A UNIQUE HYBODONTIFORM SKELETON PROVIDES NOVEL INSIGHTS INTO MESOZOIC CHONDRICHTHYAN LIFE

by SEBASTIAN STUMPF
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Abstract: Asteracanthus was one of the most common Mesozoic hybodontiform chondrichthysans, given that remains traditionally referred to this genus have been reported almost worldwide from Middle Triassic to Late Cretaceous strata so far. Asteracanthus was erected by Louis Agassiz for Late Jurassic fin spines with stellate tubercles. Later, Arthur Smith Woodward synonymized Strophodus, originally introduced by Agassiz for distinctive crushing teeth of Triassic–Cretaceous age, with Asteracanthus based on associated teeth and spines from the English Middle Jurassic. This taxonomic scheme has been accepted for more than 130 years until now, although articulated material has never been found. Here, we present a unique hybodontiform skeleton from the German Late Jurassic, displaying a striking combination of characters: tuberculate dorsal fin spines reminiscent of Asteracanthus, and multicuspid teeth that markedly differ from the crushing teeth previously referred to this genus. Using qualitative and quantitative approaches, we compared its fin spines with those that were found in association with Agassiz’s Strophodus teeth, providing evidence that Asteracanthus and Strophodus in fact represent two valid genera distinct from all other hybodontiforms. Morphological features that distinguish fin spines of Strophodus from those of all other hybodontiforms include a straight anterior border and distally distributed posterior denticles. These observations led us to present an emended diagnosis for Asteracanthus. Dentally, Asteracanthus shows strong resemblance to Hybodus, but it otherwise lacks a palatobasal process on the palatoquadrate. Therefore, and in the absence of any reliable phylogenetic framework, we recommend treating Asteracanthus as incertae familiae until hybodontiform interrelationships are resolved.

Key words: Chondrichthyes, Hybodontiformes, Mesozoic, taxonomy, Asteracanthus, Strophodus.

Extinct shark-like chondrichthysans of the order Hybodontiformes, which form the supposed sister group to Elasmobranchii (i.e. sharks, skates and rays) (Maisey et al. 2004; Maisey 2012), encompass numerous described nominal species of Palaeozoic–Mesozoic age (Cappetta 1987, 2012; Ginter et al. 2010). They are characterized by rather robust bodies with two dorsal fins supported by convex spines displaying retrose, hook-shaped denticles arranged along the posterior midline (Maisey 1978, 1982; Maisey et al. 2004). The ornamentation of hybodontiform dorsal fin spines varies between species, resulting in two general types: those exhibiting longitudinal ribs and those possessing numerous tubercles that are loosely arranged in rows. In addition, male specimens display a single or double pair of cephalic spines on the skull posterior to the orbit (Maisey 1982). Their dentition indicates diverse morpho-functional adaptations in relation to prey and feeding, ranging from crushing to grinding, clutching, tearing, and even to cutting (Cappetta 1987, 2012; Cuny 2012).

Hybodontiforms first appeared in the latest Devonian (c. 361 Ma) (Ginter et al. 2002; Hairapetian & Ginter 2009). They survived two of the big five Phanerzoic mass extinction events, and finally became extinct at the end of the Cretaceous (c. 66 Ma) (Kriwet & Benton 2004). Together with elasmobranchs, hybodontiforms formed the most dominant chondrichthyan lineage during the Mesozoic, especially during the Triassic and...
Jurassic, when they were in full swing, occurring in fully marine to continental depositional environments (e.g. Rees & Underwood 2002, 2006, 2008; Klug et al. 2010; Fischer et al. 2011; Leuzinger et al. 2017; Bhat et al. 2018). From the Early Cretaceous onwards hybodontiforms underwent a diversity decline and subsequent adaptation to freshwaters, probably in response to increasing competition with elasmobranchs, which rapidly diversified from the Early Jurassic onwards (Underwood 2006; Kriwet et al. 2009; Guinot & Cavin 2016, 2020; Stumpf & Kriwet 2019).

However, much uncertainty still surrounds the taxonomy and systematics of Mesozoic hybodontiforms. This is mainly because most species are based on isolated teeth and/or fin spines only, which commonly display morphological characters that are either ambiguous or broadly distributed among these shark-like chondrichthyans (Maisey 1978; Rees 2008; Rees & Underwood 2002, 2006, 2008). Conversely, disarticulated or articulated skeletons, which provide important taxonomic but also ecomorphological information, remain extremely rare and are restricted to a few localities only (e.g. Hauff & Hauff 1981; Maisey 1982, 1983, 1986, 1987, 1989; Gomez Pallerola 1985, 1992; Brito & Ferreira 1989), particularly because their rather poorly mineralized cartilaginous endoskeletons are subject to specific taphonomic constraints. Up to now, only a small number of taxa are known from exceptionally well-preserved skeletal material: for example, Egentonodus and Tribodus. Both genera stand out for including three-dimensionally preserved skull material, which provided substantial new insights into cranial morphology of hybodontiforms and their phylogenetic interrelationships (Maisey 1983; Maisey et al. 2004; Lane 2010; Lane & Maisey 2012), although they were never included in a computer-based phylogenetic analyses. Unlike in most hybodontiforms, the jaws of the supposed durophagous genus Tribodus are short and transversally oriented, lacking direct palatoquadrate articulations with the neurocranium and having a skeletal jaw support by the hyoid arch only (Maisey & de Carvalho 1997; Maisey 2008; Lane & Maisey 2012). The genus Asteracanthus, which is currently considered to be more closely related to Tribodus than to other hybodontiforms (Maisey et al. 2004; Lane & Maisey 2012), was one of the most common Mesozoic hybodontiforms, given that teeth and spines traditionally referred to this genus have been reported almost worldwide from Middle Triassic to Upper Cretaceous strata so far (e.g. Woodward 1888, 1889; Leriche 1910; Stromer 1927; Peyer 1946; Rippel 1981; Goto 1994; Kriwet 1995; Rees & Underwood 2008; Cuyn et al. 2007, 2009; Vincent et al. 2013; Guinot et al. 2014; Leuzinger et al. 2017; Romano et al. 2018; Citton et al. 2019). Nevertheless, the taxonomic content and systematic affinities of species assigned to the taxon remain ambiguous despite the large number of studies.

Asteracanthus was initially introduced by Agassiz (1837) for isolated dorsal fin spines from the Late Jurassic of Europe characterized by prominent stellate tubercles. More than half a century later, Woodward (1889) synonymized the genus Strophodus, originally erected by Agassiz (1838) for distinctive durophagous crushing teeth of Triassic–Cretaceous age, with Asteracanthus based on associated teeth and spines from the Middle Jurassic of England (Woodward 1888). This taxonomic scheme has generally been accepted for more than 130 years until now, despite the complete lack of articulated material.

In this study, we present a new, exceptionally well-preserved hybodontiform skeleton with dentition and fin spines from the Late Jurassic lithographic limestones of Solnhofen in Bavaria, Germany, exhibiting a striking combination of morphological characters: tuberculate dorsal fin spines reminiscent of Asteracanthus and well-defined multicuspid grasping teeth that markedly differ from the prominent durophagous crushing teeth normally referred to Asteracanthus. In an attempt to evaluate the identity and significance of this enigmatic specimen for better understanding of Mesozoic hybodontiform taxonomy and systematics, we compared its dorsal fin spines with those from the English Middle Jurassic described by Woodward (1888), providing strong evidence that both Asteracanthus and Strophodus are in fact sufficiently diagnostic to represent two valid genera distinct from all other known hybodontiforms.

**Historical background**

Along with the type species of Asteracanthus, A. ornatissimus, which was established based on isolated dorsal fin spines from the Kimmeridgian of England and Switzerland, Agassiz (1837) also introduced the species A. acutus, A. minor and A. semisulcatus, which he distinguished from A. ornatissimus based on differences in ornamentation patterns. Since that time, additional species have been proposed solely based on isolated dorsal fin spines (e.g. A. preussi Dunker, 1851a; A. granulosus Egerton, 1854; A. verrucosus Egerton, 1854; A. semiverrucosus Egerton, 1854; A. papillosus Egerton, 1854; A. tetrastrichodon Fricke, 1876; A. aegyptiacus Stromer, 1927; A. biformatus Kriwet, 1995). However, the validity of species that were recognized on the basis of isolated fin spines remains ambiguous in many cases, particularly due to the lack of discrete morphological characters for use in species differentiation.

