TEETH OF A NEW NEOSELACHIAN SHARK FROM THE BRITISH LOWER JURASSIC

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ABSTRACT. Neoselachian sharks' teeth from the lower Jurassic of Lyme Regis, Dorset, are described and assigned to *Agaleus dorsetensis* gen. et sp. nov. The teeth are large, and have a robust central cusp, one pair of lateral cusplets, and a prominent basal flange. Longitudinal ridges are present on the labial crown shoulder, and the root has a strong labial buttress. The vascularization is hemiaulacorhize. Comparison with the teeth of Recent and fossil neoselachians indicates that *Agaleus* is a benthonic orectolobiform galeomorph.

THE lower Jurassic limestones and shales of the Lyme Regis succession on the Dorset coast have long been famous for yielding whole and fragmentary vertebrate remains (Lang 1924). Amongst this vertebrate fauna, fossil elasmobranchs are represented by hybodontiforms (*Acrodus anningiae*, *A. nobilis*, *Hybodus raricostatus*, *H. delabechei*, *H. medius*, *H. reticulatus*) and a few specimens of presumed (on the basis of enameloid ultrastructure, Reif 1974) neoselachians (*Palaeospinax priscus*).

Neoselachian sharks are those belonging to the level of organization of Recent species. The fossil record of this group is well represented in the late Cretaceous and Tertiary but sporadic in the remainder of the Mesozoic. The best-known specimens have been recovered from the fine-grained limestones of the Bavarian Tithonian (upper Jurassic) in south-west Germany. Here, the squalomorphs are represented by *Notidanus*, the batoids by *Belemnobatis* and *Asterodermus*, the squatinomorphs by *Squatina*, and the galeomorphs by several orectolobids (*Corysodon*, *Phorcynis*, *Orectolobus*), a heterodontid (*Heterodontus*), carcharhiniforms (*Palaeoscyllium*, *Pristiurus*), and what may be a lamniform (*Palaeocarcharias*).

Few neoselachians are known prior to the Kimmeridgian: *Palaeospinax* has already been mentioned from the lower Lias; the remainder comprise mostly isolated teeth and fin spines of neoselachians of problematic ordinal affinity from late Triassic deposits (Duffin 1981), including *Raineria* Osswald 1928, *Nemacanthus* Agassiz 1837, *?Pseudodalatias* (Sykes 1971), *Hueneichthys* Reif 1977, *Reifia* Duffin 1980, and *Vallisia* Duffin 1982. In addition, Duffin and Ward (1983) have reported neoselachian sharks' teeth from the early Carboniferous of Britain and the Permian of the U.S.A. (*Anachronistes* spp.). Thus, considerable gaps exist in our knowledge of the early history of the neoselachians. One of the more important of these is that represented by the poorly sampled lower Jurassic deposits. In sediments of this age we should expect to find evidence of the early members of extant neoselachian orders and families. The purpose of this paper is to begin such a study with the description of a new neoselachian shark from the Blue Lias (early Jurassic) of Lyme Regis, England.

SYSTEMATIC PALAEONTOLOGY

Class CHONDRICHTHYES
Subclass ELASMOBRANCHII
Cohort NEOSELACHII
Superorder GALEOMORPHII
Order ORECTOLOBIFORMES
Family *incertae sedis*
Genus *Agaleus* gen. nov.

Derivation of name. A genus of presumed galeomorph shark named in honour of Mr. Andrew Gale.

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Diagnosis. Genus known only by large (up to 7 mm high) isolated teeth. The central cusp is large, lingually inclined, and flanked by one lateral cusplet on each side. The lateral blades are pronounced and the basal flange well developed and expanded basally. A series of horizontal ridges is present around the whole tooth at and below the crown shoulder. The ridges vary in length, and divide and converge on each other. Short vertical striations may arise from certain horizontal ridges. The horizontal ridges are particularly common along the crown shoulders of the lateral blades. The crown/root junction is deeply incised around the whole tooth. The root is deep, and has a V-shaped basal face and hemiaulacorhize vascularization. Up to two pairs of lateral canals may be developed high on the labial and lingual root faces, and up to three median canals may be present. A pronounced labial buttress of the root is present beneath the basal flange.

Agaleus dorsetensis sp. nov.

