240), highlighting the far more anterior position of pectoral and pelvic fins observable in †*P. falcifer*. Regardless, all most complete fossil specimens assigned to both †*Paracestracion* and †*Heterodontus* have dorsal fin spines, which are clearly missing in †*Palaeoscyllium* (see Kriwet and Klug 2015; Pfeil 2021; Villalobos-Segura et al. 2023). Additional poorly preserved skeletal material assigned to †*Paracestracion falcifer* and †*P. viohli* confirmed the presence of dorsal fin spines in both species (Schweizer 1964: 68; Thies and Leidner 2011: pls. 24, 25, 27; Kriwet and Klug 2015: fig. 688).

Lamniforms: The pelvic fins of extant lamniform sharks are positioned further posteriorly along the body than in †*Palaeoscyllium formosum* (Fig. 5A–K). Only in *Carcharias taurus*, the pelvic fins are aligned with the posterior margin of the first dorsal fin, which is also different from †*P. formosum* (see Fig. 5C). *Mitsukurina owstoni, Odontaspis ferox*, and *O. noronhai* have additional morphological differences in the fin arrangement compared to †*P. formosum*, such as the anal and caudal fins being placed very closely to each other (Fig. 5I, J).

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Similarly to most extant lamniforms, the exceptionally well-preserved fossil skeletons currently assigned to †*Haimirichia amonensis* and †*Cretalamna appendiculata*, as well as to various fossil odontaspid sharks, have pelvic fins that are placed more posteriorly in relation to the first dorsal fin, unlike the configuration in †*P. formosum* (Fig. 5L–N). The pelvic fin originating posterior to the first dorsal fin and the poorly developed lower caudal lobe of †*Scapanorhynchus lewisii* clearly separate it from †*P. formosum* (Fig. 5O). The skeletons assigned to †*Squalicorax* (Frickhinger 1991: text-fig. on p. 180) and †*Cretodus* (Amalfitano et al. 2022: fig. 3), unfortunately, are too poorly preserved to allow for a rigorous comparison of the fin arrangement with †*P. formosum*. While the pelvic fin of †*Ptychodus* is placed far posteriorly like in many lamniforms and differently from the condition observed in †*P. formosum*, its pectoral fin is unusually aligned with the first dorsal fin (Fig. 5P). This alignment of pectoral and first dorsal fins is quite rare among all galeomorph sharks and the only other shark sharing this fin configuration is the living carcharhiniform *Iago omanensis* (Baranes and Ben-Tuvia 1979: fig. 8; Ebert et al. 2021).

Orectolobiforms: In most extant orectolobiform sharks (Brachaeluridae, Hemiscylliidae, Orectolobidae, and Parascylliidae), the anterior margin of the pelvic fins is placed anteriorly to the first dorsal fin (see also Ebert et al. 2021), differently to what is seen in †*Palaeoscyllium formosum* (Fig. 5A–K). A poorly developed (or almost absent) lower lobe of the caudal fin is another major difference between most living orectolobiforms and †*P. formosum* (Fig. 6A–L). In hemiscylliid sharks, only a few species of *Chiloscyllium* (*C. griseum* and *C. punctatum*) show the anterior margins of pelvic and first dorsal fins being aligned with each other (Fig. 6C, D). However, the anal fin is continuous with the caudal one in all hemiscylliids, unlike in †*P. formosum* (Fig. 6C–E). *Stegostoma* (Stegostomatidae) is the only orectolobiform in which the pelvic fins originate at the midpoint of the first dorsal fin (Fig. 6H). However, the anal fin in *Stegostoma* is placed very close to the caudal fin and the latter represents almost half of the body length, which clearly separate it from †*P. formosum* (Fig. 6A, H).

Within the family Ginglymostomatidae, the anterior margins of the pelvic and first dorsal fins are almost aligned with each other in *Ginglymostoma* and *Nebrius*, while the pelvic fin is placed far more anteriorly in *Pseudoginglymostoma* (Fig. 6I–K). In addition, the anal fin is placed very close to the caudal fin in *Ginglymostoma* and *Nebrius*. The alignment of the anterior margin of the pelvic and first dorsal fins is also present in *Rhincodon* (Rhincodontidae). This orectolobiform shark also has a uniquely well-developed lower caudal lobe and the first dorsal fin is significantly larger and higher than the second dorsal fin in both juveniles and adults (Fig. 6L; see also Al-Shamary 2014; Pajuelo et al. 2018). The mentioned fin configurations thus clearly separate all extant ginglymostomatid and rhincodontid sharks from †*P. formosum* (Fig. 6I–L).

Among fossil orectolobiforms, the holotype of †*Phorcynis catulina sensu auctorum* clearly differs from †*Palaeoscyllium formosum* in having the anterior margin of the pelvic fins placed anteriorly to the first dorsal fin and close to the pectoral fin (Fig. 6M). Moreover, the small anal fin of †*Phorcynis catulina* is placed closely to the caudal fin, which also lacks a well-defined lower caudal lobe, unlike in †*Palaeoscyllium formosum* (Fig. 6M). The body configuration and shape of additional skeletons erroneously assigned to various

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genera of fossil sharks, such as †*Crossorhinus* and †*Palaeoscyllium* (Leidner 1997; Kriwet and Klug 2004; Thies and Leidner 2011), is very similar to that observed in the holotype of †*Phorcynis catulina*. Unlike †*P. formosum*, the holomorphic specimen originally assigned to †'*Orectolobus jurassicus*' (junior synonym of †*Phorcynis catulina*) by Frickhinger (1991) has pectoral and pelvic fins that are placed close to each other and the anal fin is continuous with the caudal fin (Fig. 6N). However, the anterior margin of the anal fin originates anteriorly to the second dorsal fin in this specimen, unlike in †*Phorcynis catulina*. A few other specimens identified as †*Phorcynis* (e.g., Thies and Leidner 2011: pls. 36, 37) are too poorly preserved to allow a rigorous comparison with †*Palaeoscyllium formosum*. Many doubts have recently emerged regarding the validity of the genus name †*Phorcynis* and indeed this taxon is in urgent need of revision to fix its nomenclatural and taxonomic status. Various skeletons assigned to †*Mesiteia emiliae*, †*Pararhincodon lehmani* and other (still undetermined) parascylliid sharks differ from †*Palaeoscyllium formosum* in having the origin of the pelvic fins placed anteriorly to the first dorsal fin and the anal fin placed closely to the caudal fin (e.g., Fig. 6O–Q). There is no separation between pectoral and pelvic fins in almost all shark skeletons tentatively assigned to the genus †*Cantioscyllium* and to other (still undetermined) ginglymostomatid sharks by Pfeil (2021), which set them apart from †*P. formosum* (e.g., Fig. 6R, S). Among them, only one skeleton (†Ginglymostomatidae indet.) has the anterior margins of the pelvic and first dorsal fins being aligned with each other, as well as the anal fin placed anteriorly to the second dorsal fin, unlike in †*P. formosum* (Fig. 6T). Although the poor state of preservation of the skeleton of †*Acanthoscyllium sahelalmae* does not allow for a conclusive assessment of the fin shape and arrangement, its preserved skeletal elements of the pelvic fins seem to be placed anteriorly to the first dorsal fin (see Cappetta 2012: fig. 141A–E), separating it from †*P. formosum*.