The identity of Asteracanthus' teeth remained unknown until 1888, when Woodward described associated hybodontiform remains from the Callovian Peterborough Member of the Oxford Formation near Peterborough in southeastern England. This fossil material, which is part of the
Leeds Collection and is now held at the NHMUK, encompassed five individual specimens. Two of them (now catalogued under NHMUK PV P 6869 and 6870) were of special interest to Woodward (1888), because they both included tuberculate dorsal fin spines reminiscent of Agassiz’s *Asteracanthus ornatissimus* and distinctive teeth compatible with *Strophodus*, which was originally erected by Agassiz (1838) for isolated teeth of Triassic–Cretaceous age. The remaining specimens reported by Woodward (1888) included one specimen represented by numerous cartilage fragments and associated *Strophodus* teeth (NHMUK PV P 6871), and two specimens that both consisted of fin and cephalic spine material, as well as cartilage fragments (NHMUK PV P 6867 and 6868). As a result, Woodward (1888) proposed a new taxonomic scheme, treating *Strophodus* as a junior synonym of *Asteracanthus*. Woodward, however, failed to confidently assign the Callovian material to *A. ornatissimus* due to differences in fin spine ornamentation. Therefore, he introduced the variety *A. ornatissimus var. flettonensis* for it, which he finally synonymized with *A. ornatissimus*, together with *Strophodus reticulatus* Agassiz, 1838 from the Middle Jurassic of England and *S. subreticulatus* Agassiz, 1838 from the Swiss Late Jurassic, as well as *S. medius* Owen, 1869 from the Bathonian of France (Woodward 1889). Other Jurassic *Strophodus* species originally established by Agassiz (1838) based solely on isolated crushing teeth (i.e. *S. longidens*, *S. magnus*, *S. tenuis*) were simply left as valid by Woodward (1889), but are now generally referred to *Asteracanthus* (e.g. Rees & Underwood 2008; Rigal & Cuny 2016; Leuzinger et al. 2017). Similarly, following the treatment of *Strophodus* as a junior synonym of *Asteracanthus*, Peyer (1946) introduced the species *A. smithwoodwardi* for fairly complete jaws and associated teeth from the Toarcian of Switzerland. The species *Strophodus lingualis*, initially erected by Woodward (1889) for isolated teeth from the English Bathonian, was recently transferred to a new genus, *Frangerodus*, by Rees & Underwood (2008), who also resurrected the species *Strophodus medius*, which they referred to *Asteracanthus* following the generally accepted classification scheme. Additionally, Leuzinger et al. (2017) recently proposed a new *Asteracanthus* species, *A. udulfensis*, for isolated teeth from the Kimmeridgian of Switzerland.

**MATERIAL AND METHOD**

The herein described skeleton comes from the Upper Jurassic lithographic limestones of Solnhofen in Bavaria, Germany, which are dated to the early Tithonian (Schweigert 2007, 2015). For comparison, numerous additional specimens were studied (see Stumpf et al. 2020, table 1 for a complete list of studied specimens).

**Geometric morphometric analysis**

We used geometric morphometrics to explore the morphological disparity of Early Jurassic (Hettangian) to Late Cretaceous (Cenomanian) hybodontiform dorsal fin spines to facilitate comparisons between the spines of the herein presented skeleton and those of *Asteracanthus ornatissimus var. flettonensis* from the English Middle Jurassic Oxford Clay Formation, but also to allow a more objective basis for characterizing fin spines of different genera. The shape of the fin spines was captured in lateral view in order to also allow the inclusion of spines that are still preserved on slabs, but only those spines in which the distribution of the hook-shaped denticles along the posterior midlines could be assessed.

The sample consists of a total number of 69 fin spines belonging to 63 individuals (Stumpf et al. 2020, table 1). Of the total number of fin spines used, 29 spines belonging to 23 individuals were identified at species level, including *Asteracanthus ornatissimus* Agassiz, 1837, *Hybodus reticulatus* Agassiz, 1837, *H. hauffianus* Fraas, 1895, *Acrodus nobilis* Agassiz, 1838, *A. anningiae* Agassiz, 1839, and *Strophodus reticulatus* Agassiz, 1838. This subset of fin spines was used to examine the morphological disparity between the given species. The species determination for fin spines referred to *Hybodus reticulatus*, *H. hauffianus*, *Acrodus nobilis* and *A. anningiae*, is based on dental and/or skeletal material using published work (Koken 1907; Maisey 1987; Duffin 1993, 1997, 2010). Determination for spines assigned to *Asteracanthus ornatissimus* and *Strophodus reticulatus* corresponds to the herein presented results. In addition, sex determination was possible in 9 specimens based on the presence/absence of associated cephalic spines and/or claspers. Whenever possible, the positions of the fin spines along the body were determined as well.

We established a configuration of 28 coordinates consisting of five fixed landmarks and 23 semi-landmarks that were applied to the lateral faces of the spines (Stumpf et al. 2020, fig. 1, table 2) and digitized using tpsDIG v.2.3 (Rohlf 2017). In incompletely preserved dorsal fin spines (i.e. specimens lacking the distal tip), the missing landmark coordinates were estimated using the estimate.missing function in geomorph (version 3.1.3; Adams & Otárola-Castillo 2013). The configurations were aligned using a generalized Procrustes superimposition (Rohlf & Slice 1990) to remove differences in size, rotation and orientation. The semi-landmarks were slid following the minimum Procrustes distance (Perez et al. 2006) using the gpaen function in geomorph (Adams & Otárola-Castillo 2013). The aligned coordinates were subjected to a principal component analysis to observe the shape variation in the specimens used.
In order to estimate the disparity of hybodontiform dorsal fin spines among genera (i.e. Hybodus, Asteracanthus, Acrodus and Strophodus), a permutational ANOVA was performed, followed by pairwise comparisons between the means using the functions procD.lm in the package geomorph and pairwise in RRPP (Collyer & Adams 2018). The confidence intervals (95%) were estimated on 1000 permutations.

Institutional abbreviations. GPIT, Geologisch-Paläontologisches Institut Tübingen, Universität Tübingen, Germany; NHMUK, Natural History Museum, London, UK; PBP-SOL, Wyoming Dinosaur Center, Thermopolis, USA.

SYSTEMATIC PALAEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Order HYBODONTIFORMES Patterson, 1966
Family INCERTAE SEDIS

Genus ASTERACANTHUS Agassiz, 1837

Type species. Asteracanthus ornatissimus Agassiz, 1837

Diagnosis (emended). Large-sized hybodontiform shark-like chondrichthyan (exceeding 2 m in total length) that is characterized by the following unique combination of morphological characters: body broad and robust anteriorly, tapering posteriorly behind the level of the pleural ribs; body and fins covered by monodontode dermal denticles; snout short and blunt; mouth wide and subterminal; olfactory capsules prominent and well-separated from the precranial fontanelle; occipital cotylus well-developed and deeply recessed; two pairs of cephalic spines with massive, roughly T-shaped basal plate and a large recurved cusp that extends beyond the posterior edge of the basal plate; palatoquadrate with small and deep dorsomedial articulation facet; Meckel’s cartilage elongate and low; multicuspid grasping teeth exhibiting a disjunct monognathic heterodonty and a weak denticulate heterodonty; tooth crown fairly robust and wider than high; main cusp moderately high and conical to slightly pyramidal in shape; three to five pairs of well-developed lateral cusplets diminishing in size; cutting edges continuous and well-defined; labial and lingual crown faces displaying strong vertical folds that descend from the main cusp and the lateral cusplets; presence of prominent, well-developed nodes along the labial crown base; lingual crown face with short vertical folds aligned above the crown–root junction; tooth root high and subrectangular in outline, with numerous minute, irregularly arranged foramina; dental variation passing posteriorly through the upper and lower dentition encompasses a decrease in principal cusp height; pleural ribs with rounded cross-section; pectoral fin aplesodic displaying a rounded fin apex; propterygium supports a single radial; mesopterygial and metapterygial radials single-jointed; anal fin slightly teardrop-shaped and supported by a large basal plate; hypochondral lobe of caudal fin supported by radial and interventrals; two dorsal fins supported by large, fairly robust spines displaying a gently convex-curved anterior margin; lateral surfaces of fin spines ornamented by well-developed circular to slightly oval stellate tubercles that are loosely arranged in longitudinal rows; two alternating rows of well-developed retrose, hook-shaped denticles extending almost along the entire length of the posterior border of fin spines.

Differential diagnosis. The genus Asteracanthus differs from all other hybodontiforms in the combination of: (1) two pairs of cephalic spines exhibiting a rather massive, roughly T-shaped basal plate, with a robust posterior lobe, short lateral lobes, and a large recurved cusp that extends beyond the posterior border of the basal plate; (2) presence of fairly robust, heavily ornamented multicuspid grasping teeth exhibiting prominent labial nodes and short vertical folds aligned above the lingual crown–root junction; and (3) possession of gently convex-curved dorsal fin spines displaying circular to slightly oval stellate tubercles that are loosely arranged in longitudinal rows along their lateral faces, and two alternating rows of prominent retrose denticles that extend almost along the entire length of the posterior border.

Stratigraphic range. Bathonian (Middle Jurassic) – Valanginian (Lower Cretaceous).

Geographic range. Europe (England, France, Switzerland, Germany).

