

FISH OTOLITHS FROM THE ENGLISH CRETACEOUS

by FREDERICK C. STINTON

ABSTRACT. Fish otoliths including the representatives of one new genus and four new species are described from the Neocomian, Albian, and Upper Cenomanian. Their possible affinities with earlier and later teleost groups are discussed.

ALTHOUGH teleost remains have been well known from the Upper Cretaceous Chalk for many years little is known of the fish fauna of the Lower Greensand, Gault, and Upper Greensand. Most of the literature has been concerned with skeletal remains; but teleost otoliths, which occur frequently in the English Albian, have been largely neglected, despite the fact that they are to be found in the collections of the British Museum (Natural History) dating from 1861. Koken (1891) described a single otolith from the Gault of Folkestone and Shepherd (1916) described two further otoliths from the same area. Apart from a mention by Milbourne (1956, p. 239) of the occurrence of otoliths in Bed 3 of the Gault exposed at Greatness Lane, Sevenoaks, Kent, no other work has been done on the subject.

In recent years detailed collecting at inland exposures of the Gault of Kent has produced many more otoliths, mainly fragmentary but occasionally in an excellent state of preservation. The remaining Cretaceous strata are notable for the paucity of otoliths, largely due to the decalcification of much of their thickness. Apart from the Albian (Gault) otoliths only three other sacculiths are known to date, two from the Neocomian (Speeton Clay) and one from the Upper Cenomanian (Lower Chalk). This latter specimen is largely in the form of an impression. It is probable that other otoliths occur in the Speeton Clay but they may well have been overlooked by workers who were unfamiliar with these objects.

A very few otoliths have been recorded from the Cretaceous of continental Europe and America. Priem (1908) described one species from the Neocomian of Attancourt (Haute-Marne), France, and Weiler (1969) subsequently recorded the same species from the Neocomian in the vicinity of Hanover, Germany. It is of interest to note that these forms appear to be conspecific with those described herein from the Speeton Clay and that the German specimens are recorded from the same stage as the English ones.

Strata containing an abundance of fish otoliths often appear to contain few osseous remains. The accumulation of otoliths may have originated from faecal concentrates derived from marine mammals or birds which would create a false impression of the relative numbers of teleosts occurring at that time.

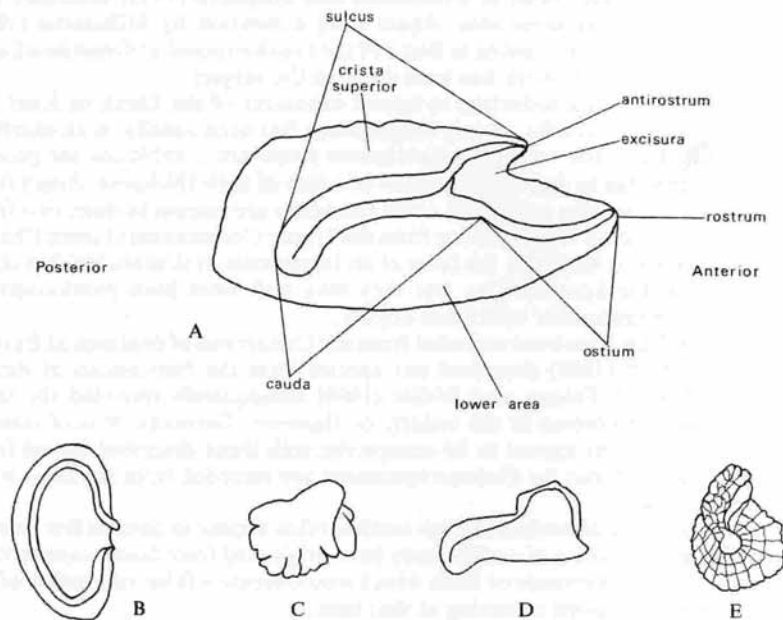
The otoliths to be described are mainly quite distinct from those of Tertiary and Recent fishes so that, in the absence of associated skeletons or suitable comparative material, a certain amount of conjecture as to their relationship is inevitable. However, certain morphological features are perpetuated from Jurassic forms through

to the present day and these offer good indicators to the possible affinities of the forms under consideration.

