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SHARKS OF THE ORDER CARCHARHINIFORMES FROM THE BRITISH CONIACIAN, SANTONIAN AND CAMPANIAN (UPPER CRETACEOUS)

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Abstract: Bulk sampling of phosphate-rich horizons within the British Coniacian to Campanian (Upper Cretaceous) yielded very large samples of shark and ray teeth. All of these samples yielded teeth of diverse members of the Carcharhiniformes, which commonly dominate the fauna. The following species are recorded and described: *Pseudoscyliorhinus reussi* (Herman, 1977) comb. nov., *Crassescyliorhinus germanicus* (Herman, 1982) gen. nov., *Scyliorhinus elongatus* (Davis, 1887), *Scyliorhinus brumarivulensis* sp. nov., ?*Palaeoscyllium* sp., *Prohaploblepharus riegrafi* (Müller, 1989) gen. nov., ?*Cretascyliorhinus* sp., Scyliorhinidae *incertae sedis* 1, Scyliorhinidae *incertae sedis* 2, *Pteroscyllium hermani* sp. nov., *Protoscyliorhinus* sp., *Leptocharias cretaceus* sp. nov., *Palaeogaleus havreensis* Herman, 1977, *Paratriakis subserratus* sp. nov., *Paratriakis tenuis* sp. nov., *Paratriakis* sp. indet. and ?*Loxodon* sp. Taxa belonging to the families ?Proscylliidae, Leptochariidae and Carcharhinidae are described from the Cretaceous for the first time. The evolutionary and palaeoecological implications of these newly recognised faunas are discussed.

Key words: Carcharhinidae, Cretaceous, Leptochariidae, Proscylliidae, Scyliorhinidae, shark, Triakidae.

THE Late Cretaceous represented a time of high shark and ray diversity, with many extant orders and families being present (e.g. Cappetta 1987; Underwood 2006). Although some localities have yielded well-preserved shark and ray skeletons (e.g. Cappetta 1980*a, b*), the majority of the Cretaceous selachian fossil record is restricted to isolated teeth. Whilst the teeth of some Cretaceous taxa, such as many lamniforms and *Ptychodus*, are large and conspicuous enough to be collected individually, a large proportion of teeth are of a size that necessitates bulk sampling. Despite this, relatively few studies of Cretaceous shark and ray faunas have involved extensive bulk sampling, and when this has been carried out, sieve mesh sizes are often too large to retain the smaller teeth (DJW, pers. obs.). Where studies of Cretaceous selachian faunas appear to have been carried out using bulk sampling, only a small proportion have included a description of the methods used. The lack of work on assemblages of sharks and rays with very small teeth has resulted in many of these smaller-toothed taxa, especially of the order Carcharhiniformes, being very poorly studied.

The Carcharhiniformes are one of the most diverse groups of sharks alive today, with species ranging in size from under 0.3 to over 6 m in length, and inhabiting virtually all marine habitats, with some taxa entering fresh water. The earliest known Carcharhiniformes are from the Middle Jurassic (e.g. Cappetta 1987; Underwood and Ward 2004), with teeth commonly being present in shark assemblages from the Late Jurassic and Early Cretaceous. Within many Late Cretaceous assemblages, teeth of Carcharhiniformes of the families Scyliorhinidae and Triakidae are abundant and diverse (e.g. Herman 1977; Underwood and Ward in press). Although cladistic studies have suggested that other families of Carcharhiniformes should have been present in the Cretaceous (e.g. Underwood 2006), their remains have not been described.

GEOLOGICAL SETTING

The Late Cretaceous was a period of globally high sea levels, and transgressive and highstand sedimentary successions are typical. Within northern Europe, much of the Upper Cretaceous succession is represented by coccolith chalk facies, with other facies being largely restricted to quartz and glauconite sands associated with structural highs. Macroscopic vertebrate remains are generally uncommon within chalk facies, with extensive museum collections largely being the result of intensive

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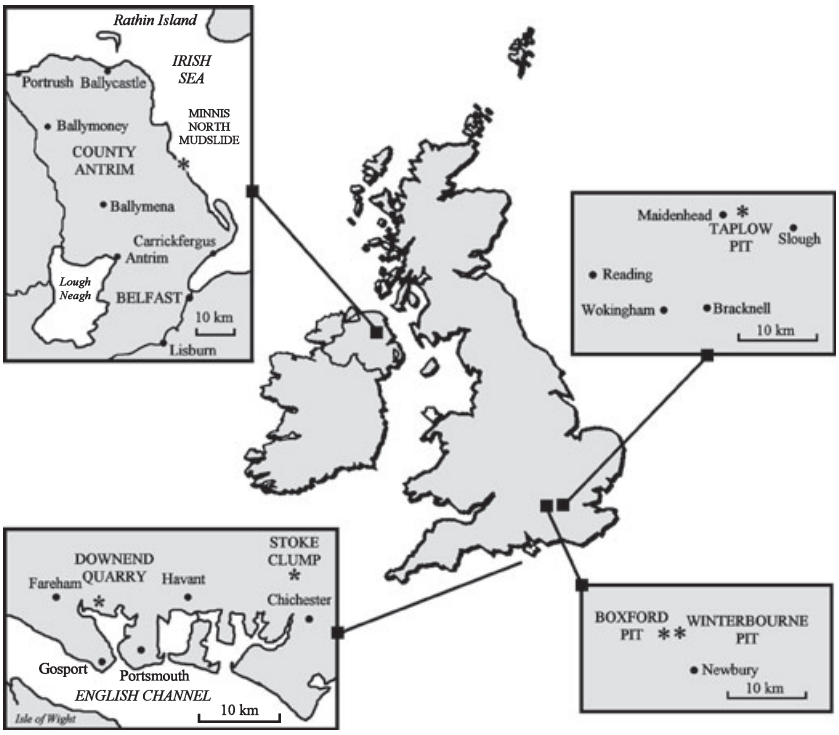


TEXT-FIG 1. Map showing the localities sampled.

collecting during former periods of active manual quarrying. The English Chalk is also a particularly poor candidate for systematic bulk sampling because of the extreme rarity of shark and ray teeth and the degree of bioerosion encountered. This is in contrast to southern Swedish chalks that can yield up to 10 tooth fragments per kg (Mikael Siverson, pers. comm. 2000). Unlike most of the English Chalk, phosphatic chalks, often immediately overlying hardgrounds, commonly contain abundant shark and ray remains. This is presumably due to a combination of current winnowing and low rate of sediment deposition and high overall levels of pore water phosphate. Many of the teeth are well mineralised and rates of bioerosion are lower than in non-phosphatic chalks. Localized areas of these phosphatic chalks are common in the Santonian and Campanian of north-west Europe and fill lenticular erosional troughs or 'cuvettes' with hardground complexes at their base (Jarvis 1980, 2006).

The majority of the English material described below was collected from chalks with a high content of phosphatic material (Text-fig. 1) during a period of fieldwork carried out by DJW in the late 1970s, which was inspired by the work of Ian Jarvis, Peter Woodruff, and Andy Gale. A Coniacian glauconitic sandstone from Northern Ireland was sampled more recently by CJU. All of these phosphatic horizons sampled yielded large numbers of shark and ray teeth of many species. The vast majority of these teeth are extremely small, and belong to small nectobenthic taxa. For details of the localities sampled and associated faunas, see the Appendix.

MATERIAL AND METHODS

All of the rock samples studied were moderately to strongly lithified, and could only be broken down by use of acids. Samples of the phosphatic chalks from southern England were crushed into 2–5-cm fragments and dissolved in buffered dilute acetic or formic acid. The residue from the 355 μm sieve fraction and above was picked for vertebrate remains. The phosphate-rich greensands from Minnis North were broken down in buffered formic acid. The residue from the 500 μm sieve fraction and above was picked for vertebrate remains, along with much of the 355 μm fraction; this fine fraction yielded very few teeth and these were highly diluted by grains of phosphate, quartz and glauconite.

A large proportion of teeth collected during this study are imperfect, with roots of the majority showing some degree of damage owing to microbial bioerosion (see Underwood *et al.* 1999). There is no sign of physical biostratinomic damage of teeth from any of the sites other than Minnis North. Where teeth of a taxon are distinctive enough to be recognisable from incomplete specimens, counts of numbers of specimens can be obtained, but where there are several taxa with similar teeth within the same sample (as with some scyliorhi-

nids) it is not possible to obtain an accurate count for the number of imperfect specimens. Counts otherwise include all teeth and partial teeth well preserved enough to be identifiable. All figured specimens from England are housed in the Natural History Museum, London (BMNH P., shortened here to 'P.'). The figured specimens from Minnis North are in Ulster Museum (BELUM K). All figured specimens were imaged by SEM. The terminology used here for parts of the selachian teeth largely follows that of Cappetta (1987).

SYSTEMATIC PALAEONTOLOGY

Cohort EUSELACHII Hay, 1902
Subcohort NEOSELACHII Compagno, 1977
Superorder GALEA Shirai, 1996
Order CARCHARHINIFORMES Compagno, 1977
Family SCYLIORHINIDAE Gill, 1862

Remarks. Sharks of the family Scyliorhinidae are abundant and diverse in the fossil record, but have received very little attention and remain poorly known. Although some Cretaceous scyliorhinids are known from articulated skeletons (e.g. Cappetta 1980*a*) the majority are known from isolated teeth. Although the teeth of many extant scyliorhinid genera are very characteristic (Herman *et al.* 1990), there have been relatively few attempts (e.g. Noubhani and Cappetta 1997) to refer fossil scyliorhinid taxa to extant or extinct genera; the majority have been referred to the genus *Scyliorhinus* Blainville, 1816. Although the type species of *Scyliorhinus*, *S. canicula* Linnaeus, 1758, has a far more diverse range of dental morphologies than recognised in the literature (Ellis and Shackley 1995; CJU, pers. obs.), a large proportion of fossil scyliorhinid dentitions cannot be accommodated within this genus. This failure to refer fossil scyliorhinid teeth to extant genera other than *Scyliorhinus* or erect new genera for species than cannot be accommodated within extant genera, has resulted in a lack of knowledge of the geological ranges of living genera and of the true diversity of the Scyliorhinidae in the past.

Genus PSEUDOSCYLIORHINUS Müller and Diedrich, 1991

Type species. Pseudoscyliorhinus schwarzhansi Müller and Diedrich, 1991, from the Cenomanian of Germany.

Pseudoscyliorhinus reussi (Herman, 1977) comb. nov.
Plate 1, figures 1–9

1977 *Scyliorhinus reussi* Herman, pl. 11, fig. 2.

in press *Pseudoscyliorhinus* sp. Underwood and Ward, fig. 1C–D.

Material. P. 66363–P. 66367 from a total of 124 teeth: 10, Boxford; 2, Winterbourne lower horizon; 2, Winterbourne upper horizon; 2, Taplow upper horizon; 71, Stoke Clump; 35, Downend; 2, Minnis North.

Description. Teeth of this species are under 3 mm wide and, when well preserved, very distinctive. The crown is relatively symmetrical and high, with erect cusps that make an angle of between 60 and 80 degrees with the basal face of the root. The main cusp is slender and nearly round in cross section, and is flanked by one, or more commonly two, pairs of much shorter lateral cusplets that are often very slightly divergent. The cusps are all straight and are either symmetrical or slightly inclined to the posterior. The cusps merge basally into a well-developed labial face of the crown, which is somewhat flared along its straight to slightly concave basal edge. The labial face of the crown is ornamented by a small number of rather irregular longitudinal ridges that reach less than half-way up the main cusp, but may reach the apex of the lateral cusplets. Where the labial base of the crown is flared, a longitudinal ridge may be present at the anterior and posterior ends of the tooth, this ridge interacting with the longitudinal ornament to form a narrow band of reticulate ornament. The lingual face of the crown is ornamented with fine longitudinal ridges that extend from the somewhat excavated crown-root junction to half-way up the main cusp. The crown slightly overhangs the root labially. The root is relatively low, but very strongly flared on all sides, projecting beyond the edge of the crown in all directions. The basal face of the root is very flat, and there is a sharp angle between this and the labial and lingual root faces. In basal view, the root is convex lingually and straight labially, with rounded lateral ends. There is no nutritive groove, but there is a distinct notch at the point where the main labial and lingual foramina enter the root close to the edge of the basal surface. A line of small, evenly spaced foramina is present just below the crown-root junction on both labial and lingual sides of the root. The basal face of the root has many small, irregular foramina.

Remarks. This genus is readily recognised by the presence of a flared and flat-based root differing from that of any other scyliorhinids. The genus was diagnosed on the Cenomanian species *P. schwarzhansi* Müller and Diedrich, 1991, with the very close similarities between this species and the previously described *Scyliorhinus reussi* Herman, 1977 evidently not having been recognised at the time. Although no photographs of the type material of *P. schwarzhansi* were published, the diagnosis of *Pseudoscyliorhinus* equally well covers *S. reussi*. It is therefore considered here that *S. reussi* should be included into *Pseudoscyliorhinus*.

Although generally very similar, *P. reussi* differs from *P. schwarzhansi* in having a more flattened root with less evident nutritive groove and reticulate ornament near base of labial face of anterior teeth. The genus therefore

has a recorded range of Cenomanian to Campanian. No extant scyliorhinids have been recorded as having teeth similar to *Pseudoscyliorhinus*; it is, therefore, not possible to assess the affinities of this genus. It has, however, been recorded that teeth of juvenile scyliorhinids have roots that are larger and more flared than in the adults (Herman *et al.* 1990, p. 230), so it is possible that the tooth morphology of *Pseudoscyliorhinus* was paedomorphic.

Genus CRASSESCYLIORHINUS gen. nov.

Derivation of name. From the thick and heavy form of the teeth compared to all other scyliorhinids.

Type species. Scyliorhinus germanicus Herman, 1982.

Diagnosis. Teeth very robust and symmetrical with moderate heterodonty. Erect central cusp conical and takes up much of crown; lateral cusplets small. Ornament of strong ridges in unworn teeth, often reticulate near base of labial crown. Labial margin of crown indented in centre. Root bulky and strongly V-shaped in basal view with somewhat flared distal lobes. Nutritive groove absent in almost all teeth.

Remarks. The only described species of scyliorhinid with a dentition similar to *Crassescyliorhinus germanicus* is *Scyliorhinus musteliformis* Herman, 1977, which differs in having teeth with lower crowns. The close similarity between these species suggests that *S. musteliformis* should also be included in *Crassescyliorhinus.* The genus has a recorded range of Santonian–Maastrichtian. The teeth of *Crassescyliorhinus* are clearly distinct from those of all other recorded post-Cretaceous scyliorhinid genera, being most similar to those of the Cretaceous genus *Cretoscyliorhinus* Underwood and Mitchell, 1999, from which they differ in being far more robust and in having less clearly separated lateral cusplets, a greater degree of heterodonty and a less 'trilobed' root basal face.

Crassescyliorhinus germanicus (Herman, 1982)
Plate 2, figures 10–18

1977 *Scyliorhinus elongatus* Herman, pl. 11, fig. 1H.
1982 *Scyliorhinus germanicus* Herman, pl. 2, fig. 10; pl. 4, figs 4–5.
1989 *Scyliorhinus germanicus* Herman; Müller, pl. 11, fig. 5, pl. 12, figs 1–4.
?2001 *Scyliorhinus* sp., Cappetta and Odin, pl. 1, fig. 8.