Other fin configurations (*incerti ordinis*): In some cases, the morphological features observed even in exceptionally well-preserved skeletons of fossil sharks may not provide sufficient information to assign the specimens conclusively to any shark order (e.g., Frickhinger 1991; Cappetta 2012; Jambura et al. 2023; Stumpf et al. 2026). For example, †*Bavariscyllium tischlingeri* undoubtedly shows a galeomorph-like body configuration, but also a combination of features, such as orectolobiform-like barbels and carcharhiniform-like teeth, which leaves its systematic position unresolved (see Stumpf et al. 2026: fig. 1). Regardless, the pelvic fin originating posteriorly to the first dorsal fin, as well as the shape of the anal and caudal fins, clearly separate †*Palaeoscyllium formosum* from †*B. tischlingeri* (Fig. 7A, B). In addition to the holotype of †*P. formosum* (Fig. 2), at least four nearly complete skeletons are currently assigned to this species (see Kriwet and Klug 2015: figs 694, 695; Villalobos-Segura et al. 2023: fig. 24B–D). The skeleton figured by Frickhinger (1991: text-fig. on p. 182) probably represents the counterpart of the articulated specimen later published by Villalobos-Segura et al. (2023: fig. 24D). All these skeletons currently assigned to †*Palaeoscyllium* share the same body configuration, with the pelvic and anal fins originating at the midpoint of the first and second dorsal fins, respectively, and the anal fin being clearly separated from the caudal fin (Fig. 7C, D, F). A deeper posterior notch dividing the well-developed upper and lower caudal lobes of the holotype is the only minor difference observable to all the other specimens. These four specimens indeed have a caudal fin with a continuous, curved postero-ventral margin running from the

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ventral tip to the subterminal notch. A further skeleton originally assigned to †*Phorcynis catulina sensu auctorum* has the same fin arrangement reported for all skeletons assigned to †*Palaeoscyllium* (Fig. 7E). A detailed study of this additional specimen, together with the other articulated skeletons of †*Palaeoscyllium* (see above) is necessary to correctly identify these specimens. The anal fin in the skeleton originally identified as †*P. minus* (currently assigned to †*Synechodus ungeri*; see Villalobos-Segura et al. 2023: fig. 14B) is most likely close to the caudal fin. However, its state of preservation does not allow any reliable comparison of its body configuration with †*P. formosum* (see also Kriwet and Klug 2015). The poor state of preservation of the two additional fragmentary specimens (scattered post-cranial elements) assigned to †*Palaeoscyllium* sp. by Schweizer (1964: 89) also prevents any reliable taxonomic identification. The skeleton assigned to †*Scyliorhinus* sp. by Pfeil (2021: pl. 20, fig. l, m) based on the morphology of its teeth shows the anterior margin of its pelvic fin being almost aligned with the origin of the first dorsal fin (Fig. 7G). Differently, all known extant species of *Scyliorhinus*, as well as all well-preserved fossil skeletons assigned to this genus, have the pelvic fin clearly placed anterior to the dorsal first fin (Fig. 3F, O, P; see also Ebert et al. 2021). Regardless of the possible re-assignment of this fossil specimen, the origin of its anal and second dorsal fins aligned with each other, as well as the absence of a well-developed lower lobe of the caudal fin, undoubtedly separate it from †*P. formosum*.

The systematic position of †*Palaeocarcharias* is also strongly debated (see Villalobos-Segura et al. 2023; Guinot et al. 2025). However, well-preserved skeletons assigned to the type species †*P. stromeri* show that the anal fin is placed very closely to the caudal fin, which clearly separates this taxon from †*Palaeoscyllium formosum* (see Villalobos-Segura et al. 2023: fig. 26A).

Comparative skeletal morphology

The morphological structures composing the endoskeleton of fossil sharks have often proved decisive in investigating and, where possible, clarifying their taxonomy and/or inter-relationships (e.g., Compagno 1999; Goto 2001; Moreira et al. 2019; Jambura et al. 2023; Vullo et al. 2024; Villalobos-Segura et al. 2025; Stumpf et al. 2026). Conversely, the significance of dermal skeletal traits for the systematics of fossil and living sharks has long been debated (e.g., Reif 1973; Leidner 1997; Johanson et al. 2008; Marshall 2011; Appleby et al. 2024). The still recognizable skeletal elements in the holotype of †*Palaeoscyllium formosum* (Fig. 2) allow for at least a general comparison.

Endoskeleton: The size and shape of the radial elements can vary greatly in galeomorph sharks depending on the fin and taxon considered (e. g., Goto 2001; da Silva and de Carvalho 2015; da Silva and Vaz 2023). Unfortunately, only the proximal region of the radials is preserved in paired and unpaired fins in the holotype of †*Palaeoscyllium formosum* (Fig. 2A, B), consequently rendering a rigorous estimate of their shape and length impossible. In galeomorph sharks, morphological features indicative for systematic assessment can also be identified in the tail endoskeleton, which typically includes the caudal region of the vertebral column together with its epaxial and hypaxial elements (e.g., Compagno 1999, 2001; Moreira et al. 2019). In †*P. formosum*, the terminal section of the

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vertebral column, which is rather horizontally directed, forms the support for the upper lobe of its heterocercal caudal fin (Fig. 2A, B). This horizontal direction of the caudal vertebrae is frequently observed in various species of carcharhiniforms, orectolobiforms, and lamniforms, which seemingly correlates with their lifestyle (e.g., Goto 2001; Kim et al. 2013; Moreira et al. 2019). Epaxial and hypaxial elements are only partially preserved in the holotype of †*P. formosum*, consisting of short epichordal radials and hypochordal processes decreasing in length posteriorly (see Fig. 2A, B). However, given the poor preservation of the caudal skeleton, the present comparison can only corroborate a vague resemblance between the general morphology of the caudal endoskeleton of †*P. formosum* and those widely documented in carcharhiniforms, lamniforms, and orectolobiforms (see also Goto 2001; Kim et al. 2013; Moreira et al. 2019).

Dermal skeleton: Morphological features and arrangement of dermal denticles are often mentioned in shark descriptions and used for taxonomic identification of fossil and extant taxa (e.g., Agassiz 1838; Woodward 1889; Maisey 1975; Thies 1995; Leidner 1997; Tanaka et al. 2002; Gilligan and Otway 2011; Martill et al. 2013; Vaz and de Carvalho 2013). However, denticle shape and ornamentation of both extant and fossil sharks can vary significantly across the body (regional variability), between sexes (sexual variability), and between developmental phases (ontogenetic variability), raising serious doubts about their reliability for taxonomic purposes (e.g., Dean 1894, 1909; Applegate 1967; Reif 1973; Raschi and Tabit 1992; Motta et al. 2012; Vullo and Guinot 2015; Dillon et al. 2017; Ankhelyi et al. 2018; Popp et al. 2020; Gabler-Smith et al. 2021; Macías-Cuyare and Oddone 2022; Vaz et al. 2023). For example, denticle shapes and ornamentations change across different body regions (e.g., Reif 1985; Motta et al. 2012). Notably, such morphologies can also vary across skin areas relatively close to each other, such as the anterior and posterior margin of the same fin (see Motta et al. 2012: figs 4C1–C3, 4P1–P3; 6C1–C3, 6P1–P3). In some species (e.g., *Lamna nasus* and *Scyliorhinus retifer*), the morphology of the denticles can even change completely across very small dermal patches, such as the interbranchial skin (sometimes only a few millimeters wide; see Gabler-Smith et al. 2021: figs 2, 7, 8). Denticle features can also be shared across different taxa (e.g., Motta et al. 2012; Gabler-Smith et al. 2021), possibly creating further issues and ambiguities for the identification of isolated or fragmentary fossil specimens. For instance, denticles with almost identical morphologies are located at the anterior margins of pectoral and caudal fins of *Carcharhinus limbatus* and *Isurus oxyrinchus*, which belong to two completely different orders, Carcharhiniformes and Lamniformes, respectively (see Motta et al. 2012: figs 4, 6). Therefore, possible taxonomic misidentifications and interpretations based on isolated denticles, whose original body position is difficult to determine, must be treated with caution (Feichtinger et al. 2021; Naylor et al. 2021). Reif (1978) was among the first to categorize different denticle types in extant and fossil sharks based on their morphogenesis (“placoid type”, “hybodontid type”, and “ctenacanthid type”; see also Cappetta 2012: 39). However, he soon recognized their striking morphological variability, judging denticle traits as unreliable, especially for the identification of disarticulated specimens (see also Reif 1973: 1). In some cases, an acceptable taxonomic resolution based on denticle ornamentation can be reached at most for the family level (see also Dillon et al. 2017, 2021; Appleby et al. 2024). The possible significance of denticle morphological and histological traits

