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BY

ERROL IVOR WHITE, F.R.S.

Pp. 1–45 ; 3 *Plates* ; 51 *Text-figures*

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THE HEAD OF
DIPTERUS VALENCIENNESI
Sedgwick & Murchison

By ERROL IVOR WHITE

SYNOPSIS

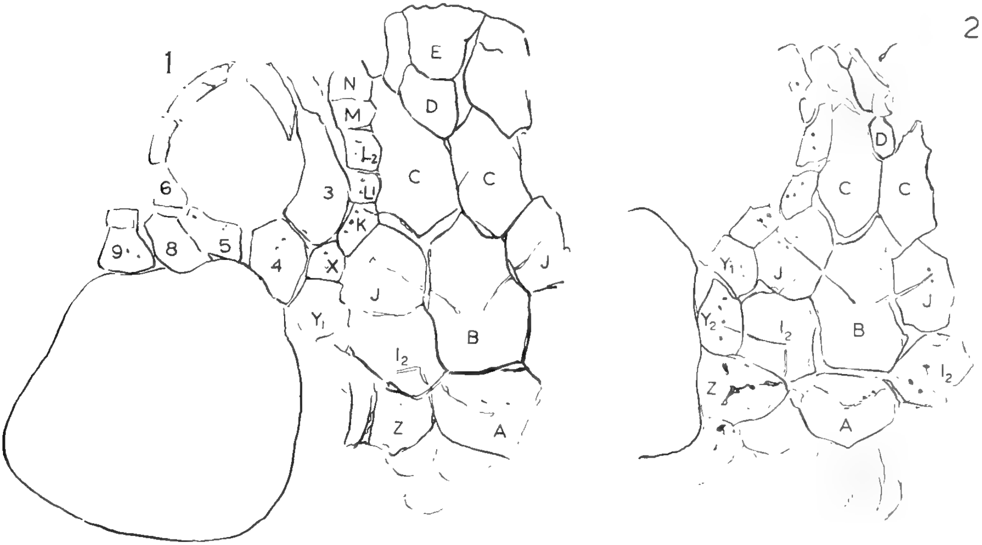
There is only one known species of *Dipterus* from the Middle Old Red Sandstone of Scotland, *D. valenciennesi* Sedgwick & Murchison. The split between the dipnoan and crossopterygian stocks took place at the mosaic stage of evolution of the skull-roof bones, and the nomenclature of the consequent roofing-plates in one group has no relevance to that in the other; entirely independent systems must be used. A modified version of Forster-Cooper's alphabetical system is accepted for the dipnoans, the pattern being developed by invasion and loss rather than by fusion. There has been a gradual loss of rows of plates at the back of the dipnoan head with consequent movement forward of the occipital cross-commissure. The details of the neurocranium are described.

The Name

Specimens of *Dipterus* from the Middle Old Red Sandstone of Scotland have generally been referred to a single species, *Dipterus valenciennesi* Sedgwick & Murchison, although from time to time attempts have been made (e.g. Pander 1858 : 7 ; Watson & Day 1916 : 29) to separate the solid-snouted forms under Agassiz's (1844 : 29) specific name of *platycephalus*. More recently Westoll (1949 : 127–128) decided that the Banniskirk specimens showed sufficient peculiarities in the skull-roof pattern to warrant their separation as a distinct species, and in the belief that all Sedgwick & Murchison's (1829 : 143, pl. 15, figs. 1–3, pl. 16, figs. 1, 3, pl. 17, figs. 1–3) original specimens of their three species, *D. brachypygopterus*, *D. macropygopterus* and *D. valenciennesi* came from Banniskirk quarry, has used the first of these names, *D. brachypygopterus*, for the Banniskirk form which he considered distinct, dropping the names *D. macropygopterus* and *D. valenciennesi* altogether as synonyms of *D. brachypygopterus*, and has revived Agassiz's name of *platycephalus* for all the other Scotch specimens of *Dipterus*, with or without solid snouts.

Unfortunately the provenance of all Sedgwick & Murchison's figured material, now in the collection of the Geological Survey, is not so certain. Only one of the specimens, a co-type of *Dipterus macropygopterus* (pl. 15, fig. 2 ; G.S. no. 6448) was originally labelled "Banniskirk", all the others being labelled "Thurso". "Thurso" indeed was used in early days to cover Banniskirk, which is some 8 miles to the south-east of the town, but it also covered many other quarries in the neighbourhood, and identification of the locality must depend on the recognition of matrix, a very doubtful procedure in these variable rocks. Sedgwick & Murchison's remark about "those from Banniskirk" (1829 : 142) refers to the "small number (sent to Cuvier) of the whole series afterwards examined by Messrs. Valenciennes and Pentland" (p. 142, footnote), and indeed on the previous page Sedgwick & Murchison are at pains to point out that "when the attention of geologists was first drawn to these ichthyolites, it was not known that specimens of them were to be found in any other quarry than that of Banniskirk. The authors of this memoir have however, since discovered that similar remains are extensively . . . spread over the Caithness deposit, etc. etc. . . ." This refers to Old Red fishes in general, but clearly puts to question the origin of the specimens they figured, which are from the " more perfect remains" sent to Valenciennes & Pentland.

But even more important is the lack of substance in the supposition that the Banniskirk forms have a special pattern of their head plates, qualifying them for specific recognition. None of Sedgwick & Murchison's figured specimens shows the head-pattern clearly, and so are irrelevant to this point, whether they come from Banniskirk or not. All the five specimens from Banniskirk figured by Westoll (1949 : 137–139, text-fig. 4) show to some degree *brachypygopterus* features, that is, the paired bones C are replaced by the forward extension of B, and to a small extent by the medial growth of some of the lateral series K–M, although he notes that it is possible that something very like the Achanarras type (" *D. platycephalus* ") occurs very rarely at Banniskirk.



FIGS. 1, 2. *Dipterus valenciennesi* S. & M. Skull-roof showing normal pattern. Banniskirk, Caithness. Fig. 1, Geol. Surv. No. 6464. Fig. 2, R.S.M. 1859.33.623 (Hugh Miller Coll.). Both ×3.

One such individual was figured by Pander (1858, pl. 1, fig. 2), and his diagram (pl. 3, fig. 1) is essentially " normal " in pattern (Text-fig. 10). Of the six specimens available to me that bear *original* Banniskirk labels and show the roof pattern clearly, four (G.S. 6464, R.S.M. 1859.33.623, and R.S.M. 1876.18.31; Text-figs. 1–3) and R.S.M. 1859.33.626[1] show the typical normal pattern with 2 " C " plates

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[1] The initials R.S.M. indicate that the specimen came from the Royal Scottish Museum ; D.M.S.W. from Professor Watson's collection ; G.S. from the Geological Survey ; and M.M. from Manchester Museum. Other specimens numbered with or without an initial P, are in the British Museum (Natural History).

and a median " D ", as does a fifth (33149I, Text-fig. 4) whose supposed provenance from Banniskirk has been subsequently added in pencil, presumably on the basis of the matrix. None of these five specimens would have called for comment in regard to its skull-roof.