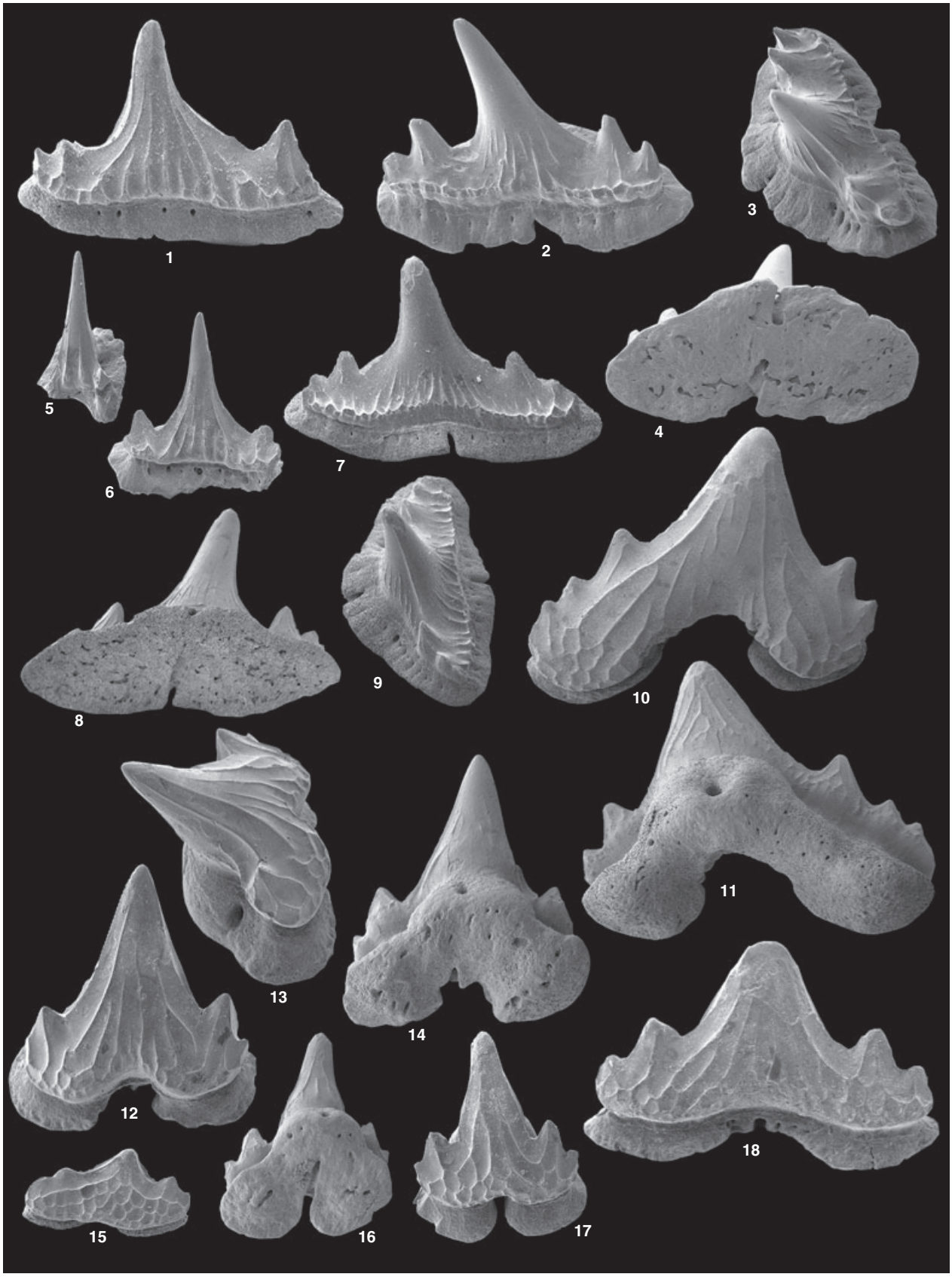
Material. P. 66368–P. 66372 from a total of several hundred teeth: 54, Boxford; 68, Winterbourne lower horizon; 43, Winterbourne upper horizon; 9, Taplow lower horizon; 18, Taplow upper horizon; several hundred, Downend.

Description. Teeth of this species are very robust and show a moderate degree of monognathic heterodonty. Some presumed anterior teeth are higher than wide, but the majority of teeth are wider than high, reaching a width of 3 mm. Teeth from most positions are symmetrical, with a low degree of asymmetry being present in posterior teeth. Over half of the width of the crown is taken up with a robust main cusp. This is conical and only slightly flattened on the labial face, and is of similar width to height on all except extreme anterior and posterior teeth. This is flanked by one or two pairs of short but robust lateral cusplets that are typically wider than high; a third cusplet may be present on the anterior side of large, presumed anterolateral teeth. The ends of the crown are rounded, with the basal edge of the crown on the labial side having a strong and smoothly curved indentation on all except posterior teeth. The labial face of the crown is typically highly ornamented with strong and sharp-edged ridges, although these may be less well developed on some of the largest and most robust lateral teeth. The labial ornament comprises widely spaced longitudinal ridges, with up to six on the main cusp, that bifurcate towards the crown base to form a polygonal pattern, and reach the apex of the cusps where not removed by wear. Ornament on the lingual face of the crown is similar if not so strongly developed and rather more irregular. The crown is a similar width or slightly narrower than the root, and strongly overhangs it labially. The root is low, and distinctly V-shaped when viewed basally. The basal face of the root is flat, and is flared at its lateral ends. There is a bulbous lingual apex of the root with a large, central foramen. Opposite this on the

EXPLANATION OF PLATE 1

Figs 1–9. *Pseudoscyliorhinus reussi* (Herman, 1977) comb. nov. 1, P. 66363, Lower Campanian, Downend, labial view. 2–4, P. 66366, Boxford, in 2, labial, 3, oblique lateral, and 4, basal views. 5, P. 66364, Lower Campanian, Winterbourne, upper phosphate level, ?parasymphaseal tooth, labial view. 6, P. 66365, Lower Campanian, Winterbourne, upper phosphate level, ?small anterior tooth, labial view. 7–9, P. 66367, Lower Campanian, Winterbourne, upper phosphate level, in 7, labial, 8, lingual, and 9, oblique lateral views. 1–6, × 35; 7–9, × 20.

Figs 10–18. *Crassescyliorhinus germanicus* (Herman, 1982). 10–11, P. 66368, Upper Santonian, Winterbourne, lower phosphate level, large anterolateral tooth in 10, labial, and 11, lingual views. 12–14, P. 66369, Middle Santonian, Boxford, anterior tooth in 12, labial, 13, oblique lateral, and 14, lingual views. 15, P. 66370, Middle Santonian, Boxford, posterior tooth, labial view. 16–17, P. 66371, Boxford, anterior tooth in 16, labial, and 17, lingual views. 18, P. 66372, Middle Santonian, Boxford, posterolateral tooth, labial view. 10–11, × 20; 12–18, × 35.



UNDERWOOD and WARD, *Crassescyliorhinus*, *Pseudoscyliorhinus*

lingual side is a notch or groove containing the lingual foramen. An open nutritive groove is rarely present. The lingual faces of the root are concave and have a small number of well-developed foramina. Numerous small foramina are present on the basal face of the root.

Remarks. The teeth recorded here are very similar to those previously figured (e.g. Herman 1977, 1982; Müller 1989), although the small number of specimens figured before has not previously allowed recognition of the degree of heterodonty within the species recognised here, and the teeth figured here are largely of morphologies not previously illustrated.

Genus SCYLIORHINUS Blainville, 1816

Type species. Squalus canicula Linnaeus, 1758.

Remarks. Scyliorhinus has commonly been used as a convenient genus within which to place virtually all fossil scyliorhinid (and sometimes other carcharhiniform) teeth. Despite this, it is one of 16 extant scyliorhinid genera, and recent studies (e.g. Noubhani and Cappetta 1997) have recognised a number of additional extinct genera. Several workers (Herman *et al.* 1990; Halter 1994) have noted the distinctive dental morphology of extant *Scyliorhinus*, and that relatively robust anterior teeth without well-developed cusplets are characteristic of the genus. Despite this, studies of jaws of the type species have revealed very strong sexual heterodonty (Ellis and Shackley 1995; J. Southion and A. Chappel, pers. comm. 2006). The robust teeth morphology is only present in mature males, with females and juveniles having smaller, more gracile teeth with well-developed lateral cusplets. The pattern of heterodonty shown in other extant species of *Scyliorhinus* has not been documented, but it is possible that in some species, such as *S. stellaris*, the robust tooth morphology is seen in both sexes (A. Chappel, pers. comm. 2006).

Scyliorhinus elongatus (Davis, 1887)
Plate 2, figures 1–9

1887 *Thyellina elongata* Davis; pl. 14, figs 2–3 (teeth not figured).
1889 *Scyllium elongatus* (Davis); Woodward, pl. 16, fig. 5 (teeth not figured).
1977 *Scyliorhinus elongatus* (Davis); Herman, pl. 11, fig. 11.1G, I–J.
1980a *Scyliorhinus elongatus* (Davis); Cappetta, pl. 21, fig. 2; pl. 22, figs 2–7; pl. 23, figs 1–4 (teeth only), fig. 30.
?1997 *Scyliorhinus* aff. *elongatus* (Davis), Noubhani and Cappetta, pl. 24, figs 1–6.

Material. P. 66373–P. 663775 from a total of 78 teeth: 5, Boxford; 10, Winterbourne lower horizon; 4, Winterbourne upper horizon; 1, Taplow lower horizon; 5, Taplow upper horizon; 53, Downend.

Description. Teeth of this species show a high degree of monognathic heterodonty, with distinctly different anterior and lateral tooth morphologies. Heterodonty is similar to that recorded previously (Cappetta 1980*a*). All teeth are higher than wide. Anterior teeth are large, up to 3 mm high, poorly ornamented and asymmetrical, with teeth becoming smaller, more gracile and more strongly ornamented in lateral positions. Anterior teeth are robust and have a straight main cusp flanked by a pair of short but robust cusplets. Labial and lingual faces of all cusps are similarly convex. Ornament is weak and largely restricted to the lateral parts of the crown. The labial face of the main cusp has little or no ornament, with 2–3 strong longitudinal ridges being present on the lateral cusplets, being strongest at the basal edge of the crown. The lingual face of all cusps has weak longitudinal ridges reaching close to the apex. The basal edge of the crown on the lingual side strongly overhangs the root and is strongly excavated below the main cusp. The entire crown is inclined towards the commissure. The root is robust and strongly bilobate and V-shaped, if somewhat asymmetrical, in basal view. The lingual foramina are well developed and in the centre of the somewhat swollen lingual part of the root. The labial foramen forms an elongate opening on the basal face of the root at the sharply angled junction of the root lobes. The root lobes are slightly flared basally and are only weakly expanded at their labial ends. The basal face of the root is flat. A series of large foramina is present on the labial faces of the root, with small and irregular foramina being present on the basal face of the root. The crowns of lateral teeth are somewhat similar to those of anteriors, but are more gracile with more elongate main and lateral cusps. The labial faces of both main cusp and lateral cusplets have an ornament of strong longitudinal ridges that do not bifurcate, and most reach almost to the apices of the cusps. The lingual faces have very fine longitudinal ridges. The basal edge of the crown is less excavated than in anterior teeth, but is still always concave, and overhangs the root to a moderate degree. The roots of lateral teeth are similar to those of anterior teeth, but are somewhat lower and less robust, with the root lobes being somewhat more flared.

Remarks. Both anterior and lateral teeth are almost identical to those figured by Cappetta (1980*a*) and Herman (1977). This species thus appears to be relatively widespread, being present in the Santonian of Lebanon (Cappetta 1980*a*) and Campanian of Belgium (Herman 1977) in addition to the records given here. Teeth from Morocco (Noubhani and Cappetta 1997) agree well with material of *S. elongatus*, suggesting that this species may have ranged up to Late Maastrichtian. The overall dental morphology is very similar to that of *Scyliorhinus antiquus* (Agassiz, 1843) as figured by Cappetta (1977), differing in having stronger ornamentation and more robust anterior teeth. The tooth morphology and heterodonty

are very similar to that of the male morph of *S. canicula*; it is, therefore, probable that this species belongs to *Scyliorhinus s.s.* No gracile anterior teeth similar to those possessed by female and juvenile *S. canicula* were recognised; it is, therefore, likely that there was little or no sexual heterodonty in this taxon.

Scyliorhinus brumarivulensis sp. nov.
Plate 2, figures 10–18

Derivation of name. Direct Latin translation of Winterbourne, from the common occurrence of this species there.

Holotype. BMNH P. 66378.

Material. P. 66379–P. 66382 from a total of several hundred teeth: 158, Boxford; 110, Winterbourne lower horizon; 24, Winterbourne upper horizon; 10, Taplow lower horizon; 8, Taplow upper horizon; several hundred, Downend.

Diagnosis. Teeth show moderate degree of gradient monognathic heterodonty, with more compressed, smoother anterior teeth and more ornamented laterals. All teeth under 1.5 mm wide, with teeth from most jaw positions at least as wide as high. Main cusp straight and flanked by two pairs of short, pointed lateral cusplets, the outer pair poorly developed or absent in anterior teeth. Ornament varies with jaw position; labial face of anterior teeth flat and smooth, that of all cusps of lateral teeth with small numbers of very strong longitudinal ridges that bifurcate strongly towards the base and reach most of the way to the apex of the cusps; similar but weaker ornament on teeth from transitional positions. Crown of teeth from most positions inclined towards commissure. Labial basal edge of crown straight to weakly concave and strongly overhangs root. Root low and hemiaulacorhize. Basal face of root flat and flared, especially on lingual edges of root lobes.

Description. The teeth of this species are uniformly small, being less than 1.5 mm wide, and show distinctive monognathic heterodonty and probable dignathic heterodonty. The width of the majority of teeth is similar to their height, although some extreme anterior teeth are rather higher than wide. The crown is erect and comprises a main cusp, which is somewhat longer than wide, flanked by two pairs of small, sharply pointed lateral cusplets, except in some anterior teeth where the outer pair of cusplets may be very reduced and incipient. The base of the main cusp occupies about half of the width of the crown. All cusps are somewhat flattened labially, with some of the largest and least well ornamented teeth having a labial face that is almost flat. By analogy with extant scyliorhinid dentitions, these are assumed to be from lower anterior positions. All teeth have a continuous and well-developed cutting edge. The labial face of the crown of lateral teeth is ornamented with 10–15, somewhat discontinuous, longitudinal ridges. These ridges are sharply edged and reach at least three-quarters of the way to the apices of all cusps. Towards the base of the crown, the labial ridges bifurcate, and commonly join to form a narrow strip with a reticulate pattern. In presumed upper anterior teeth a similar but weaker and more irregular ornament is present. Presumed lower anterior teeth have a labial ornament of short longitudinal ridges on the basal and lateral parts of the crown, or may have no labial ornament. The basal edge of the labial face of the crown is faintly concave to almost straight, and strongly overhangs the root. The lingual face of the crown is ornamented by several weak, and rather irregular, longitudinal ridges in most teeth, but is smooth in presumed lower anterior teeth. This lingual ornamentation reaches neither the apex of the cusps nor base of the crown. The root is low and lacks a nutritive groove. The root is V-shaped in basal view, with concave outer lingual faces of the root lobes in lateral teeth making them appear rather recurved. The basal part of the root is flared along the labial edge and at the lateral extremities. The basal face of the root is flat, and the edge between the basal and lingual or labial faces is sharply angled. There are well-developed foramina at the lingual apex of the root and at the junction of the root lobes. Well-developed foramina are present on the lingual faces of the root, and on the basal face of the root lobes, with smaller and more irregular foramina also being present across much of the root.