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in systematics often was hypothesized, but rarely tested in a phylogenetic context (e.g., Taniuchi and Garrick 1986; Johanson et al. 2008; Martill et al. 2013; Mello et al. 2013; Soares and Mathubara 2022; Vaz et al. 2023). Conversely, numerous studies including both extant and fossil taxa have shown that arrangement, shape, and ornamentation of dermal denticles often are indicative of one or more ecological functions (e.g., hydrodynamics and defence; Reif 1985; Raschi and Tabit 1992; Southall and Sims 2003; Vullo and Guinot 2015; Dillon et al. 2017; Gabler-Smith et al. 2021; Vaz et al. 2023; Sayama et al. 2024). Their high and intricate morphological variability, together with a likely shape-function link, makes the study of shark taxonomy and evolutionary history problematic and challenging when based solely on dermal denticles (see also Applegate 1967). In particular, morphological comparisons based on denticles collected from unspecified body regions raise serious doubts and concerns (see also Marshall 2011). However, denticle morphologies may still be useful for taxonomic identification as supporting evidence if combined with other diagnostic characters and provided that their exact body region of provenance is known (see also Gilligan and Otway 2011; Marshall 2011; Vaz and de Carvalho 2013; Mollen and Hovestadt 2018; Rodríguez-Cabello et al. 2020; Carrasco-Martínez et al. 2021; Appleby et al. 2024). Possible ontogenetic variations and sexual dimorphism also should be carefully documented or at least considered (e.g., Reif 1973; Vaz and de Carvalho 2013; Macías-Cuyare and Oddone 2022; Vaz et al. 2023). In this perspective, detailed coded categorizations of denticle characters (e.g., Tway 1979; Rubin et al. 2025), together with comprehensive and in-depth comparative studies on extant taxa (e.g., Marshall 2011; Vaz and de Carvalho 2013; Dillon et al. 2017; Vaz et al. 2023), are essential to provide a solid framework of reference to fully understand their morphological variability and to identify possible indicative traits in both fossil and living taxa (see also Johanson et al. 2008; Appleby et al. 2024). Nevertheless, the use of denticle morphologies in palaeontology for taxonomic purposes, even when observable in articulated and well-preserved fossil skeletons, requires further in-depth considerations (see Viohl 1994; Bieńkowska 2004). Denticle structures themselves have great potential for preservation compared to other skeletal parts (e.g., cartilaginous elements) and exceptionally well-preserved fish specimens appear to often retain much of their fossil dermal skeleton relatively intact during fossilization (e.g., Bieńkowska 2004; Underwood et al. 2015; Dillon et al. 2017, 2021). However, a prolonged decay of a carcass in marine environments could greatly alter and deteriorate the status of soft tissues supporting the dermal denticles (e.g., connective tissues and muscle fibres; Sansom et al. 2013). Consequently, taphonomic processes can at least partially alter the position of small dermal elements (e.g., denticles) in fossil specimens, compromising their correct identification and interpretation even when comparing palaeontological material collected from Lagerstätten deposits (e.g., Solnhofen Archipelago; see also Viohl 1994). Therefore, taxonomic identifications based on denticles, which are already challenging in extant neoselachians, present even greater uncertainties when examining fossil specimens (articulated and isolated).

Arrow-shaped denticles like those described here for †*Palaeoscyllium formosum* (morphotype α and β; Fig. 2C, D) were identified in various extant galeomorph sharks (e.g., *Carcharhinus falciformis, Cephaloscyllium ventriosum, Galeocerdo cuvier, Mustelus canis*, and *Triakis scyllium*; see Rubin et al. 2025). However, their morphological similarities

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with the denticles of †*P. formosum* do not extend beyond the general shape (see Rubin et al. 2025: appendix 3). In particular, the ridges on the crown in extant species rarely converge posteriorly like in †*P. formosum*. Instead, they have diverging or parallel patterns often ending on multiple cusps (e.g., Raschi and Tabit 1992; Gilligan and Otway 2011; Marshall 2011; Motta et al. 2012; Mello et al. 2013; Carrasco-Martínez et al. 2021; Macías-Cuyare and Oddone 2022; Vaz et al. 2023; Sayama et al. 2024). Exceptions can be found among carcharhiniform sharks with converging ridges on denticles from the anterior area to the first dorsal fin in *Mustelus canis* (see Ankhelyi et al. 2018: fig. 2c) and the side region anterior to the pelvic fin in *Scyliorhinus retifer* (see Dillon et al. 2017: fig. 2c, AP). Smooth oval denticles like those observed on the anal fin of †*P. formosum* (morphotype γ; Fig. 2C, D) were commonly reported from the anterior-most region of the head in lamniforms (e.g., *Carcharodon carcharias*; see Sayama et al. 2024) and carcharhiniforms (e.g., *Galeus mincaronei* and *Mustelus canis*; see Ankhelyi et al. 2018; Macías-Cuyare and Oddone 2022). Similar rounded and smooth denticle morphologies were also reported in the interbranchial area of some carcharhiniforms (e.g., *Triakis semifasciata* and *Scyliorhinus retifer*) and lamniforms (e.g., *Alopias vulpinus, Carcharodon carcharias, Isurus oxyrinchus*, and *Lamna nasus*; see Gabler-Smith et al. 2021). In *Isurus oxyrinchus*, smooth oval denticles are also documented from the region anterior to the anal fin (see Motta et al. 2012), while they are arranged across the anterior margin of the upper caudal lobe in *Alopias vulpinus* (see Popp et al. 2020).

Thies (1995: 469) was the first to mention the denticles of the holotype of †*P. formosum*, briefly comparing them with those of other isolated and articulated fossil specimens. Among them, only an isolated denticle (IGPH 93-I-15, “morphotype 6”; see Thies 1995: fig. 5F) was figured and considered similar in morphology (morphotype α; Fig. 2C, D) to those collected from the dorsal side of the holotype (SNSB-BSPG AS I 1365) and from an additional skeleton (JME SOS 3151; Villalobos-Segura et al. 2023: fig. 24C), which was also considered to be †*P. formosum*. Unfortunately, the original position of the isolated denticle on the body is difficult to determine, preventing any rigorous comparison (see also above). For example, almost identical arrow-shaped denticles (morphotype α; Fig. 2C, D) also were described and figured from both the dorsal spines of †*Paracestracion falcifer* (ex †*Heterodontus falcifer*) and the mouth area of †*Paraorthacodus jurensis* (ex † ‘*Synechodus jurensis*’; see Reif 1973: figs 3e, f, 7g). Conversely, the morphological features of denticles collected from the articulated skeleton JME SOS 3151 are still unknown due to the lack of any published description or figure of its dermal structures. Differently from the holotype of †*P. formosum*, only pointed, arrow-shaped denticles (morphotype α; Fig. 2C, D) with a rather homogeneous morphology across the body were extracted from the holomorphic skeleton SNSB-BSPG AS I 589a-b, which also was originally assigned to †*P. formosum* (see Leidner 1997: 39–42; see also Thies and Leidner 2011: pl. 47–49). The presence of pointed denticles in the area anterior to the anal fin of SNSB-BSPG AS I 589a-b is an additional difference compared to the holotype of †*P. formosum* (SNSB-BSPG AS I 1365), which instead has rounded denticles (morphotype β; Fig. 2C, D) in the same body region. Differences between denticle morphologies of †*Palaeoscyllium*, †*Corysodon*, and †*Phorcynis sensu auctorum* were used previously for separating these three fossil genera taxonomically and, therefore, the features of their dermal skeleton mandate further