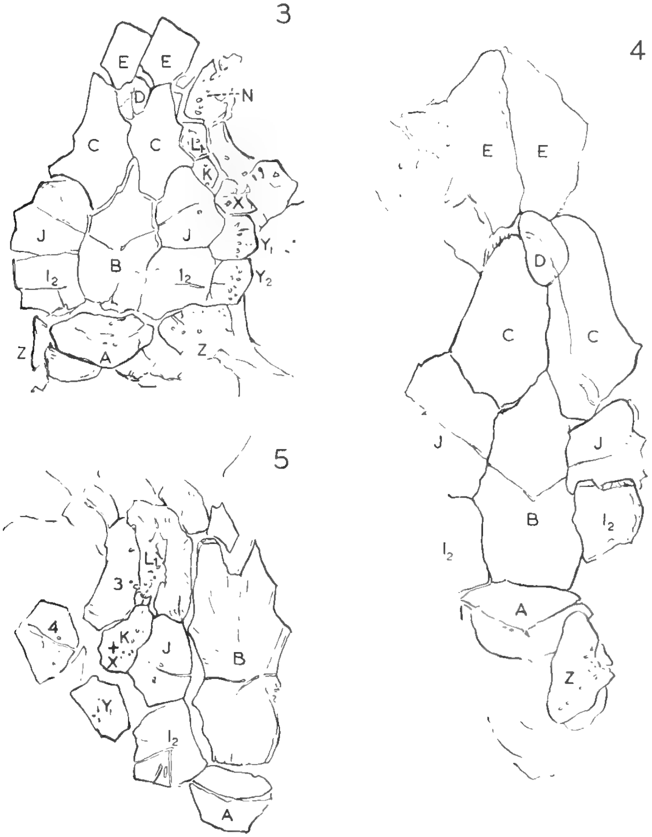
However, on a slab recently collected at Banniskirk by Mr. Jack Saxon is a small nearly complete fish whose head certainly does call for comment, but for another reason (P.46762D, Text-fig. 8). Two C's, a D and 2 E's are well developed in the normal way, but the hinder part of the skull is completely asymmetrical with no J on the left side, its space being largely occupied by B much swollen in front, but with some help from L_1 and K, on to which the rather unusual anterior pit-line extends to meet the supraorbital sensory canal. There is no indication of fusion here whatever, and indeed it is most likely that this arrangement is due to the invasion by B, and to a lesser extent by L_1 and K, of the area where J has failed to develop, in accordance with the sensible principle laid down by Parrington (1950 : 537–540) that fusion should not be postulated unless clearly indicated.

Only two of the six specimens with original Banniskirk labels show the " brachypygopterus " pattern with the greatly enlarged plate B and no C's (42480, R.S.M. 1859.33.624, Text-figs. 5, 6), and both these specimens seem to indicate by the structure of plate B, which in each shows radiation from a single centre, that in these specimens also we have instances of plates (B) invading areas where the growth of the normal plates has been inhibited. But that it was not always entirely a matter of simple invasion is shown by one of Peach's specimens, a small skull-roof collected in 1858 at Sandside, some 10 miles west of Thurso. In this (R.S.M. 1887.35, Text-fig. 7) B is much enlarged forwards and the L bones, two on the left and one on the right side, are wide; but between their anterior ends are two very small C plates, partly fused together and partly fused to B. The front part of the skull, well separated by a *post mortem* displacement from the hinder part, shows a small M on the left, a larger M on the right, large N's on both sides, a wide single E incompletely separated from the snout, and behind this a wide plate which is evidently compound. Whether this last represents D^+ is not very important, but the definite natural break behind the well-defined posterior border does seem to establish that it was not part of C.

A reasonable and simple explanation of the form of the B and C and L bones in this specimen is provided by Parrington's (1956 : 395–404) " Patterns of dermal bones ": the development of the C bones has been retarded and much of their space occupied by B and the L bones before its growth began, and when it did make progress growth-pressure to the rear induced partial fusion with B and lateral pressure induced fusion between the two C's. That neither C bone tended to fuse with its lateral neighbour L, is noteworthy, for Westoll (1949 : 135) has already remarked on the reluctance of " general " bones to fuse with " lateral line bones ", and figured only two possible examples of this (1949 : text-figs. 2*B*, 3*E*).

The " brachypygopterus " pattern is not a specific character but an occasional variation, not uncommon at Banniskirk but occurring infrequently elsewhere, as at Achanarras (Parrington 1950 : 540, text-figs. 4, 5). Most of the specimens showing this pattern are small, but not all, witness Parrington's second specimen.

So far as present knowledge goes one is dealing with a single variable species, and for this all three of Sedgwick & Murchison's specific names of 1828 are available (the fourth name *macrolepidotus* refers to an osteolepid, *Thursius*—see Woodward 1891 : 373) ; but Agassiz's *platycephalus* of 1844 is not (Text-fig. 8). And Agassiz (1835 : 115) having used the inadmissible name " *macrolepidotus* ", Pander (1858 : 6) as the first acceptable reviser, had the right to select whichever of the three available names that he wished for the specific name (Article 24, Internat. Code Zool. Nomenclature, XV Internat. Congr. Zool. 1961) : and his choice of " *valenciennesi* " was fully supported by Woodward (1891 : 236). So the name of the species remains *Dipterus valenciennesi* Sedgwick & Murchison. The term " brachypygopterus-type " may be used for the form of *D. valenciennesi* described by Westoll from Banniskirk, but from any locality, in the way that platycephalus-type has been used for the solid-snouted forms. In regard to this last form the original head-shield, the lectotype, upon which Agassiz based his " *Polyphractus platycephalus* " is unusually wide and small, for the numerous resorption lines and large openings of the foramina seem to indicate



Figs. 3–5. *Dipterus valenciennesi* S. & M. Fig. 3, Skull-roof showing normal pattern. Banniskirk, Caithness. R.S.M. 1876.18.31. ×3. Fig. 4, Skull-roof showing normal pattern. ?Banniskirk. 33149(I). ×3. Fig. 5, Skull-roof showing " brachypygopterus " pattern. Banniskirk. 42480 (Peach Coll.). ×2·25.

an aged fish (P. 3373*a*, Text-fig. 51). Its small adult size, a little over 4 cm. in length, is rather unusual in the "platycephalus-type". Forster-Cooper (1937 : 231) noticed a general correlation between size and the development of the snout, and it seems true that while the hard snout can occur occasionally in rather small specimens, such as this and the original of Text-fig. 7, it is invariably present in large specimens. This does not support Marshall's (1962 : 314) remark that the difference between the soft and hard snouted forms "may be explained as seasonal differences": they seem more likely to be linked with size and age.

It is difficult to give absolute measurements of breadth and length in these skulls, but in general the larger skulls tend to be relatively narrower, up to about 15%, and while the smaller specimens, those measuring under 6·0 cm. from the back of B to the tip of the hard snout, have only 2 or 3 plates along the sensory canal series as a rule, *i.e.* Y_2–N, not all the larger specimens show multiplication. But there are obvious exceptions to both these tendencies.