Asteracanthus ornatissimus Agassiz, 1837

1837 Asteracanthus ornatissimus Agassiz, pl. 8, figs 1–6.
1843 Hybodus obtusus Agassiz, pl. 23, figs 43, 44.
1851a Asteracanthus preussi Dunker [sic], pl. 26, fig. 3.
1851b Asteracanthus ornatissimus Agassiz; Dunker, pl. 37, figs 1–7.
1855a Asteracanthus granulosus Egerton, pl. 1, figs 1–5.
1855b Asteracanthus verrucosus Egerton, pl. 2, figs 1, 2.
1876 Asteracanthus preussi Dunker [sic]; Fricke, pl. 22, fig. 1.
1887 Hybodus obtusus Agassiz; Platnauer, pl. 1, figs 1–15.
1888 Asteracanthus ornatissimus, var. flettonensis Woodward, pl. 12, figs 7, 8.
1889 Hybodus obtusus Agassiz; Woodward, pl. 11, figs 8–11.
1911 Hybodus obtusus Agassiz; Priem, pl. 1, fig. 11.
1911 Asteracanthus ornatissimus Agassiz; Priem, pl. 6, figs 5–7.
1916 Asteracanthus granulosus Egerton; Woodward, fig. 9.
1946 Asteracanthus, sp.; Peyer, pl. 10, fig. 1; pl. 11, figs 1–3.
1978 Asteracanthus ornatissimus Agassiz; Maisey, text-fig. 1B (I), (III), C, D; p. 663, pl. 72, fig. 5.
Solnhofen, Bavaria, Germany; Altmühltal Locality and age.

of the fragment shown in Agassiz (1837, pl. 8, figs 9–11). The syntype series of

'Dynacodus' obtusus (Agassiz); Candoni, figs 1, 2.

'Hybodus' obtusus Agassiz; Underwood, fig. 3a.

Hybodus obtusus Agassiz; Rees & Underwood, pl. 2, figs 1–3.

Asteracanthus granulosus Egerton; Duffin & Sweetman, fig. 17.7c.

Hybodus obtusus Agassiz; Kriwet & Klug, fig. 678.

Asteracanthus obtatissimus Agassiz; Martill, pl. 36, figs 2, 8; pl. 37, fig. 4.

1982 Asteracanthus ornatisimus Agassiz; Maisey, fig. 16a–f.

1991 Hybodus obtusus Agassiz; Minier, pl. 36, figs 2, 8; pl. 37, fig. 4.

2001 'Polycodus' obtusus (Agassiz); Candoni, figs 1, 2.

2002 'Hybodus' obtusus Agassiz; Underwood, fig. 3a.

2008 Hybodus obtusus Agassiz; Rees & Underwood, pl. 2, figs 1–3.

2011 Asteracanthus granulosus Egerton; Duffin & Sweetman, fig. 17.7c.

2015 Hybodus obtusus Agassiz; Kriwet & Klug, fig. 678.

2016 Asteracanthus ornatisimus Agassiz; Furic, fig. 2.1a, b.

2016 Hybodus obtusus Agassiz; Furic, fig. 2.4a–c.

Diagnosis. Same as for genus (by monotypy).

Type locality and age. The syntype series of Asteracanthus ornatisimus consists of four specimens: a fairly complete dorsal fin spine lacking its distal tip from the Kimmeridgian of Solothurn, Switzerland (Agassiz 1837, pl. 8, figs 1–6; housed in the fossil fish collection of the Muséum national d’Histoire naturelle, Paris, France, and catalogued under MNHN JRE 543) and three fin spine fragments (Agassiz 1837, pl. 8, figs 7–11). Although the provenance of the fragment shown in Agassiz (1837, pl. 8, figs 9–11) remains unknown, those shown in Agassiz (1837, pl. 8, figs 7, 8; catalogued under NHMUK PV P 461, 462) originate from the Kimmeridgian Clay Formation of Shotover in south-eastern England.

Referred specimen. PBP-SOL-8003, a large, almost completely articulated female individual lacking part of the neurocranium and caudal (Figs 1–5).

Locality and age. Solnhofen, Bavaria, Germany; Altmühltal Formation, Hybonotum Zone, Rueppelianus Subzone, early Tithonian.

Description

General features. PBP-SOL-8003 is represented by a nearly complete articulated female individual c. 2 m long with dentition, lacking part of the neurocranium and most of the caudal fin (Fig. 1A, B). The specimen is for the most part strongly compressed, except for the more robust parts, which still exhibit a certain degree of relief for identifying morphological features. It is exposed in dorsal view anteriorly, with the pectoral girdle and the right pectoral fin being partially visible. Posterior to the pleural ribs, the specimen is bent to the left and twisted, so that the posterior half of the trunk is visible in right lateral aspect.

The specimen is almost completely covered with densely arranged dermal denticles, outlining the body and fins, except for the dorsal fins. The anterior and posterior dorsal fin spines are well preserved and exposed in right lateral view (Fig. 1C, D). The body is remarkably broad anteriorly, tapering posteriorly, particularly behind the pleural ribs.

Head and cranium. The head of PBP-SOL-8003 is longer (c. 63 cm) than wide (c. 52 cm). The mouth is wide and in ventral position. The skull is partially preserved. The neurocranium lacks the orbitotemporal region and postorbital processes, part of the ethmoid and otico-occipital region, and much of the basicranium, exposing the dentition underneath. The mandibular arches, which remain less compressed, are fairly well-preserved and aligned in natural position. Both the upper and lower jaws display abundant, regularly arranged teeth. The hyoid arch is not preserved. The gill arches remain poorly preserved and largely covered by placoid scales.

Neurocranium. The neurocranium of PBP-SOL-8003 is incomplete, lacking the orbitotemporal region and postorbital processes, part of the ethmoid and otico-occipital region, plus much of the basicranium (Fig. 2A, B). The ethmoid region is fragmentary and incomplete posteriorly, lacking the portion where the ethmoidal processes would be expected to be. It overlies the paired palatoquadrate anteriorly and appears to have been proportionally wide and anteriorly blunt. The precerebral fontanelle of PBP-SOL-8003 is incompletely preserved but appears to have been of moderate size and wider than long. The presence of a median rostral bar anterior to the precerebral fontanelle could not be identified in PBP-SOL-8003. The right olfactory capsule is preserved, but remains incomplete and fragmentary, being accessible from behind (Fig. 2C). The corresponding olfactory canal is missing. The olfactory capsule, as preserved, is comparatively large, wider than long, and set away from the precerebral fontanelle.

The orbitotemporal region, postorbital processes and otic capsules are missing, providing access to the posterior part of the basicranium, which is accessible in dorsal view. The occipital region of PBP-SOL-8003 is incomplete and fragmentary (Fig. 2B). It projects posteriorly and preserves the occipital cotylus, foramen magnum and paired foramina that house the shared exits of the glossopharyngeal (IX) and vagus (X) nerves. The foramen magnum, which is positioned just above the occipital cotylus, remains incomplete dorsally. The endolymphatic fossa is not preserved. The occipital cotylus is well-developed and deeply recessed to form two prominent posteriorly projecting lateral processes.

Mandibular arch. The mouth gape of PBP-SOL-8003 is wide and subterminal, with the palatoquadrate protruding the Meckel’s cartilage anteriorly (Fig. 2A). The palatoquadrates are elongated and aligned in natural position, damaged posteriorly at the level of the quadrate region and obscured anteriorly by the ethmoid region of the neurocranium. The exposed portions of the palatoquadrates are straight and increase in width posteriorly, with the left palatoquadrate displaying a well-developed articular knob that articulates with the articular cotylus of the left Meckel’s cartilage. The posterior-most portion of the right palatoquadrate is covered by the right Meckel’s cartilage, so that the articular cotylus of the latter one is visible. The palatoquadrate lacks a dorsomedial palatal process, unlike in most other hybodontiforms. Instead, there is a small and deeply recessed dorsomedial articulation facet located approximately two-thirds the distance along the palatoquadrate (Fig. 2D), presumably for the articulation with the ethmoid of the neurocranium.
FIG. 1. *Asteracanthus ornatissimus* Agassiz, 1837, PBP-SOL-8003, from the lower Tithonian of Solnhofen, Bavaria, Germany. A, interpretative line drawing. B, slab containing specimen. C, close-up view of anterior dorsal fin spine. D, close-up view of posterior dorsal fin spine. E, tentative life reconstruction of female *A. ornatissimus* (by Fabrizio De Rossi). Abbreviations: adfs, anterior dorsal fin spine; af, anal fin; bv, basiventral; cf, caudal fin; ebr, epibranchial; lal, lateral line; Mc, Meckel’s cartilage; nc, neurocranium; notc, notochord; pcf, pectoral fin; pdfs, posterior dorsal fin spine; plr, pleural rib; pq, palatoquadrate; pvf, pelvic fin; scc, scapulacoracoid. Scale bars represent: 50 cm (A, B); 10 cm (C, D).
FIG. 2. *Asteracanthus ornatissimus* Agassiz, 1837, PBP-SOL-8003, from the lower Tithonian of Solnhofen, Bavaria, Germany. A, head in dorsal view. B, preserved posterior part of the neurocranium. C, close-up view of right olfactory capsule. D, close-up view of dorso-medial articulation facet on left palatoquadrate (arrow). Abbreviations: artcot, articular cotylus; artfa, articular facet; artkn, articular knob; fm, foramen magnum; Mc, Meckel’s cartilage; occot, occipital cotylus; pq, palatoquadrate; prcf, precerebral fontanelle; IX, glossopharyngeal nerve foramen; X, vagus nerve foramen. Scale bars represent: 10 cm (A); 5 cm (B); 2 cm (C, D).
FIG. 3. *Asteracanthus ornatissimus* Agassiz, 1837, PBP-SOL-8003, from the lower Tithonian of Solnhofen, Bavaria, Germany. A, photograph of dentition. B, interpretation. **Abbreviations:** LA, lower anterior teeth; LL, lower lateral teeth; LP, lower posterior teeth; S, lower symphyseal teeth; UA, upper anterior teeth; UL, upper lateral teeth; UP, upper posterior teeth; (l), left; (r), right. Scale bars represent 5 cm.
The Meckel’s cartilages of PBP-SOL-8003 are poorly preserved and in part covered by the neurocranium. They are elongate and rather low. Their posterior halves, which are visible in medial view, form deeply convex posterodorsal margins that merge into prominent articular condyles at their posterodorsal corners. The anterior junction of the paired Meckel’s cartilages is obscured by teeth. Labial cartilages could not be identified.