TERMINOLOGY

The terminology is that proposed by Koken (1884, p. 525) whose original names for the morphological features of the otolith are still applicable. Chaîne and Duvergier (1934) described further specialized features which appear in a few teleost groups. The original names for the different types of otoliths were revised by Adams (1940). He suggested terms which directly related the otoliths to their sites within the labyrinth and these are adopted here in preference to the original terms.

The generalized percoid features of the three otolith types are shown in text-fig. 1A, B, D, while the utriculiths of two primitive teleosts, *Notopterus notoapterus* Pallas (text-fig. 1C) and *Esox lucius* Linnaeus (text-fig. 1E) show the variable sculpture of this type of otolith. The characters of the lagenalith are relatively constant in all teleost groups and are insufficiently variable to be of use for generic determination. Similarly, among the many percoid groups, the utriculith shows little variation in detail and is of little use in generic determination. Among the more primitive fishes



TEXT-FIG. 1. A, Schematic percoid left sacculith, medial view. B, Generalized features of a percoid lagenalith approximately, $\times 12$. C, Utriculith of *Notopterus notoapterus* Pallas, $\times 12$. D, Percoid utriculith (*Gaterin gaterinus* Forskål), $\times 21$. E, Utriculith of *Esox lucius* Linnaeus, $\times 10$.

and among the siluroids the utriculiths are very variable, and those of the Ariidae are characteristic of the various genera. They are large, biconvex, circular to oval objects occurring frequently in the Upper Eocene and, because of their size, are well known to palaeontologists who work in the English Bartonian.

SYSTEMATIC DESCRIPTIONS

Subclass TELEOSTEI

Order ELOPIFORMES

Family MEGALOPIDAE

Genus MEGALOPS Lacépède 1803, p. 289

Type species. *Megalops filamentosus* Lacépède = *Clupea cyprinoides* Broussonet, monotypic.

Megalops bicrenulatus sp. nov.

Plate 31, figs. 1-3

Holotype. P. 51770/1. Paired sacculiths, one utriculith and associated scales and bones, the remains of a single individual.

Dimensions. P. 51770 (pl. 31, figs. 1a, b), length 5.68 mm, width 3.38 mm

P. 51770 (pl. 31, figs. 2a, b), length 5.74 mm, width 3.48 mm

P. 51771, utriculith (pl. 31, figs. 3a, b), length 1.38 mm, width 0.96 mm

Description. The sacculiths (pl. 31, figs. 1a, b, 2a, b) are rather thick, biconvex, rounded posteriorly, and bluntly pointed anteriorly. Dorsal rims bicrenulate anteriorly and very slightly rounded posteriorly, coalescing completely with the rounded posterior rim which in turn coalesces with the regularly rounded ventral rim; slightly undulant anterior rims. Outer faces smooth, somewhat undulant, and depressed in the postero-dorsal area. Inner faces smooth. Sulcus opening obliquely on the anterior rim and not reaching the posterior rim. It consists of a short, wide, triangular ostium with a concave lower rim and a long, slightly arcuate, rather narrow cauda expanding slightly towards its pointed extremity. A depression above the crista superior, accentuating it. A very slight lower angle and a marked upper angle at the junction of ostium and cauda, the upper angle being formed by the crista superior recurving nearly vertically to the junction of the anterior and dorsal rims. Blunt rostrum, slight excisura, but no antirostrum or collicula present.

The utriculith (pl. 31, figs. 3a, b) is a rather triangular, biconvex right otolith. The ventral rim is finely crenulated while the smooth anterior and posterior rims form a dorsal point. Outer face smoothly rugose with a central concavity in the ventral area producing a keeled ventral rim. No characters of specific value are present.

Discussion. The sacculiths have a distinct resemblance to the Jurassic forms described as *Pholidophorus* by Stinton and Torrens (1968), both in the character of the sulcus and in peripheral details, but lack the denticulated ventral rims of the Jurassic forms besides being thicker. It was suggested that the otolith described as *Pholidophorus paradoxicus* Stinton and Torrens, might be a precursor of *Megalops* and the present form has a distinct resemblance to sacculiths of *Megalops cyprinoides*

(Broussonet) which today inhabits the Indo-Pacific. Both forms have a similar sulcus and peripheral characters but the fossil form has a shorter rostrum while the smooth ventral rim also differs from the serrated one of the Recent species. Dr. C. Patterson has examined the accompanying scales and states (pers. comm.) that they bear some resemblance to those of the Recent genus *Megalops* but cannot be definitely identified with it.