Nomenclature of the Bones of the Skull-roof

From the first the identification of the dermal bones of the skull-roof in lung-fishes gave rise to much difficulty, in the fossil forms because they had too many plates for exact correlation with those of the general run of fishes, and in the living because they had too few; and usually the earlier zoologists, such as Günther (1871), Huxley (1876) and Bridge (1898) wisely treated them with caution. The first serious attempt to identify the plates of the head of the fossil forms according to the nomenclature in general use for vertebrates was made by D. M. S. Watson (Watson & Day 1916 : 29–32; Watson & Gill 1923), but his interpretation met with flat contradiction from Goodrich (1930 : 305).

Since then efforts to bring order into the labelling of dipnoan roofing bones has developed along two very divergent lines: one a purely arbitrary alphabetical notation, proposed by Forster-Cooper (1936): and the other the compound nomenclature of Holmgren & Stensiö (1936), which seems in effect a more or less spatial use of the general vertebrate terms based on the assumption of widespread fusion of plates.

In a recent study of the skull-roof of a dipterine from Belgium (White 1962) the alphabetical notation of Forster-Cooper (1937 : 228–229) was used without conviction or enthusiasm, merely because the alternatives seemed even less desirable. Romer's (1936 : 242, text-fig. 9) code-system, if more logical in intention, is, as Westoll (1949 : 126) has pointed out, incorrect in application.

On the other hand Lehman's (1959 : 6) advocacy of Holmgren & Stensiö's (1936 : 365, text-figs. 280 *A–C*) terminology, based on the theory of widespread fusion, is only acceptable if the homologies of the component bones are generally agreed, which they certainly are not.

Jarvik (1948 : 81, 291), while strongly supporting the fusionists, does admit that complex bones in different groups of fishes given the same name, rarely, if ever, are strictly homologous, "even in closely allied groups". He further remarks (p. 83) that "It is true that dermal bones are variable in shape and sometimes may invade the territories of adjoining bones. Thus it seems likely that the individual variations in

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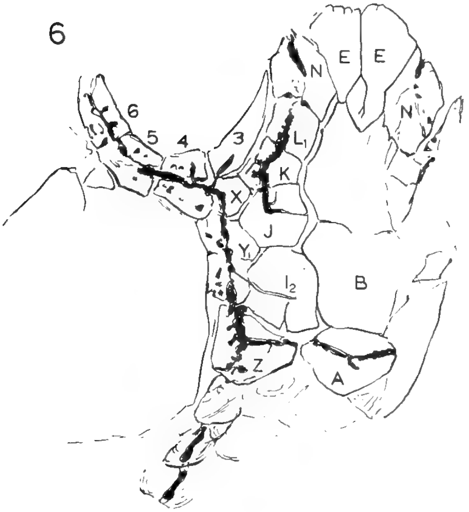

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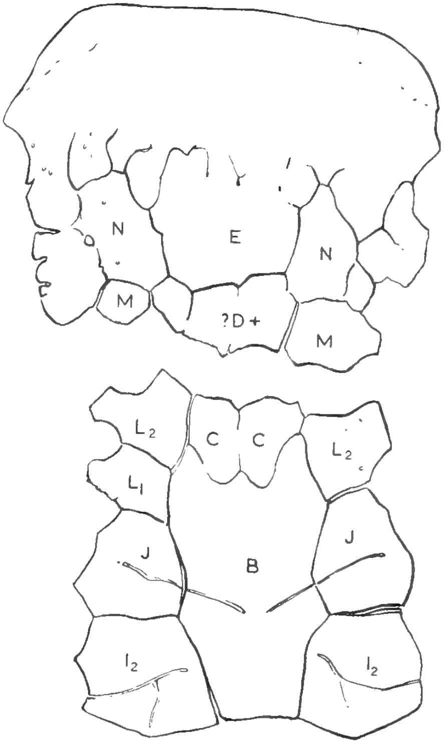

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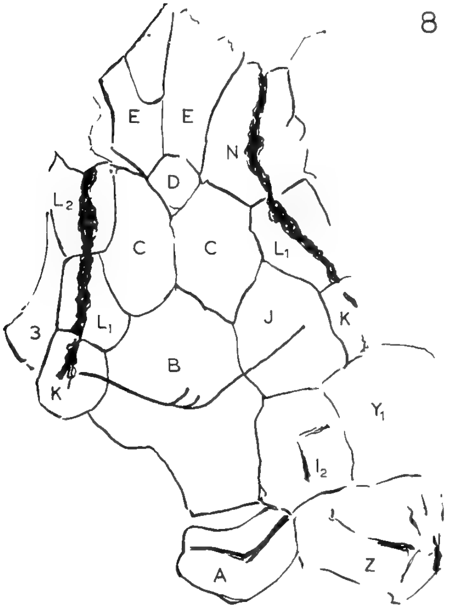
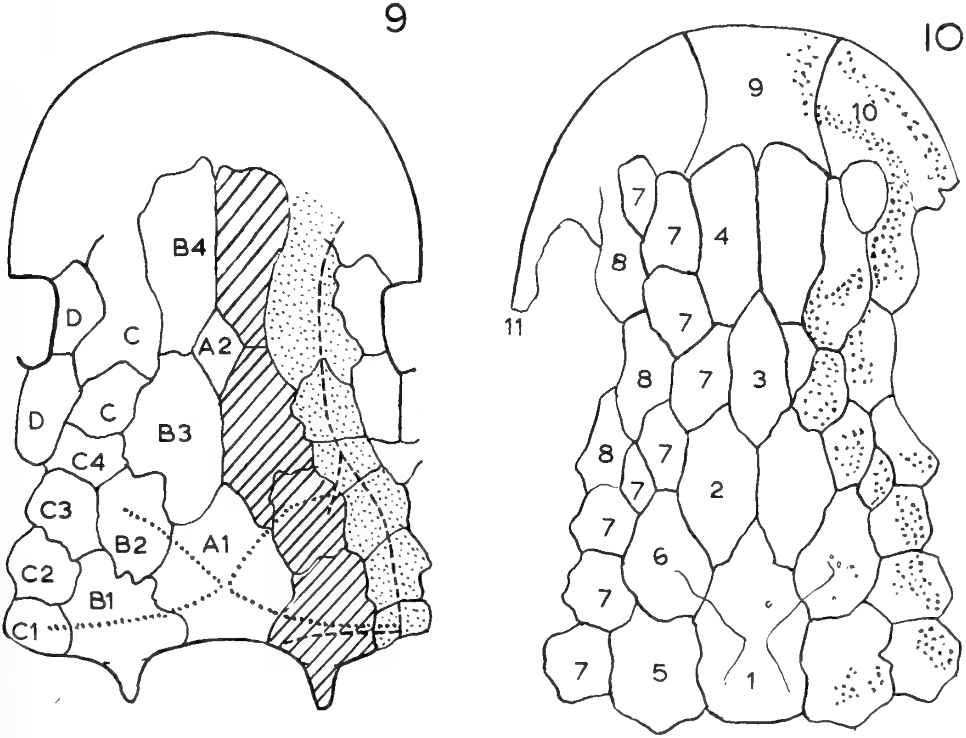