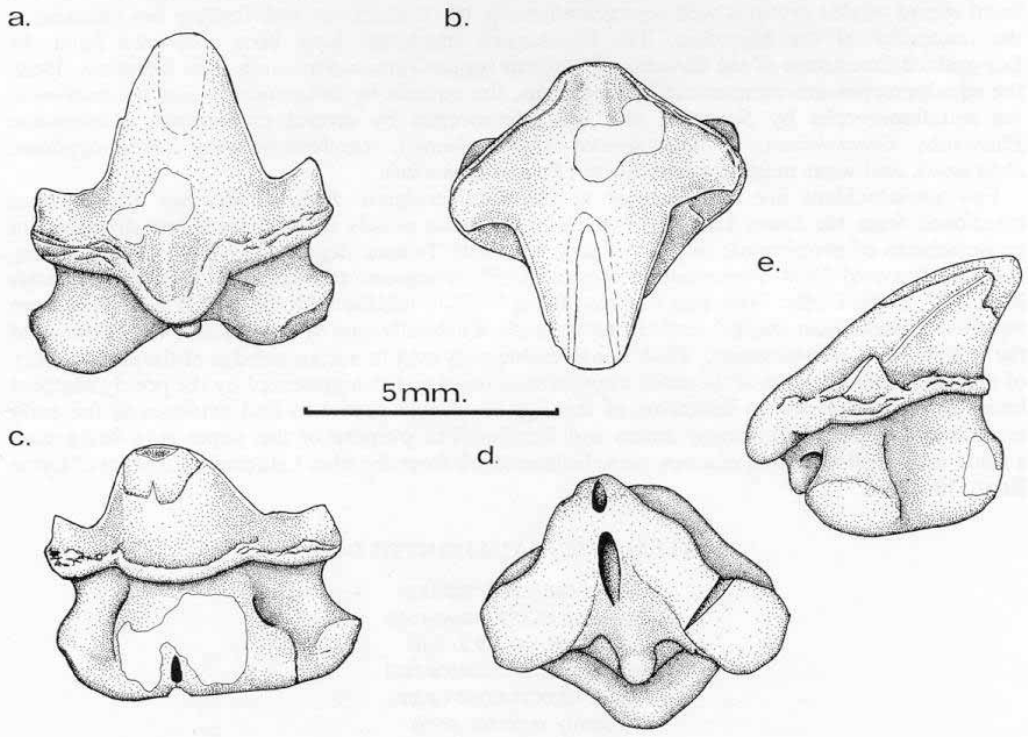
Text-figs. 1*a–e*, 3*a–e*

Diagnosis. As for genus.

Derivation of name. After Dorset, the county in which the teeth were found.

Holotype. P.60788 BM(NH), a complete tooth (text-figs. 1*a–e*), collected by Mr. A. Gale from a fallen block below Church Cliff, Lyme Regis.

Other Material. Two teeth; P.60789 BM(NH), an isolated crown, collected by Mr. D. Kemp in 1975 from a fallen block below Church Cliff, Lyme Regis; GSM 117084 (text-fig. 3), complete tooth, collector unknown.



TEXT-FIG. 1. Holotype of *Agaleus dorsetensis* (BM(NH) P.60788) from the lower Jurassic of Lyme Regis, Dorset. *a*, labial view; *b*, oclusal view; *c*, lingual view; *d*, basal view; *e*, lateral view.

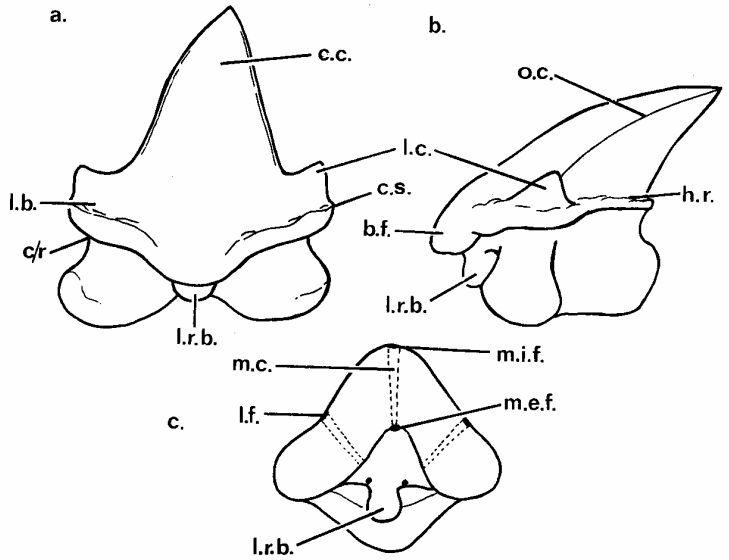
Age. P.60788 and P.60789 are from the Blue Lias, ?Lower Sinemurian, lower Jurassic. GSM 117084 is labelled 'Lower Lias' only.