Remarks. The teeth of this species are very similar in overall morphology and the general form of ornament to those of *Scyliorhinus arambourgi* Cappetta, 1980*a* (see Cappetta 1980*a*, fig. 27) from the Cenomanian of Lebanon. Teeth of *S. brumarivulensis* sp. nov. differ principally in the greater amalgamation of ribs near the basal edge of the labial crown face, forming a reticulate pattern in most teeth. There are also strong similarities between teeth of *S. brumarivulensis* sp. nov. and those of *S. sulcidens* Noubhani and Cappetta, 1997 from the Palaeocene of Morocco, which differs in having more elongate lateral cusplets and a sparser ornamentation. The teeth of this species show a very similar overall morphology and heterodonty to that of female *Scyliorhinus canicula*. It is unknown whether *S. brumarivulensis* sp. nov. shows sexual heterodonty, but the presence of uncommon large anterior teeth suggests that it is possible that enlarged teeth were only present in a proportion of individuals, possibly mature males. The presence of a dentition very similar to that of female *S. canicula* suggests that this species should be included in *Scyliorhinus* despite not conforming to the tooth morphology of the genus as defined by Herman *et al.* (1990) and Halter (1994). Despite being very common within the samples studied here, teeth of this taxon appear not to have

been recognised in earlier studies, presumably because of their small size.

Scyliorhinus aff. *S. brumarivulensis* sp. nov.
Plate 3, figures 1–2

Material. BELUM K29670, a single tooth from Minnis North.

Description. This single tooth is 1 mm high and generally well preserved. The crown is slightly asymmetrical, with the cusps inclined to the posterior. The main cusp is triangular in profile, and basally comprises more than half of the crown width. This is flanked by a pair of short but robust lateral cusplets, about as wide as high, with a minute additional cusplet on the posterior side. A continuous but weak cutting edge is present across the entire width of the crown. The labial face of all cusps is slightly convex, the lingual face is strongly convex. The labial crown face is ornamented by a series of short, irregular longitudinal ridges, reaching less than half of the way up the main cusp and not reaching the apex of the undamaged cusplet. These labial ridges reach the crown-root contact, and some bifurcate. The lingual face of the crown is ornamented with weak longitudinal ridges reaching close to the apex of the main cusp. The crown overhangs the root on all sides. The root is wider than the crown, and relatively low. It is flared basally towards the lateral ends, and has a flat basal face. A series of well-developed foramina is present near the centre of the labial root face, and a large foramen at the lingual root apex. A row of foramina is present along the root lingual face.

Remarks. This tooth is very similar to those assigned to *Scyliorhinus brumarivulensis* sp. nov., but differs in having the combination of a weak and irregular ornament and poorly developed lateral cusplets; teeth of this morphology were not recognised within the large sample sizes of *S. brumarivulensis* teeth seen at other sites, whereas 'typical' *S. brumarivulensis* teeth were not found in association with this tooth. It is, therefore, possible that this tooth may either represent an extreme morphology of *S. brumarivulensis* or another, related species. The latter would not be unreasonable considering the very different facies and age of the Minnis North site compared to the other sites studied.

Genus PALAEOSCYLLIUM Wagner, 1857

Type species. Palaeoscyllium formosum Wagner, 1857 from the Tithonian of Germany.

Palaeoscyllium striatum sp. nov.
Plate 3, figures 3–9

Derivation of name. After the evenly striated ornament on the teeth.

Holotype. BMNH P. 66383.

Material. P. 66384 and P. 66385 from a total of 86 whole and partial teeth: 21, Boxford; 22, Winterbourne lower horizon; 3, Winterbourne upper horizon; 1, Taplow lower horizon; 7, Taplow upper horizon; 9, Stoke Clump; 23, Downend.

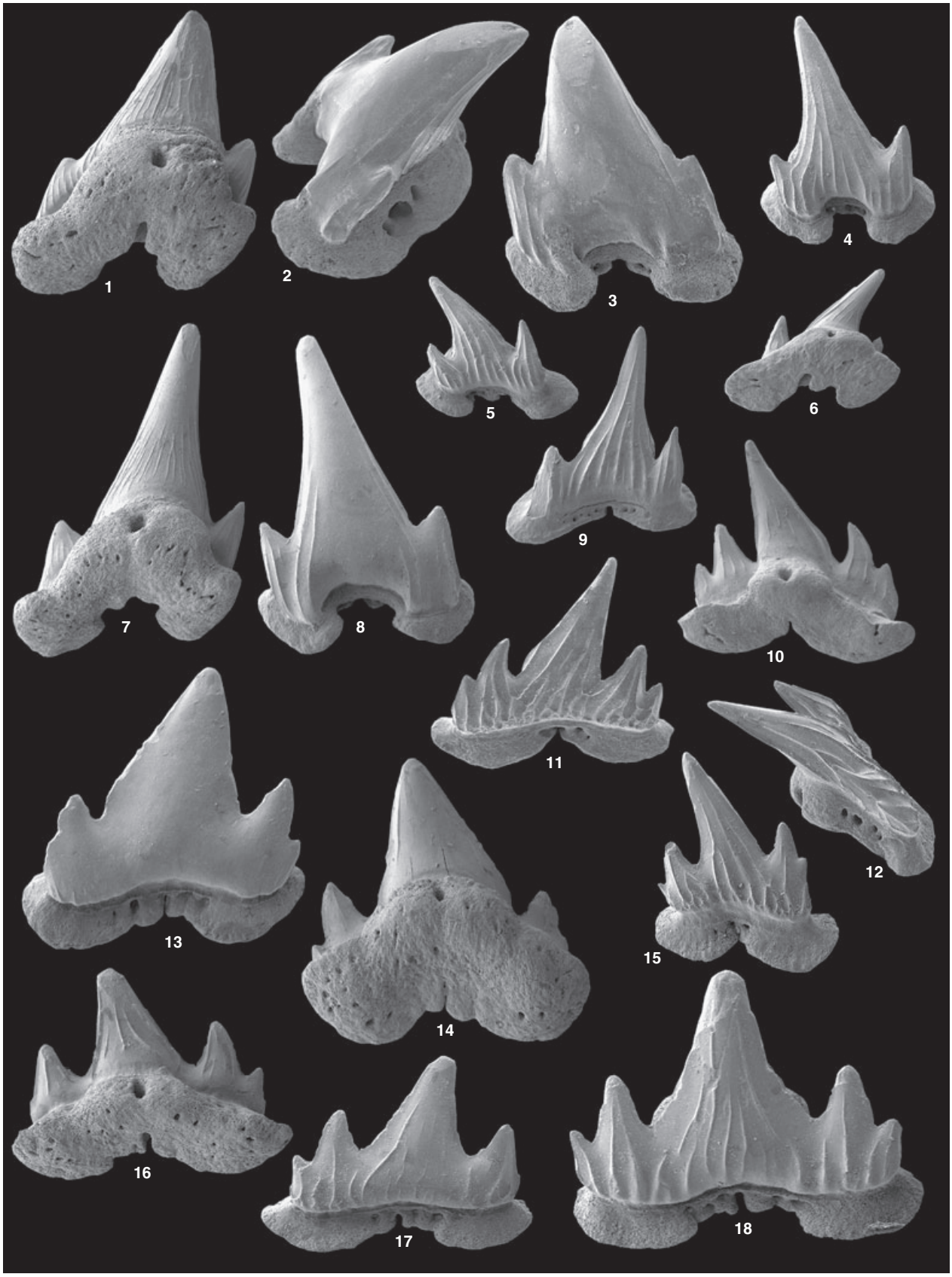
Diagnosis. Dentition apparently showing low degree of gradient monognathic heterodonty. Teeth higher than wide, with main cusp more than twice as high as wide and a single pair of lateral cusplets. Main cusp straight or curved to posterior. Labial face of all cusps with straight to slightly sinuous longitudinal ridges, reaching apex of cusplets but not main cusp. Ridges do not bifurcate or reach base of crown and are of constant width along their length. Lingual ornament similar but finer. Crown does not overhang root labially. Root low and with flat basal face, which is flared labially to give distinct three-lobed appearance to basal face. No nutritive groove and main lingual foramen small; labiobasal foramen in short groove on basal face. Well-developed foramina on lateral and labial faces of root.

Description. Teeth of this taxon are larger than those of most of the co-occurring scyliorhinids, being up to 3 mm high. They are

EXPLANATION OF PLATE 2

Figs 1–9. *Scyliorhinus elongatus* (Davis, 1887). 1–3, P. 66373, Boxford, anterior tooth in 1, labial, 2, oblique lateral, and 3, lingual views. 4, P. 66374, Upper Santonian, Winterbourne, lower phosphate level, lateral tooth, labial view. 5–6, P. 66375, Upper Santonian, Winterbourne, lower phosphate level, posterolateral tooth in 5, labial, and 6, lingual views. 7–8, P. 66376, Upper Santonian, Winterbourne, lower phosphate level, anterior tooth in 7, lingual, and 8, labial views. 9, P. 66377, Upper Santonian, Winterbourne, lower phosphate level, lateral tooth. All × 25.

Figs 10–18. *Scyliorhinus brumarivulensis* sp. nov. 10–12, P. 66378, holotype, Middle Santonian, Boxford, lateral tooth in 10, lingual, 11, labial, and 12, oblique lateral views. 13–14, P. 66379, Upper Santonian, Winterbourne, lower phosphate level, anterior tooth in 13, labial, and 14, lingual views. 15, P. 66380, Upper Santonian, Winterbourne, lower phosphate level, posterolateral tooth, labial view. 16–17, P. 66381, Upper Santonian, Winterbourne, lower phosphate level, anterolateral tooth in 16, lingual, and 17, labial views. 18, P. 66382, Upper Santonian, Winterbourne, lower phosphate level, anterior tooth, labial view. All × 32.



UNDERWOOD and WARD, *Scyliorhinus*

all higher than wide, and have an elongate main cusp and a single pair of short, sharply pointed lateral cusplets. The main cusp is straight in some teeth, but in the largest (presumed to be anterolateral) is quite strongly curved towards the commissure. Lateral cusplets are short and straight in all teeth. The labial face of the crown has an ornament of relatively strong longitudinal ridges. These follow the cusps and reach close to the apex of the main cusp and the apex of well-preserved lateral cusplets. There is no bifurcation of the ridges, although occasional short ridges are present between the more continuous ones. The ridges all fade out a short distance above the base of the crown. There is a well-developed cutting edge along all of the cusps. The lingual face of the cusps is more convex than the labial, and is ornamented with very fine longitudinal ridges that almost reach both the cusp apex and base of the crown. The basal edge of the crown on the labial side is concave and does not obviously overhang the root, merging into the top of the root on the lateral parts of the tooth. The root is low and very strongly V-shaped in basal view, with a swollen lingual apex. The basal face of the root is flat. There is a small foramen at the centre of the lingual root apex, and a foramen at the junction of the root lobes, which commonly forms a short deep but narrow groove on the basal face. The root lobes are weakly flared. The labiolateral and lingual faces of the root have many small foramina, and small foramina are irregularly distributed across the root basal face.

Remarks. The small number of specimens of teeth of this species make the heterodonty pattern difficult to assess, but it is probable (by comparison with extant scyliorhinids) that the large, curved teeth were in anterolateral positions, with straighter teeth in lateral and extreme anterior jaw positions. Although the curved teeth seen in this species have not been documented in other species of *Palaeoscyllium*, this is considered here to be unimportant for generic level assignment. This would represent the latest occurrence of *Palaeoscyllium*, and one of the few Cretaceous occurrences (e.g. Rees 2005; Sweetman and Underwood 2006). Teeth of this species may be separated from other species of *Palaeoscyllium* by the generally smaller lateral cusplets, presence of a curvature in some teeth and especially by the labial ornament, with the ridges on the labial face of other species bifurcating and becoming swollen towards the base, and reaching the basal edge of the tooth crown. It should be noted that the mid-Cretaceous species *Palaeoscyllium reticularis* Underwood and Mitchell, 1999 was referred to this genus before the gracile female dental morph of *Scyliorhinus* was recognised; it is possible that it should be placed within *Scyliorhinus* and not *Palaeoscyllium*.

Genus PROHAPLOBLEPHARUS gen. nov.

Derivation of name. From the close similarity to teeth of the extant species *Haploblepharus edwardsii* (Schinz, 1822).

Type species. Scyliorhinus ?riegrafi Müller, 1989.

Diagnosis. Teeth small, high and symmetrical with apparent low heterodonty. Teeth higher than wide with straight main cusp and two pairs of divergent cusplets. Labial ornament of strong longitudinal ridges, swollen at base; weaker ornament on lingual face. Crown strongly overhangs root. Root low and similar in width to crown with short root lobes showing no flaring at base. No nutritive groove but well-developed labial and lingual foramina present.

Remarks. The form of the crown of teeth of this species is very similar to that of the extant genus *Haploblepharus* Garman, 1913 (see Herman *et al.* 1990), but varies in possessing a narrow, compact root without a flat and flared basal face. There is also a strong similarity to teeth of the Palaeogene genus *Casieria* Noubhani and Cappetta, 1997, but they differ in having an incomplete root nutritive groove and more clearly divergent cusplets.

Prohaploblepharus riegrafi (Müller, 1989) comb. nov.
Plate 3, figures 10–17

1989 *Scyliorhinus ?riegrafi* Müller, pl. 14, figs 2–10.

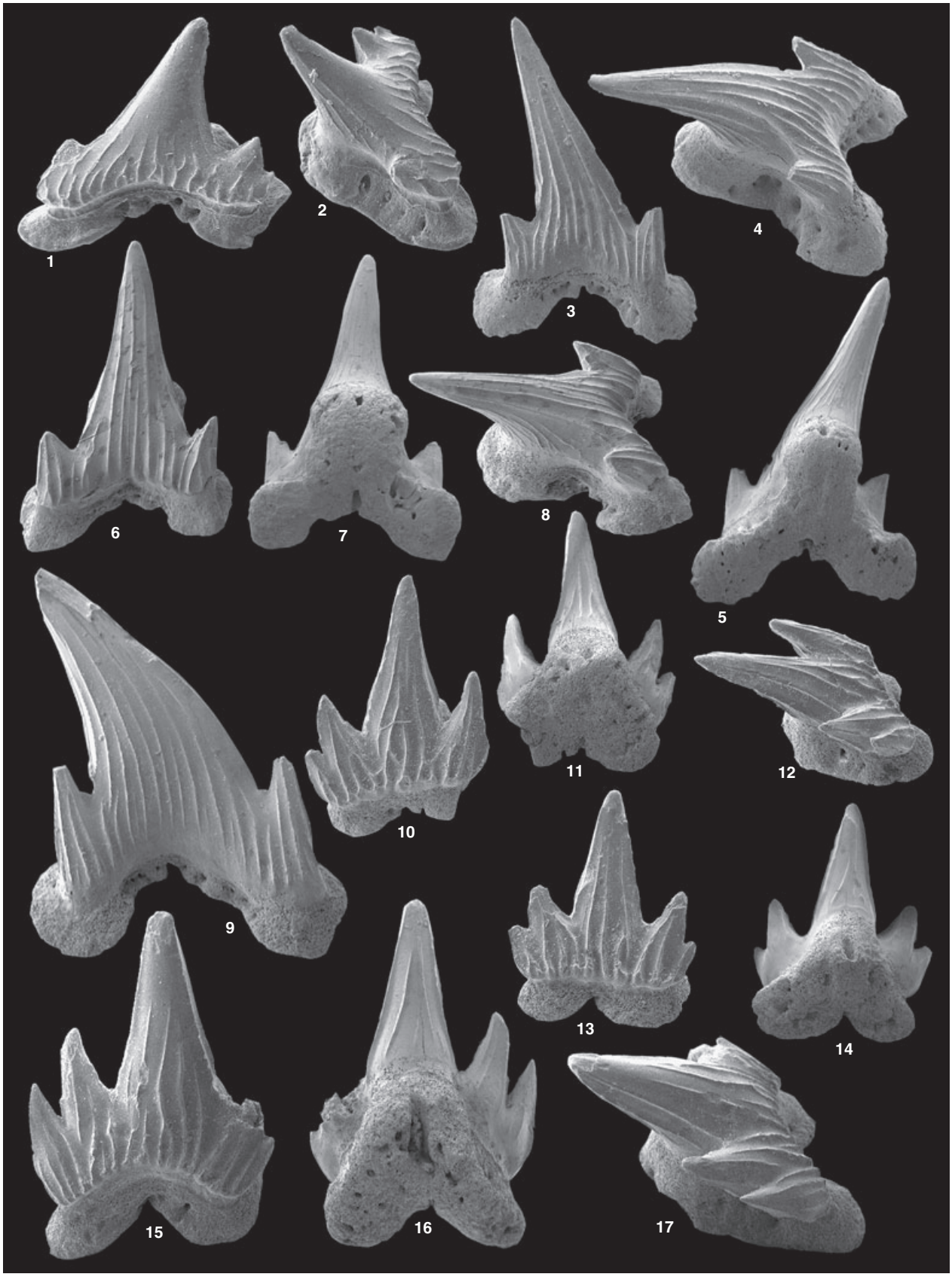
Material. P. 66386–P. 66388 from a total of nine teeth: 1, Winterbourne lower horizon; 2, Winterbourne upper horizon; 3, Taplow upper horizon; 2, Downend; 1, Minnis North.