FIGS. 6–8. *Dipterus valenciennesi* S. & M. Fig. 6, Skull-roof, with left cheek, showing "brachypygopterus" pattern. Banniskirk, Caithness. R.S.M. 1859.33.624 (Hugh Miller Coll.). ×3. Fig. 7, Skull-roof showing pattern intermediate between normal and "brachypygopterus" types. Sandside, Caithness. R.S.M. 1887.35 (Peach Coll.). ×3. Fig. 8, Skull-roof of very small fish showing extremely asymmetrical hinder end. Banniskirk. P.46762D (Colld. J. Saxon, 1964). ×3·5.

shape and extent of the dermal bones of the cranial roof in *Osteolepiformes* . . . are not always to be explained by various fusions, etc. ", which comes quite near to Westoll's (1944 : 114) assertion that " the compound form (of nomenclature) . . . expresses no more than geographical extent . . .", and certainly weakens the argument for too rigid adherence to the hypothesis of universal fusion without unduly encouraging those who pin their faith overmuch on the apparently contradictory idea of "loss and invasion "—" *aut Caesar aut nihil* " may be a good political precept but it is usually a poor biological principle—indeed, Truth in Nature has a habit of falling between two schools of thought.

In spite of what has been said by their proponents concerning the advantages of either philosophy for establishing the identity or homologies of bones or their supposed components in Dipnoi, it is in practice often very difficult to identify bones by any system satisfactorily, and important mistakes and many doubtful identifications have been made on both sides. Not the smallest source of error has been due to attempts to establish the course of the canals by the openings of the tubuli on the surface of the bones; and this in the nature of things is often inevitable, since it is not always desirable or possible to dissect out the canals.



FIGS. 9, 10. Diagrams of skull-roof of *Dipterus*. Fig. 9, Diagram showing Romer's (1936 : 243, text-fig. 1c) alphabetical notation. Fig. 10, Pander's diagram of the skull-roof (1858 : 55, pl. 3, fig. 1).

Forster-Cooper's alphabetical notation (*FCAN*)

Forster-Cooper's (1937 : 228, text-fig. 3) alphabetical notation (FCAN) was based on a very simple plan, but unfortunately he never developed it fully, and sometimes used it incorrectly (*e.g.* pl. 7, figs. 13, 14).

It should be noted that this scheme was quite arbitrary and not based on the sensory canals and pit-lines : indeed, it is quite plain that Forster-Cooper had no clear idea of their true course. In almost every specimen that he figured and labelled he relied on the external openings of the tubuli of the sensory canals to determine their position, and sometimes mistook damaged tubercles of the ornament and *post mortem* cracks for pores and pit-lines (1937 : 233, pl. 5, fig. 9, text-fig. 5).

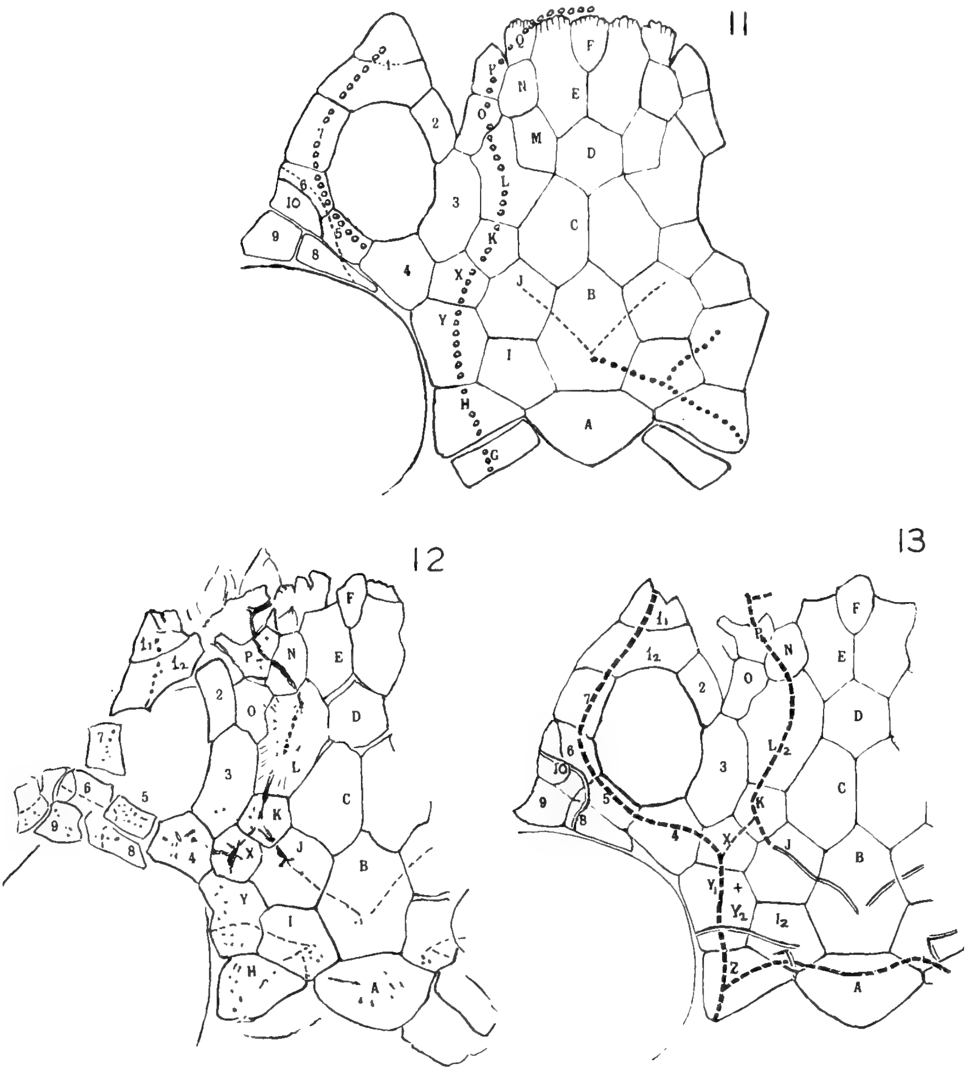
His description of the lateral lines is indeed most puzzling : " The course of the main lateral line from the body on to the head appears to run across the supracleithrum to the bone H. It then runs to I, where it branches, one branch going through Y, the other to B, where it meets its fellow of the opposite side. This junction is more noticeable in the *platycephalus* condition than in that of *valenciennesi*. Just in front of this point there is a V-shaped pit line pointing forwards whose arms run through the paired J bones from each side ".

In the next paragraph he stated that " The pores marking the underlying sense-organ canals always occur on the same series of bones in a line running from G through H, Y, X, K, L, O, P, Q, and then round the front of the snout at the anterior edges of E and F ".