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clarifications (see also Thies 1995; Leidner 1997; Thies and Leidner 2011). The holotype of †*Corysodon cirinensis* (MHNL 15.297; see Thies and Leidner 2011: pl. 53) has arrow-shaped denticles on the proximal region of the pelvic fin, unlike in the holotype of †*P. formosum*, which shows oval denticles (morphotype γ; Fig. 2C, D) in this area. In addition, the smooth oval denticles collected from the region anterior to the pelvic fin in the skeleton MHNL 15.297 differ from those of †*P. formosum* (morphotype β; Fig. 2C, D). Another articulated skeleton assigned to †*C. cirinensis* (see Thies and Leidner 2011: pl. 54–56) shows arrow-shaped denticles on the anterior and posterior trunk region similar to those observed in †*P. formosum* (morphotype α; Fig. 2C, D). However, the poor preservation of this additional specimen of †*C. cirinensis* does not allow to accurately determine the area of origin of the denticles and, therefore, does not allow any detailed comparison. Thies (1995) briefly mentioned the morphological similarity between the denticles (morphotype α; Fig. 2C, D) extracted from the dorsal side of the holotype of †*P. formosum* (SNSB-BSPG AS I 1365) and other skeletons (NHMUK PV P 5541 and JME SOS 3150a) currently assigned to the problematic taxon †*Phorcynis catulina*. According to Thies (1995: 469), †*P. catulina* has denticles with a “coronal bulge bearing a strong and prominent lateral fold on each side”, which differ from those of †*Palaeoscyllium formosum*. Denticles from the holotype of †*P. minus* (NHMUK PV P 5541; junior synonym of †*Phorcynis catulina*) with various shapes were figured by Thies and Leidner (2011: pl. 35). Although poorly preserved, the arrow-shaped denticles of NHMUK PV P 5541 (see Thies and Leidner 2011: pl. 35, figs B–F, H–J) clearly have a narrower crown with a single main bulge and no ridges in contrast to those of †*Palaeoscyllium formosum* (morphotype α and β; Fig. 2C, D). In addition, an oval denticle with a smooth surface was extracted from NHMUK PV P 5541 (Thies and Leidner 2011: pl. 35, fig. G). Unfortunately, there is no information about the body regions from which this denticle was sampled, preventing any accurate comparison. The denticle morphology of JME SOS 3150a is still unknown due to the lack of any description or figure. Dermal denticles were collected only from the head region of the holotype of the type species †*Phorcynis catulina* (MHNL 15.293; see Thies and Leidner 2011: pl. 29; see also De Saint-Seine 1949: text-fig. 6). These are narrower and more pointed than those from the head region of †*Palaeoscyllium formosum* (morphotype α; Fig. 2C, D). Two other poorly preserved skeletons (BSPHG 1960-XVIII-55 and MHNL 15.294; see Thies and Leidner 2011) allegedly belonging to the genus †*Phorcynis* have similar arrow-shaped and oval denticles to those observed in MHNL 15.293 (holotype of †*P. catulina*) and NHMUK PV P 5541. Most denticles collected from BSPHG 1960-XVIII-55 are arrow-shaped and smooth, with only a few of them having short ridges on their anterior margin (Thies and Leidner 2011: pls. 37, 38). In addition, oval, smooth denticles were sampled, but only from the head region of BSPHG 1960-XVIII-55. Oval denticles were collected from both the pectoral fins and the caudal region of MHNL 15.294 (see Thies and Leidner 2011: pl. 36). Some of these denticles have short crests that are restricted to the anterior margin of the crown. The denticles from the caudal region of MHNL 15.294 show three-bulged, arrow-shaped denticles like those described for of †*Palaeoscyllium formosum* (morphotype α; Fig. 2C, D).

Even after comparing all available fossil dermal remains in detail (see above), a conclusive taxonomic determination for †*P. formosum* based on denticle features alone is impossible due to the frequent lack of appropriate morphological documentation of the denticles

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mentioned in literature and/or precise indication of their original position across articulated fossil specimens. Given the high variability of dermal denticles documented in several extant and fossil sharks (see above), any systematic assumptions and/or interpretations based on the limited and scattered fossil record known to date for the taxa discussed in the present study must be regarded as tentative and highly speculative.

Taxonomic and systematic implications

The skeletal structures and evolution of pectoral, pelvic, dorsal, and anal fins have been the main focus of attention in clarifying the systematics of both fossil and extant neoselachians (e.g., Shirai 1992; Goto 2001), rather than their absolute or relative position along the body. One of the few exceptions is the presence of an anal fin, as it is a characteristic unique to the galeomorph sharks amongst the neoselachians (e.g., Shirai 1992). Conversely, the shape and arrangement of the fins along the body are often used as recognizable or even diagnostic features for both extant and fossil neoselachian taxa (e.g., Wagner 1862; Woodward 1889; Compagno 1977; Cappetta 2012; Ebert et al. 2021). Although the absolute position of the fins along the body may vary slightly within the same species for various reasons (e.g., ontogeny and/or sexual dimorphism), their general configuration and relative position allow for rigorous comparisons between different galeomorph taxa (see also Ebert et al. 2021). Such comparative evaluation can reveal new sets of features useful to improve and strengthen the current taxonomic classification of extant and fossil neoselachians (see also below).

The position and morphological features of both paired and unpaired fins of †*Palaeoscyllium formosum* are undeniably crucial in defining its taxonomic identity (see the Amended diagnosis section, above). The fin configuration characterizing †*P. formosum* is definitely unique among extant and fossil galeomorph sharks (see Figs 3–5) and, consequently, represents an unambiguous morphological trait for a correct determination of the species (see also the Comparative body morphology section, above). Conversely, the endoskeletal structures of †*P. formosum* are too poorly preserved to provide any further useful information for a better taxonomic classification of the species (see Fig. 2B). Seemingly, the general similarities and/or differences in shapes and ornamentations of the dermal denticles between the holotype of †*P. formosum* and other extant and fossil taxa can not be used for unambiguously characterizing the type species, which is the focus of the present study (see also the Comparative skeletal anatomy section, above).

The presence of the same distinctive fin configuration in SNSB-BSPG AS I 1365 (holotype of †*P. formosum*) as well as in CM 4780, SMNK-PAL 44950, SNSB-BSPG AS I 589a-b, and JME SOS 7885 (see above) suggest that these holomorphic specimens could belong to the genus †*Palaeoscyllium*. Conversely, the few differences observed in the dermal skeleton of some of these fossil specimens (see above) do not represent a reliable and sufficient line of evidence justifying their potential separation in different genera. Nevertheless, the possibility that CM 4780, SMNK-PAL 44950, SNSB-BSPG AS I 589a-b, and JME SOS 7885 belong to a different species within the genus †*Palaeoscyllium* cannot be ruled out and this needs to be properly clarified in future reassessments. In addition, the poor state of preservation of the skeleton JME SOS 3151 hampers a correct taxonomic identification,

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despite it was previously assigned to †*P. formosum* (see also Villalobos-Segura et al. 2023: fig. 24C).

Wagner (1857: 291; 1861: 12) originally assigned †*P. formosum* to the "family Scyllien" (≈ Scyliorhinidae *sensu lato*) within the group "Squali" stating that "the first dorsal fin is above or behind the pelvic fins" in this family (see also Wagner 1862). Based on current, and certainly more advanced, understanding of the morphology of living sharks, all extant members of the family Scyliorhinidae (*sensu stricto*) show pelvic fins originating anterior to the first dorsal fin (see Ebert et al. 2021). However, such a fin arrangement is shared by members of numerous extant families belonging to both orectolobiforms (e.g., Brachaeluridae, Hemiscylliidae, Orectolobidae, and Parascylliidae) and carcharhiniforms (e.g., Pentanchidae and Scyliorhinidae). Furthermore, the fin configurations of these shark groups and that of †*P. formosum* clearly differ from each other (see the Comparative body morphology section, above). Wagner (1857) also mentioned a supposed similarity between †*P. formosum* and the living genus *Ginglymostoma*, which is a member of the family Ginglymostomatidae (Orectolobiformes). Later, Wagner (1862: 289) hypothesised a close relationship between †*P. formosum* and †*Scyliorhinus angustus* (ex †'*Thyellina angusta*') belonging to the family Scyliorhinidae. However, clear differences in the position of the pelvic and anal fins occur between †*P. formosum* and all scyliorhinids and ginglymostomatids (see the Comparative body morphology section, above). Thus, the assignment (or affinity) of †*P. formosum* to the families indicated by Wagner (1857) based solely on the alleged similarities in their fin arrangements is rejected here. Later, Leidner and Thies (1999) assigned †*Palaeoscyllium* to Carcharhiniformes, rather than to Orectolobiformes (see Cappetta 1987), based on the morphology of the dermal denticles. The denticles with mono-cuspidate posterior margins of the holotype of †*P. formosum*, as well as their disposition across the body, resemble more those of demersal sharks (e.g., the orectolobiform *Ginglymostoma*; see Dillon et al. 2017, 2021). Conversely, †*P. formosum* lacks the multi-cuspi-date denticles commonly observed in numerous extant carcharhiniform sharks (e.g., Dillon et al. 2017, 2021). Despite early efforts by Dingerkus and Koestler (1986), denticle morphologies in orectolobiforms remain poorly documented in comparison to those of carcharhiniforms and detailed studies are too scarce to draw any conclusive interpretations. In addition, some denticle shapes are not exclusive or typical of a single clade but shared across multiple shark orders (see also above). Although teeth are completely missing in the holotype of †*P. formosum*, Underwood (2002) and Cappetta (2012) supported the carcharhiniform affiliation of †*Palaeoscyllium* based on tooth morphologies preserved in other skeletons assigned to the same genus (e.g., Thies and Leidner 2011: pls. 50, 51). Nevertheless, proposing high-ranking affiliations and phylogenetic relationships based on tooth traits solely can be problematic and potentially misleading without solid phylogenetic testing (Villalobos-Segura et al. 2025; Stumpf et al. 2026). This is particularly true when shark groups characterised by great morphological diversity in their dentitions are considered (e.g., Carcharhiniformes; see Zanini and Soares 2025). Entirely different tooth characters are, in fact, clearly recognizable even among species belonging to the same extant carcharhiniform family, such as the scyliorhinid *Scyliorhinus capensis* (upper and lower multi-cuspidate dentitions) and *S. stellaris* (upper and lower mono-cuspidate dentitions; see Soares and De Carvalho 2019; Berio 2021; Ebert