Locality of holotype. Albian (Gault), Folkestone, Kent. Exact horizon unknown.

Other material. P. 47558/9 Lower Gault, *niobe* subzone, B.P.C.M. Pit, Small Dole, Sussex. H. A. Toombs Colln. P. 51772 Gault, *varicosum* zone, Folkestone, Kent. A. Gale Colln. P. 51783 Gault, Trottscliffe, Kent. G. Freeman Colln.

Family ELOPIDAE

Genus *Elops* Linnaeus 1766

Type species. *Elops saurus* Linnaeus.

'*Elops*' *neocomiensis* (Priem)

Plate 31, figs. 4-5

1908 *Otolithus (Clupeidarum) neocomiensis* Priem, p. 37, text-figs. 11-14.

1965 *Palealbula neocomiensis* Frizzell, p. 97, pl. 4, fig. 8.

1969 *Palealbula neocomiensis* Weiler, pp. 358-361, text-figs. 2, 3, 5, 7, 8.

Material and locality. Left sacculith (P. 15954) and right sacculith (P. 15953), Lower Cretaceous (Neocomian), Hauterivian zone D1, Speeton Clay, Yorkshire. G. W. Lamplugh Colln.

Dimensions. Right sacculith (pl. 31, fig. 4a, b), length 13.94 mm, width 8.90 mm.

Left sacculith (pl. 31, fig. 5a, b), length 14.30 mm, width 8.05 mm.

Description. Both otoliths are eroded, rather thick, with convex inner faces and concave outer faces. Dorsal rims probably somewhat eroded but show an irregular, slightly rounded periphery; posterior rim of the right specimen is nearly vertical and smoothly rounded; ventral rims of both specimens smoothly rounded; anterior rims eroded but probably rather oblique. Outer faces rugose with compressed peripheries to form keeled rims. The sulcus is arcuate, evidently opening widely on the anterior rim and terminating on or near the posterior rim. It consists of a short obtusely triangular ostium with a steeply descending lower rim and a long, arcuate cauda

EXPLANATION OF PLATE 31

- Figs. 1-3. *Megalops bicrenulatus* sp. nov. 1a, b, Syntype P. 51770, right sacculith, inner and outer faces, $\times 4$. 2a, b, Syntype P. 51770, left sacculith, inner and outer faces, $\times 4$. 3a, b, Syntype P. 51771, utriculith, inner and outer faces, $\times 16$.
- Figs. 4-5. '*Elops*' *neocomiensis* (Priem). 4a, b, P. 15953, right sacculith, inner and outer faces, $\times 1.6$. 5a, b, P. 15954, left sacculith, inner and outer faces, $\times 1.6$.
- Fig. 6a, b, *Pteralbula cantiana* (Shepherd). Syntype P. 17, left sacculith, inner and outer faces, $\times 1.6$.
- Fig. 7a, b, *Albula obesa* sp. nov. Holotype P. 51773, right sacculith, inner and outer faces, $\times 2$.
- Fig. 8a, b, *Pterothrissus galtinus* (Koken). P. 51767, right sacculith, inner and outer faces, $\times 4.8$.
- Fig. 9a, b, '*Osmerus*' *lobatus* sp. nov. Holotype P. 23274, left sacculith, inner and outer faces, $\times 10.4$.
- Fig. 10. *Sphaeronchus rotundus* sp. nov. Holotype P. 51766, right sacculith, inner face, $\times 2.4$.
- Fig. 11. Fragment of sacculith, P. 51769, simulating the utriculith of a Recent Ariid. Inner face, $\times 4$.



STINTON, fish otoliths

which is deep and widens somewhat towards the posterior end before narrowing to a rounded point. Crista superior raised and there is a very narrow excavation between it and the dorsal rim. A rounded lower angle and an oblique upper angle produced by a recurving of the crista superior, at the junction of ostium and cauda. A rostrum probably present but no evidence of an antirostrum or excisura. No collicula.