Not only are these two statements contradictory, but both are wrong. For convenience they have been translated on to Forster-Cooper's original diagram (Text-fig. 11), the first statement shown by solid dots on the right side, the second by hollow dots on the left. Neither is supported by any of his own touched-up photographic illustrations, including that of his standard specimen (Forster-Cooper 1937 : 228, pl. 4, fig. 7, text-fig. 3) on which his diagram was based.

Apparently these statements were based on Goodrich's (1925 : 83, text-figs. 1, 3, 4) descriptions and figures, which do place the occipital commissure across Goodrich's " tabular " (H), " Post-parietal " (I) and " dermal supraoccipital " (B) just behind the anterior pit-lines, with some indication in *Dipterus* of a forward branch in the " post-parietal ", while the " supra-temporal " and " supraorbital " canals run in a continuous sinuous curve very much as Forster-Cooper describes. It may be noted that the much earlier diagram of that very acute observer C. M. Pander (1858 : 55, pl. 3, fig. 1), is a perfectly accurate representation of the skull-roof of *Dipterus* and its sensory canals (Text-fig. 10).

The general course of the canals and pit-lines is now well known, thanks to the work of Graham-Smith & Westoll (1937 : 244, text-fig. 2*a*), Westoll (1949 : 126, text-figs. 2, 3 etc.) and Parrington (1950 : 536, text-fig. 1). In the first paper Graham-Smith & Westoll partly rationalized Forster-Cooper's notation, using a rather better preserved head, P.22189 from Achanarras, as the standard specimen ; plate G, which in Forster-Cooper's specimen (see Text-figs. 11, 12, 21) was a body-scale unconnected with the lateral line, was dropped; Y was allotted to two plates, and so was L on the right side as the normal pattern, the single plate on the left being considered the result of fusion. For no apparent reason Q was substituted for P. However, Westoll's remarks (1949 : 130–134) that " All these latero-sensory canal bones are



FIGS. 11–13. *Dipterus valenciennesi* S. & M. Fig. 11, Forster-Cooper's "Generalized diagram" (1937 : 228, text-fig. 3) with the sensory canals and pits added from his description (p. 233), the solid dots on the right side show "the course of the main lateral line"; the rings on the left, the occurrence of the "pores marking the underlying sense-organ canals." Fig. 12, Sketch of the specimen on which Fig. 11 was based showing the distribution of the pores of the sensory canals (and of the canals themselves on the partly dissected plates X, J, K, L, N, P) and of the pit-lines. Achanarras, Caithness. P.22187. ×2·3. Fig. 13, Corrected diagram of the same specimen with emended lettering.

extremely constant in their development, with the exception . . . that adjacent members 'fuse' ", and " There is never any difficulty in deciding where 'fusion' has occurred at least in the skull-roof " seems to the present writer to be very optimistic. Indeed Westoll's figures (1949, text-figs. 2, 3 etc.), like the earlier figures of Stensiö, are diagrammatic sketches, and the supposed source of the sensory canals was similarly based on the external pores.

Lack of more precise information doubtless accounts for Westoll's (1949 : 136) remark that " these canals show no abnormalities in the specimens studied ".

Dissections have been carried out in a number of specimens, including both Forster-Cooper's and Graham Smith & Westoll's standard specimens with interesting results.

In Forster-Cooper's specimen (*P.* 22187) part of the left side of the head has been prepared (Text-fig. 12) and the pattern is shown in diagrammatic form (Text-fig. 13). In the latter it will be noted that there is some alteration of the original lettering. G, which has already been noted as a scale, is omitted ; H, since it belongs to the main sensory canal series with Y and X, is changed to Z. But of much more significance is the absence of L_1 and M and the labelling of Y as $Y_1 + Y_2$.[1] Here we are brought up against the main problem of fusion and/or replacement.

Westoll (1949 : 126, 128) although keenly critical of the fusionist tendencies of Stensiö and his school in relation to large bones, nevertheless stated that " Ontogenetical studies on living bony fishes such as *Amia* show that true fusion of adjacent bone rudiments developed along a latero-sensory canal is a normal feature of the development of large bones. It is here accepted that fusion of this type occurs in *Dipterus* " and gives (1949 : 132) some 45 instances where fusion of lateral-line elements are supposed to have occurred.

Positive detection of such fusion in more or less adult fossil skulls would presumably depend on how rudimentary the bone-rudiments were at the time of fusion : complete fusion of the earliest stages would not probably be traceable, and whether it took place or not must depend on other indirect evidence, if any.

Parrington (1950 : 545), in the second of his three important and refreshingly sane papers relating to the development of skull-bones, comments upon these supposed fusions along the lateral line series and suggests that " fusion is a result of dermal bones meeting at a time when their growth-rates exceed that of the surrounding tissues by a certain amount. The earlier appearance of neuromast rudiments would increase their chances of growing to contact other neuromast rudiments and this would increase at least the possibility of fusion ". Parrington goes on to quote the possible correlation between the increasing tendency of lateral-line elements to " fuse" with decrease in length of skull, but notes the outstanding exception, in reverse, of the long headed *Fleurantia*, where " fusion " is still marked. Later he emphasized the possibility of "almost complete capture of vacated territory " (1956) 406).

In the author's opinion Parrington's most important contributions to the questions concerning the growth and form of bones and their relationships to the sensory canals are these (Parrington 1949 : 69, 76 ; 1956 : 405, 408 etc.), which may be called " Parrington's axioms ".

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[1] Y_1 and Y_2 are reversed from Westoll's notation so as to be in logical sequence, and I is labelled I_2 for reasons stated on p. 26.

1. " . . . it is unwise to assume bone fusions without the evidence of multiple centres of radiation of either the ornament or the bone structure ".

2. " . . . precursors of the dermal bones attract the growing primordia of the lateral line system and that changes in the number and positions of the dermal bones can therefore cause changes in the relations of the lateral line canals ".

Examination of the partly dissected heads here figured does seem to show that if these two principles are accepted a reasonable interpretation can be made of the bones and canals, and further for this purpose Forster-Cooper's alphabetical system of identification of the bones, as now modified, is infinitely preferable to attempts to name the bones, especially as it will be shown that the fusions postulated are only too frequently not substantiated.

The Sensory Canals and Pit-lines

Before proceeding with the question of invasion or fusion of the dermal roof-bones it is necessary to confirm the course of the sensory canals of the pit-lines.