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et al. 2021). Using tooth features in systematic evaluations without a previous careful and detailed examination of their dental morphologies can cause further issues due to the variation between different ontogenetic stages and sexes of the same species (e.g., Soares and De Carvalho 2019). For instance, adult females of *S. capensis* have multi-cusped anterior teeth, whereas those of adult males have only a single cusp (see Soares and De Carvalho 2019: figs 23, 24). In *S. canicula*, the shape and size of lateral tooth cusplets changes between juveniles and adults of the same sex (see Berio 2021). Future detailed comparisons between tooth morphologies of extant galeomorph sharks and potential fossil carcharhiniforms (e.g., †*Palaeoscyllium*) are crucial to identify dental traits (if any) that might be useful for systematic purposes.

Notwithstanding the unique fin configuration characterizing all the specimens considered here as belonging to †*Palaeoscyllium* (SNSB-BSPG AS I 1365, CM 4780, SMNK-PAL 44950, SNSB-BSPG AS I 589a-b, and JME SOS 7885), they still bear a vague resemblance to the body shape of some lamniforms and carcharhiniforms. In particular, the fin shape and size in the holotype of †*P. formosum* are quite similar to those of *Carcharias taurus* (Lamniformes) and *Triakis scyllium* (Carcharhiniformes; see Figs 3, 5). More striking differences in both general body configuration and fin morphologies occur between †*P. formosum* and other galeomorph sharks, such as members of Heterodontiformes and Orectolobiformes (see the Comparative body morphology section, above). Nonetheless, the general similarity in body shape highlighted here between these groups should be regarded with caution. The high variability of fin shapes and arrangements documented for numerous genera of living galeomorphs raises doubts about the significance of such morphological traits for establishing relationships at higher systematic ranks, especially when skeletal features are not properly considered in the same phylogenetic context. In addition, a specific fin configuration is not always an exclusive trait of a single family and/or order of extant galeomorph sharks and often occur in different clades. For examples, the position of the pelvic fin anterior to the first dorsal fin, together with the close proximity of the anal fin and the caudal fin, is documented in various shark families within both orectolobiforms (e.g., Brachaeluridae, Hemiscylliidae, Orectolobidae, and Parascylliidae) and carcharhiniforms (e.g., Pentanchidae; see Ebert et al. 2021). The pelvic and anal fins posterior to the first and second dorsal fins, respectively, are commonly found in both lamni-forms (e.g., Odontaspididae and Pseudocarchariidae) and carcharhiniforms (e.g., Hemigaleidae and Leptochariidae; see Ebert et al. 2021). Although sharks of various families (e.g., Orectolobidae, Lamnidae, Hemigaleidae, and Proscylliidae) show a quite consistent fin arrangement, it is not always distinctive and homogenous within an entire group (see Ebert et al. 2021). For instance, the position of the anal fin changes between the carcharhinids *Carcharhinus* and *Scoliodon*, between the pentanchids *Figaro* and *Galeus*, and between the pseudotriakids *Pseudotriakis* and *Gollum* (see Ebert et al. 2021). Interestingly, the relative position of pectoral, pelvic, and dorsal fins is mostly uniform across genera belonging to the same family, with sporadic exceptions (see Ebert et al. 2021).

The fin configurations, although potentially useful for mere taxonomic determination at the level of species (here morphospecies) in peculiar cases (e.g., †*Palaeoscyllium formosum*), can be misleading for establishing and/or supporting relationships at higher taxonomic ranks (e.g., families and orders). Fin shape and position can also be linked to one or

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multiple ecological functions as well as to their swimming efficiency and manoeuvrability in different habitats (e.g., Flammang et al. 2011; Maia and Wilga 2013; Hoffmann et al. 2019; Seamone et al. 2024). In particular, pectoral fins primarily contribute to turning, while dorsal fins provide stability, especially by resisting roll, and may also generate additional thrust (e.g., Maia and Wilga 2013; Hoffmann et al. 2019). The caudal fin is the main source of propulsion. In most sharks, the heterocercal tail generates both thrust and hydrodynamic lift by directing water backwards and downwards (e.g., Wilga and Lauder 2002; Flammang et al. 2011). In larger blue sharks, a more symmetrical caudal fin is expected to direct water mainly backwards, producing greater thrust but less hydrodynamic lift (e.g., Wilga and Lauder 2002; Flammang et al. 2011).

In this complex scenario, extensive and detailed studies based on both fossil skeletons and dentitions (e.g., Jambura et al. 2023; Villalobos-Segura et al. 2025; Stumpf et al. 2026) represent crucial first steps towards a more stable systematic classification and call for a future and continuous re-evaluation of both extinct and living sharks. Recently, the systematic positions of the galeo-morph sharks †*Palaeoscyllium* and †*Bavariscyllium* was re-evaluated in a phylogenetic context based on exceptionally well-preserved skeletons and using multiple approaches (cladistics and morphometry; Stumpf et al. 2026). Even adopting a multidisciplinary approach, it is not yet possible to establish a conclusive assignment to a supra-generic rank for both †*Palaeoscyllium* and †*Bavariscyllium*, and further investigations are required (Stumpf et al. 2026). For †*Palaeoscyllium* specifically, a future re-evaluation of the already solid phylogenetic scaffold established by Stumpf et al. (2026), incorporating additional holomorphic skeletons and associated teeth will be critical to ensuring a correct interpretation of this enigmatic fossil taxon and clarify its taxonomic content and systematic position.

Conclusions

The present reassessment, focusing on the holotype of †*Palaeoscyllium formosum* Wagner, 1857, confirmed the taxonomic validity and applicability for both genus and species based on the detailed comparison with morphologically similar galeomorph sharks (extant and fossil). The anterior margin of the pelvic and anal fins originating at the midpoint of the first and second dorsal fins, respectively, are confirmed here as useful features for the taxonomic identification of the type species †*P. formosum*. The separation between the anal and caudal fins is added to the set of species-specific characters necessary to identify this enigmatic fossil taxon. The combination of these distinctive characteristics reveals a fin configuration that has not been found in any living or fossil shark to date.

The few known skeletons (CM 4780, SMNK-PAL 44950, SNSB-BSPG AS I 589a-b, and JME SOS 7885) that show an identical fin configuration are considered here as possible members of the genus †*Palaeoscyllium*, pending future evaluations. The accurate redescription of the denticle morphologies of †*P. formosum* did not provide any additional traits unique for the species, but it confirmed only additional secondary features probably more related to its lifestyle. In general, morphological information from the dermal skeleton must be interpreted with caution in both taxonomy and systematics, given the extensive variability and ecological influences potentially shaping these dermal structures. Although

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no tooth morphology can be unequivocally assigned to the type species based on the holotype, a careful reassessment of the other articulated skeletons of †*Palaeoscyllium* preserving associated teeth will be critical for establishing unambiguous dental traits for this taxon with a consequent amendment and improvement of the diagnosis at genus level in the future.

The few skeletal structures preserved in the holotype of †*Palaeoscyllium*, combined with its fin number and general configuration, supports its affiliation with galeomorph sharks. Although the general appearance and body configuration of †*P. formosum* resembles those observed in some carcharhiniforms and lamniforms, its inclusion in a suprageneric rank, either at family or order level, remains dubious and in need of further clarifications.