Discussion. These otoliths show an obvious affinity to sacculiths of the modern Elopidae in the character of the dorsal periphery, the arcuate sulcus, and the very short, triangular ostium with its position on the anterior rim. Erosion has shortened the rostrum so that it is impossible to ascertain whether it was comparable in length with that of the Recent forms.

It has not been possible to compare these specimens directly with those from the French and German Cretaceous but illustrations indicate that they are identical. The origin of the French holotype from the Lower Cretaceous and the German specimens from the contemporaneous Hauterivian stage of the Lower Cretaceous near Hanover further confirms the identity of the English and continental specimens.

Frizzell (1965) related these forms to an albulid complex, suggesting that Priem's species was a precursor of *Albula*. He also ascribed two forms from the Upper Cretaceous of the United States—*Prealbula weileri* Frizzell and *Protalbula sohli* Frizzell to this same complex. However, none of these forms shows the ostium opening in the characteristic position of the albulids nor do they have the almost continuous anterior and dorsal rims. Furthermore, they lack the produced posterior area which appears to be an established character of albulid sacculiths.

Family ALBULIDAE
Genus *Pteralbula* gen. nov.

Type species. (*Atherina*) *cantiana* Shepherd 1916, p. 203.

Rectangular sacculiths with a prominent vertical extension of the postero-dorsal area. They are biconvex. Sulcus occupying the dorsal half of the otolith, opening on the antero-dorsal corner and running diagonally towards the postero-ventral corner but terminating before reaching the periphery. Sulcus consisting of a very short, angular ostium and an almost straight cauda. Undulant dorsal rim and all other rims regularly rounded. Osteological details unknown at present.

Pteralbula cantiana (Shepherd)

Plate 31, fig. 6

1916 *Otolithus* (*Atherina*) *cantiana* Shepherd, p. 203, text-fig. 157.

Syntype. P. 17, Albian (Gault), Folkestone, Kent. Gardner Colln.

Dimensions. Length 12.86 mm, width 10.83 mm.

Description. An adult left sacculith, somewhat eroded. Morphological characters as for the genus. Smooth, irregularly undulant outer face with depressed antero-dorsal and postero-dorsal areas. Dorsal area of inner face compressed, accentuating the crista superior. A rounded lower angle and upper right angle at the junction of ostium and cauda. No rostrum, antirostrum, excisura, or collicula. A wide, smooth, semicircular lower area.

Discussion. The salient feature of this otolith is the marked vertical projection of the postero-dorsal area, a character previously only seen in typical albulid sacculiths. Also, the sulcus occupies a similar position on the inner face with the ostium opening on the antero-dorsal edge. On the other hand, the rather rectangular outline and the diagonal course of the sulcus resemble pterothrissid sacculiths and it is considered that this fish was ancestral to both *Albula* and *Pterothrissus*. One might expect to find the genus represented in the Jurassic and it seems probable that it extended into the Cretaceous before becoming replaced by modern forms of *Albula* and *Pterothrissus*.

A realignment of the postero-dorsal extension to a horizontal posterior extension, the rounding and narrowing of the otolith with the necessary realignment of the sulcus to conform with these morphological changes would result in a typical albulid sacculith. Similarly, the entire loss of the posterior extension would result in a relatively typical otolith of *Pterothrissus* without any further morphological changes. Such changes would also require modifications of the cranial structures in the area of the auditory bullae to accommodate these alterations in the design.

Shepherd (1916) suggested that this form compared with that described as *Otolithus (Atherina) austriacus* Schubert because of a supposed similarity between the sulcus of each species. However, atherine sacculiths have a median, narrow sulcus quite dissimilar from the present form.

Other material and localities. P. 51774 Gault, *intermedius/subdelaruei* zone, Folkestone, Kent. A. Gale Colln. 41358 Gault, Folkestone, Kent. Horizon unknown. B. N. Wright Colln. 47213 Gault, Folkestone, Kent. Horizon unknown. Gardner Colln. P. 15727 Gault, Bed VIII, Copt Point, Folkestone, Kent. W. A. McFadyen Colln. 36115 Gault, Folkestone, Kent. Horizon unknown. W. Griffiths Colln. 36321 Gault, Folkestone, Kent. Horizon unknown. W. Griffiths Colln. P. 47710-47716 Gault, level 2, ?*E. latus* zone, B.P.C.M. Old Pit, Small Dole, Sussex. Bernard Cooper Colln. P. 47587-47588 Gault, basal level below nodule bed, B.P.C.M. Pit, Small Dole, Sussex. Bernard Cooper Colln. P. 49805 Gault, A.P.C.M. Pit, Small Dole, Sussex. S. Cragg Colln.