Dentition and heterodonty. The dentition is preserved in situ and encompasses functional and numerous rows of well-mineralized replacement teeth (Figs 3, 4). Only a few teeth are displaced. The upper left jaw half contains nine tooth files (i.e. two anterior, four lateral and three posterior teeth; see below for distinguishing features), while the upper right half consists of eight tooth files (i.e. two anterior, four lateral and two posterior teeth; see below for distinguishing features). The lower jaw includes a symphyseal tooth file that is accompanied on each side by nine tooth files (i.e. two anterior, four lateral and three posterior teeth). Accordingly, teeth of both the upper and lower jaw halves would have alternated with each other when the mouth was closed.

The dentition consists of relatively large, up to 25 mm wide, fairly robust multicuspid grasping teeth (Fig. 4), displaying a disjunct monognathic heterodonty and a weak dognathic heterodonty. The tooth crowns are slightly inclined lingually and wider than high, with a moderately high and robust, conical to pyramidal main cusp and three to four pairs of lateral cusplets, which diminish in size away from the principal cusp, measuring up to one-third the height of the main cusp. The crowns are heavily ornamented and exhibit continuous, well-defined cutting edges and strong vertical folds that descend from the main cusps and the lateral cusplets. In addition, there are short, discontinuous, non-bifurcating, weak to moderately well-developed vertical folds covering both the lingual and labial faces of the crown. Labially, there is a series of well-defined bulbous nodes aligned along the base of the crown. The nodes are usually ornamented with short, apically merging folds. Lingually, the crowns display a series of very short but well-defined folds, which are aligned along the lower part of the crown, slightly above the crown–root junction. The root seems to be nearly as high as the crown and subrectangular in outline, possessing numerous minute, irregularly arranged foramina, which gives a somewhat trabecular appearance to the root. Variation in dental morphology passing through the upper and lower dentition encompasses a decrease in central cusp height, with teeth of posterior positions displaying a reduced, inconspicuous main cusp that is subequal in height to the lateral cusplets present to either side of it.

Upper anterior teeth are prominent and up to 25 mm wide and characterized by a symmetrical tooth crown with an upright, moderately high, rather conical main cusp that is flanked by up to four pairs of lateral cusplets (Fig. 4A). Upper lateral teeth closely resemble those of upper anterior positions, but differ from...
FIG. 5. *Asteracanthus ornatissimus* Agassiz, 1837, PBP-SOL-8003, from the lower Tithonian of Solnhofen, Bavaria, Germany. A–B, right pectoral girdle and fin: A, photograph; B, interpretative line drawing. C, right pelvic girdle and fin. D, anterior dorsal fin. E, posterior dorsal fin. F, anal fin. G, preserved caudal fin skeleton. H, lateral line. Abbreviations: bp, basal plate; bpt, basipterygium; cbrf, coracobranchial fossa; cor, coracoid; hs, haemal spine; hyp, hypural; iv, interventral; pcf, pectoral fin; plr, pleural rib; pro, propterygium; pvg, pelvic girdle; rad, radial; scc, scapulocoracoid; scp, scapular process; scpb, scapular buttress. Scale bars represent: 5 cm (A–G); 2 cm (H).
the latter in displaying a slightly asymmetrical tooth crown with a distally inclined central cusp and up to four pairs of lateral cusplets (Fig. 4B). Teeth of upper posterior positions are up to 20 mm wide and rather slender with a low, only slightly distally inclined main cusp that is flanked by three to four very low and reduced lateral cusplets (Fig. 4C).

Lower symphyseal teeth, which are restricted to a single tooth file, are rather more stoutly built and c. 15 mm wide, forming a symmetrical tooth crown with a prominent, pyramidal main cusp and three to four lateral cusplets on either side of it (Fig. 4D). The labial nodes aligned along the base of the crown are particularly well-developed in symphyseal teeth, resembling the condition in the neighbouring lower anterior teeth. The latter, however, are wider, exhibiting a rather conical than pyramidal main cusp that is flanked by three, sometimes four lateral cusplets (Fig. 4E). Lower lateral teeth are rather slender and up to 20 mm wide, with a less stoutly built and slightly distally inclined conical central cusp and up to five pairs of lateral cusplets (Fig. 4F). Like upper posterior teeth, those of lower posterior positions are up to 20 mm wide and characterized by low and slender crowns possessing a reduced, inconspicuous central cusp and three to four pairs of low lateral cusplets (Fig. 4G).

Hyoid and gill arches. Only part of the right branchial region is visible, including five branchial arches, located between the right Meckel’s cartilage and the right scapulocoracoid. The accessible elements are here tentatively interpreted as epibranchials (Fig. 1A, B). No further morphological information can be retrieved due to the state of preservation.

Axial skeleton. The axial skeleton, as preserved, is for the most part covered by densely arranged dermal denticles. Accessible elements include 11 right and six left pleural ribs, numerous basiventrals, which extend up to the level of the pelvic fin, and haemal arches located in the posteriormost body portion, starting from the region between anal and caudal fins (Fig. 1A, B). The pleural ribs are long and slender, exhibiting a rounded cross-section. The proximal ends are indiscernible and remain obscured by skin.

The basiventrals are re-curved and somewhat sickle-shaped, displaying an expanded proximal region and a longitudinal groove that extends along the distal portion.

There is an elevated ridge that runs along the body midline, extending from the occipital cotylus to the posterior dorsal fin spine (Fig. 1A, B), which is here tentatively interpreted as remnants of the notochord.

Pectoral girdle and fin. The paired scapulocoracoids are fairly well preserved, with their coracoid portions being largely obscured by dermal denticles. The right scapulocoracoid, which is broken at the level where the scapular process meets the coracoid, is exposed in lateral view (Fig. 5A, B). The left scapulocoracoid, as preserved, is fragmentary and has been flipped so that the medial side of the scapular process can be identified. The scapular process is elongate, slender, and curved in its distal portion. A prominent groove extends along the length of the scapular process, which is anteriorly delimited by a strongly developed scapular buttress that extends ventrally to meet the coracoid.

The proximal portion of the right coracoid is preserved, displaying the coracobranchial fossa that extends along the anterior leading edge. The posterior margin is incomplete, showing no sign of a glenoid fossa or surface for articulation with the basal fin elements. Foramina for the diazonal nerves are not discernible.

The right pectoral fin is preserved, exposing its dorsal aspect (Fig. 5A, B). The posterior margin is obscured by the anterior trunk region. The pectoral fin is clearly apleodic and covered by densely arranged dermal denticles so that ceratotrichia could not be identified. The fin, as preserved, is relatively long, and appears to have been rather wide, displaying a slightly convex anterior margin that smoothly merges into a rounded apex. The propterygium is accessible, while the meso- and metapterygium are not. The propterygium is roughly rectangular in shape, longer than wide, forms a convex distal articulation surface, slightly convex leading edge, and a well-calcified, rather sharp-angled proximal articulation surface. The propterygial trailing edge is difficult to discern, but appears to have been straight. The propterygium supports a single pointed radial, which is roughly triangular in outline and displays a concave proximal articulature surface. In addition, there are numerous regularly jointed radials aligned adjacent to the single propterygial radial, including three pairs of mesopterygial and at least five pairs of metapterygial radials. The mesopeterygial radials include two single-jointed cartilages, while the metapterygial radials encompass three single-jointed cartilages. Distal radials are elongated and pointed, forming a straight to slightly concave leading edge and a slightly convex trailing edge.

Pelvic girdle and fin. The right pelvic fin is identifiable. It is triangular in outline and covered by densely arranged dermal denticles (Fig. 5C). The proximal part of the fin is largely obscured by dermal denticles of the body. There is a large, elongate cartilage that is almost entirely covered by skin, which is here identified as basipterygium. An additional piece of cartilage, which remains largely obscured by the basipterygium, is tentatively determined as the pelvic girdle. In addition, there are at least nine elongate, bluntly terminating proximal and at least four pointed distal radials.