In addition to the unique fin configuration described here for †*P. formosum*, the extensive and comprehensive comparison of fin arrangements across galeomorph sharks employed here highlights the unusual fin configuration in some fossil galeomorph sharks. Some of these fin configurations do not occur in extant members of the same orders, such as the close-set pectoral and pelvic fins in the heterodontiform †*Paracestracion* from the Jurassic and the alignment of pectoral and dorsal fins in the lamniform †*Ptychodus* from the Cretaceous. This could suggest a potential reduction in the body configuration diversity and/or disparity within some orders of sharks through time. However, the assignment of a new or unusual fin arrangement to a pre-existing shark family or order, especially if based solely on fossil taxa, can have major repercussions on the overall understanding of their morphological and structural variability. Further in-depth studies and detailed comparisons of additional groups of both living and fossil sharks will be vital to properly investigate a possible decline in the variety of their body configuration from the Mesozoic era to the present day.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Data availability

All data necessary to reproduce the results of the manuscript are fully available and included in the present publication.

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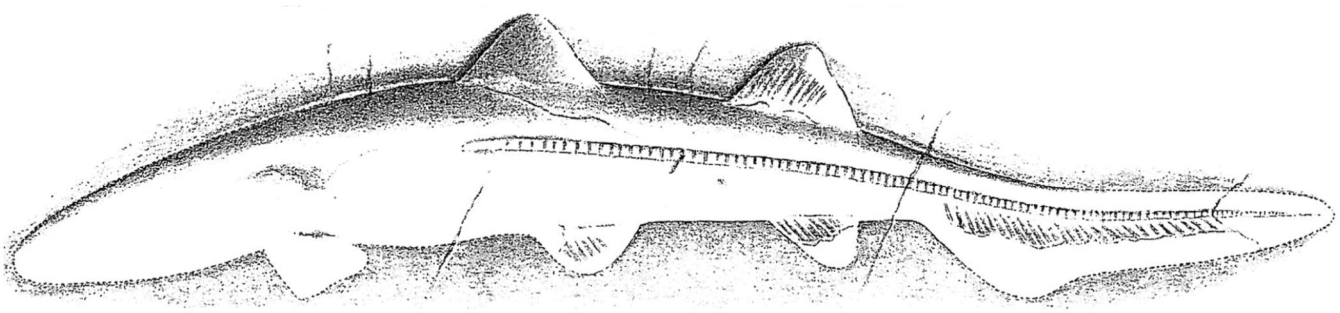


Figure 1.
Historical pictures of the holotype (SNSB-BSPG AS I 1365) of †*Palaeoscyllium formosum* (after Wagner 1861: pl. 5, fig. 2) from the lower Tithonian (Upper Jurassic) of the Solnhofen area (southern Germany).

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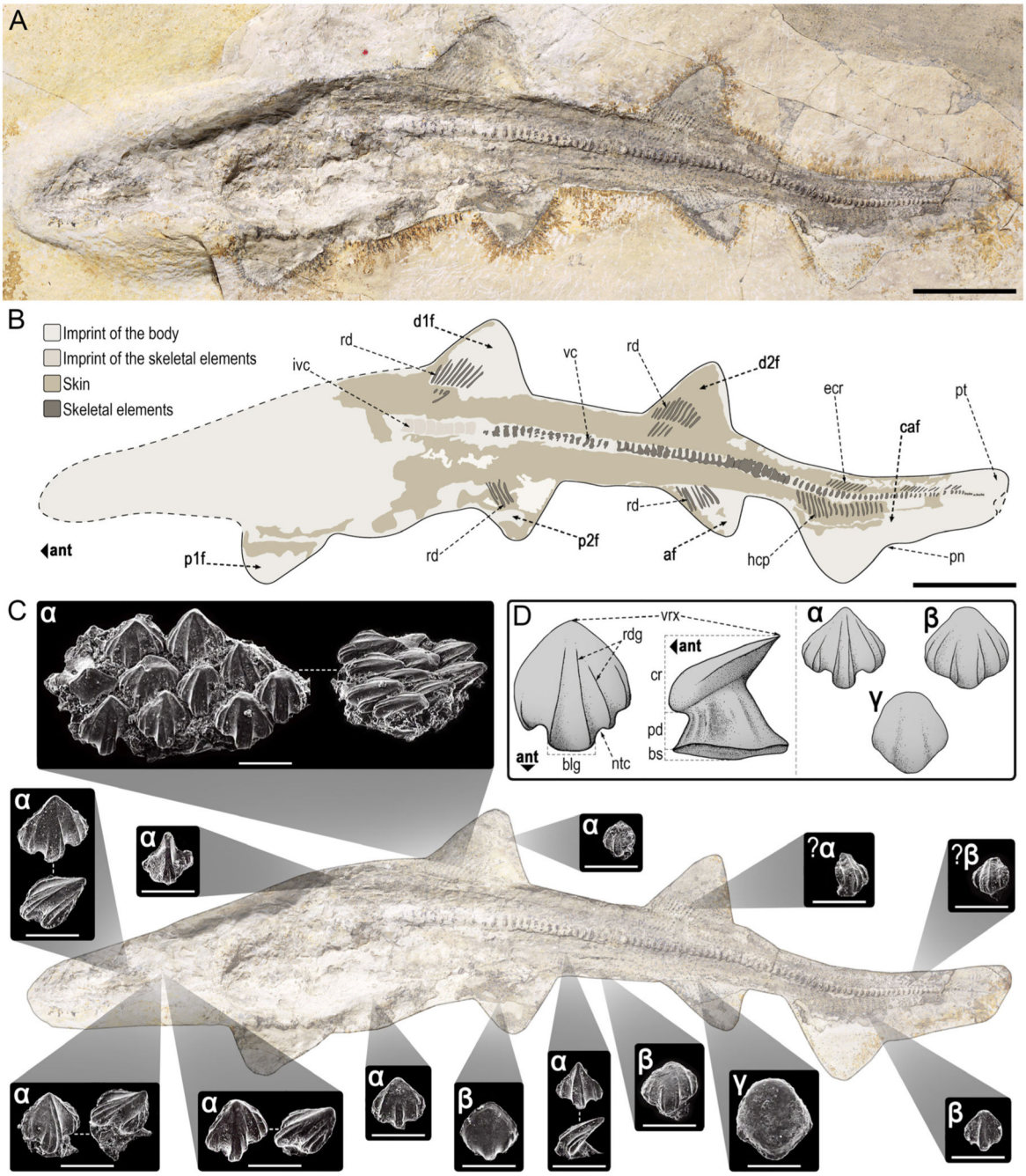


Figure 2. The holotype (SNSB-BSPG AS I 1365) of †*Palaeoscyllium formosum* from the lower Tithonian (Upper Jurassic) of the Solnhofen area (southern Germany).

A. Fossil specimen; **B**. Illustrative drawing of the preserved body structures; af, anal fin; ant, anterior side; caf, caudal fin; d1f, first dorsal fin; d2f, second dorsal fin; ecr, epichordal radials; hcp, hypochordal processes; ivc, imprints of vertebral centra; p1f, pectoral fin; p2f, pelvic fin; pn, posterior notch; pt, posterior tip; rd, radials; vc, vertebral centra; **C**. Denticles originally detached from the holotype (see morphotypes α, β, and γ) and their position across the specimen (based on Leidner 1997 and Thies and Leidner 2011); **D**. Dermal

denticles terminology and morphotypes (α, β, and γ; modified after Thies and Leidner 2011 and based on Rubin et al. 2025); ant, anterior side; blg, bulge; bs, base; cr, crown; ntc, anterior notch; pd, peduncle; rdg, ridge; vrx, posterior vertex. Scale bar equals 50 mm (**A, B**) and 200 μm (**C**).