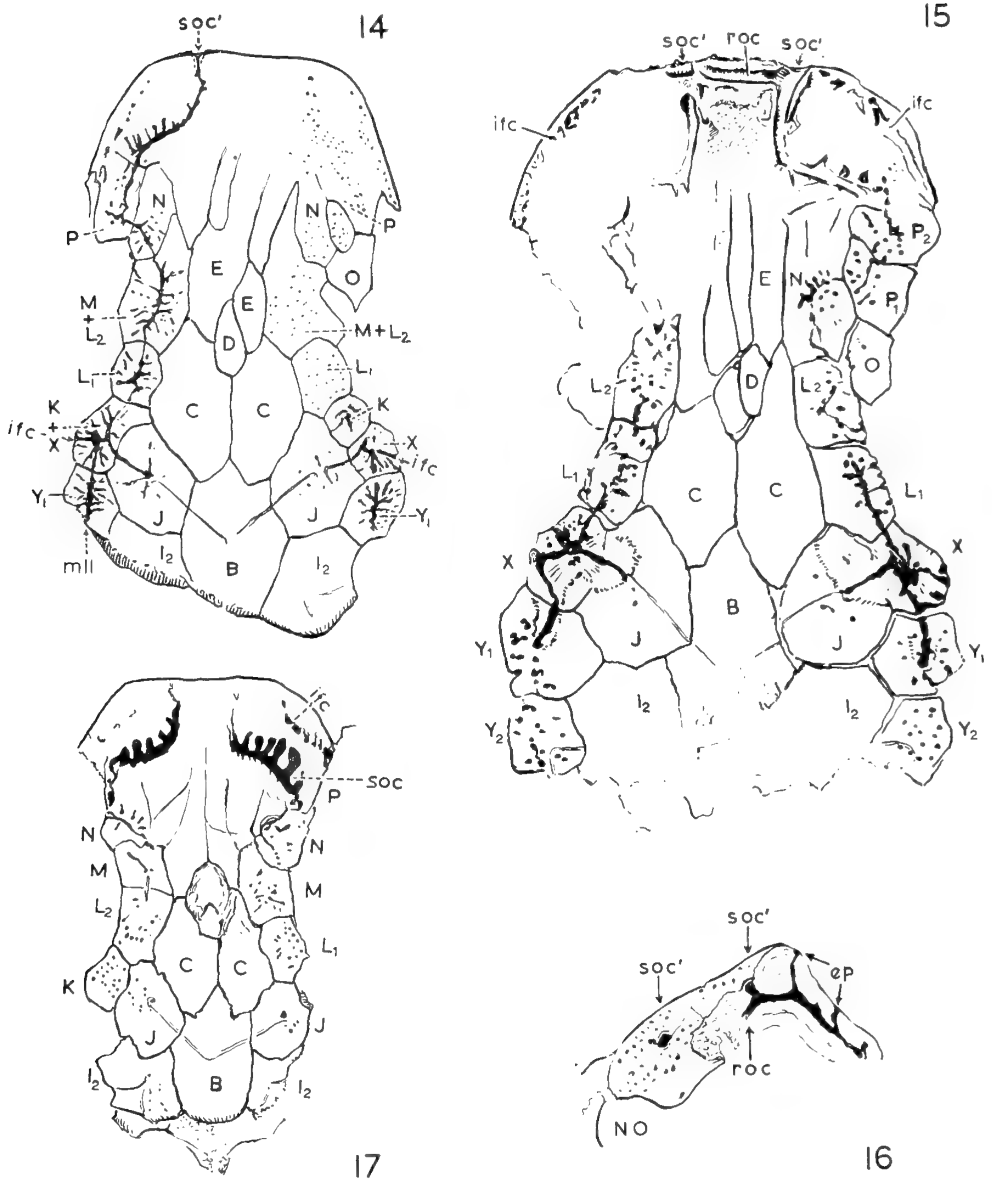
The pit-lines do vary, especially the middle and posterior lines in old specimens, but it is a variation in detail and seldom approaches the more aberrant patterns shown by Forster-Cooper's (1937 : 233, text-fig. 5). The anterior line runs forwards diagonally from B to J, and the two sides may meet in the middle or have small loops.

The middle line runs transversely from I_2 into Y_2 and the posterior backwards from I_2 to Z. They may be in contact in I_2 and have terminal twists and curls, rarely partial duplication. A well marked additional line is shown in Text-fig. 42 (P.17410).

The general distribution of the sensory canals, as already noted, is well known, but not in any detail, especially in the snout region. The course of the supraorbital with many of the canaliculi is shown in no. 33165 (Text-fig. 14), in which the canal of the left side has been fully developed.

The supraorbital canal runs normally from the end of the anterior pit-line in J to K, and so forwards through the usual series labelled L_1, L_2 and M to N where it turns outwards to P. This plate is often incompletely separated in front from the snout. Thence the canal continues forwards, curving inwards and then again forwards and so downwards to the opening on the upper lip. This opening is so large in some specimens of *Rhinodipterus* (see White 1962 : 4, pl. 2, text-fig. 3) that Gross (1956 : 23, pl. 5, fig. 5, text-fig. 14*C*) identified it as the anterior nasal opening, and Ørvig (1961 : 15, pl. 3, fig. 3, text-figs. 8*B*, *C*,9*C–E*) as " probably openings for glands of some sort ".

The canals of the extreme rostral region are still better demonstrated in Text-fig. 15 (P.6087), in which the rostral commissure has been naturally weathered out, in P.34547 and in a broken section in 33166 (Text-fig. 16). In another weathered but much flattened snout (P.34546, Text-fig. 17) the supraorbital canal, as it turns inwards in P, apparently gives off forwards six or seven pouch-like cavities instead of the usual rounded tubuli, and such " pouches " are also indicated in P.34558. This is almost certainly the effect of crushing and weathering, accentuated by resorption of the bone in the immediate neighbourhood of the tubuli. An intermediate stage is shown in Text-fig. 19 (P.46690), which also shows the presence of smaller openings on the hinder side of the canal.



FIGS. 14–17. *Dipterus valenciennesi* S. & M. Fig. 14, Skull-roof in which the sensory canals have been wholly dissected out on the left side, partly on the right. Thurso, Caithness. 33165. ×1·3. *mll*, main lateral line. For other lettering see Fig. 15. Fig. 15, Skull-roof in which the sensory canals of the snout have been naturally weathered out and some of the remainder dissected out. "Caithness". P.6087. ×2. *ifc*, infraorbital canal. *roc'*, rostral commissure. *soc'*, anterior aperture of the supraorbital canal. Fig. 16, Median part of upper lip showing both external apertures of the supraorbital canal (*soc'*), with part of rostral commissure (*roc'*) and supraorbital canal itself and branches leading to external pores (*ep*) exposed by a natural longitudinal fracture. Thurso, Caithness. 33166. ×2. Fig. 17, Skull-roof with part of canals on snout naturally weathered out. Foreshore, Clardon Haven, Caithness. P.34546. (Colld. D. L. Dineley, 1957). ×1·3. *ifc*, infraorbital canal. *soc*, supraorbital canal.

The main canal runs through Z, in which it gives off the occipital commissure, first to the hinder end of I_2 and then through A. From Z the main canal normally passes through Y_2 and Y_1, to X, in which it turns down to pass through circumorbital 4 to form the infraorbital canal, at the same time sending a short branch to K to anastomose with the supraorbital canal.

The infraorbital canal runs through the circumorbital plates 5, 6, 7, I_2, I_1 up on to the snout, crossing the antero-lateral corners, as may be seen in most hard-snouted specimens. It may finish in a pore under the snout like the supraorbital canal, but if so the pore is often very small, and not always to be distinguished easily from the others present in this region; for the whole canal under pressure tends very readily to dissolve in the system of pores and spaces which permeate the bone there.