Unpaired fins. Specimen PBP-SOL-8003 possesses two dorsal fins, both of which are supported by a single prominent convex spine displaying retrote denticles arranged along the posterior margin (Fig. 5D, E). The anterior dorsal fin originates at the level of the pectoral girdle and the posterior dorsal fin at the level of the posterior pelvic fin margin (Fig. 1A, B). Both dorsal fins bear a single subtriangular basal plate that interlocks anteriorly with the basal slot in the lower posterior part of the fin spine. Although the anterior dorsal fin exhibits a single large radial posterior to the basal plate, at least three parallel-arranged radials are present in the posterior dorsal fin posterior to the basal plate.

The anal fin is well-separated from the pelvic fin, rather large, higher than wide, and somewhat teardrop-shaped, with a gently
convex anterior but a strongly convex posterior margin, which both merge distally into a rounded tip (Fig. 5F). The endoskeleton of the anal fin encompasses a prominent subrectangular basal plate, which is situated just above the anal fin base, and two well-calculated radial cartilages, one being in contact with the ventral margin of the basal plate along its entire length, and the other one being placed posteroventrally to the basal plate running almost parallel to the dorsoventral long-axis of the anal fin.

The caudal fin is heterocercal, lacking most of its epichordal lobe (Fig. 5G). There is a series of well-calculated, somewhat sigmoid-shaped haemal spines, extending from the level between the anal and caudal fin. Haemal arches are absent. The hypocordal lobe is well-developed, has a nearly symmetrical outline with a smoothly rounded tip, and is supported by eight elongated, pointed radials, with the four anteriormost caudal fin radials being separated from the corresponding haemal spines by four intercalated short and rather stoutly built interventrals.

**Dorsal fin spines.** The fin spines are exposed in right lateral view and gently curved, particularly in their distal halves (Figs 1C, D, 5D, E). The anterior fin spine is longer (c. 34 cm) than the posterior one (c. 30 cm) and more robust. The lateral surfaces display a shiny enameloid covering that is ornamented by well-developed and densely arranged oval to rounded tubercles that are loosely arranged in longitudinal rows, which extend approximately two-thirds the way down the apicobasal length of the spines. The tubercles occasionally display a star-shaped ornamentation pattern and merge distally into faint longitudinal ribs. The posterior border is slightly concave and raised into an elevated ridge that slightly increases in size proximally to form a distinct bulge at approximately midway down the length of the tuberculate portion of the spine, representing the upper delimitation of the basal slot in the lower posterior part of the fin spine.

The elevated ridge that runs along the posterior border displays two alternating rows of well-developed hook-shaped denticles, which strongly increase in size proximally, with the youngest generation of denticles being located close to the elevated bulge. The fin spine base is elongated in both spines, but more gracile in the posterior one. As typical for hybodontiform fin spines, the posterior border of the fin spine base forms a weak posterior concavity at the level of the proximal-most portion of the ornamentation.

**Dermal denticles.** The body and the fins of PBP-SOL-8003 are covered by dermal denticles that correspond to the ‘non-growing’ (monodontode) type. They all show a circular base and an upright, cone-like cusp displaying numerous vertical folds that extend from the apex to the base of the cusp. Dermal denticles of the ‘growing’ (polyodontode) type could not be observed.

**Lateral line.** At the level of the caudal fin, just above the haemal spines, there is a thin, occasionally interrupted calcified structure of a few millimetres in diameter that runs parallel with the body axis (Figs 1A, B, 5H), which might represent a preserved part of the lateral line system.

**DISCUSSION**

**Comparison**

In the following section, a comparison between PBP-SOL-8003 and other hybodontiforms, particularly those that are known from skeletal material (e.g. *Hybodus Agassiz, 1837; Onychoselache Dick, 1978; Egertonodus Maisey, 1987; Hamiltonichthys Maisey, 1989; Crassodus Brito & Ferreira, 1989; Crassodus Maisch & Matzke, 2016*) and closely related outgroup taxa to basal hybodontiforms (e.g. *Tristychius Agassiz, 1837; Acronemus Rieppel, 1982*) is drawn (note that *Homalodontus Mutter et al., 2008* is here tentatively regarded as belonging to Hybodontiformes, although its precise systematic position remains open to question). In addition, the species identity of PBP-SOL-8003 is discussed based on a comparison with both *Asteracanthus ornatissimus sensu Agassiz, 1837* and *A. ornatissimus var. flettonensis Woodward, 1888*.

**Comparative anatomy and species identity.** In PBP-SOL-8003, the ethmoid region of the neurocranium, although partially preserved, appears to have been proportionally wide, resembling the condition in *Hamiltonichthys* (Maisey 1989) rather than in *Onychoselache, Hybodus* and *Egertonodus*, the neurocrania of which display more slender ethmoid regions (Maisey 1983, 1987; Coates & Gess 2007). The precerebral fontanelle of PBP-SOL-8003 appears to have been rather small, as in most other hybodontiforms, except for *Tribodus*, which has a large precerebral fontanelle that extends far posteriorly to the level of the orbitae (Lane 2010). However, similar to the condition in *Tribodus*, the olfactory capsule is rather large in PBP-SOL-8003 and set away from the precerebral fontanelle. Comparatively large olfactory capsules are present in *Tristychius*, which is further characterized by a rather large, posteriorly extending precerebral fontanelle (Coates & Tietjen 2018). However, unlike in hybodontiforms, the olfactory capsules of *Tristychius* are not widely separated from each other.

The occipital region of PBP-SOL-8003 is reminiscent of that of *Hybodus* and *Egertonodus*, particularly in displaying a deeply recessed occipital cotylus. Conversely, the occipital cotylus of *Tribodus* is less well-developed and shallowly concave (Lane 2010). A very deep occipital cotylus also occurs in *Acronemus* (Maisey 2011), unlike in *Tristychius*, the occipital cotylus of which more closely resembles that of *Tribodus* (Lane 2010; Coates & Tietjen 2018). PBP-SOL-8003 shares with *Hybodus, Egertonodus* and *Tribodus* a combined exit for the glossopharyngeal and vagus nerves, a feature generally regarded as unique to hybodontiforms (Coates & Tietjen 2018).
FIG. 6. Hybodontiform material from the Callovian Peterborough Member, Oxford Clay Formation, UK, initially assigned to Asteracanthus ornatissimus var. flettonensis Woodward, 1888, here referred to Asteracanthus ornatissimus Agassiz, 1837. A–M, NHMUK PV P 6867: A–D, anterior dorsal fin spine in left lateral, right lateral, anterior and posterior views; E–H, posterior dorsal fin spine in left lateral, right lateral, anterior and posterior views; I–J, right cephalic spine in dorsal and mesial views; K–M, left cephalic spine in lateral, mesial and basal aspects. N–U, NHMUK PV P 6868: N–Q, ?anterior dorsal fin spine in left lateral, right lateral, anterior and posterior views; R–U, ?posterior dorsal fin spine in left lateral, right lateral, anterior and posterior aspects. Scale bars represent: 10 cm (A–H, N–U); 3 cm (I–M).
Similar to most other hybodontiforms, the palatoquadrates of PBP-SOL-8003 are elongated and, as preserved, they are in natural position and obscured anteriorly by the ethmoid region of the neurocranium, which is indicative of a hyostylic jaw suspension (sensu Lane & Maisey 2012). However, PBP-SOL-8003 is readily distinguished from most other hybodontiforms by lacking a palatobasal process on the palatoquadrate. Conversely, PBP-SOL-8003 bears a small but well-developed articulation facet that is located about two-thirds the distance along the palatoquadrate, presumably for the articulation with the ethmoid of the neurocranium. An articulation of the ectethmoid process with the palatoquadrate has been described in *Homalodontus*, which otherwise seems to possess a postorbital articulation on the palatoquadrate (Mutter et al. 2007, fig. 4), a feature present in *Acroneurus* and many other chondrichthyan taxa basal to hybodontiforms (Maisey 2008, 2011). In *Tribodus*, the palatoquadrates are short, transversally oriented, and lack any direct articulation with the neurocranium, although there may have been a ligamentous connection between the palatoquadrates and the neurocranium (Maisey & de Carvalho 1997; Lane & Maisey 2012).

The elongate and low overall profile displayed by the Meckel’s cartilages of PBP-SOL-8003 is rather more similar to that of *Hybodus* and *Egertonodus* (Maisey 1982, 1983, 1987) than to that of *Acrodus* and *Crassodus*, which have relatively massive and deep Meckel’s cartilages (Maisey 1982; Maisch & Matzke 2016).

The anterior margin of the scapular process in PBP-SOL-8003 is distinctively buttressed, resembling the condition in *Hybodus*. The coracoid of PBP-SOL-8003 bears a well-developed coracobranchial fossa, a feature also found in *Onychoselache, Lissodus* and *Hybodus* (Maisey 1982; Coates & Gess 2007). This contrasts with *Tribodus*, in which the coracobranchial fossa is reduced and less well-developed (Lane & Maisey 2009).