Two examples (Nos. 112229, 112230), Gault, Folkestone, Price Colln., are contained in the museum collections of the Institute of Geological Sciences.

Genus ALBULA Scopoli 1777

Type species. *Esox vulpes* Linnaeus.

Albula obesa sp. nov.

Plate 31, fig. 7

Holotype. P. 51773.

Dimensions. Length 10.67 mm, width 6.23 mm.

Description. A thick, eroded, biconvex right sacculith. Slightly rounded dorsal rim; rounded, slightly produced posterior rim; fairly deeply rounded ventral rim; rounded anterior rim. Smooth convex outer face with a slight depression at the postero-dorsal corner. Convex inner face with an indistinct sulcus, due to erosion, apparently opening on the antero-dorsal corner of the otolith and extending somewhat diagonally to parallel the dorsal and posterior rims. It terminates near the postero-ventral corner of the otolith. Details of sulcus obscure but it appears to consist of a short, wide ostium and a long, slightly undulant, relatively wide cauda. A very

slight depression on the dorsal rim. No apparent rostrum, antirostrum, excisura, or collicula. A wide, smooth lower area.

Discussion. Despite the very worn condition of this specimen it shows a marked similarity to sacculiths of Tertiary and Recent albulids in its peripheral contours, position, and alignment of the sulcus and especially in the characteristic extension of the posterior rim. It appears that this may well have come from a true *Albula*.

In the Cenozoic the first typical albulid otolith recorded is that figured by Priem (1908, p. 84, text-figs. 45, 46) from the Palaeocene, Thanétien, Sables de Châlons-sur-Vesles (Marnes) which he named *Otolithus (Trachini ?) bellevoiyii*, a species which is very similar to, if not synonymous with, the English species *Albula eppi* Frost, from the Ypresian, Blackheath Beds. This more rounded outline persists throughout the Eocene and Oligocene eventually becoming further modified to the more elongate and narrower sacculith seen in the Recent forms.

Locality. Gault, *varicosum* subzone, Small Dole, Sussex. D. Ward Colln.

Family PTEROTHRISSIDAE
Genus PTEROTHRISSUS Hilgendorf 1877

Type species. *Pterothrissus gissu* Hilgendorf.

Pterothrissus galtinus (Koken)

Plate 31, fig. 8

1891 *Otolithus galtinus* Koken, p. 138, text-fig. 27.

Material and locality. Right sacculith P. 51767 Gault, Bed 11, *intermedius* zone, B.P.C.M. Pit, Small Dole, Sussex. G. Freeman Colln.

Dimensions. Length 4.33 mm, width 2.50 mm.

Description. A beautifully preserved right sacculith. Nearly horizontal, crenulated dorsal rim; rounded, crenulate posterior rim; long, rounded denticulate ventral rim; short, irregularly denticulate anterior rim. Convex outer face prominently umbonated on the dorsal area. Compressed posterior and ventral areas peripherally ornamented with short, tuberoso ribs. Almost flat inner face with a somewhat diagonal sulcus which opens very slightly on the upper part of the anterior rim and terminates near the postero-ventral corner. Sulcus consisting of an almost enclosed, rather wide, oval ostium and a long, narrow, straight cauda which turns down slightly near its pointed extremity. An indistinct sulculus extends vertically from the end of the cauda to the postero-dorsal corner of the otolith. Slightly rounded lower angle and an acute upper angle, produced by the recurved upper ostial rim, present at the junction of ostium and cauda. A shallow depression above the crista superior, accentuating it. No rostrum, antirostrum or collicula but an excisura present. Lower area finely latticed.