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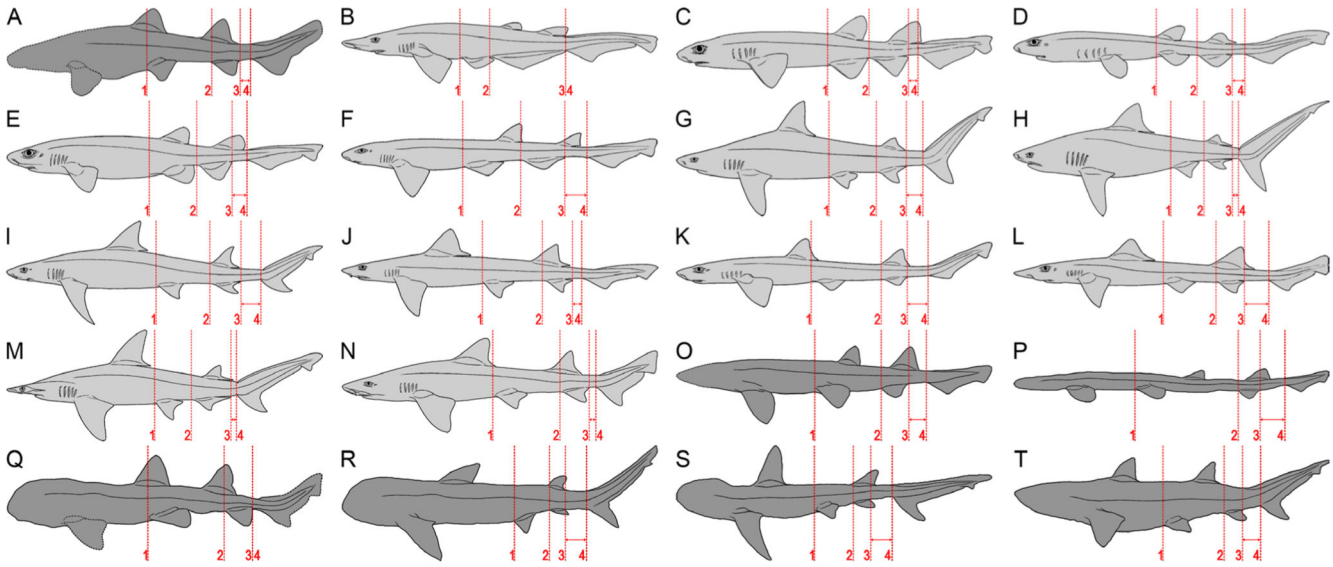


Figure 3.

Fin configuration of †*Palaeoscyllium formosum* (**A**) based on the holotype (SNSB-BSPG AS I 1365) and compared with those of selected carcharhiniform sharks (**B**–**T**); **B**. Pentanchidae (based on *Apristurus canutus*); **C**. Pentanchidae (based on *Bythaelurus giddingsi*); **D**. Pentanchidae (based on *Cephalurus cephalus*); **E**. Pentanchidae (based on *Parmaturus angelae*); **F**. Scyliorhinidae (based on *Scyliorhinus canicula*); **G**. Carcharhinidae (based on *Carcharhinus acronotus*); **H**. Galeocerdidae (based on *Galeocerdo cuvier*); **I**. Hemigaleidae (based on *Hemigaleus microstoma*); **J**. Leptochariidae (based on *Leptocharias smithii*); **K**. Proscylliidae (based on *Proscyllium magnificum*); **L**. Pseudotriakidae (based on *Gollum attenuatus*); **M**. Sphyrnidae (based on *Sphyrna tiburo*); **N**. Triakidae (based on *Triakis scyllium*); **O**. †*Scyliorhinus angustus*; **P**. †*S. elongatus*; **Q**. †*Corysodon cirinensis*; **R**. †*Eogaleus bolcensis*; **S**. †*Galeorhinus cuvieri*; **T**. ?Carcharhinid (undetermined). Interpretative drawing of extant (light grey) and fossil (dark grey) sharks are based on individuals and specimens figured in relevant literature (see also Suppl. material 1: table S1). The black dotted lines indicate body regions missing in the original fossil specimens (speculative reconstruction). The red dotted lines indicate the origin of the pelvic fin (1), anal fin (2), and distance between the end of the anal fin and the beginning of the lower lobe of the caudal fin (3, 4), if present. All shark drawings not to scale.

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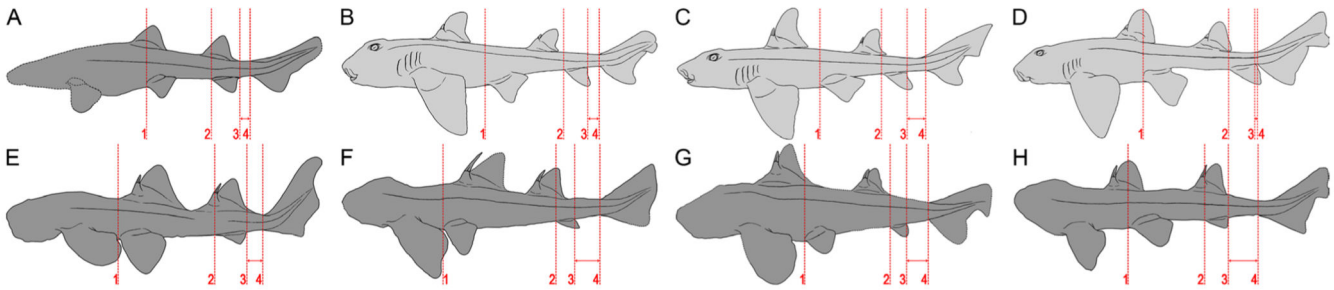


Figure 4.

Fin configuration of †*Palaeoscyllium formosum* (**A**) based on the holotype (SNSB-BSPG AS I 1365) and compared with those of selected heterodontiform sharks (**B**–**H**); **B**. Heterodontidae (based on *Heterodontus omanensis*); **C**. Heterodontidae (based on *H. ramalheira*); **D**. Heterodontidae (based on *H. quoyi*); **E**. †*Paracestracion danieli*; **F**. †*Paracestracion falcifer*; **G**. †*Heterodontus* sp.; **H**. †*H. zitteli*. Interpretative drawing of extant (light grey) and fossil (dark grey) sharks are based on individuals and specimens figured in relevant literature (see also Suppl. material 1: table S1). The black dotted lines indicate body regions missing in the original fossil specimens (speculative reconstruction). The red dotted lines indicate the origin of the pelvic fin (1), anal fin (2), and distance between the end of the anal fin and the beginning of the lower lobe of the caudal fin (3, 4), if present. All shark drawings not to scale.

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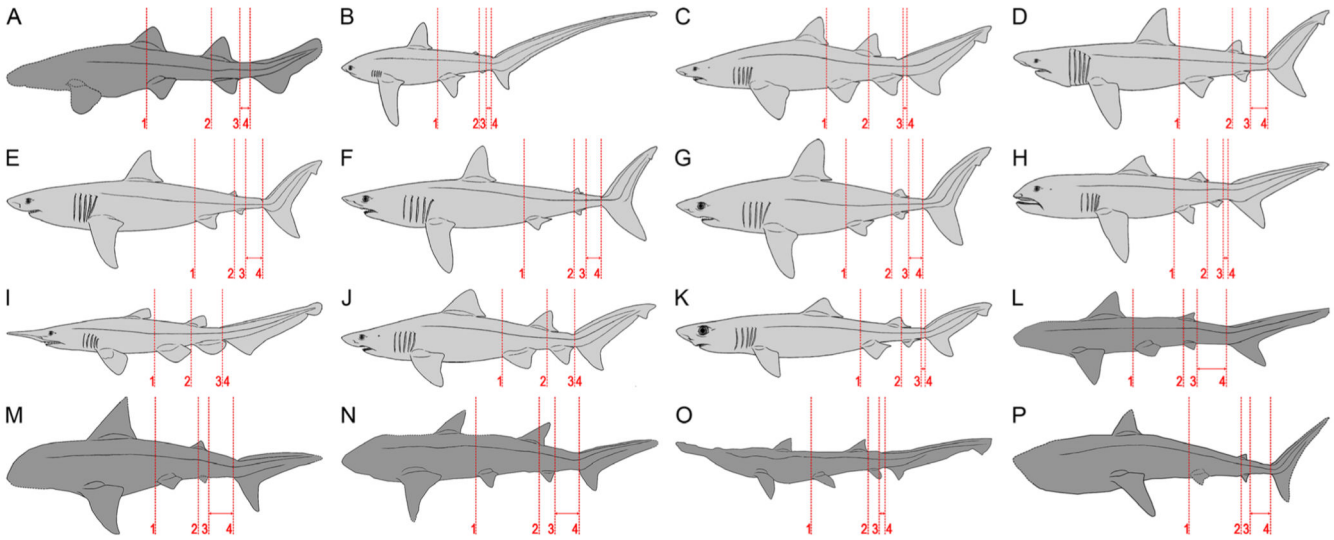


Figure 5.