The pectoral fin endoskeleton of PBP-SOL-8003 is apleodic, a condition shared with taxa such as *Hamiltonichthys, Hybodus, Lissodus*, and possibly *Tribodus* (Maisey 1982, 1989; Lane & Maisey 2009), contrasting with *Onychoselache*, the pectoral fins of which are plesodic (Coates & Gess 2007). However, PBP-SOL-8003 with its apically rounded pectoral fins is dissimilar to *Hamiltonichthys* and *Hybodus*, which both display pectoral fins with pointed apices (Koken 1907; Maisey 1989). Overall, the pectoral fin endoskeleton of PBP-SOL-8003 seems to be morphologically close to that of *Lissodus* (Maisey 1982), but this must be regarded as tentative until more complete material is available for study.

The dorsal fins of PBP-SOL-8003 are positioned similar to those in *Hamiltonichthys, Gansuselache, Lissodus* and *Hybodus*, in which the anterior fin emerges at the level of the pectoral girdle and the posterior one at the level of the posterior pelvic fin margin (Koken 1907; Brough 1935; Maisey 1989; Wang et al. 2009). This contrasts with *Homalodontus* and *Onychoselache*, as well as more distantly related forms, in which the posterior dorsal fin is set slightly further anteriorly (Coates & Gess 2007; Mutter et al. 2007; Sallan & Coates 2014).

The endoskeleton supporting the anal fin resembles that of *Tristychius* (Dick 1978) rather than that of *Hamiltonichthys* and *Hybodus*, which both possess a more complex anal fin endoskeleton (Koken 1907; Coates & Gess 2007).

In PBP-SOL-8003, the hypochordal lobe of the caudal fin bears a well-calciﬁed endoskeletal support made up of elongated radials and few interventrals intercalated between the latter and the haemal spines. A similar arrangement seems also to be present in *Hybodus* (SS, pers. obs.), unlike in *Hamiltonichthys*, which lacks interventrals (Maisey 1989).

Although growing dermal denticles could not be observed in PBP-SOL-8003, it cannot be completely ruled out that they might actually be present, particularly because denticles of this type are assumed to have been restricted to the oropharynx in at least some, if not all, hybodontiforms (Maisey & Denton 2016).

The fairly robust and gently convex-curved overall morphology displayed by the dorsal fin spines of PBP-SOL-8003, combined with the presence of well-deﬁned, regularly arranged stellate tubercles along the lateral faces, and the possession of two alternating rows of well-developed hook-shaped denticles along almost the entire posterior border of the spines, are morphological characters that are traditionally considered as consistent with referral to dorsal fin spines of *Asteracanthus ornatisimus* Agassiz, 1837, which were reported from several European localities of Bathonian–Kimmeridgian age (e.g. Dunker 1851b; Woodward 1889; Priem 1911; Feyer 1946; Martill 1991; Furic 2016). Surprisingly, however, the teeth of PBP-SOL-8003 markedly differ from the prominent crushing teeth that are traditionally referred to *A. ornatisimus*. Indeed, the fairly robust multisiduous tooth morphology, together with the presence of well-developed labial nodes, plus the occurrence of short vertical folds that are arranged along the lower lingual crown face, are dental characters that are consistent with those of *Hybodus obtusus* Agassiz, 1843, which represents a frequently reported European species known from isolated teeth of Bathonian–Kimmeridgian age only (e.g. Platnauer 1887; Woodward 1889; Martill 1991; Underwood 2002; Rees & Underwood 2008; Furic 2016). Teeth traditionally assigned to *H. obtusus* resemble those of *H. hauffianus* from the Lower Jurassic of Germany to some extent, particularly due to the presence of nodes aligned along the lower labial crown face, which are, however, less well-developed and usually form small, inconspicuous swellings in teeth of *H. hauffianus*. 


In addition, teeth of *H. hauffianus* display more labio-lingually flattened and less heavily ornamented crowns with a high, conical and sharply pointed main cusp that is flanked by slender and quite high lateral cusplets, similar to teeth of the *Hybodus*-type species, *H. reticulatus*, from the Lower Jurassic of England (Maisey 1987; Duffin 1993, 2010). A high-crowned and labio-lingually compressed multicusp tooth morphology also characterizes teeth of *Egertonodus* (Maisey 1983; Rees & Underwood 2008; Duffin & Sweetman 2011). Moreover, articulated dentitions of *E. basanus* (Egerton, 1845) possess a lower symphyseal tooth file plus up to 10 tooth files in each lower jaw and up to 12 tooth files in each upper jaw (Maisey 1983; Duffin & Sweetman 2011). This condition is similar to that of PBP-SOL-8003, the lower jaw of which exhibits a symphyseal tooth file that is accompanied on each side by nine tooth files and whose upper jaw halves contain up to nine tooth files. In conclusion, one could argue that this striking combination of morphological characters present in PBP-SOL-8003 is sufficiently diagnostic to represent a valid genus distinct from all other hybodontiforms. However, by comparing the fin spines of PBP-SOL-8003 with those present in the Callovian specimens from Peterborough, England, for which Woodward (1888) originally proposed the variety *A. ornatisimus var. flettonensis*, significant morphological differences can be observed, particularly in those spines that were actually found in association with low and widely expanded crushing teeth initially described as *Strophodus* (NHMUK PV P 6869 and 6870; Fig. 7A–L). These include: (1) a more slender overall morphology with a straight rather than convex-curved anterior margin; (2) an ornamentation consisting of small and more irregularly distributed stellate tubercles; and (3) the presence of very small, inconspicuous posterior denticles that are restricted to the distal half of the posterior border only.

The rather straight overall gross morphology, together with the presence of posterior denticles that are distributed distally along a small portion of the spine, are features that are especially interesting, because this combination of characters has not yet been reported in any hybodontiform. On the contrary, dorsal fin spines present in the remaining specimens, or more precisely those that were originally found in association with cephalic spines (NHMUK PV P 6867 and 6868; Fig. 6), show closest morphological resemblance to *A. ornatisimus sensu* Agassiz, 1837 (and also to PBP-SOL-8003), thus indicating two separate identities for the Callovian specimens initially named *A. ornatisimus var. flettonensis*.

We therefore conclude that the dorsal fin spines of *A. ornatisimus var. flettonensis* that were found associated with *Strophodus* teeth are in fact sufficiently diagnostic to confidently separate them from those of *A. ornatisimus sensu* Agassiz, 1837. As a result, we recommend treating *Strophodus Agassiz, 1838* as valid to include all species previously referred to *Asteracanthus*, except for those established based on isolated dorsal fin spines. Finally, with these considerations in mind, we conclude that the herein described specimen PBP-SOL-8003 in fact constitutes the first articulated skeleton that can positively be referred to the genus *Asteracanthus*, which is here provisionally re-defined as monotypic to include the single species *A. ornatisimus* only.

Additional skeletal material attributable to *A. ornatisimus* is housed in the Etches Collection, Kimmeridge, England, and represents an articulated skull including teeth, cephalic spines, and a partially preserved tuberculate dorsal fin spine from the lower Kimmeridge Clay Formation, which was identified as *Hybodus obtusus* (Underwood 2020). Most notably, this specimen possesses two pairs of cephalic spines with massive, roughly T-shaped basal plates, each carrying a prominent re-curved cusp that extends beyond the posterior edge of the basal plate.

Among the *Asteracanthus* species that have been introduced on the basis of isolated fin spines, *A. preussi* from the Kimmeridgian of Germany, *A. granulosus* from the English Berriasian, and *A. verrucosus* from the Valanginian of England are placed in synonymy with *A. ornatisimus* due to superficial similarities in overall fin spine morphology, despite minor differences in ornamentation, which are not necessarily reliable indicators of separate identities. However, the presence of *A. ornatisimus* in the Early Cretaceous is here considered tentative, particularly because teeth of this species have not yet been reported from post-Jurassic deposits.

The status of the remaining species initially established based on isolated dorsal fin spines (e.g. *A. acutus*, *A. aegyptiacus*, *A. biformatus*, *A. papillosus*, *A. minor*, *A. semisulcatus*, *A. semiverrucosus* and *A. tetrastrichodon*) remains dubious and unresolved for the moment, either because they are based on poorly preserved, fragmentary material or because they exhibit characters that do not firmly support an inclusion in *Asteracanthus*. For instance, partially preserved dorsal fin spines described under the name *A. aegyptiacus* from the Upper Cretaceous of North Africa exhibit a unique ornamentation pattern different from what can be observed in stratigraphically older fin spines referred to *Asteracanthus*, including numerous well-organized small unicuspitate, non-stellate tubercles (Stromer 1927; Werner 1989, 1994), thus making a positive referral to *Asteracanthus* unlikely. Dorsal fin spines attributed to *A. aegyptiacus* co-occur with prominently ribbed dorsal fin spines traditionally referred to *Hybodus aschersoni* Stromer, 1927 as well as teeth of distobadid hybodontiforms (e.g. Werner 1989, 1994; Dutheil 1999; Ibrahim et al. 2020). Teeth
approaching the dental morphology of Asteracanthus, Hybodus and Strophodus are otherwise absent in the Upper Cretaceous of North Africa. This may suggest that A. aegyptiacus in fact could be congeneric with one of the co-occurring distobatid species (Werner 1994; Pfeil 2011), pending more complete material. Partial tuberculate dorsal fin spines also were described from the Lower and Upper Cretaceous of North America, where they commonly occur associated with teeth of Meristodonoides Underwood & Cumbaa, 2010, tentatively suggesting a congeneric relationship (Case & Cappetta 2004; Underwood & Cumbaa 2010; Cicimurri et al. 2014).