Discussion. The present species was originally established by Koken on a somewhat eroded specimen from the Folkestone Gault and he assigned it to his '*umbonatus*' (= *Pterothrissus*) group. However, this sacculith is so similar to those of the living species that it can only be referred to the Recent *Pterothrissus*. It suggests that the Pterothrissidae evolved fully during the Cretaceous at least as far as the otoliths

are concerned. Many adult sacculiths up to 15 mm length have been found at various Gault exposures indicating that this fairly common fish grew to a large size. The adult otoliths usually show evidence of erosion and it is frequently difficult to separate them from similarly affected otoliths of other species which accompany them.

Other material and localities. P. 23274 Gault, zone VI, Copt Point, Folkestone, Kent. W. A. Macfadyen Colln. 36105 Gault, Folkestone, Kent. Horizon unknown. W. Griffiths Colln. P. 23275 Gault, zone VIII, Copt Point, Folkestone, Kent. W. A. Macfadyen Colln. 35879 Gault, Folkestone, Kent. Horizon unknown. W. Griffiths Colln. 41358 Gault, Folkestone, Kent. Horizon unknown. B. N. Wright Colln. 47213 Gault, Folkestone, Kent. Horizon unknown. Gardner Colln. P. 10818 Gault, Folkestone, Kent. Horizon unknown. Hilton Price Colln. P. 47717-47719 Gault, level 2 (?*E. latus* zone), B.P.C.M. Old Pit, Small Dole, Sussex. Bernard Cooper Colln. P. 47680-47681 Gault, level 1, base of old pit, B.P.C.M. Pit, Small Dole, Sussex. Macdonald Colln. P. 47620-47662 Gault, basal level (below nodule bed), B.P.C.M. Pit, Small Dole, Sussex. Bernard Cooper Colln. P. 47587-47588 Gault, basal level (below nodule bed), B.P.C.M. Pit, Small Dole, Sussex. Bernard Cooper Colln. P. 48669 Lower Gault, *bennettianus* zone, Bed 1, top shell seam, A.P.C.M. Pit, Small Dole, Sussex. H. Owen Colln. P. 51784 Gault, Leighton Buzzard, Bedfordshire. Horizon unknown. Buteux Colln.

Order SALMONIFORMES

Family OSMERIDAE

Genus OSMERUS Lacépède 1803

Type species. *Salmo eperlanus* Linnaeus.

'Osmerus' lobatus sp. nov.

Plate 31, fig. 9

Holotype. P. 23274 Gault, zone VI, Copt Point, Folkestone, Kent. W. A. Macfadyen Colln.

Dimensions. Length 2.42 mm, width 1.59 mm.

Description. A rather thin, oval left sacculith which is slightly eroded. Crenulated, nearly horizontal dorsal rim; short, nearly vertical posterior rim with a small central point and a notch above it; a moderately rounded ventral rim, indistinctly crenulated on the posterior half; oblique anterior rim. Slightly convex outer face with indistinct tuberculations on the dorsal area and very faint radial ribbing on the ventral area. Inner face very slightly convex with a slightly diagonal sulcus opening obliquely on the anterior rim and terminating almost on the postero-ventral point. Sulcus consisting of a short, wide, triangular ostium and a long, rather narrow cauda which is open-ended. A depression above the crista superior, accentuating it. A rounded upper angle and a slight, rounded lower angle at the junction of ostium and cauda. A very blunt rostrum and a slight excisura but no antirostrum or collicula present. A smooth, semicircular lower area.

Discussion. This otolith resembles those of the Recent subspecies *Osmerus eperlanus mordax* (Mitchill) in its outline and in the over-all characters of the sulcus. It lacks the serrated anterior part of the ventral rim but this characteristic osmeroid feature might be present in unworn specimens in view of the faint ribbing on the outer face. In the absence of corroborative osteological remains and considering the evident affinity of this sacculith to modern osmeroid forms it is probable that this represents an ancestral type of *Osmerus*.

Other material and localities. P. 51768 Gault, Lower Bed XI, Ford Place, Kent. G. Freeman Colln. P.47663 Gault, basal level below nodule bed, B. P.C.M. Pit, Small Dole, Sussex. Bernard Cooper Colln.

Order BERYCIFORMES

Family BERYCIDAE *sensu lato*

Genus *Sphaeronchus* Stinton and Torrens 1968

Type species. *Sphaeronchus dorsetensis* Stinton and Torrens, 1968, p. 250.