EXPLANATION OF PLATE 3

Figs 1–2. *Scyliorhinus* aff. *brumarivulensis* sp. nov., BELUM K29670, Coniacian, Minnis North. 1, labial view. 2, oblique lateral view; × 40.

Figs 3–9. *Palaeoscyllium striatum* sp. nov. 3–5, P. 66383, holotype, Lower Campanian, Winterbourne, upper phosphate level, in 3, labial, 4, oblique lateral, and 5, lingual views. 6–8, P. 66384, Middle Santonian, Boxford, in 6, labial, 7, lingual, and 8, oblique lateral views. 9, P. 66385, Upper Santonian, Winterbourne, lower phosphate level, labial view. All × 30.

Figs 10–17. *Prohaploblepharus riegrafi* (Müller, 1989) comb. nov. 10–12, P. 66386, Lower Campanian, Downend in 10, labial, 11, lingual, and 12, oblique lateral views. 13–14, P. 66387, Lower Campanian, Downend, in 13, labial, and 14, lingual views. 15–17, P. 66388, Lower Campanian, Winterbourne, upper phosphate level, in 15, labial, 16, lingual, and 17, oblique lateral views. All × 35.



UNDERWOOD and WARD, Carcharhiniformes

Description. The few available teeth show low degrees of heterodonty. All are higher than wide, and the largest tooth is under 2 mm high. A straight, erect main cusp comprises about half of the height and a third of the width of each tooth. This is flanked by either two pairs of lateral cusplets, or two cusplets on one side of the tooth and one on the other. All cusplets are well developed and somewhat divergent. All cusps are rounded in cross section, although a well-developed cutting edge is continuous across all of the cusps. The labial face of the crown is ornamented by strong, sharp-edged, longitudinal ridges. There are 2–5 somewhat irregular ridges per cusp, and these reach close to the apex. Basally the ridges become swollen and there is some degree of bifurcation. Lingual ornament is of sparse but strong longitudinal ridges. The crown tapers somewhat basally, so that the lateralmost cusplets overhang the crown base. The crown overhangs a low, compact root. The root is U-shaped in basal view, and the root lobes are short and not flared. There is no nutritive groove on the flat basal face of the root, with well-developed foramina being present on the labial and lingual faces of the root.

Remarks. Although very few teeth of this species were recorded, they are very distinctive and clearly separated from all other scyliorhinids by the presence of a constriction at the base of the crown and divergent lateral cusplets. These specimens agree very closely with the type material from the Campanian of Germany. The general form and ornament of teeth of this taxon are very similar to those of *Scyliorhinus brumarivulensis* sp. nov. and could easily be mistaken for symphyseal teeth of this species. Despite this, the greater maximum size, form of the root and very different distribution enable teeth of this species to be differentiated from it.

Genus CRETASCYLIORHINUS Underwood and Mitchell, 1999

Type species. Scyliorhinus destombesi Cappetta, 1977, from the Albian of France.

?*Cretascyliorhinus* sp.
Plate 4, figures 1–2

Material. BELUM K29671, a single damaged tooth from Minnis North.

Description. The single tooth is incomplete, lacking one root lobe and one lateral cusplet. The tooth appears almost symmetrical. The main cusp is robust and conical, being slightly curved lingually. The preserved lateral cusplet is short and conical, and projects slightly laterally. The cusps are nearly round in cross section and have a very weak but continuous cutting edge. The labial faces of the cusps are almost unornamented, with just some very weak longitudinal ridges on the sides of the main cusp. The lingual face of the main cusp is ornamented with faint, rather irregular, longitudinal ridges. The crown does not overhang the root on either the labial face or the lateral extremities. The root is relatively low and would have been strongly V-shaped in basal view. The basal face of the root is flat and there is no nutritive groove, although the main lingual and labial foramina are elongate and form a partial groove. The labial extremities of the root are very strongly flared, giving a very rounded profile in basal view; the lateral faces are strongly concave below the position of the lateral cusplet; the lingual apex is faintly swollen. There are well-developed foramina on the lateral and basal faces of the root.

Remarks. This single tooth does not closely resemble that of any of the other species recorded here. Although differing from the majority of teeth of *Cretascyliorhinus destombesi* in being considerably more gracile and lacking the strong ornament, this tooth strongly resembles the extreme anterior teeth of *C. destombesi* and for that reason has been tentatively referred to *Cretascyliorhinus*.

Scyliorhinidae *incertae sedis* 1
Plate 4, figures 3–10

Material. P. 66389–P. 66391 from Downend (1 tooth) and Winterbourne, upper level (2 teeth), and several isolated crowns.

Description. The teeth referred to this taxon are all at least twice as high as wide and are very gracile in overall design. One tooth, presumed to be from an anterior position, differs from the rest in lacking a strong ornament and having a low degree of asymmetry. These differences are here considered to be within the range of monognathic heterodonty of scyliorhinids, and it is referred to the same taxon as the other, more strongly ornamented, teeth. The presumed anterior tooth has a broken cusp but is otherwise well preserved. The single cusp is robust and straight, being slightly compressed in cross section. The cusp makes up most of the width of the crown, with the lateral parts of the crown being small and strongly labially directed. There is some trace of a poorly developed cutting edge at the base of the crown. The ornament is restricted to a small number of short, irregular folds on the labial surface of the lateral parts of the base of the crown. The crown overhangs the root labially and lingually, and is slightly narrower than the root. The crowns of the other teeth are elongate and at least twice as high as wide, and are inclined or curved towards the posterior. One tooth lacks lateral cusplets, whereas others have a small, sharply pointed distal cusplet but no anterior cusplet. A well-developed cutting edge is present on all teeth. The slightly convex labial face of the teeth is ornamented by up to eight strong, almost straight longitudinal ridges. These ridges do not reach either the apex of the cusps or the base of the crown, and do not bifurcate. The strongly convex lingual face of the cusps has scattered, fine longitudinal ridges. The labial face of the crown does not over-

hang the root laterally, where it merges with the top of the root lobes, but does to some degree near the centre. The roots of all teeth are low and very strongly V-shaped in basal view, with the root lobes being of unequal length. The basal face of the root is flat, and there is a sharp angle between this and the lateral root faces. In one tooth the lingual part of the root is rather elongate and has a shallow longitudinal groove. There is little flaring of the root and its lingual extremity is not swollen. There is a well-developed foramen at the lingual end of the root, and another within a narrow but deep slot on the basal face at the junction of the root lobes. There are smaller foramina on both the basal and lateral faces of the root.

Remarks. The single incomplete tooth of this species has a strong superficial resemblance to teeth of the orectolobiform *Pararhincodon*, but the morphologies of the crown and root demonstrate that this is a scyliorhinid. There are very close morphological similarities between this tooth and anterior teeth of '*Scyliorhinus*' *entomodon* Noubhani and Cappetta, 1997, from the Palaeocene of Morocco, although there are significant differences, including the strong crown overhang of the root and the partly closed nutritive groove in '*S.*' *entomodon*; it is considered here that the overall similarities are likely to be superficial. Teeth of this taxon are also similar to some of the anterior teeth of *Leptocharias smithi* Müller and Henle, 1839 (M. Harris, pers. comm. 2006), but the lack of crown overhang and an ornament not reaching the base of the crown are very different to the situation in co-occurring *Leptocharias* teeth; it is very unlikely that these belong to the same dentition. The affinities of this species are, therefore, uncertain, but it is unlikely that it should be placed in any previously described genus. More material is required before the nature of the dentition of this species can be understood, and the genus properly described.

Scyliorhinidae *incertae sedis* 2
Plate 4, figures 11–13

Material. P. 66392, one other poorly preserved tooth and several tooth crowns from Stoke Clump.

Description. All teeth seen were under 2 mm high and higher than wide. The crown of all was damaged to some degree, but their overall shape is similar. The straight and elongate main cusp takes up at least half of the width of the crown, and is round in cross section. There is a single pair of short but robust lateral cusplets. There appears to be a weak but continuous cutting edge. The labial face of the crown is smooth or with ornament restricted to short, weak longitudinal ridges near the basal edge. Longer, but still weak, longitudinal ridges are present on the lingual face. The crown is similar in width to, or slightly wider than, the root, and overhangs it very strongly on all sides. The root is high and has short lobes that only extend a short distance labially below the lateral cusplets. The basal face of the root is flat and not flared; the lingual faces are straight and make a sharp angle with the basal face, with no swollen lingual extremity. A large lingual foramen is present within a vertical fold below the main cusp. A row of small foramina is present about two-thirds of the way up the linguolateral faces of the root.

Remarks. Although none of the specimens of this species has well-preserved crown surfaces, the general form of the crown and the form of the root are clear. The general form of the crown and overall lack of ornament are very similar to the Albian–Cenomanian '*Scyliorhinus*' *dubius* (Woodward 1889), although this differs in having a far lower root with a flared basal face and more elongate lateral cusplets (see Cappetta 1977). Better preserved material is required before this species can be described satisfactorily.

Carcharhiniformes *incertae sedis*
Plate 4, figures 14–17

Material. P. 66394, a single tooth from the lower level at Winterbourne.

Description. The tooth is nearly 3 mm high and has a very characteristic appearance. There is a single cusp, which comprises about half of the total height of the tooth. This is slender and straight, and has a poorly developed cutting edge. Basally, two lateral blades extend from the lateral parts of the cusp, and project labially quite strongly. The proximal parts of the lateral blades bear a cutting edge, although this is absent distally. The crown is largely unornamented, with a row of short, widely spaced ridges near the base on the labial face. The crown overhangs the root labially and laterally. The root is high, irregular, and somewhat asymmetrical. The basal face of the root is roughly U-shaped and has a wide, well-developed nutritive groove with a pair of foramina in the central part; numerous additional very small foramina are scattered across the basal face. Lateral, lingual and, to some extent, labial faces of the root have numerous, irregularly spaced vertical grooves. These grooves contain foramina and extend from the sharply angled contact with the basal face to at least half-way up the root faces.

Remarks. P. 66394 has a unique morphology, differing from all other teeth seen in these samples. Although the form of the tooth superficially resembles that of *Squatina* and some orectolobiforms, the lack of uvulae, the vascularisation of the root, and the form of the crown suggest scyliorhinid affinities. There are no figured teeth of fossil or extant scyliorhinids showing a close resemblance to this specimen, so it is considered here that this represents an as yet undescribed genus. More specimens would be needed for a diagnosis of this taxon.

Family *incertae sedis*

Genus PTEROSCYLLIUM Cappetta, 1980*a*

Type species. Pteroscyllium signeuxi Cappetta, 1980*a*, from the Santonian of Lebanon.

Remarks. The general shape of *Pteroscyllium* teeth, presence of specialised parasymphaseals (P. 66400) and angular fins may suggest lamniform affinities (Underwood 2004, 2006), although body form and the presence of numerous functional files of small teeth are very scyliorhinid. This may represent an intermediate group (Underwood and Ward in press) close to the divergence of the two clades. *Pteroscyllium* was considered by Cappetta (1992) to form a monogeneric subfamily, the Pteroscylliinae, within the Scyliorhinidae. It probably deserves full familial status, but it would be premature to define a new family without further examination of skeletons of the type species.

Pteroscyllium hermani sp. nov.
Plate 5, figures 1–12

1977 *Scyliorhinus reussi* Herman, pl. 7, fig. 9.
in press *Pteroscyllium* sp. Underwood and Ward, fig. 1H–I.

Derivation of name. After Jacques Herman for his work on Cretaceous and extant sharks.

Holotype. BMNH P. 66395.

Material. P. 66396–P. 66400 from a total of 73 teeth: 11, Boxford; 44, Winterbourne lower horizon; 15, Winterbourne upper horizon; 1, Taplow lower horizon; 1, Taplow upper horizon; 1, Downend.

Diagnosis. Teeth very gracile and higher than wide. Main cusp comprises at least half of height of tooth. Main cusp flanked by single pair of short cusplets. Main cusp and cusplets all at least three times as long as wide. Strong ornament of sharp, longitudinal ridges on lower half of labial crown face, their upper edge being at about the level of a constriction at the base of the main cusp. No ornament on lingual cusp face. Bilobed root low with well-developed nutritive groove. Basal face of root concave to convex without well-defined edge at contact with lateral root faces.

Description. Teeth of this species are up to 4 mm high and have an overall very gracile appearance. The majority of teeth are close to being symmetrical, with a straight main cusp flanked by a single pair of lateral cusplets. In all but supposed posterior teeth the main cusp is considerably more than twice as high as wide and round in cross section. In many teeth the middle third of the cusp is parallel-sided, flaring basally close to its contact with the root. A single pair of small, extremely slender lateral cusplets is present in all teeth, arising from the lateral extremities of the crown. These are parallel to the main cusp or very slightly divergent. The labial face of the crown is ornamented with a series of robust, sharp edged longitudinal ridges. These reach less than a third of the length of the main cusp, but can reach almost to the apices of the lateral cusplets. The ridges are straight to slightly curved and only rarely bifurcate. They thicken towards the base, and are swollen close to the base of the crown in presumed posterolateral teeth. There is a very well-developed cutting edge on the lateral cusplets and on the basal part of the main cusp, but this is weak or absent on much of the main cusp. The lingual face of each cusp is unornamented. The root is slightly wider than the crown, and distinctly U-shaped. It is clearly divided into two lobes by a deep, prominent nutritive groove. The root lobes taper somewhat towards a rounded tip, and only extend a short distance beyond the base of the lateral cusplets. The basal face of the root is flat to slightly concave, and there is no sharp edge between the basal and other faces of the root. A single large foramen is present in the central part of the nutritive groove, and small foramina are irregularly distributed across the root basal face. A row of small foramina is present on the labial face of the root just below the base of the crown.