Locality. P.60788 and P. 60789 are from Church Cliff, Lyme Regis, Dorset, England. ST345925. The locality for GSM 117084 is unknown.

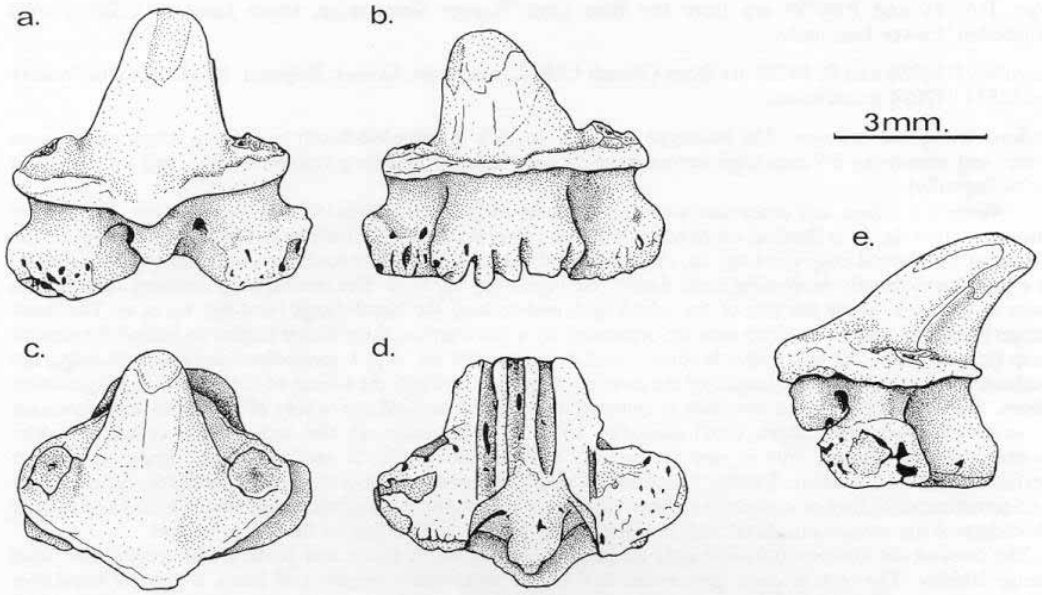
Description of the holotype. The holotype (text-fig. 1*a–e*) is a complete tooth sustaining some antemortem wear, and measuring 6·9 mm high (crown apex to root base), 6 mm long (mesiodistally), and 6·5 mm wide (labiolingually).

The crown is robust and comprises a central lingually inclined cusp with circular cross-section. The central cusp (c.c., text-fig. 2) is flanked on either side by one lateral cusplet (l.c.) which is less than one-sixth of the height of the central cusp (text-fig. 1*a*, *c*). The lateral blades (l.b.) of the tooth are well developed and there is a prominent basally projecting basal flange (b.f.) (text-fig. 1*a*, *b*, *e*). The central cusp sustains antemortem wear at the apex, along the top of the labial face, and toward the basal flange (text-fig. 1*a*, *c*, *e*). The basal flange possesses two depressions labially, separated by a low vertical ridge which begins to ascend the central cusp (text-fig. 1*a*). The labial face is shorter and concave (text-fig. 1*e*). A mesiodistal longitudinal ridge, the occlusal crest (o.c.), runs the length of the crown and passes through the apices of the cusps, forming cutting edges. The top of the crown shoulder is somewhat expanded around the whole of the tooth and possesses a series of horizontal ridges (h.r.) (text-fig. 1*a–c*, *e*). The ridge at the top of the crown shoulder is the most prominent, but is not continuous around the tooth. It contains many gaps, and short vertical ridges arise from it. Further longitudinal ridges are present below the crown shoulder, often broken and sometimes dividing or converging. These accessory ridges are more pronounced on the labial and lingual shoulders of the mesial and distal lateral blades (text-fig. 1*a*, *c*). There is no further ornament.