Fin configuration of †*Palaeoscyllium formosum* (**A**) based on the holotype (SNSB-BSPG AS I 1365) and compared with those of selected lamniform sharks (**B**–**P**); **B**. Alopiidae (based on *Alopias vulpinus*); **C**. Carchariidae (based on *Carcharias taurus*); **D**. Cetorhinidae (based on *Cetorhinus maximus*); **E**. Lamnidae (based on *Carcharodon carcharias*); **F**. Lamnidae (based on *Isurus oxyrinchus*); **G**. Lamnidae (based on *Lamna nasus*); **H**. Megachasmidae (based on *Megachasma pelagios*); **I**. Mitsukurinidae (based on *Mitsukurina owstoni*); **J**. Odontaspidae (based on *Odontaspis ferox*); **K**. Pseudocarchariidae (based on *Pseudocarcharias kamoharai*); **L**. †*Haimirichia amonensis*; **M**. †*Cretalamna appendiculata*; **N**. †*Odontaspis aculeatus*; **O**. †*Scapanorhynchus lewisii*; **P**. †*Ptychodus* sp. Interpretative drawing of extant (light grey) and fossil (dark grey) sharks are based on individuals and specimens figured in relevant literature (see also Suppl. material 1: table S1). The black dotted lines indicate body regions missing in the original fossil specimens (speculative reconstruction). The red dotted lines indicate the origin of the pelvic fin (1), anal fin (2), and distance between the end of the anal fin and the beginning of the lower lobe of the caudal fin (3, 4), if present. All shark drawings not to scale.

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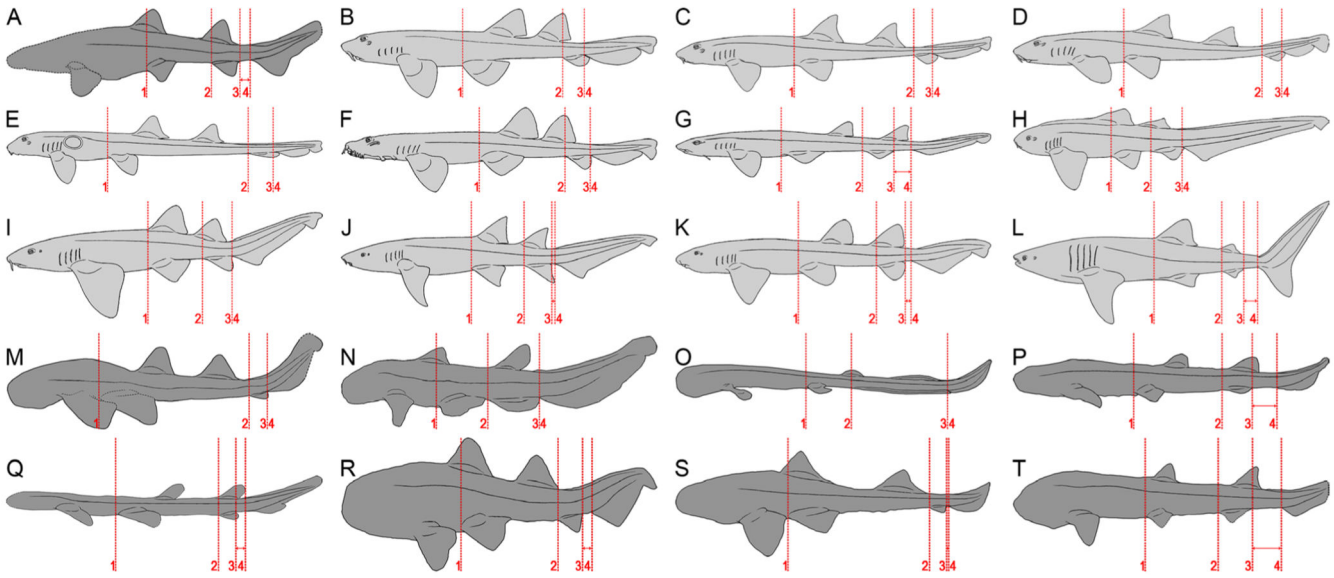


Figure 6.

Fin configuration of †*Palaeoscyllium formosum* (**A**) based on the holotype (SNSB-BSPG AS I 1365) and compared with those of selected orectolobiform sharks (**B**–**T**); **B**. Brachaeluridae (based on *Brachaelurus waddi*); **C**. Hemiscylliidae (based on *Chiloscyllium punctatum*); **D**. Hemiscylliidae (based on *Chiloscyllium griseum*); **E**. Hemiscylliidae (based on *Hemiscyllium ocellatum*); **F**. Orectolobidae (based on *Orectolobus japonicus*); **G**. Parascylliidae (based on *Cirrhoscyllium expolitum*); **H**. Stegostomidae (based on *Stegostoma tigrinum*); **I**. Ginglymostomatidae (based on *Ginglymostoma unami*); **J**. Ginglymostomatidae (based on *Nebrius ferrugineus*); **K**. Ginglymostomatidae (based on *Pseudoginglymostoma brevicaudatum*); **L**. Rhincodontidae (based on *Rhincodon typus*); **M**. †*Phorcynis catulina sensu auctorum*; **N**. †'*Orectolobus jurassicus*'; **O**. †*Mesiteia emiliae*; **P**. †*Pararhincodon lehmani*; **Q**. †Parascylliidae indet.; **R**. †*Cantioscyllium decipiens*; **S**. †Ginglymostomatidae indet.1; **T**. †Ginglymostomatidae indet.2. Interpretative drawing of extant (light grey) and fossil (dark grey) sharks are based on individuals and specimens figured in relevant literature (see also Suppl. material 1: table S1). The black dotted lines indicate body regions missing in the original fossil specimens (speculative reconstruction). The red dotted lines indicate the origin of the pelvic fin (1), anal fin (2), and distance between the end of the anal fin and the beginning of the lower lobe of the caudal fin (3, 4), if present. All shark drawings not to scale.

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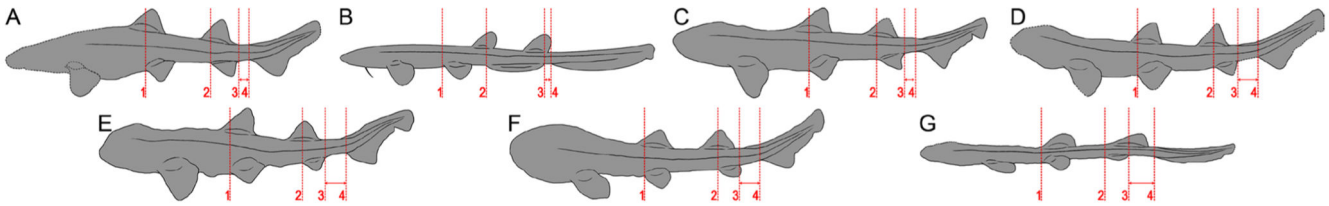


Figure 7.

Fin configuration of †*Palaeoscyllium formosum* (**A**) based on the holotype (SNSB-BSPG AS I 1365) and compared with those of other fossil galeomorph sharks (**B**–**G**, *incerta ordinis*); **B**. †*Bavariscyllium tischlingeri*; **C**. †*Palaeoscyllium* sp. (SMNK-PAL 44950); **D**. †*Palaeoscyllium* sp. (SNSBBSPG AS I 589 A); **E**. †*Palaeoscyllium* sp. (CM-4780); **F**. †*Palaeoscyllium* sp. (JME SOS 7885); **G**. †?*Scyliorhinus* sp. Interpretative drawing of fossil sharks are based on individuals and specimens figured in relevant literature (see also Suppl. material 1: table S1). The black dotted lines indicate body regions missing in the original fossil specimens (speculative reconstruction). The red dotted lines indicate the origin of the pelvic fin (1), anal fin (2), and distance between the end of the anal fin and the beginning of the lower lobe of the caudal fin (3, 4), if present. All shark drawings not to scale.

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