Remarks. This species is similar to other named species of the genus, being closest to *P. nolfi* Müller and Diedrich, 1991 but more gracile overall with finer lateral cusplets. It

EXPLANATION OF PLATE 4

Figs 1–2. ?*Cretascyliorhinus* sp., BELUM K29671, Coniacian, Minnis North. 1, labial view. 2, lingual view; × 40.

Figs 3–10. Scyliorhinidae *incertae sedis* 1. 3–5, P. 66389, Lower Campanian, Downend, in 3, labial, 4, oblique lateral view, and 5, lingual views. 6–7, P. 66390, Upper Santonian, Winterbourne, lower phosphate level, in 6, labial, and 7, lingual views. 8–10, P. 66391, Middle Santonian, Boxford in 8, lingual, 9, oblique lateral, and 10, labial views. All × 35

Figs 11–13. Scyliorhinidae *incertae sedis* 2, P. 66392, Lower Campanian, Stoke Clump, in 11, labial, 12, oblique lateral, and 13, lingual views; × 35.

Figs 14–17. Carcharhiniformes *incertae sedis*, P. 66394, Upper Santonian, Winterbourne, lower phosphate level, in 14, occlusal, 15, labial, 16, oblique lateral, and 17, lingual views; × 20.

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also differs from *P. lamranii* Noubhani and Cappetta, 1997, which has more irregular ornament and no constriction at the base of the main cusp. This species is more gracile than the coeval *P. dubertreti* Cappetta, 1980*a* and differs from this, *P. signeuxi* Cappetta, 1980*a*, and *P.* aff. *signeuxi* (of Antunes and Cappetta 2002) in having longer, straighter ridges on the labial face of the crown.

Family TRIAKIDAE Gray, 1851

Genus PALAEOGALEUS Gurr, 1962

Type species. Scyllium vincenti Daimeries, 1888.

Palaeogaleus havreensis Herman, 1977
Plate 5, figures 13–21

1977 *Palaeogaleus havreensis* Herman, pl. 12, fig. 1.
1989 *Palaeogaleus havreensis* Herman; Müller, pl. 15, figs 5–6.

Material. P. 66401–P. 66406 from a total of 394 teeth, many poorly preserved: 109, Boxford; 3, Winterbourne lower horizon; 86, Winterbourne upper horizon; 2, Taplow upper horizon; 30, Stoke Clump; 164, Downend, but commonly poorly preserved.

Description. Teeth of this species are up to 3 mm wide and show a high degree of heterodonty. Ornament on the labial faces of tooth crowns varies considerably, especially within low, presumed lateral teeth, where it may be either strongly ornamented with longitudinal ridges or have ornament restricted to weakly developed folds near the base. The lack of intermediate forms suggests that this is owing to dignathic heterodonty. This difference is less pronounced in higher, presumed anterior, teeth. Comparison with the dentitions of extant triakids suggests that teeth with a strong ornament are probably from the upper jaw, with weakly ornamented teeth probably from the lower jaw. The crown of anterior teeth is higher than wide, with over half of the width being taken up by a central cusp that is straight but somewhat inclined posteriorly. There are typically two pairs of small lateral cusplets, although a third pair of incipient cusplets may also be present, with the anterior cusplets being slightly smaller than the posterior. All cusps are rather compressed and share a continuous cutting edge. The basal edge of the crown very strongly overhangs the root labially and has a slight central indentation. Ornament is restricted to the labial face of the crown. In probable lower teeth this comprises a strong crenulation of the basal edge of the crown, with the basal projections continuing as short but strong longitudinal ridges, reaching less than half of the height of the base of the main cusp. In probable upper teeth, the basal crenulations are finer, typically with more than 20 folds. These continue upwards into strong, sharp-edged, folds that are slightly sinuous and reach at least as far as the base of the cusps; in many teeth some folds continue onto the labial face of the cusps. These folds only rarely bifurcate. The crowns of lateral teeth are similar overall to those of the anterior, but are wider than high and have a cusp that is strongly posteriorly inclined, almost reaching the level of the posterior end of the tooth. The leading edge may be straight, slightly convex (mostly on presumed upper teeth) or slightly concave (mostly on presumed lower teeth). Two pairs of lateral cusplets are usually present, with the posterior pair being larger than the anterior. Cusplets are less well developed on presumed lower teeth, where anterior cusplets may be present as poorly differentiated swellings on the leading edge of the crown. Presumed lower teeth have a weak ornament of a variably crenulated crown basal edge with little or no development of longitudinal ridges. By contrast, presumed upper teeth have a strong ornament similar to that in anterior teeth, but more commonly having ridges continuing onto the labial face of the cusps, sometimes reaching the apex. Crowns of posterior teeth have an ornament similar to that of laterals, but are low and have a poorly developed main cusp with no lateral cusplets. The low but bulky root of all teeth is similar, and is similar to the crown in size. This is distinctly bi-lobed and quite symmetrical, with

EXPLANATION OF PLATE 5

Figs 1–12. *Pteroscyllium hermani* sp. nov. 1–3, P. 66395, holotype, Upper Santonian, Winterbourne, lower phosphate level, anterior tooth, in 1, labial, 2, oblique lateral, and 3, lingual views; × 25. 4–6, P. 66396, Middle Santonian, Boxford, lateral tooth in 4, labial, 5, lingual, and 6, oblique lateral views; × 25. 7–8, P. 66397, Upper Santonian, Winterbourne, lower phosphate level, anterior tooth in 7, labial, and 8, lingual views; × 25. 9, P. 66398, Lower Campanian, Winterbourne, upper phosphate level, anterior tooth, labial view; × 35. 10, P. 66399, Lower Campanian, Winterbourne, upper phosphate level, posterolateral tooth, labial view; × 35. 11–12, P. 66400, Upper Santonian, Winterbourne, lower phosphate level, parasymphaseal tooth, in 11, labial, and 12, lingual views; × 35.

Figs 13–21. *Palaeogaleus havreensis* Herman, 1977. 13–14, P. 66401, Middle Santonian, Boxford, ?lower lateral tooth, in 13, labial, and 14, lingual views; × 20. 15–17, P. 66402, Middle Santonian, Boxford, ?upper anterior tooth, in 15, lingual, 16, labial, and 17, oblique lateral views; × 20. 18, P. 66403, Middle Santonian, Boxford, ?lower anterolateral tooth, labial view; × 20. 19, P. 66404, Lower Campanian, Winterbourne, upper phosphate level, commissural tooth, labial view; × 35. 20, P. 66405, Lower Campanian, Downend, ?upper posterolateral tooth, labial view; × 20. 21, P. 66406 Middle Santonian, Boxford, parasymphaseal tooth, labial view; × 35.

UNDERWOOD and WARD, *Palaeogaleus*, *Pteroscyllium*

anterior and posterior root lobes being separated by a very well developed nutritive groove. The root is somewhat flared laterally and labially, with the flat basal faces of the root lobes having convex labial and concave lingual margins. A large central foramen is present within the central groove, with a row of smaller foramina present on the lingual faces of the root. In addition to these larger foramina, very abundant small pores are spread over much of the root.

Remarks. The teeth described here are very similar to those recorded by Herman (1977) from the Campanian. Despite this, the dignathic heterodonty of this species has not been recorded previously, presumably because of the small number of specimens available when this taxon was first described. Dignathic heterodonty within species of *Palaeogaleus* was recognised by Noubhani and Cappetta (1997), although all of the Maastrichtian and Palaeogene species they described show a lower degree of heterodonty than recorded here. This is the first pre-Campanian record of the genus.

Genus PARATRIAKIS Herman, 1977

Type species. Paratriakis bettrechiensis Herman, 1977.

Paratriakis subserratus sp. nov.
Plate 6, figures 1–9

in press *Paratriakis* sp. Underwood and Ward, fig. 1P.

Derivation of name. From the incipient serration on the distal cusp.

Holotype. BMNH P. 66407.

Material. P. 66408–P. 66411 from a total of 271 teeth: 95, Boxford; 30, Winterbourne lower horizon; 17, Winterbourne upper horizon; 2, Taplow upper horizon; 17, Stoke Clump; 110, Downend.

Diagnosis. Teeth up to 3 mm wide showing relatively low degrees of heterodonty. Tooth wider than high and strongly asymmetrical. Crown unornamented with flat to concave labial face, the basal margin being swollen in presumed lateral teeth. Main cusp reaches as far back as posterior end in most teeth; there are no anterior cusplets and one or rarely two very poorly developed posterior cusplets. Root low and lacking nutritive groove, but with notch at position of labial foramen.

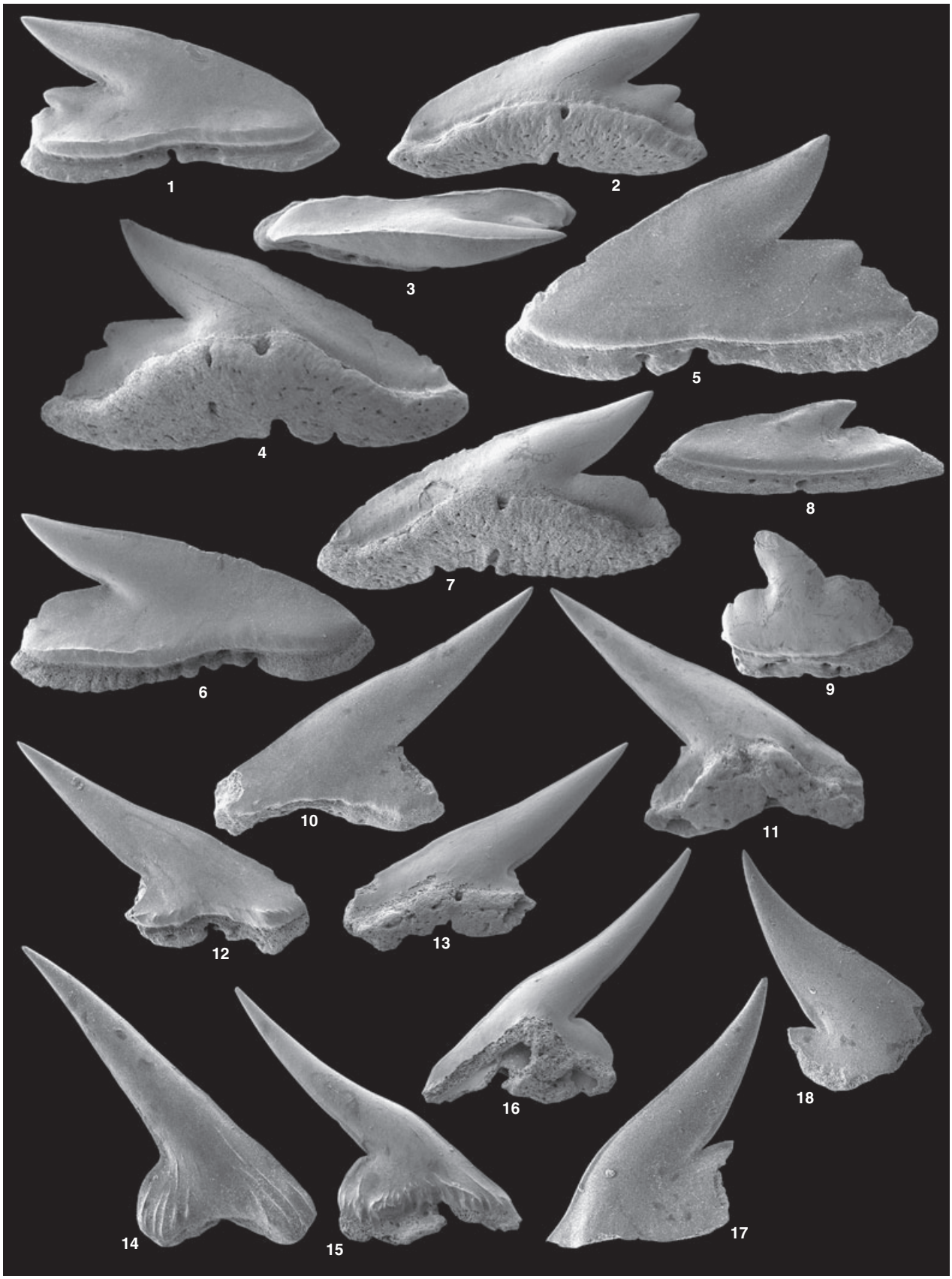
Description. These teeth demonstrate a relatively low degree of monognathic heterodonty, and no dignathic heterodonty was recognised. All are wider than high, with presumed lateral teeth being at least twice as wide as high. The crown is generally unornamented and very strongly overhangs the root labially; the majority (all but the largest) of the presumed lateral teeth have a swollen labial edge to the crown that forms a narrow horizontal ledge. In rare cases this ledge has a fine but sharp enameloid ridge. The labial face of the crown is flat in presumed anterior teeth, becoming concave where the basal ridge is present. A single well-developed cusp is highly compressed and strongly posteriorly inclined, with the anterior edge forming an angle of between 20 degrees (in lateral teeth) and 35 degrees (in anterior teeth) with the basal edge of the crown. The leading edge of the crown and cusp is straight to slightly convex and has a continuous, sharp cutting edge. In most teeth, the cusp extends as far posteriorly as the posterior edge of the tooth, where it overhangs a relatively poorly developed distal heel. In virtually all teeth, the distal heel is interrupted by one, or rarely two, notches indicating the presence of one or more incipient to very poorly developed distal cusplets. The root and crown are similar in size. The lingual face of the root is slightly convex and quite strongly excavated along its basal edge. The root is very low and only slightly flared basally. The basal face of the root is flat, and gently curved (concave labially) within all but the most anterior teeth, tapering at both ends, slightly recurving at the anterior edge in some teeth. This curvature is far stronger in anterior teeth, with both ends being noticeably recurved. There is no nutritive groove, but the main labial and lingual foramina are very well developed, the labial foramen being at the contact of the basal and labial faces of the root, giving a distinct

EXPLANATION OF PLATE 6

Figs 1–9. *Paratriakis subserratus* sp. nov. 1–3, P. 66407, holotype, Middle Santonian, Boxford, lateral tooth in 1, labial, 2, lingual, and 3, occlusal views. 4–5, P. 66408, Lower Campanian, Winterbourne, upper phosphate level, anterior tooth in 4, lingual, and 5, labial views. 6–7, P. 66415, Upper Santonian, Winterbourne, lower phosphate level, lateral tooth in 6, labial, and 7, lingual views. 8, P. 66410, Lower Campanian, Downend, posterior tooth, labial view. 9, P. 66411, Winterbourne, lower phosphate level, parasymphaseal tooth, labial view. All × 25.

Figs 10–16. *Paratriakis tenuis* sp. nov. 10–11, P. 66412, Lower Campanian, Stoke Clump, in 10, labial, and 11, lingual views. 12–13, P. 66413, holotype, Middle Santonian, Boxford, in 12, labial, and 13, lingual views. 14, P. 66414, Lower Campanian, Stoke Clump, labial view. 15–16, P. 66409, Upper Santonian, Winterbourne, lower phosphate level, in 15, labial, and 16, lingual views. All × 40.

Figs 17–18. *Paratriakis* sp. indet. 17, P. 66417, Lower Campanian, Downend, labial view. 18, P. 66416, Lower Campanian, Downend, labial view. Both × 33.



UNDERWOOD and WARD, *Paratriakis*

notch in the root profile. Very abundant small foramina are spread over much of the root.