The crown/root junction (c/r) is deeply incised around the whole tooth and particularly beneath the basal flange labially. The root is deep (just under half of the total tooth height) and has a V-shaped basal face whose apex is directed lingually (text-fig. 1*d*). The lateral arms of the V are expanded labially. The vascularization is hemiaulacorhize; a median canal (m.c.) is partially roofed and connects a medio-internal (m.i.f.) and medio-external foramen (m.e.f.). There is one pair of lateral internal and external foramina (l.f.)



TEXT-FIG. 2. Diagram to illustrate technical descriptive terms used in the text. Tooth in *a*, labial view; *b*, lateral view; *c*, basal view. c.c. central cusp; l.c. later cusplet; l.b. lateral blade; b.f., basal flange; o.c., occlusal crest; h.r., longitudinal ridge; c/r, crown/root junction; m.c., median canal; m.i.f., medio-internal foramen; m.e.f., medio-external foramen; l.f., lateral foramen; l.r.b., labial root buttress; c.s., crown shoulder.



TEXT-FIG. 3. Tooth of *Agaleus dorsetensis* (GSM 117084) in *a*, labial view; *b*, lingual view; *c*, occlusal view; *d*, basal view; *e*, lateral view.

situated half-way up the labial and lingual root walls (text-fig. 1*c*, *e*). Just beneath the basal flange, a short but robust labial root buttress (l.r.b.) is developed, separating the two lateral labial foramina (text-fig. 1*a*, *d*, *e*).

Variation. P.60789 comprises an isolated crown, measuring 7 mm from central cusp apex to the base of the basal flange, and 5 mm mesiodistally. The specimen agrees with the general morphology of the holotype and has sustained less antemortem wear. The basal expansion of the basal flange is not quite so pronounced as in the holotype, and longitudinal ridges at the crown shoulder are fewer in number and mostly restricted to the lingual side. Also, there are isolated vertical ridges ascending the mesial and distal edges of the central cusp and lateral cusplets for a short distance (1·5 mm).

GSM 117084 (text-fig. 3*a–e*) is identical to the holotype in the structure of the crown and distribution of antemortem wear. The lateral cusplets have been removed by post-mortem abrasion. The overall root morphology is as for the holotype, with the exception of the vascularization. The labial extremities of the lateral root prongs and the lingual apex of the V-shaped flat basal root face are markedly expanded. The basal root face has been somewhat eroded (text-fig. 2*d*). Three open median canals are present crossing the basal root face labiolingually. A fourth median canal of identical orientation is present in a more lateral position.

DISCUSSION

Agaleus dorsetensis possesses a well-differentiated crown and root and hemiaulacorhizoid root vascularization (Casier 1947). This combination of characters exists only in the neoselachian sharks (Duffin and Ward 1983). Although a thick enameloid layer is present in *Agaleus*, its ultrastructure has not been investigated owing to the scarcity of specimens.

The neoselachians are divided into four superordinal groups (Compagno 1973): Batoidea, Squatinomorphii, Squalomorphii, and Galeomorphii, all of which are represented in Jurassic deposits. Squalomorph sharks usually possess teeth which are strongly labiolingually compressed, acting as scissor blades (e.g. *Isistius*) with an anaulacorhizoid vascularization. Batoid teeth are low-crowned, usually non-cuspidate, with anaulacorhizoid or holaulacorhizoid root vascularization. The hemiaulacorhizoid root vascularization shown by *Agaleus* is restricted to galeomorph and squatinomorph sharks (Table 1).

TABLE 1. Comparison of the teeth of *Agaleus dorsetensis* with those of Recent and fossil neoselachians. +, character present; −, character absent; H, hemiaulacorhize vascularization; Ho, holaulacorhizoid vascularization; A, anaulacorhizoid vascularization.