Further consideration of the sacculiths of *Sphaeronchus* assigned by Stinton and Torrens (1968, p. 50) to the Pycnodontidae suggests that they are more likely to have been derived from fishes related to the Berycoidei. The circular outline of the otolith together with the short, oval, wide ostium and nearly straight cauda could be interpreted as berycoid features and could logically be expected to evolve into the sacculiths seen today in the genera *Beryx*, *Gephyroberyx*, *Cleidopus*, *Monocentris*, *Hoplostethus*, *Trachichthodes*, *Trachichthys*, and *Antigonia*. The Antigoniidae were assigned to the Berycoidei by myself (Stinton 1967) on the evidence of the sacculiths, which are remarkably similar to those of the Recent Australian berycoid *Trachichthys australis* Shaw and Nodder.

Sphaeronchus rotundus sp. nov.

Plate 31, fig. 10

Holotype. P. 51766 Lower Chalk (Upper Cenomanian), *subglobosus* zone, Gayton, Norfolk. A. Gale Colln.

Dimensions. Length 6.50 mm, width 5.67 mm.

Description. A partial impression of the inner face of a right sacculith, the original substance of the otolith having been decalcified. It is circular in outline and the rims appear to be continuous. The inner face is slightly convex. The median sulcus opens widely on the anterior rim and just reaches the posterior rim. It consists of a short, wide, somewhat semicircular ostium and a long, rather narrow, slightly arcuate cauda. A slightly rounded lower angle and a near right-angled upper angle at the junction of ostium and cauda. A depression above the crista superior, accentuating it. A blunt rostrum present but no apparent antirostrum. An excisura is probably present but there are no collicula.

Discussion. This otolith has the characters of the genus *Sphaeronchus* Stinton, described from the Inferior Oolite, but it differs from the Jurassic form in its ostial characters and more circular periphery. It is the only known otolith from the Chalk at present.

It is common to find objects simulating utriculiths of modern ariids at all Gault horizons where determinable otoliths occur. One such specimen (P. 51769, Pl. 31, fig. 11), demonstrates this similarity when examined cursorily. However, a closer inspection reveals that a trace of a sulcus still remains (seen as a straight line at the top of fig. 11 on Pl. 31). When a large series of these objects is examined it will be seen that they are the remains of large otoliths, probably mostly pterothrissids, which have suffered fracture and/or erosion of the dorsal area, the weakest part of

the sacculith. This results in a truncated, conic object which further erosion by rolling rounds off the fractured edges. It also removes the patina of the inner face to show the underlying laminated structure of the otolith. Many specimens have the remnants of the sulcus reduced to a small, spheroid central depression. The outer face usually retains the patina so that one may be easily misled into supposing that these were utriculiths of ariids.

CONCLUSIONS

The frequently occurring sacculiths of *Pterothrissus* associated with elopid-like otoliths, *Albula* and a probable precursor of *Megalops* in the Gault, offer reasonable evidence of the geographical and climatic conditions pertaining at that time. Today the Pterothrissidae are restricted to two comparatively narrow areas, one off the west coast of Africa between latitudes 16° N. and 20° S. (Poll 1951-1959, p. 16) and the second around the 42° N. parallel in the Tsugare Straits, Japan (Jordan and Herre 1906, p. 619). The West African species *P. bellocci* Cadenat is commonest off the Congo region at depths of 120-250 m. It becomes rarer northwards but occurs fairly frequently off the coast of Senegal (Cadenat 1950) where the pelagic/littoral genera *Megalops*, *Elops*, and *Albula* are not uncommon. Thus the conditions prevailing during the deposition of the Gault may well have been comparable with those now obtaining in West African seas. The presence of the Japanese pterothrissid in more temperate waters beyond the range of the tropical *Elops*, *Megalops*, and *Albula* suggests an anachronism but in the depths at which both *Pterothrissus* species live it is probable that temperatures and habitats are similar.

The common occurrence of rolled fragments of otoliths suggests inshore wave and current action although it has been proved that currents of considerable strength may be encountered at all depths. The absence of otoliths comparable with those of other modern teleost groups in the Gault is noteworthy but this may be due to collecting methods so far used as these may tend to miss the smaller otoliths which often make up the bulk of the specimens in Tertiary and Recent deposits. There is no reason to suppose that the same situation did not obtain during the Cretaceous era.