Remarks. This species is readily distinguished from other species of *Paratriakis*. It differs from the rather similar *P. decheni* (von der Marck, 1863, as *Palaeoscyllium*, a name that was preoccupied; see Müller 1989) in having an incipient distal cusplet, a generally convex anterior cutting edge and a main cusp that never extends beyond the posterior end of the root. It also differs from *P. curtirostris* (Davis, 1887) in having an incipient cusplet in the distal heel and a ridge parallel to the base of the labial crown face. It lacks the elongate erect cusp of *P. bettrechiensis* Herman, 1977. Although a lack of cusplets was regarded by Cappetta (1987) as characteristic of the genus, the presence of cusplets here is not considered to be of generic importance as all other features of the teeth are typical of the genus.

Paratriakis tenuis sp. nov.
Plate 6, figures 10–16

?1982 *Paratriakis* sp. Herman, pl. 2, fig. 7.

Derivation of name. From the very slender and delicate cusp.

Holotype. BMNH P. 66413.

Material. P. 66414 and P. 66415; only two teeth have a moderately complete root including P. 66412. Total of 4 teeth, Boxford; 2, Winterbourne lower horizon; 1, Winterbourne upper horizon; 14, Stoke Clump.

Diagnosis. Tooth under 3 mm wide, gracile and highly compressed. Cusp very elongate and strongly inclined to posterior; free part of cusp at least as long as width of crown. Small distal heel present but no cusplets. Labial edge of crown swollen laterally but concave in centre.

Description. These teeth are small and extremely gracile. The crown is dominated by a single, elongate cusp that is at least three times as high as wide. This is slender and highly compressed, and is inclined to the posterior, typically forming an angle of 30–40 degrees to the crown base. The leading edge of the crown and cusp are straight to faintly sigmoidal. The cusp (as measured along the posterior edge) is at least as long as the basal part of the crown is wide, and is unornamented. There are no cusplets, but a poorly developed, semicircular, distal heel is present. A continuous cutting edge is present along the occlusal edge of the tooth. The labial face of the crown is rather swollen towards the ends of the tooth, but is concave in the central part. The swollen labial basal edges of the crown commonly have a longitudinal ledge, and commonly have short, irregular ridges, either restricted to the basal edge or extending a short distance onto the labial crown face. The labial edge of the crown strongly overhangs the root, but the lingual edge is somewhat indented. The root is small and very low, and is similar in size and shape to the base of the crown. The basal face of the root is flat and slightly flared labially. There is no nutritive groove, but labial and lingual foramina are well developed. Small foramina are present on the short labial face of the root as well as on the basal face.

Remarks. These teeth are similar to those of *P. bettrechiensis* Herman 1977, but differ in having a more elongate cusp and smaller basal parts of crown and smaller root.

Paratriakis sp. indet.
Plate 6, figures 17–18

?1982 *Paratriakis* sp. Herman, pl. 2, fig. 7.
?1989 *Paratriakis* sp. Müller, pl. 15, fig. 3.
?2001 *Paratriakis* sp. Cappetta and Odin, pl. 1, fig. 6.

Material. P. 66416 and P. 66417 from a total of 14 partial teeth: 2, Taplow upper horizon; 4, Stoke Clump; 8, Downend.

Description. None of the teeth of this species has a preserved root or complete crown. The cusp is strongly distally inclined and typically about twice as long as wide. The cusp is moderately compressed and has a well-developed cutting edge. The anterior edge of the cusp has a distinct sigmoidal curvature in all but the more erect (presumed anterior) teeth. There is a distal heel, but this is never complete. There is no evidence of ornament on the teeth.

Remarks. These teeth differ from those of *Paratriakis tenuis* sp. nov. and *P. bettrechiensis* in having a shorter and more robust crown with a stronger sigmoidal curvature. The cusp is more elongate, erect and curved than in *P. subserratus* sp. nov. It is likely that these teeth are conspecific with poorly preserved material described from the European Campanian (Müller 1989) and Maastrichtian (Herman 1982; Cappetta and Odin 2001), but the poor preservation of all material prevents further comparisons.

Family LEPTOCHARIIDAE Gray, 1851

Genus LEPTOCHARIAS Smith, *in* Müller and Henle 1838

Type species. Leptocharias smithii Müller and Henle 1839.

Leptocharias cretaceus sp. nov.
Plate 7, figures 1–12

in press *Leptocharias* sp. Underwood and Ward, fig. 1J–M.

Derivation of name. From occurrence in the Cretaceous.

Holotype. BMNH P. 66418.

Material. P. 66419–P. 66421 from a total of 14 teeth: 2, Boxford; 5, Winterbourne lower horizon; 3, Winterbourne upper horizon; 1, Taplow lower horizon; 1, Taplow upper horizon; 2, Downend.

Diagnosis. Teeth highly asymmetrical showing moderate monognathic and probable dignathic heterodonty. Straight and robust main cusp inclined to posterior, single pair of lateral cusplets small but robust and parallel to main cusp. Incipient second pair of cusplets may be present. Labial ornament of variably strong, regular, longitudinal ridges reaching apex of cusplets but not main cusp. Ridges reach base of crown and bifurcate towards base. Fine and more irregular ridges on lingual face. Root very bulky, high and far wider than crown. Root lobes with strongly angular profile, with 'corners' projecting labially and linguolaterally. Root lobes are of similar size but asymmetrical. Nutritive groove seen on one tooth, but usually absent.

Description. These highly characteristic teeth are up to 2.5 mm high, and have a variation in the ornament of teeth of otherwise similar appearance that suggests that either sexual or dignathic heterodonty was present. The crown comprises a straight and rather conical main cusp, higher than wide, with a single pair of small but robust lateral cusplets. On some teeth a second pair of incipient cusplets is also present. The main cusp and cusplets are inclined posteriorly and are parallel. Anterior and posterior lateral cusplets are of similar size. The basal edge of the crown on the labial side is concave and smoothly arched. The labial face of the crown is ornamented by straight to gently curved longitudinal ridges. These ridges reach at least half-way up the main cusp, and reach the apex of lateral cusplets. In some teeth these ridges are very robust and swollen close to their base at the base of the crown; in others they are fine and reach the base of the crown without obvious swelling. There is some degree of bifurcation of the ridges towards the base, but this never forms a reticulate ornament. The lingual face of the cusps is ornamented with fine, somewhat irregular longitudinal ridges that reach about half-way up the main cusp. The crown weakly overhangs the root labially and laterally, but the junction between the crown and root is clearly visible in labial view. The root is large and bulky and the most characteristic feature of these teeth. It is considerably wider than the crown and relatively high. The anterior and posterior sides of the root are of similar size, but there is considerable asymmetry of the shapes of the root lobes other than within the single specimen of a symmetrical, presumed parasymphaseal tooth. The profile of the root is very angular, with 'corners' of the root projecting lingually and labiolaterally. On the anterior side of the tooth, the labial projection of the root is less well defined, and the root lobe is rather square in profile, with the root lobe having a straight lingual edge. On the posterior root lobe, the angularity is more pronounced, and the root lobe is hammerhead-shaped, with a concave lingual edge. The basal face of the root of all teeth is flat, and makes a sharp edge with other faces. There are many small foramina irregularly spaced over the root basal face. The largest tooth recovered has a deep, wide nutritive groove with a central foramen, but all other teeth have large lingual and labial foramina and no nutritive groove. Other foramina are large and obvious, with a row near the centre of the labial face of the root, and 1–4 large foramina on each side of the lingual faces of the root.

Remarks. The teeth of this taxon are extremely similar to those of the extant *Leptocharias smithii*. The large, angular and highly asymmetrical root of *L. cretaceus* sp. nov. is present in *L. smithii*, but is unlike the root of any extant scyliorhinid (Herman *et al.* 1990), other extant carcharhiniform (e.g. Herman *et al.* 1991) or any fossil carcharhiniform of known affinity (i.e. preserved as an entire skeleton). This root morphology is, therefore, considered here to be a character unique to *Leptocharias*. In addition, the presence of a straight but strongly inclined main cusp present in both *L. cretaceus* and *L. smithii* is unknown in extant scyliorhinids. These characters, apparently unique to *Leptocharias*, are also seen in the Palaeogene '*Scyliorhinus*' *ptychtus* Noubhani and Cappetta, 1997; we think that this species should, therefore, also be referred to *Leptocharias* (Underwood and Ward in press). Anterior teeth of *L. smithii* show strong sexual dimorphism (e.g. Herman *et al.* 1991). The variation in ornamentation of teeth of *L. cretaceus* may also be a result of sexual dimorphism.

Family CARCHARHINIDAE Jordan and Evermann, 1896

Genus LOXODON Müller and Henle 1838

Type species. Loxodon macrorhinus Müller and Henle 1838.

?*Loxodon* sp.
Plate 7, figures 13–16

in press ?*Loxodon* sp. Underwood and Ward, fig. 1R–T.

Material. P. 66422 and P. 66423, complete and partial teeth, respectively, from the Santonian of Winterbourne.

Description. The teeth are wider than high and highly compressed. There is a single cusp that is strongly inclined posteriorly. The cusp has straight anterior and posterior edges. There is a very weakly developed distal heel, which takes the form of a straight blade that is parallel to the base of the crown and extends approximately as far posteriorly as the cusp. The base of the cusp is straight on both labial and lingual faces, and does not overhang the root on either side. The crown-root

junction is excavated on both labial and lingual faces, and there is faint crenulation of the enameloid just above the junction. There is otherwise no ornamentation on the teeth. The region of the root-crown junction is noticeably concave below the base of the cusp on the labial side, and near the anterior and posterior ends of the tooth on the lingual side. The root is relatively small and compressed, being no deeper than the crown. The root labial face is continuous with the anterior and posterior parts of the crown, but is indented below the centre of the cusp at the labial end of the nutritive groove. There is an acute angle between the labial and basal faces of the root, and the lingual root face is very reduced. The root is cut by a deep but narrow nutritive groove containing a well-developed foramen. A row of small foramina is present half-way up the root labial face, with a row of smaller foramina being present just below the crown-root junction on the lingual side. Small, irregularly distributed, foramina are present across the basal face of the root.

Remarks. These teeth appear superficially similar to those of *Paratriakis*, but may be readily separated by the presence of a large nutritive groove. They can be referred to a member of the Carcharhinidae and not the Triakidae by the morphology of the root, and in particular the lack of a labial overhang of the crown, a feature that appears to be present in all triakids. These teeth are similar to those of a number of Cenozoic and recent carcharhiniform genera. Although the small quantity of material renders generic assignment uncertain, the lack of incipient serrations and posterior cusplets makes it unlikely that these teeth belong to *Rhizoprionodon*, whereas the lack of torsion of the cusp makes assignment to *Scoliodon* unlikely. This record represents the earliest occurrence of the Carcharhinidae, and the first evidence of the family in the Mesozoic (Underwood and Ward in press).

Family ?PROSCYLLIIDAE Fowler, 1941

Genus PROTOSCYLIORHINUS Herman, 1977

Type species. Protoscyliorhinus bettrechiensis Herman, 1977.

Protoscyliorhinus sp.
Plate 7, figures 17–19

Material. BELUM K28672, a partial tooth from the Coniacian of Minnis North.

Description. The single partial tooth is about 2 mm wide, but is missing the posterior part. The crown comprises a low, triangular main cusp with one small lateral cusplet and a further two incipient cusplets. The tip of the main cusp has been removed by wear, but otherwise there is a continuous cutting edge along the occlusal edge. The labial face of the crown is ornamented with short, irregular longitudinal ridges. These bifurcate towards the base and partly merge to form small, triangular raised portions. The lingual face of the cusps has short, fine longitudinal ridges. The crown overhangs the root along its labial and lateral edges, with the basal edge of the crown forming a smooth curve on the labial face. The root is low and of a similar thickness along its preserved width. There is a wide but shallow nutritive groove with a central foramen, although it is unclear whether this has been modified by corrosion. The root is only slightly flattened, and there is no well-defined edge between the basal and other root faces. There is a row of very small foramina on the labial root face, and scattered small foramina on the basal part of the root.

Discussion. The tentative assignment of *Protoscyliorhinus* to the Proscylliidae follows that of Underwood (2006) and Underwood and Ward (in press) as the teeth possess a deep labial face to the crown joining the main and lateral cusps and a root of uniform thickness without a flared basal face, a combination of characters seen in extant *Proscyllium* but not any extant scyliorhinids (see Herman *et al.* 1990, 1991). This tooth represents the youngest recorded occurrence of *Protoscyliorhinus*.

EVOLUTIONARY IMPLICATIONS

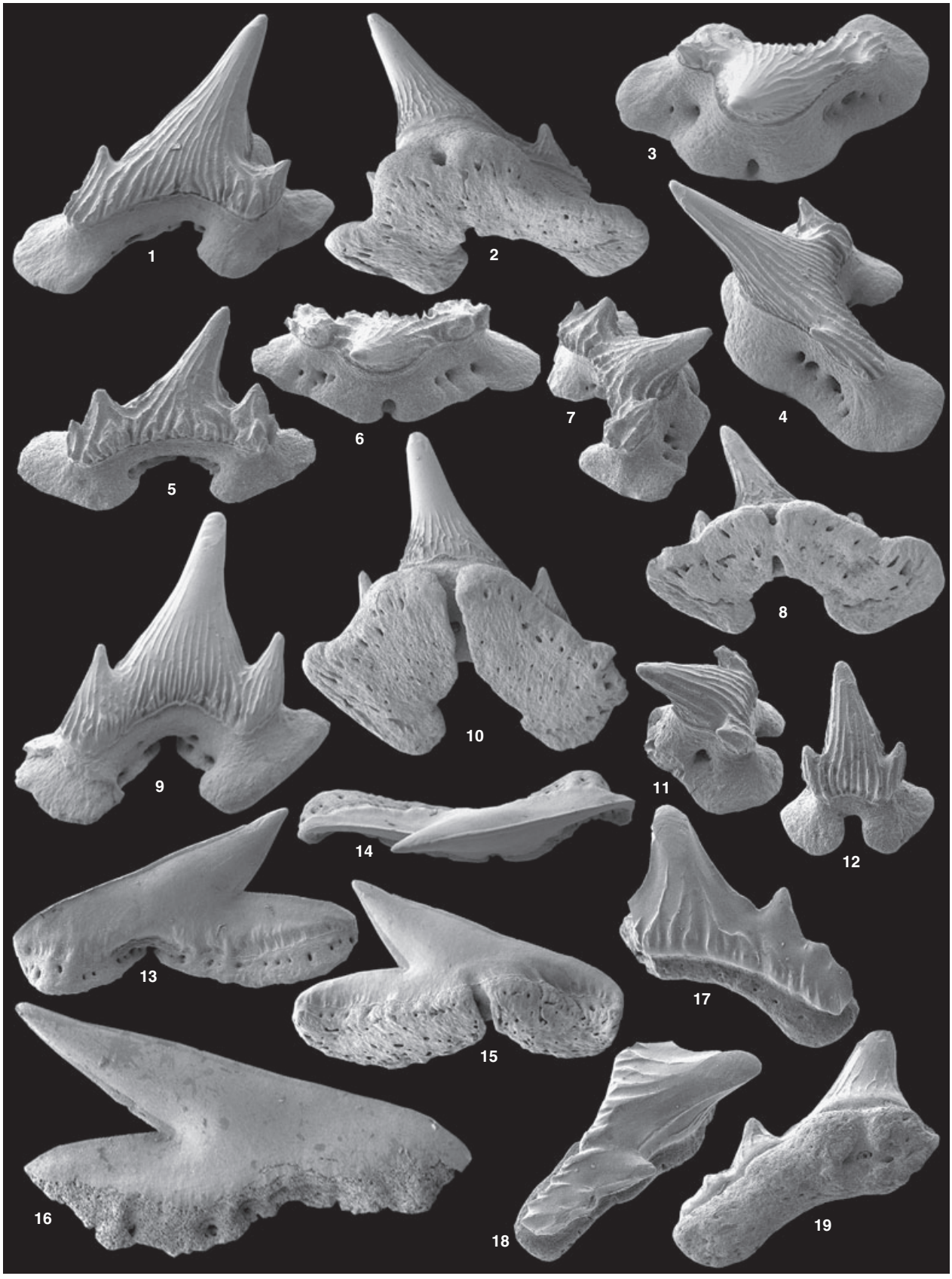
The specimens recorded in this study represent the first indications of a number of extant Carcharhiniforme families in the Cretaceous (Underwood and Ward in press).