The Callovian Strophodus specimens initially assigned to A. ornatissimus var. flettensis Woodward (1888) are here referred to the species S. reticulatus Agassiz, 1838 due to the presence of distinctively ornamented tooth crowns with frequently branching folds on the upper parts of the crown and a fine reticulate pattern that is restricted to the lower parts of the crown (Rees & Underwood 2008). Numerous additional specimens housed in the fossil fish collection of the NHMUK, which are represented by teeth, cartilage fragments, and a few poorly preserved fin spine fragments, suggest that this species was the most common hybodontiform encountered in the Oxford Clay Formation, followed by Asteracanthus ornatissimus. The latter species is represented by fin and cephalic spines, as well as teeth. Cephalic spines of S. reticulatus remain unknown. Apart from specimens housed at the NHMUK, additional material is located at the GPIT, including the hitherto most completely preserved dorsal fin spine of S. reticulatus (Fig. 8E–I).

Finally, following the here proposed taxonomic scheme, the genus Asteracanthus has a rather constrained temporal distribution, ranging from the Bathonian to possibly the Valanginian. Strophodus, by contrast, shows an even wider stratigraphic range, which spans from the Anisian–Ladinian to the Hauterivian (Peyer 1946; Rieppel 1981), if not Aptian (Pictet & Campiche 1858).

**Geometric morphometric analysis.** To provide additional support for our taxonomic conclusions to consider Asteracanthus and Strophodus as distinct, valid genera, we performed a geometric morphometric analysis for hybodontiform fin spines. The results of this analysis, which included a total number of 69 hybodontiform dorsal fin spines ranging from the Early Jurassic to Early Cretaceous, are best described by principal component (PC)1 and PC2 (Fig. 9B), which account for 71.76% of the variance, while PC3 and PC4 account for 11.14 and 6.99% of the variance, respectively. The associated shape changes are depicted by wireframes around the morphospace. Negative values of PC1 (54.89%) correspond to comparatively short fin spines with a straight anterior margin and posterior denticles that are distributed more distally. Conversely, fin spines with positive values of PC1 are generally more convex-curved along the anterior margin and concave-curved along the posterior margin, and display denticles that are widely distributed along the latter. The shape changes observed along PC2 (16.86%) largely involve the overall gross morphology of the spine, which ranges from relatively slender and distinctively more convex-curved spines for negative values to spines that are less convex-curved and robust at positive values.

As revealed by the overall morphospace occupation shown in Figure 9B, fin spines of Early Jurassic age are widely scattered and located at both negative and positive values of PC2, contrasting with those of Middle Jurassic to Late Cretaceous age, which tend to cluster mainly in positive values of PC2, suggesting a tendency towards generally more stoutly built dorsal fin spines in hybodontiforms from the Middle Jurassic onwards. This pattern, however, should be treated with caution because it might not necessarily reflect a real signal due to the unevenly distributed sample sizes, for which Early Jurassic fin spines comprise 50.73% of the whole dataset.

When comparing the species subset (Fig. 10A), a considerable overlap can be observed between the morphspaces of Hybodus hauffianus and Asteracanthus ornatissimus, with that of H. hauffianus occupying the largest portion, mainly along positive scores of PC2. What also can be observed is that sex and position of the fin spines along the body seem not to have any notable effect on the shape in fin spines of H. hauffianus. The species H. reticulatus is represented by a single dorsal fin spine only, which is positioned in negative values of PC2 within the morphospace.
occupation of *Acrodus anningiae*. The resulting mean shape for dorsal fin spines of the genus *Hybodus* therefore roughly matches that computed from the whole dataset (Fig. 10B).

Dorsal fin spines of *Asteracanthus ornatissimus* are generally placed in positive values of PC2, which results in a mean shape that is very close to that of *Hybodus*, displaying a slightly more robust profile (Fig. 10C).

Fin spines of *Acrodus anningiae* are positioned in negative values of PC2 and remain well-separated from those of *Asteracanthus ornatissimus* and *Hybodus hauffianus*. Conversely, the single fin spine of *Acrodus nobilis* is placed in positive scores of PC2, occupying a position within the morphospace of both *Asteracanthus ornatissimus* and *Hybodus hauffianus*. In general, fin spines of *Acrodus* display a slightly thinner profile compared with that of *Asteracanthus* and *Hybodus* (Fig. 10D). However, similar to fin spines of the aforementioned two genera, the denticles along the posterior midline are generally widely distributed.

Finally, dorsal fin spines of *Strophodus reticulatus*, which are represented by two specimens (Figs 7E–H, 8E–I), are placed well apart from all other spines due to their extreme shapes, which are in fact closer to those shapes located at negative values of PC1. The main differences explaining the distinct placement of dorsal fin spines of *Strophodus reticulatus* mainly relate to the anterior border, which is straight rather than convex-curved, combined with the reduced and distally projected distribution of denticles along the posterior midline (Fig. 10E).

Procrustes ANOVA revealed that there are differences in the shape of the fin spines depending on the generic identity (df, 3; SS, 0.042526; MS, 0.0141754; r², 0.30329; F, 3.6276; p = 0.004). In addition, the pairwise comparison between the means also revealed that fin spines of *Strophodus* still markedly differ from all the others (Stumpf *et al.* 2020, table 3). This, however, should be considered with caution because of the small sample size.
Systematic affinities

The dentition of *Asteracanthus* consists of high-crowned multicuspid teeth that are rather more similar to those of *Hybodus* than to those of other hybodontiforms. Maisey (1989) regarded the presence of high-crowned multicuspid teeth as diagnostic for the subfamily Hybodontinae, which he included within Hybodontidae. He also placed Acrodontinae, which usually incorporates genera characterized by well-defined durophagous crushing teeth, such as *Acrodus* and *Tribodus*, as well as *Strophodus* (Rees & Underwood 2006, 2008; Lane 2010) in Hybodontidae. The main character used by Maisey (1989) for placing the subfamilies Hybodontinae and Acrodontinae within Hybodontidae is the presence of an osteodont tooth histotype, which he regarded as a derived feature among hybodontiforms. Conversely, genera characterized by low-crowned teeth displaying the orthodont tooth histotype were considered by Maisey (1989) to form an array of phylogenetically plesiomorphic hybodontiforms. This classification scheme has generally been accepted, but remains open to discussion, particularly because detailed histological analyses of teeth have been omitted from most studies up to now.

Two tooth histotypes are traditionally considered to occur in hybodontiforms (and chondrichthyans generally), following the classification scheme of Glikman (1964), who distinguished between: (1) orthodonty, with teeth displaying a hollow pulp cavity that is surrounded by a layer of orthodentine; and (2) osteodontoxy, with teeth having a pulp cavity that is filled by osteodentine. More recent studies dealing with tooth histology patterns in chondrichthyans, however, revealed the presence of three tooth histotypes in modern sharks (Jambura et al. 2018,
2019, 2020), which are defined as follows: (1) orthodonty, teeth with central hollow pulp cavity encapsulated by orthodentine; (2) pseudoosteodonty, teeth in which the orthodentine surrounds a dentinal core composed of osteodentine; and (3) osteodonty, teeth with no orthodentine but a dentinal core filled by osteodentine. As in modern sharks, all of these three tooth histotypes also occur in hybodontiforms, as clearly inferred from already

**FIG. 10.** Morphospace of hybodontiform dorsal fin spines based on principal component analysis (PCA) and wireframes illustrating the shape changes from the mean along the first two principal components in spines that could be assigned to genus level. A, morphospace plot showing principal component values sorted by taxonomic determination (arrows indicate fin spines that belong to a single specimen, pointing to the first anterior dorsal fin spine). B–E, wireframes illustrating differences between mean shape of fin spines referred to the genera: B, *Hybodus*; C, *Asteracanthus*; D, *Acrodus*; E, *Strophodus* (black lines and circles indicate mean shape of genera; grey lines and circles indicate mean shape computed from the whole dataset).
published data (e.g. Jaekel 1889; Peyer 1946; Lane & Maisey 2012; Maisch & Matzke 2016; Bhat et al. 2018). In consequence, *Strophodus* and *Tribodus* are currently the only known hybodontiforms with osteodont teeth, which are further characterized by displaying a columnar dentinal structure, commonly referred to as columnar osteodentine (Peyer 1946; Lane & Maisey 2012). Tooth histology patterns of *Palaeobates* and *Polyacrodus* correspond to the orthodont histotype (Jaekel 1889). Pseudoosteodonyt seems to have widely been distributed among hybodontiforms, given that it occurs in quite distinctly related taxa, such as *Acrodus*, *Crassodus* and *Pristrisodus* (Jaekel 1889; Maisch & Matzke 2016; Bhat et al. 2018). Interestingly, teeth of *Hamiltonichthys*, which is generally assumed to be placed at the base of Hybodontiformes, probably also correspond to the pseudoosteodont tooth histotype (Maisey 1989, fig. 28), pending a more detailed analysis. Unfortunately, the tooth histology patterns of genera traditionally grouped within Hybodontinae, such as *Hybodus*, *Egertonodus* and *Planohybodus*, remain unknown.