	Agaleus dorsetensis	Squalomorphs	Batoids	*Squatina*	*Heterodontus*	Lamniforms	Carcharhiniforms	*Parascyllium*	*Cirrhoscyllium*	*Hemiscyllium*	*Chiloscyllium*	*Synchismus*	*Eostegostoma*
CROWN CHARACTERS													
Basal flange	+	+	−	+	+	−	−	+	−	−	−	−	+
Lingual apron	+	+	−	−	−	−	−	−	−	+	+	+	+
Lateral cusplets	1	0–1	0	0	0–4	0–2	0–4	1	1	0–1	0–1	0–1	1
Longitudinal ridge	+	−	−	−	−	−	−	−	−	−	−	−	−
ROOT CHARACTERS													
Vascularization	H	A	Ho/A	H	H	Ho	Ho/A	Ho	H	H	H	H	H
Root buttress	+	−	−	−	−	−	−	−	−	−	−	−	−

	Stegostoma	*Rhiniodon*	*Palaeorhiniodon*	*Ginglymostoma*	*Protoginglymostoma*	*Nebrius*	*Eucrossorhinus*	*Orectolobus*	*Brachaelurus*	*Squatirhina*	*Anachronistes*	*Doratodus*	*Almascyllium*
CROWN CHARACTERS													
Basal flange	−	+	+	+	−	+	+	+	+	+	+	−	+
Lingual apron	+	+	+	+	+	+	+	+	+	+	−	−	+
Lateral cusplets	1	0	0–1	2–5	1–3	2–12	0	0	1	0–1	1	1	1
Longitudinal ridge	−	−	−	−	−	−	−	−	−	−	+	+	+
ROOT CHARACTERS													
Vascularization	H/Ho	H	H	H	H	H	Ho/H	H	H	Ho	H	?	H
Root buttress	−	−	−	−	−	−	−	−	−	−	+	?	−

Our knowledge of squatinomorph sharks' teeth is restricted to the single extant genus *Squatina*, and a small number of fossil species. The general tooth morphology comprises an elongate central cusp flanked by non-cuspidate lateral blades. *Agaleus* shares the possession of a hemiaulacorhizoid root with *Squatina*, and the presence of a strong labial flange at the base of the crown. It differs markedly in crown architecture, however, having strong lateral cusplets flanking a low central cusp.

Among Galeomorphii, hemiaulacorhizoid root vascularization is seen only in *Heterodontus* and the orectolobiforms (Table 1). The dentition of mature *Heterodontus* shows stong monognathic heterodonty in which only the anterior teeth are cuspidate; the lateral teeth form a crushing pavement. Also, only juvenile *Heterodontus* show the development of a basal flange (Reif 1976 figs. 23, 24); a small pair of lappets overhangs the crown root junction in adult anterior teeth (Reif 1976, fig. 23).

The basal flange in *Agaleus* is strongly developed, a feature seen in the teeth of a number of orectolobid genera (Table 1). *Agaleus* combines this feature with a single pair of lateral cusplets on the crown, a combination of features seen in the teeth of *Brachaelurus* amongst extant orectolobid sharks, and *Mesiteia* amongst fossil species. Thus the teeth of *Agaleus* superficially resemble those of *Brachaelurus* and *Mesiteia* most closely among orectolobids. *Mesiteia* is recorded from the Upper Cretaceous of Lebanon (Cappetta 1980) and the U.S.A. (Estes 1964, Cappetta 1973, Herman 1977). The extant genus *Brachaelurus* has been cited from the Turonian (upper Cretaceous) of South Dakota, U.S.A. (Cappetta 1973).

Teeth of *Agaleus* differ from those of all extant orectolobid genera, however, in possessing a labial root buttress which underlies the basal flange of the crown. This feature is known only in the Carboniferous and Permian genus *Anachronistes* (Duffin and Ward 1983), a presumed neoselachian of doubtful ordinal status. In addition, *Agaleus* possess well-defined horizontal ridges on the labial and lingual crown shoulders. This feature is not present in any Recent sharks tooth, to our knowledge. Amongst fossil neoselachians, it is weakly developed in *Anachronistes*. The problematic genus *Doratodus* (Duffin 1981) has a simpler horizontal ridge on the labial and lateral crown shoulders (Table 1).

The teeth of *Agaleus* are larger than those of any extant orectolobiform genera excepting *Nebrius* and *Ginglymostoma*. The labial buttress of the root may indeed have been instrumental in adding extra structural advantage to the crown during occlusion. We assume from the tooth shape and antemortem wear that *Agaleus* was of benthonic habit and durophagous diet, in common with most orectolobid species.

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