EXPLANATION OF PLATE 7

Figs 1–12. *Leptocharias cretaceus* sp. nov. 1–4, P. 66418, holotype, Upper Santonian, Winterbourne, lower phosphate level, in 1, labial, 2, lingual, 3, occlusal, and 4, oblique lateral views. 5–8, P. 66419, Lower Campanian, Winterbourne, upper phosphate level, in 5, labial, 6, occlusal, 7, oblique lateral, and 8, lingual views. 9–10, P. 66420, Upper Santonian, Winterbourne, lower phosphate level, in 9, labial, and 10, lingual views. 11–12, P. 66421, Lower Campanian, Winterbourne, upper phosphate level, parasymphaseal tooth, in 11, oblique lateral, and 12, labial views. 1–8, 11–12, × 25; 9–10, × 20.

Figs 13–16. ?*Loxodon* sp. 13–15, P. 66422, Upper Santonian, Winterbourne, lower phosphate level, in 13, labial, 14, occlusal, and 15, lingual views. 16, P. 66423, Upper Santonian, Winterbourne, lower phosphate level, lingual view. All × 25.

Figs 17–19. *Protoscyliorhinus* sp. BELUM K28672, Coniacian, Minnis North, in 17, labial, 18, oblique lateral, and 19, lingual views; × 20.



UNDERWOOD and WARD, Carcharhiniformes

Previous studies have suggested that fossils from the Jurassic may be assignable to the Proscylliidae (e.g. Underwood and Ward 2004), a family predicted to be close to the base of the carcharhiniforme clade (see Underwood 2006 and references therein). The Leptochariidae are also likely to be a basal family within the order (Underwood and Ward in press), and their presence in the Cretaceous is not unexpected. The Carcharhinidae (including the Sphyrnidae if they are to be considered monophyletic) are the most morphologically diverse of the extant carcharhiniform families, with a number of genera being known from the Palaeocene, even though much of the diversification had occurred within the Neogene (e.g. Cappetta 1987). The occurrence of Cretaceous Carcharhinidae therefore extends the earliest record of the group to a point before the first recorded radiation within the family.

PALAEOECOLOGY

The diverse carcharhiniforms recorded in all of the samples studied form part of diverse shark and ray faunas, with the majority of specimens in all of the Chalk samples belonging to taxa with small teeth. The only samples with the majority of larger teeth are those from the greensands of Minnis North, where low numbers of small teeth may be a result of biostratinomic sorting and physical and biological destruction. These small teeth (with the possible exception of those of some of the batoids) would have belonged to small taxa, by comparison with modern relatives, the majority less than 50 cm in length. Most of these small taxa (Scyliorhinidae and most Orectolobiformes) have pointed, clutching (Cappetta 1986) teeth, and would have been slow swimmers with an elongate body form. These are likely to have been nectobenthic generalist feeders, consuming diverse small organisms. Other taxa, particularly of the Triakidae, had a more cutting dentition and were probably more active hunters of small fish, cephalopods and crustaceans. Other probable ecological types are present among associated selachians. Medium to large predatory lamniformes are present in all samples, although it is only in the Downend and Minnis North samples that they are common, with taxa possessing both cutting and piercing dentitions being present in all samples. Selachians with a durophagous dentition are rare in all of the Chalk samples, and restricted to a small number of batoids and rare *Heterodontus*. The exception to this is the sample from Minnis North, where *Heterodontus* and batoids are common, and teeth of *Ptychodus* were recorded. Teeth of small ambush predators, such as *Squatina*, are present but uncommon in all samples.

This dominance of selachian faunas by diverse, small, nectobenthic taxa appears to be common within the European Cretaceous. Previous studies of selachian faunas from European chalk facies have yielded high diversities of small taxa from horizons in the Albian (Underwood and Mitchell 1999), Cenomanian (e.g. Müller and Diedrich 1991), Campanian (e.g. Müller 1989) and Maastrichtian (e.g. Siverson 1993), although all of these studies are from within the North Sea Basin or associated Boreal regions, as opposed to the more Tethyan-influenced Anglo-Paris Basin of the Chalk samples described here. Although there are many similarities with regard to the overall ecological composition of all of these European assemblages, squalids are a major part of all of the more boreal assemblages; it is likely that the absence of squalids in the samples described here is owing to their more boreal distribution. Other, less systematic, studies of selachians from the Anglo-Paris Basin (e.g. Herman 1977) yielded very similar faunas to those described here, and lack squalids. Very high diversity selachian faunas dominated by small nectobenthic taxa therefore appear to be characteristic of the European Upper Cretaceous.

Selachian faunas from the Western Interior Seaway of North America are well known from near-shore facies (e.g. Case 1978), but there have been few systematic studies of selachians from neritic facies (see Welton and Farish 1993; Case and Cappetta 1997). Although studies typically show high diversities of Lamniformes and batoids, most samples contain very few taxa of small nectobenthic sharks (except in Case and Cappetta 1997); in some samples even batoids are extremely rare and the faunas are almost entirely composed of larger mid-water predators (e.g. Cumbaa *et al.* 2006).

Other Late Cretaceous selachian faunas are less well known than those of northern Europe and North America. Diverse Maastrichtian sharks are well known from North African phosphorites, and very diverse assemblages have been described from Morocco (e.g. Noubhani and Cappetta 1997). These contain a number of Carcharhiniforme taxa along with many Lamniformes and other selachian groups. Although the species composition of these assemblages is well recorded, the proportions of different species and ecogroups have not been documented.

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REFERENCES

AGASSIZ, L. J. R. 1833–44. *Recherches sur les poissons fossiles, 3*. Imprimerie de Petitpierre, Neuchâtel, 390 + 32 pp.

ANTUNES, M. T. and CAPPETTA, H. 2002. Sélaciens du Crétacé (Albien–Maastrichtien) d'Angola. *Palaeontographica, Abteilung A*, **264**, 85–146.

BLAINVILLE, H. M. D. DE 1816. Prodrome d'une distribution systématique du regne animal. *Bulletin de la Société Philomatique de Paris*, **8**, 105–124.

BONE, A. and BONE, D. 2002. Lavant Stone: a late medieval building stone from the Chalk (Upper Cretaceous) of West Sussex. *Proceedings of the Geologists' Association*, **111**, 193–203.

—— —— 2004. Lavant Stone: a Roman and medieval building stone in West Sussex. *Sussex Archaeological Collections*, **142**, 63–78.

CAPPETTA, H. 1973. Selachians from the Carlile Shale (Turonian) of South Dakota. *Journal of Paleontology*, **47**, 504–514.

—— 1977. Observations sur quelques selaciens du Crétacé Supérieur d'Angleterre avec la description d'un genre nouveau. *Geobios*, **10**, 479–485.

—— 1980*a*. Les selaciens du Cretace superieur du Liban. I: Requins. *Palaeontographica, Abteilung A*, **168**, 69–148.

—— 1980*b*. Les Selaciens du Cretace Superieur du Liban. II: Batoides. *Palaeontographica, Abteilung A*, **168**, 149–229.

—— 1986. Types dentaires adaptatifs chez les sélaciens actuels et post-Paléozoiques. *Palaeovertebrata*, **16**, 57–76.

—— 1987. Mesozoic and Cenozoic elasmobranchii. Chondrichthyes II. *In* SCHULTZE, H. P. (ed.). *Handbook of paleoichthyology, Part 3B*. Gustav Fischer Verlag, Stuttgart, 193 pp.

—— 1992. Carchariniformes nouveaux (Chondrichthyes, Neoselachii) de l'Yprésian du bassin de Paris. *Geobios*, **25**, 639–646.

—— and ODIN, G. S. 2001. Les sélaciens du Campanien–Maastrichtien de Tercis les Bains (SO France). 645–651. *In* ODIN, G. S. (ed.). *The Campanian-Maastrichtian boundary characterization and correlation from Tercis-les-Bains (Landes, SW France) to Europe and other continents*. IUGS Special Publication, **36**, 679–685.

CASE, G. R. 1978. A new selachian fauna from the Judith River Formation (Campanian) of Montana. *Palaeontographica, Abteilung A*, **160**, 176–205.

—— and CAPPETTA, H. 1997. A new selachian fauna from the Late Maastrichtian of Texas (Upper Cretaceous/Navarroan; Kemp Formation). *Münchener Geowissenschaftlich Abhandlungen, A*, **27**, 5–63.

COMPAGNO, L. J. V. 1977. Phyletic relationships of living sharks and rays. *American Zoologist*, **17**, 303–322.

CUMBAA, S. L., SCHRÖDER-ADAMS, C., DAY, R. G. and PHILLIPS, A. J. 2006. Cenomanian bonebed faunas from the northeastern margin, Western Interior Seaway, Canada. *New Mexico Museum of Natural History and Science Bulletin*, **35**, 139–155.

DALINKEVICIUS, J. A. 1935. On the fossil fishes of the Lithuanian Chalk. I. Selachii. *Mémoires de la Faculté des Sciences de l'Université de Vytautas le Grand*, **9**, 247–305.

DAIMERIES, A. 1888. Notes ichthyologiques I. *Annales de la Société Royal de Malacologie, Belgique, Bulletin des Séances*, **23**, 42–43.

DAVIS, J. W. 1887. The fossil fishes of the chalk of Mount Lebanon, in Syria. *Scientific Transactions of the Royal Dublin Society, Series 2*, **3**, 457–636.

DINELEY, D. L. and METCALF, S. J. 1999. *Fossil fishes of Great Britain*. Geological Conservation Review Series, **16**. Joint Nature Conservation Committee, Peterborough, 675 pp.

ELLIS, J. R. and SHACKLEY, S. E. 1995. Ontogenetic changes and sexual dimorphism in the head, mouth and teeth of the lesser spotted dogfish. *Journal of Fish Biology*, **47**, 155–164.

FLETCHER, T. P. 1977. Lithostratigraphy of the Chalk (Ulster White Limestone) in Northern Ireland. *Reports of the Institute of Geological Sciences*, **77** (24), 1–33.

FOWLER, H. W. 1941. The fishes of the groups Elasmobranchii, Holocephali, Isospondyli, and Ostariophysi obtained by US Bureau of Fishing Steamer *Albatross* in 1907 to 1910, chiefly in the Philippine Islands and adjacent seas. *Bulletin of the United States Natural History Museum*, **100**, 1–879.

GALE, A. S. 1980. Penecontemporareous folding, sedimentation and erosion in Campanian Chalk near Portsmouth, England. *Sedimentology*, **27**, 137–151.

GARMAN, S. 1913. The Plagiostomia (sharks, skates and rays). *Memoirs of the Museum of Comparative Zoology, Harvard College, Cambridge*, **36**, 1–515.

GILL, T. 1862. Analytical analysis of the order of Squali and revision and nomenclature of genera. *Annals of the Society of Natural History of New York*, **7**, 367–408.

GRAY, J. E. 1851. *List of specimens of fish in the collection of the British Museum, Part 1*. British Museum (Natural History), London, 160 pp.

GURR, P. R. 1962. A new fish fauna from the Woolwich Bottom Bed (Sparnacian) of Herne Bay, Kent. *Proceedings of the Geologists' Association*, **73**, 419–447.

HALTER, M. C. 1994. Additions to the fish fauna of N.W. Europe. 3. Three new species of the genus *Scyliorhinus* from the late Cretaceous (Campanian and Maastrichtian) of the Limburg area (Belgium and the Netherlands) with the reassignment of four additional species to the genus *Scyliorhinus sensu stricto*. *Professional Paper of the Belgian Geological Survey*, **278**, 65–110.

HAY, O. P. 1902. Bibliography and catalogue of the fossil vertebrata of North America. *Bulletin of the United States Geological Survey*, **179**, 1–868.

HERMAN, J. 1977. Les Sélachians néocrétacés et paléocénes de Belgique et des contrées limitrophes eléments d'une biostratigraphie intercontinentale. *Mémoires pour servir à l'Explication des Cartes Géologiques et Minières de la Belgique*, **15**, 1–450.

—— 1982. Die Selachier-Zahne aus der Maastricht-Stufe von Hemmoor, Niederelbe (NW-Deutschland). *Geologisches Jahrbuch, A*, **61**, 129–159.

—— HOVESTADT-EULER, M. and HOVESTADT, D. C. 1990. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of chondrichthyan fishes. *In* STEHMANN, M. (ed.). *Part A: Selachii. No. 2b: Order: Carcharhiniformes – Family: Scyliorhinidae*. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie, **60**, 181–230.

——— ——— ——— 1991. Contributions to the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of chondrichthyan fishes. *In* STEHMANN, M. (ed.). *Part A: Selachii. No. 2c: Order: Carcharhiniformes – Families: Proscylliidea, Hemigaleidae, Pseudotriakidae, Leptocharias and Carcharhinidae*. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie, **61**, 73–120.

JARVIS, I. 1980. The initiation of phosphatic sedimentation, the Senonian (Cretaceous) of the Anglo-Paris Basin. 167–192. *In* BENTOR, Y. K. (ed.). *Marine phosphorites, geochemistry, occurrence, genesis*. SEPM Special Publication, **29**, 249 pp.

—— 2006. The Santonian–Campanian phosphatic chalks of England and France. *Proceedings of the Geologists' Association*, **117**, 219–237.

—— and WOODROOF, P. 1981. The phosphatic chalks and hardgrounds of Boxford and Winterbourne, Berkshire – two tectonically controlled facies in the Late Coniacian to early Campanian (Cretaceous) of southern England. *Geological Magazine*, **118**, 175–187.

JORDAN, D. S. and EVERMANN, B. W. 1896. The fishes of North and Middle America: a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the isthmus of Panama. Part I. *Bulletin of the United States National Museum*, **47**, 1–1240.

LERICHE, M. 1906. Contribution à l'étude des poissons fossiles du Nord de la France et des régions voisines. *Mémoires de la Société Géologique du Nord*, **55**, 1–430.

LINNAEUS, C. 1758. *Systema naturae*. Tenth edition. Salvi, Stockholm, 824 pp.

MARCK, W. VON DER 1863. Fische, Krebse und Pflanzen aus dem Plattenkalk der jüngeren Kreide aus Westfalen. *Paleontographica*, **11**, 1–83.

MORTIMORE, R. N., WOOD, C. J. and GALLOIS, R. W. 2001. *British Upper Cretaceous stratigraphy*. Geological Conservation Review Series, 23. Joint Nature Conservation Committee, Peterborough, 585 pp.

MÜLLER, A. 1989. Selachier (Pisces, Chondrichthyes) aus dem höheren Campanium (Oberkreide) Westfalens (Nordrhein-Westfalen, NW-Deutschland). *Geologie und Paläontologie in Westfalen*, **14**, 1–161.

—— and DIEDRICH, C. 1991. Selachier (Pisces, Chondrichthyes) aus dem Cenomanium von Ascheloh am Teutoberger Wald (Nordrhein-Westfalen, NW-Deutschland). *Geologie und Paläontologie in Westfalen*, **20**, 1–105.