Notably, although showing close dental resemblance to *Hybodus* and *Egertonodus*, the palaatoquadrate of *Asteracanthus* lacks a distinct palatalobal process, a feature that readily distinguishes it from *Hybodus* and *Egertonodus* (Maisey 1982, 1989). Cephalic spines of *Asteracanthus* display a massive, uniquely shaped basal plate with a robust posterior lobe and short and reduced lateral lobes (Fig. 6I–M), whereas those of *Hybodus* and *Egertonodus* as well as *Planohybodus* share a wide, distinctively T-shaped basal plate (Maisey 1982, 1983; Rees & Underwood 2008). In addition, *Egertonodus* exhibits one pair of cephalic spines, contrasting with *Hybodus* and *Planohybodus* as well as *Asteracanthus*, which possess two pairs of cephalic spines. The phylogenetic significance of these differences, however, needs to be tested.

All these inconsistencies can only be resolved by providing more-comprehensive comparative analyses of hybodontiform tooth histologies, combined with a subsequent phylogenetic analysis using strict cladistic principles. This, however, is beyond the scope of the present paper and will be published elsewhere. In consequence, *Asteracanthus* cannot confidently be referred to any existing family and is left here within Hybodontiformes as *incertae familiae*, pending further analyses.

Likewise, it still remains uncertain as to whether the columnar osteodentine in teeth of *Strophodus* and *Tribodus* carries a phylogenetic or rather functional signal (i.e. due to similar feeding ecologies). In addition, differences in overall dental morphology and tooth arrangement but also jaw architecture (Peyer 1946; Rees & Underwood 2008; Cappetta 2012; Lane & Maisey 2012; Rigal & Cuny 2016) suggest a rather distant phylogenetic relationship between *Strophodus* and *Tribodus*. Therefore, we recommend treating *Strophodus* also as *incertae familiae* and suggest that *Tribodus* might in fact be placed within the family Distobatidae together with genera such as *Distobates* Werner, 1989 and *Reticulodus* Murry & Kirby, 2002 due to very similar tooth morphologies, in particular the presence of hexagonal-shaped tooth crowns (Cappetta 2012).

Palaeoecology

Chondrichthyan teeth display important adaptive traits for inferring possible diet preferences (Cappetta 1987, 2012). However, dental morphology alone does not consistently mirror trophic adaptations in chondrichthyans, and provides only a broad idea about their actual biological roles (Whitenack & Motta 2010; see also Huber et al. 2019 for further discussion). Therefore, the proposed diet preferences addressed below should be treated with care, given that the prey ranges were most probably wider than expected when it comes to tooth morphologies alone.

*Asteracanthus* seemingly formed a common and widely distributed component within European Middle Jurassic – Early Cretaceous marine ecosystems, and in particular during the Late Jurassic, as inferred from the high number of documented teeth and spines (e.g. Dunker 1851a, b; Fricke 1876; Platnauer 1887; Woodward 1889; Priem 1911; Peyer 1946; Candoni 1995; Underwood 2002; Furic 2016). Records attributable to *Asteracanthus* only were rarely reported from marginal marine sediments, suggesting that the genus might have predominantly been bound to open marine environments.

As suggested by specimen PBP-SOL-8003, teeth of *Asteracanthus* are arranged such that multiple tooth rows were functional at the same time, forming a well-developed grasping dentition. The variation in dental morphologies characterizing the dentition of *Asteracanthus* suggests that the higher and more robust anterior teeth were used for grasping and handling prey items, while it is more likely that those of lateral and posterior positions performed a crushing function, thus suggesting a rather taxonomically diverse dietary spectrum that probably ranged from soft to moderately hard-shelled organisms, such as crustaceans, echinoderms and hard-shelled molluscs, to even unshelled prey items such as belemnites and fish. In addition, the prominent labial nodes at the tooth crown bases might have provided further protection against hard-shelled and morphologically well-defended organisms (Rees & Underwood 2008). Scavenging behaviours have also been suggested for *Asteracanthus* based on teeth that were found associated with marine reptile remains (Martill 1991). These considerations, in combination with the presence of well-rounded pectoral fins, imply that *Asteracanthus* was a rather sluggish swimmer adapted
towards a more epibenthic mode of life, which would be indicative of it occupying an intermediate trophic level. In Hybodus, which is dentally quite similar to Asteracanthus, a more active mode of life might have been prevalent, as suggested from a specimen reported from the German Toarcian preserving numerous belemnite rostra in its stomach region (Schmidt 1921). In addition, indirect evidence for hybodontiform predation on cephalopods was reported based on a Kimmeridgian ammonite preserving potential bite marks and a tooth of Planohyodus (Vullo 2011).

Asteracanthus was certainly one of the largest hybodontiforms that ever existed, reaching a body length between 2 and 3 m, similar to Hybodus, which was a common and widespread member of Early Jurassic marine ecosystems (e.g. Maisey 1987; Duffin 1993, 1997, 2010; Urlichs et al. 1994; Stumpf & Kriwet 2019). Additional large-bodied hybodontiforms that roamed the Jurassic seas alongside Hybodus and Asteracanthus include Acrodus, Strophodus and Planohyodus. These forms were all geographically widespread and predominantly occurred in open marine environments, contrasting with smaller hybodontiforms such as Lissodus and Parvodus, which seem to have been rather restricted in their facies distribution, occurring mainly in marginal marine settings with reduced salinity conditions (Duffin & Thies 1997; Rees 1998; Rees & Underwood 2006, 2008; Stumpf & Kriwet 2019). By the Early Cretaceous, hybodontiforms had become rare in open marine depositional environments (Guinot et al. 2013, 2014) and were almost entirely restricted to marginal marine and brackish water habitats, where they flourished and inhabited a wide range of ecological niches until they finally went extinct at the end of the Cretaceous (e.g. Patterson 1966; Duffin & Sigogneau-Russell 1993; Rees 2002; Underwood & Rees 2002; Guny et al. 2006, 2008; Bermúdez-Rochas 2009; Underwood & Cumbaa 2010; Duffin & Sweetman 2011; Rees et al. 2013; Cook et al. 2014; Sweetman et al. 2014; Soler-Gijón et al. 2016; Gates et al. 2019; Teng et al. 2019). It is generally assumed that the diversity decline of fully marine Mesozoic hybodontiforms was shaped through a competitive displacement by elasmobranchs (i.e. modern sharks, skates and rays), which rapidly diversified taxonomically and ecologically from the late Early Jurassic onwards to become the dominant group of chondrichthians during the later part of the Mesoozoic (Underwood 2006; Kriwet et al. 2009; Guinot & Cavin 2016, 2020; Stumpf & Kriwet 2019). Notably, large hybodontiforms are comparatively rare in post-Jurassic hybodontiform faunas, suggesting a potential ecologically controlled selectivity, probably in relation to the availability of preferred food resources. As such, it is also possible that the apparent decline of large, fully marine hybodontiforms might have been linked to diversity drops among ammonites and other potential food resources caused by the global environmental perturbation episodes at the Jurassic–Cretaceous boundary (Tennant et al. 2017 and references therein), which in fact would be indicative of an opportunistic replacement rather than a competitive displacement (Benton 1996), whereby elasmobranchs rapidly filled the free ecospaces that were left by their more plesiomorphic relatives.

**CONCLUSION**

Qualitative and quantitative comparisons between dorsal fin spines of a new, exceptionally well-preserved hybodontiform skeleton from the Tithonian of Germany and fin spines of specimens assigned to Asteracanthus ornattissimus var. flettonensis provide strong evidence that the Mesozoic hybodontiforms Asteracanthus and Strophodus, which are traditionally regarded as synonymous, in fact represent two well-separated genera distinct from all other known hybodontiforms. Both forms are common and widespread, particularly during the Middle and Late Jurassic, where they formed typical elements within marine vertebrate associations, probably occupying intermediate trophic levels. Strophodus displays uniquely shaped jaws and a distinctive dentitional pattern composed of specialized teeth well-adapted to durophagous diet, contrasting with Asteracanthus, which exhibits well-defined multicuspid teeth quite similar to those of Hybodus and Egertonodus, suggesting closer phylogenetic relationships.

Asteracanthus otherwise lacks a palato basal process on the palatoquadrate, a feature that readily distinguishes it from all other hybodontiforms with high multicuspid teeth. Additionally, cephalic spines of Asteracanthus are unique among hybodontiforms in displaying a massive basal plate with a robust posterior lobe and short lateral lobes, but the phylogenetic significance of this feature remains ambiguous. Therefore, and in the absence of any quantitative phylogenetic framework, we recommend treating Asteracanthus as incertae famiiae. Likewise, the systematic position of Strophodus remains unclear for the moment and needs to be re-evaluated.

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**DATA ARCHIVING STATEMENT**

Data for this study are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.fqz612jr5

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