To give a general impression of the canal-system, the details from Text-figs. 14, 15 etc. have been superimposed on the left side of the outline of a well known, more complete skull of " platycephalus " type (P.7834, Text-fig. 18) to which plates Z–A–Z have been added and, in fig. A (P.6507), the upper lip of another specimen. The skull-roof has been figured by three other authors (Jarvik 1950, text-fig. 6; Gross 1956, text-fig. 13*B*; Ørvig 1961, text-fig. 7*B*), each giving a somewhat different interpretation of the plates, and all different from that given here. The right side shows the actual distribution of the pores in this specimen.

From this general pattern there are a number of significant deviations, as there are from the standard patterns of the head-plates, and since they are interdependent, sensory canals and head-plates will be considered together, in the light of Parrington's axioms (p. 11 *supra*) and of his theory of " Patterns of dermal bones " (1956).

It is in the lateral line series, Z–X and K–P that most difficulties arise, but there are four plates and areas that have sufficiently constant features to make them readily recognizable, Z and Y_1 at the back of the skull-roof and N and P near the front.

Z, formerly H, is the hindmost plate and always roughly triangular. It receives the main-line canal from the supracleithrum and passes it on to Y_2 after the canal has been joined by the occipital commissure. Only once in the series available is it in any way abnormal.

Y_1 always occupies the same position, just overlapping the front of the operculum, and so having a characteristic projecting angulation on the outer side. On the mesial side it lies alongside the hinder part of J and a small part of I_2. Very rarely is it replaced by, or fused with, X (Text-fig. 25; Westoll 1949, text-fig. 2*B*).

N is the plate, often fused with the snout, where the supraorbital canal turns outwards at the start of the sigmoid curve in front, and P (Westoll's " Q ") is the plate or area in which the canal turns forward again.

A survey of the available material will make clear the advantage of a purely alphabetical system of bone nomenclature.

The first specimen to be considered must obviously be Forster-Cooper's standard specimen (P.22187, Text-figs. 11–13). Fig. 12 shows the actual specimen as it now is, partly dissected. It also shows the original lettering except that G and M are omitted, G because it was only a scale and M because its supposed presence was due to a crack in L.

The sensory canals are perfectly orthodox, as may be seen in the revised diagram (Text-fig. 13), but the series of lateral line bones show two interesting deviations, apart from the absence of M. A single bone occupies the space not only of M but of both the " L " bones and there is clearly only a single centre of growth, which from its central position is judged to be that of the middle bone of the three, L_2. There is

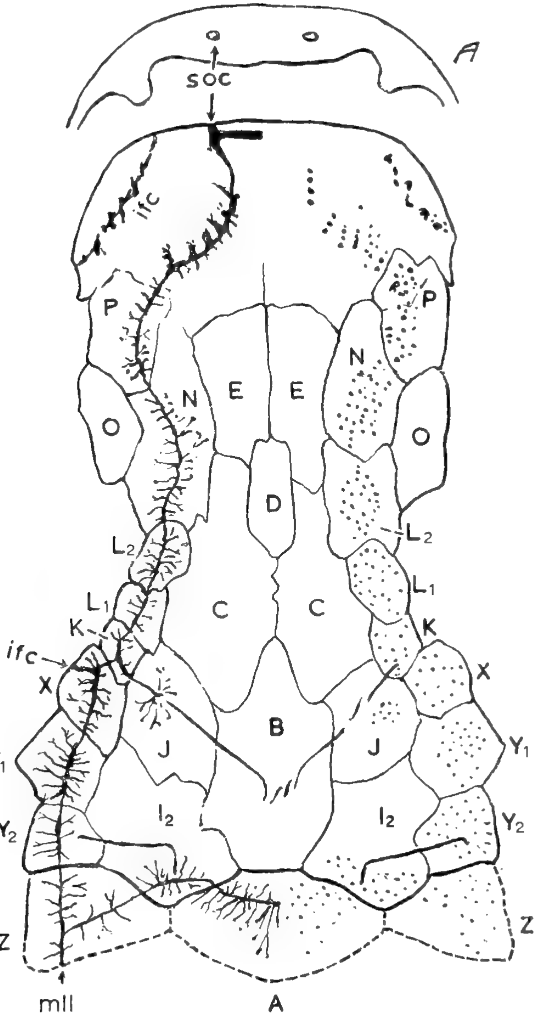


FIG. 18. *Dipterus valenciennesi* S. & M. Skull-roof of large head with plates Z–A–Z added, showing external pores of sensory canals on right side, and restoration of the canals on the left side, based on Figs. 14, 15. (*cf.* Jarvik 1950, text-fig. 6; Gross 1956, text-fig. 13B; Ørvig 1961, text-fig. 7B). Coast near Thurso, Caithness. P.7834. ×1·5. A, underside of snout of similar specimen. Toldale Quarry, between Thurso and Reay, Caithness. P.6507. ×1·5. *ifc*, infraorbital canal. *mll*, main lateral line. *soc*, supraorbital canal and aperture.

also only a single Y bone, but this is judged to be compound, $Y_1 + Y_2$, by reason of its shape and the distribution of the pores which seem to indicate two centres.

In 33165 (Text-fig. 14) the two sides make a most interesting contrast. On the wholly dissected left side a large single bone in the M–L_2 area does seem to have had two centres and is accordingly labelled as a compound bone, and the large odd-shaped bone between L_1 and Y_1, is almost certainly a compound K + X. On the partly dissected right side the L_1 to M region is similar to the left, but the K and X area is very different, for K is not only small but is excluded from contact with C by an extension of L_1 and has lost to X the beginning of the supraorbital canal where it passes out of J. This is most unusual, but the result can be simply explained à la Parrington, by delay in the development of K's rudiment, which has allowed the capture of the beginning of the supraorbital canal by X and the invasion of this territory on the other side by L_1.

P.6087 (Text-fig. 15) shows the suppression of M on both sides, in favour of N on the right, and probably of L_2 on the left.

On both sides the important K–X region is occupied by a single, not very large bone, with a single growth centre but containing both the turn-down of the main canal at the beginning of the infraorbital canal, typical of X, and the continuation of the supraorbital canal from J, typical of K. It is not clear which has been suppressed, but it is probably K, for L_1 on both sides is much larger than usual and extends further backwards into the K area to meet J, as it also does on the right side in the previous figure.

In a short-headed specimen (P.34546, Text-fig. 17) two bones only occupy the M–L position, each with a single centre and those of the left side are only superficially separated. It is probable from their forward position that the anterior bone on each side represents M, but that the hinder bone on the left side, judging by the position of the growth-centre, seems to be L_2, whereas on the right L_1 is the more probable survivor, particularly as M is unusually large, as if it had partly replaced L_2.