MÜLLER, J. and HENLE, J. 1838–41. *Systematische beshreibung der plagiostomen*. Veit, Berlin, 200 pp.

NOUBHANI, A. and CAPPETTA, H. 1997. Les Orectolobiformes, Carchariniformes, et Myliobatiformes (Elasmobranchii, Neoselachii) des bassins à phosphate du Maroc (Maastrichtian–Lutétien basal). *Palaeo Ichthyologica*, **8**, 1–327.

REES, J. 2005. Neoselachian shark and ray teeth from the Valanginian, Lower Cretaceous, of Wąwał, central Poland. *Palaeontology*, **48**, 209–221.

SCHINZ, H. R. 1822. *Das Thierreich eingetheilt nach dem Bau der Thiere als Grundlage ihrer Naturgeschichte und der vergleichenden Anatomie*. Mit vielen Zusätzenversehen von H. R. Schinz, Cotta, Stuttgart and Tübingen das Thierreich, i–xvi, 1–83.

SHIRAI, S. 1996. Phylogenetic interrelationships of neoselachians (Chondrichthyes: Euselachii). 9–34. *In* STIASSEY, M. L. J., PARENTI, L. R. and JOHNSON, G. D. (eds). *Interrelationships of fishes*. Academic Press, San Diego, CA, 496 pp.

SIMMS, M. J. 2003. Minnis North Mudflow. Geological Sites in Northern Ireland, Earth Science Conservation Review: http://www.habitas.org.uk/escr/summary.asp?Item=114

SIVERSON, M. 1993. Late Cretaceous and Danian neoselachians from southern Sweden. *Lund Publications in Geology*, **110**, 1–28.

SWEETMAN, S. C. and UNDERWOOD, C. J. 2006. A neoselachian shark from the non-marine Wessex Formation (Wealden Group: Early Cretaceous, Barremian) of the Isle of Wight, southern England. *Palaeontology*, **49**, 457–465.

UNDERWOOD, C. J. 2004. Barremian and Aptian (Cretaceous) sharks and rays from Speeton, Yorkshire, NE England. *Proceedings of the Yorkshire Geological Society*, **55**, 107–118.

—— 2006. Diversification of the Neoselachii (Chondrichthyes) during the Jurassic and Cretaceous. *Paleobiology*, **32**, 215–235.

—— and MITCHELL, S. H. 1999. Albian and Cenomanian selachian assemblages from North East England. *Special Papers in Palaeontology*, **60**, 9–59.

——— ——— and VELTKAMP, C. J. 1999. Microborings in mid Cretaceous fish teeth. *Proceedings of the Yorkshire Geological Society*, **52**, 269–274.

—— and WARD, D. J. 2004. Environmental distribution of Bathonian (Middle Jurassic) neoselachians in southern England. 111–122. *In* TINTORI, A. and ARRATIA, G. (eds). *Mesozoic fishes 3 – systematics, palaeoenvironments and biodiversity*. Verlag Dr. Friedrich Pfeil, München, 649 pp.

——— ——— in press. The Mesozoic record of the Carcharhiniformes. *In* ARRATIA, G., SCHULTZE, H.-P. and WILSON, M. V. H. (eds). *Mesozoic fishes 4*. Verlag Dr. Friedrich Pfeil, München.

WAGNER, J. A. 1857. Charakteristik neuer Arten von Knorpelfischen aus den lithographischen Schiefern der Umgegend von Solnhofen. *Gelehrte Anzeiger der Bayerischen Akademie der Wissenschaften*, **44**, 288–293.

WELTON, B. J. and FARISH, R. F. 1993. *The collector's guide to fossil sharks and rays from the Cretaceous of Texas*. Before Time, Lewisville, TX, 203 pp.

WHITE, H. G. O. and TREACHER, L. 1906. The phosphatic chalks of Winterbourne and Boxford (Berkshire). *Quarterly Journal of the Geological Society of London*, **62**, 499–522.

WILLCOX, N. R. 1953. The origin of the beds of phosphatic chalk with special reference to those at Taplow. 119–133. *In Origin des gisements de phosphates de chaux*. Comptes Rendus de la Dix-neuvième Session, Alger, Congrès Géologiques International, Algiers.

WOODROOF, P. B. 1980. Field Meeting: The Chalk of the Newbury and Lambourne area, Berkshire, 25 June 1978. *Proceedings of the Geologists' Association*, **91**, 349–350.

WOODWARD, A. S. 1889. *Catalogue of the fossil fishes in the British Museum. Part 1*. British Museum (Natural History), London, 474 pp.

APPENDIX

Field sites and provisional faunal lists

Locality. Boxford, Berkshire.
Coordinates. SU 431 719.
Section description. A small overgrown quarry, located 340 m north-north-west of Boxford Church, on the east side of a country lane that runs parallel to the River Lambourne. The pit exposes a complex of slump folded hardgrounds overlain by phosphatic chalk.
Stratigraphy. Uppermost Seaford or basal Newhaven Chalk Formation, *M. coranguinum* Zone, mid-Santonian.
Samples. 95 kg sample of soft pelletal phosphatic chalk was collected from high in the northern face of the quarry, 30 cm above the 'Upper Hardground'. A rich and diverse selachian fauna was recovered.
References. White and Treacher (1906), Jarvis and Woodroof (1981), Ward in Dineley and Metcalf (1999), Mortimore *et al.* (2001).
Associated selachian fauna. *Synechodus* sp., *Squatina decipiens* Dalinkevicius, 1935, *Squatina* sp., *Carcharias* sp., *Cretalamna appendiculata* (Agassiz, 1843), *Protolamna* sp., '*Palaeoanacorax*' sp., ?*Pseudocorax laevis* Leriche, 1906, *Squalicorax falcatus* (Agassiz, 1843), *Heterodontus* cf. *havreensis* Herman, 1977, *Chiloscyllium greeni* (Cappetta, 1973), *Cretorectolobus* sp., *Pararhincodon groesseni* Herman, 1982, *Pseudospinax pusillus* Muller and Diedrich, 1991, *Parasquatina* sp., ?*Rhombopterygia* sp., ?*Rhynchobatus* sp., *Sclerorhynchus* sp., *Rhinobatos casieri* Herman, 1977, ?*Squatirhina* sp. indet., Hybodontidae indet.

Locality. Winterbourne, Berkshire.
Coordinates. SU 448 722.
Section description. A shallow pit in the middle of a field exposing up to 6 m of upper Santonian and lower Campanian chalk (*Marsupites* and *pilula* zones), *c.* 1.7 km east of Boxford. Two phosphatic levels were sampled.
Stratigraphy. Newhaven Chalk Formation; lower phosphatic horizon is *Marsupites testudinarius* Zone, upper Santonian; upper phosphatic horizon is *Offaster pilula* Zone, lower Campanian.
Samples. 165 kg of pelletal (Santonian) chalk from immediately above the (lower) Phosphatic Hardground, and 180 kg of similar, lower Campanian, chalk, 2 m higher in section, just above the Upper Hardground. Both levels yielded a rich and diverse selachian fauna.
References. White and Treacher (1906), Woodroof (1980), Jarvis and Woodroof (1981), Mortimore *et al.* (2001).
Associated selachian fauna. Lower phosphatic level: *Hexanchus* sp., *Squatina decipiens* Dalinkevicius, 1935, *Squatina* sp., *Carcharias* sp., *Cretalamna appendiculata* (Agassiz, 1843), *Protolamna* sp., '*Palaeoanacorax*' sp., *Pseudocorax laevis* Leriche, 1906, *Squalicorax kaupi* (Agassiz, 1843), *Paracorax* sp., *Heterodontus* sp., *Chiloscyllium greeni* (Cappetta, 1973), *Cretascyllium* ?*expansum* Müller and Diedrich, 1991, *Pararhincodon groesseni* Herman, 1982, *Parasquatina* sp., ?*Rhombopterygia* sp., *Sclerorhynchus* sp., *Rhinobatos casieri* Herman, 1977. Upper phosphatic level: *Squatina decipiens* Dalinkevicius, 1935, *Squatina* sp., *Carcharias* sp., *Cretalamna appendiculata* (Agassiz, 1843), *Protolamna* sp., *Scapanorhynchus* sp., '*Palaeoanacorax*' sp., *Pseudocorax laevis* Leriche, 1906, ?*Squalicorax kaupi* (Agassiz, 1843), *Chiloscyllium greeni* (Cappetta, 1973), *Cederstroemia havreensis* (Herman, 1977), *Cretascyllium* ?*expansum* Müller and Diedrich, 1991, *Pararhincodon groesseni* Herman, 1982, *Parasquatina* sp., ?*Rhombopterygia* sp., *Sclerorhynchus* sp., *Rhinobatos casieri* Herman, 1977.

Locality. Stoke Clump, West Sussex.
Coordinates. SU 835 098.
Section description. A series of shallow pits in farmland that were infilled in the early 1940s. However, lumps of brown phosphatic chalk, known as Lavant Stone, can still be found in the field 475 m north-east of Stoke Clump.
Stratigraphy. Old Nore or Peacehaven Beds, Newhaven Chalk Formation; *Offaster pilula* Zone, lower Campanian.
Samples. Approximately 220 kg of phosphatic chalk was collected, crushed, and screened. This site yielded a relatively low diversity fauna dominated by *Chiloscyllium*. There are also abundant sponge spicules, isolated asteroid and ophiuroid ossicles and phosphatised bony fish otoliths.
References. Mortimore (1986), Bone and Bone (2002, 2004).
Associated selachian fauna. *Paraorthacodus* sp., *Squatina decipiens* Dalinkevicius 1935, *Anomotodon* sp., '*Palaeoanacorax*' sp., *Squalicorax kaupi* (Agassiz, 1843), *Chiloscyllium greeni* (Cappetta, 1973), *Cederstroemia havreensis* (Herman, 1977), ?*Rhombopterygia* sp., *Sclerorhynchus* sp., *Rhinobatos casieri* Herman, 1977, *Rhinobatos* sp.

Locality. South Lodge Pit, Taplow, Buckinghamshire.
Coordinates. SU 906 819.
Section description. South Lodge Pit is an abandoned quarry on the east bank of the River Thames near Taplow. The pit originally exposed two hardgrounds of middle and late Santonian age, overlain by a brown pelletal phosphatic chalks. It is currently somewhat degraded and only the upper horizon is visible.
Stratigraphy. Taplow Phosphatic Chalk Member, Newhaven Chalk Formation; lower phosphatic horizon is *Uintacrinus socialis* Zone, mid Santonian; upper phosphatic horizon is *Marsupites testudinarius* Zone, upper Santonian.
Samples. About 180 kg of soft brown pelletal phosphatic chalk was taken from immediately above both hardgrounds. Vertebrate faunas from both were poor and yielded few well-preserved teeth.
References. Willcox (1953), Mortimore *et al.* (2001).
Associated selachian fauna. Lower phosphatic level: *Squatina decipiens* Dalinkevicius, 1935, *Carcharias* sp., ?*Scapanorhynchus* sp., '*Palaeoanacorax*' sp., *Pseudocorax laevis* Leriche, 1906, *Squalicorax kaupi* (Agassiz, 1843), *Chiloscyllium greeni* (Cappetta, 1973), *Pseudospinax pusillus* Müller and Diedrich, 1991, *Sclerorhynchus* sp., *Rhinobatos casieri* Herman, 1977. Upper phosphatic level: *Squatina decipiens* Dalinkevicius, 1935, *Carcharias* sp., *Cretalamna appendiculata* (Agassiz, 1843), ?*Scapanorhynchus* sp., '*Palaeoanacorax*' sp., *Pseudocorax laevis* Leriche 1906, *Squalicorax kaupi* (Agassiz, 1843), *Chiloscyllium greeni* (Cappetta, 1973), *Cretorectolobus* sp., *Cretascyllium* ?*expansum* Müller and Died-

rich, 1991, *Pararhincodon groesseni* Herman, 1982, ?*Rhombopterygia* sp., *Rhinobatos casieri* Herman, 1977.

Locality. Downend, Hampshire.
Coordinates. SU 601 065.
Section description. A large, mostly back-filled, quarry on the south-west margin of Portsdown Hill, immediately adjacent to the M27 motorway. The middle part of the south-east face exposed faulted and contorted Campanian chalks with hardgrounds and locally developed calcarenites.
Stratigraphy. ?Spetisbury Member, Culver Chalk Formation; *G. quadrata* and *B. mucronata* Overlap Zone, lower Campanian.
Samples. About 150 kg of calcarenite was crushed and sieved from immediately above the Downend Main Hardground. Selachian remains were diverse and included very abundant teeth of *Squalicorax*. Many of these are of a similar size and appear to represent a partial associated dentition.
References. Gale (1980), Mortimore *et al.* (2001).
Associated selachian fauna. *Squatina decipiens* Dalinkevicius, 1935, *Squatina* sp., *Carcharias* sp., *Cretalamna appendiculata* (Agassiz, 1843), *Scapanorhynchus* sp., *Palaeoanacorax* sp., *Pseudocorax laevis* Leriche, 1906, ?*Squalicorax kaupi* (Agassiz, 1843), *Heterodontus* sp., *Chiloscyllium greeni* (Cappetta, 1973), *Cederstroemia havreensis* (Herman, 1977), *Cretorectolobus* sp., *Pararhincodon groesseni* Herman, 1982, *Parasquatina* sp., ?*Rhombopterygia* sp., *Rhinobatos casieri* Herman, 1977.

Locality. Minnis North Mudflow, County Antrim, Northern Ireland.
Coordinates. D 339 135.
Section description. This site is a mudslide on the Antrim Coast Road (A2) north of Drumnagreagh Port. Cretaceous rocks occur as blocks within the slipped Jurassic clays at the base of the hill and on the beach below the road, and sometimes as partly slipped blocks on the hillside.
Stratigraphy. Phosphatic pebble bed in Kilcoan Sands Member, Hibernian Greensand Formation; *M. cortestudinarium* Zone, Coniacian.
Samples. About 160 kg of glauconitic sandstone was dissolved in acid. Vertebrate remains were seen in the field and vary in their mode of preservation. Many teeth are dark coloured, strongly abraded and have any cavities filled by glauconite, whilst others, including all of the specimens figured here, are pale in colour, appear unabraded and have porous roots. The composition of these two assemblages is somewhat different, but it is not clear whether they indicate two different assemblages (indigenous and reworked) or whether the differences are due to differential biostratinomy.
References. Fletcher (1977), Simms (2003).
Associated selachian fauna. Abraded teeth: *Synechodus* sp., *Cretalamna appendiculata* (Agassiz, 1843), *Protolamna* sp., *Paranomotodon* sp., *Squalicorax falcatus* (Agassiz, 1843), *Heterodontus lonzeensis* Herman, 1977, *Heterodontus* sp., *Turoniabatis* sp., ?*Ptychotrygon* sp. Hybodontidae indet., *Ptychodus* sp. Unabraded teeth: *Protosqualus* sp., *Carcharias* sp., *Cretalamna appendiculata* (Agassiz, 1843), *Protolamna* sp., *Paranomotodon* sp., *Scapanorhynchus* sp., *Squalicorax falcatus* (Agassiz, 1843), *Heterodontus lonzeensis* Herman, 1977, *Chiloscyllium greeni* (Cappetta, 1973), *Cantioscyllium* sp., *Pararhincodon* sp., ?*Rhombopterygia* sp., *Rhinobatos* sp., *Turoniabatis* sp., *Squatirhina lonzeensis* Herman, 1977, *Meristodon* sp.