The record of the two otoliths from the Speeton Clay suggests that intense collecting would bring to light other forms for it is evident that this clay is a suitable medium for their preservation. It may be mentioned here that while '*Elops*' *neocomiensis* (Priem) has predominantly elopid features the over-all shape of the otolith and the ostium have certain resemblances to percoid sacculiths and it is possible that this particular species could have evolved into certain of the modern percoids. The true elopid otoliths are relatively thin and small and the denseness of this fossil form suggests that the fish lived at some depth, rather than being pelagic. Frost (1925, p. 153) in his work on Recent otoliths makes the statement that 'Clupeoidea exhibit . . . primitive simplicity unapproached in other groups and that we may take these as the basic form from which the otoliths of later and more specialized fishes have been derived.' While this is undoubtedly true for some groups of modern teleosts this premiss is unacceptable for some of the groups mentioned below.

The osmeroid type of otolith exhibits some characteristics of modern osmeroids. Again, Frost (1925, p. 158) suggests that the sacculiths of the living *Osmerus eperlanus* Linnaeus, indicate an affinity with the berycoids and other unnamed groups.

In the absence of any comparable morphological features between the sacculiths this statement is also untenable. The Gault osmeroid sacculith does show a distinct affinity to the salmonid fishes and may well be related to the Salmoniformes. Patterson (in Harland *et al.* 1967, p. 658) listed a number of suborders under the order Salmoniformes of which only the Salmonoidei, Argentinoidei, and Galaxioidei have sacculiths of a type which could have evolved from the fossil '*Osmerus lobatus* sp. nov. Patterson (1970) later described in detail two salmoniform Cenomanian species (*Gaudreyella audryi* and *Humbertia operta*) suggesting that they showed an affinity to the Recent genus *Hypomesus* and to the argentinoid/osmeroid fishes generally. It might well be that the sacculiths of '*Osmerus lobatus* represent a fish referable to this group. The sub-orders listed by Gosline (1960, p. 361) and McAllister (1968, p. 52) also include these salmonoid groups.

One might reasonably expect to find berycoid otoliths in the Chalk in view of the typical berycoid skeletons which are a feature in some areas, especially as the Chalk forms appear to differ little from the Recent ones. However, the very nature of the Chalk deposits precludes the likelihood of any otoliths being found apart from casts similar to those described herein.

Patterson (1964) in his studies on Mesozoic acanthopterygians postulated three sub-orders, Polymixioidei, Dinopterygoidei, and Berycoidei, which together had evolved from a polymixiid stock. He included the genera *Beryx*, *Gephyroberyx*, *Cleidopus*, *Monocentris*, *Hoplostethus*, *Trachichthodes*, and *Trachichthys* within the Berycoidei together with certain other families including the Holocentridae. However, the sacculiths of Recent species of *Polymixia* are quite distinct from the true berycoids in their characters, as are the holocentrids and myripristids which appear to have some affinity with the polymixiids as far as the sulcus characters are concerned. Rosen and Patterson (1969, p. 460) divorced the Polymixioidei entirely from the Beryciformes, including them in the superorder Paracanthopterygii while the Beryciformes were transferred to the series Percomorpha within the superorder Acanthopterygii. This regrouping is consistent with the evidence of the otoliths of *Sphaeronchus* for these could well have evolved into the true berycoids of today and also certain modern deep-bodied percoids such as the Scorpididae, Monodactylidae, Sparidae, Lactariidae, and perhaps the Chandidae. In discussing the possible origin of the Perciformes Patterson (1964, p. 467) lists the Scorpididae, Monodactylidae, and Sparidae, together with some other groups including the Kyphosidae as being possible relatives of the berycoids. However, the sacculiths of *Kyphosus* bear no resemblance to typical berycoid sacculiths but have a distinct relationship to certain carangid otoliths. The characters of carangid sacculiths indicate that they probably evolved from an ancestral stock distinct from the berycoids.

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All of the described specimens are lodged in the collections of the Department of Palaeontology, British Museum (Natural History), and bear the registration numbers of the museum.

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