The fine narrow head from near Thurso (P.7834, Text-fig. 18, p. 13 *supra*) is undissected, the sensory canals on the left side being diagrammatic. It is one of the longest heads examined, 6·9 cm. from the hinder margin of B to the tip of the snout, being only two millimetres or so shorter than the Toldale head (P.6507, Forster-Cooper 1937, pl. 7, fig. 14) and a specimen from Edinburgh (1859.33.622), but 8 mm. less than the record head in that Museum (1901.153.2) which measures 7·7 cm. The head in Text-fig. 18 shows quite markedly contradictory tendencies, a tendency to the decrease in size of plates in the middle lateral regions (K, L_1, L_2) especially on the left side ; but in front there is a very obvious increase in size through the suppression of M, to the advantage of N only on the left side, but also for the benefit of L_2 on the right. A marked difference in development of the sensory canal plates of the two sides is illustrated by a Clardon Haven specimen (P.46690, Text-fig. 19).

Of considerable interest in showing the relationship between the distribution of pores and the actual course of the canals is the specimen (P.22189) on which Westoll (Graham-Smith & Westoll 1937 : 244, text-fig. *2a* ; Westoll 1943 : 89, text-fig. *7c* ; 1949 : 126, text-fig. 1) based his modified scheme of lettering.

In the original somewhat diagrammatic and restored drawings X and K are shown as a compound plate. The supraorbital canal entered this plate from J on its posterior-inner side, and almost opposite this the main canal is supposed to have come in from the anterior Y plate and then turn down into circumorbital " 4 " to form the infraorbital canal. In fact dissection (Text-fig. 20) shows that the main canal never reaches the " X and K " bone but turns down in Y_1 (Y_2 of Westoll), and that the connection between the main and supraorbital canals is not only drawn out but apparently double. Examination of the structure of this supposedly compound plate shows clearly enough that it had a single growth-centre ; X has failed to

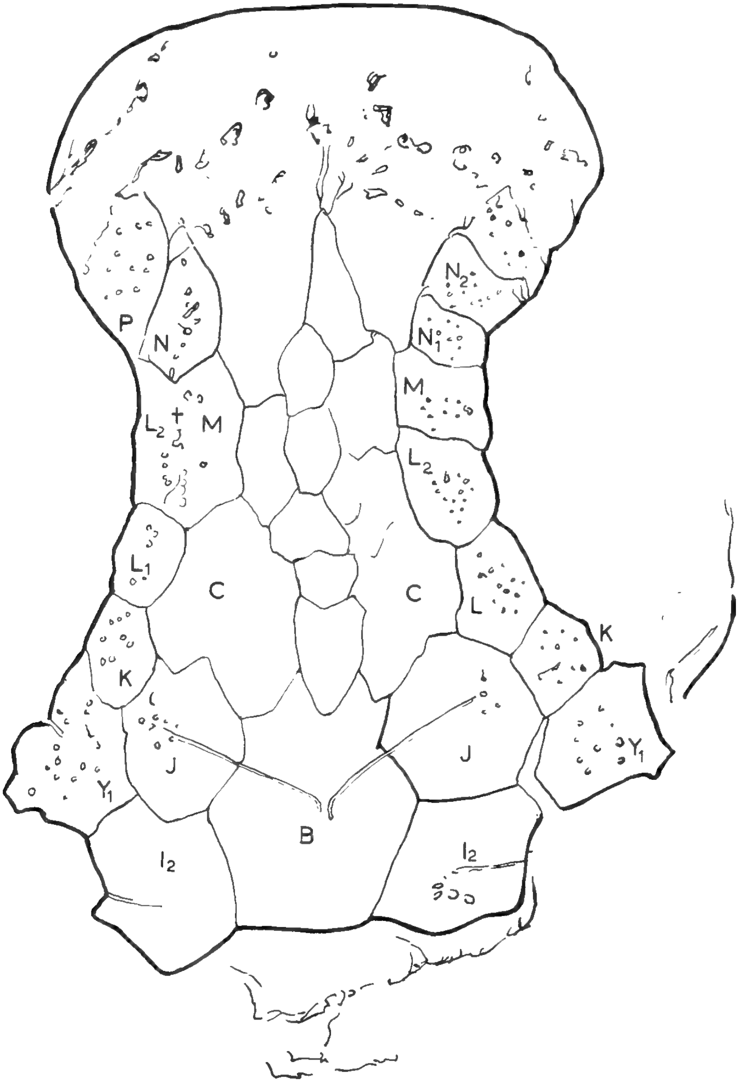


FIG. 19. *Dipterus valenciennesi* S. & M. Skull-roof showing asymmetrical development of lateral line plates. Clardon Haven, Caithness. P.46690 (Colld. R. V. Collier, 1964). × 2·25.

develop and its space has been largely taken by K, but the lateral line has been largely captured by Y_1. The L plate is also shown as a compound $L_1 + L_2$, but this has a single centre and seems to be composed of L_1 only which has taken over the territory of a missing L_2.

The pores in the very small head illustrated in Text-fig. 41 (P.22194) seem to indicate a similar situation in regard to the XK area, and here also the area of M has apparently been taken over by L_2.

The capture of the infraorbital curve by Y_1, is even more clearly demonstrated in Text-fig. 21 in a very abnormal short-headed fossil from Achanarras (P.17642, *cf.*

FIG. 20. *Dipterus valenciennesi* S. & M. Left side of skull-roof and cheek of original of Westoll's standard specimen (see Graham-Smith & Westoll 1937 : 244, text-fig. 2*a* ; Westoll 1949 : 126, text-figs. 1A, C) with sensory canals partly dissected out and plates partly re-lettered. Achanarras, Caithness. P.22189. ×3·5.

Forster-Cooper 1937, pl. 5, fig. 9). Plate X apparently did not develop, to judge from single-centred K, but there seems to have been some opposition by K to the annexation of the main canal by Y_1, judging by its subdivision. This fragmentation of canals owing to disturbance by fusion or elimination of plates is probably not unusual (Text-figs. 22–24). In 42403 (Text-fig. 22), a much resorbed specimen from near Wick, K and X do seem to have fused to show what appear to be double centres of growth, but nevertheless the start of the infraorbital canal has gone to Y_1.

In Text-fig. 21 another most interesting abnormality is illustrated. The supra-occipital commissure shows much disturbance owing to the non-appearance of Y_2, but instead of its space being occupied by Y_1, that bone is of the average size, and Z has grown forwards taking with it the outer end of the commissure, which crosses I_2 much further forward than usual. In contrast, the occipital cross-commissure in two other fishes from Achanarras (P.17641, P.17643, Text-figs. 23, 24), instead of its usual path Z–I_2–A–I_2–Z, misses I_2 altogether, although these plates seem normally developed.

In P.17641 (Text-fig. 23) K and X seem undoubtedly to have fused on the left side, but on the right K has been eliminated to the advantage of L_1, which is rather unusual (but see P.6087, Text-fig. 15). Generally K is a better " stayer " than X, and it is worth noting that its division from J is often only superficial, the basal layers being completely fused (cf. Text-figs. 15, 22 etc.). On both sides the start of the infra-orbital canal has been largely captured by Y_1 and only a small subdivision of it is retained by X.

There is some doubt whether the missing plate on the right side is K or X, but the arrangement is partly paralleled in Text-fig. 15 where there was similar expansion of L_1 into the K area and disarrangement of the canals. L_1 and L_2 in P.17643 (Text-fig. 24) show a very obvious case of imperfect fusion.

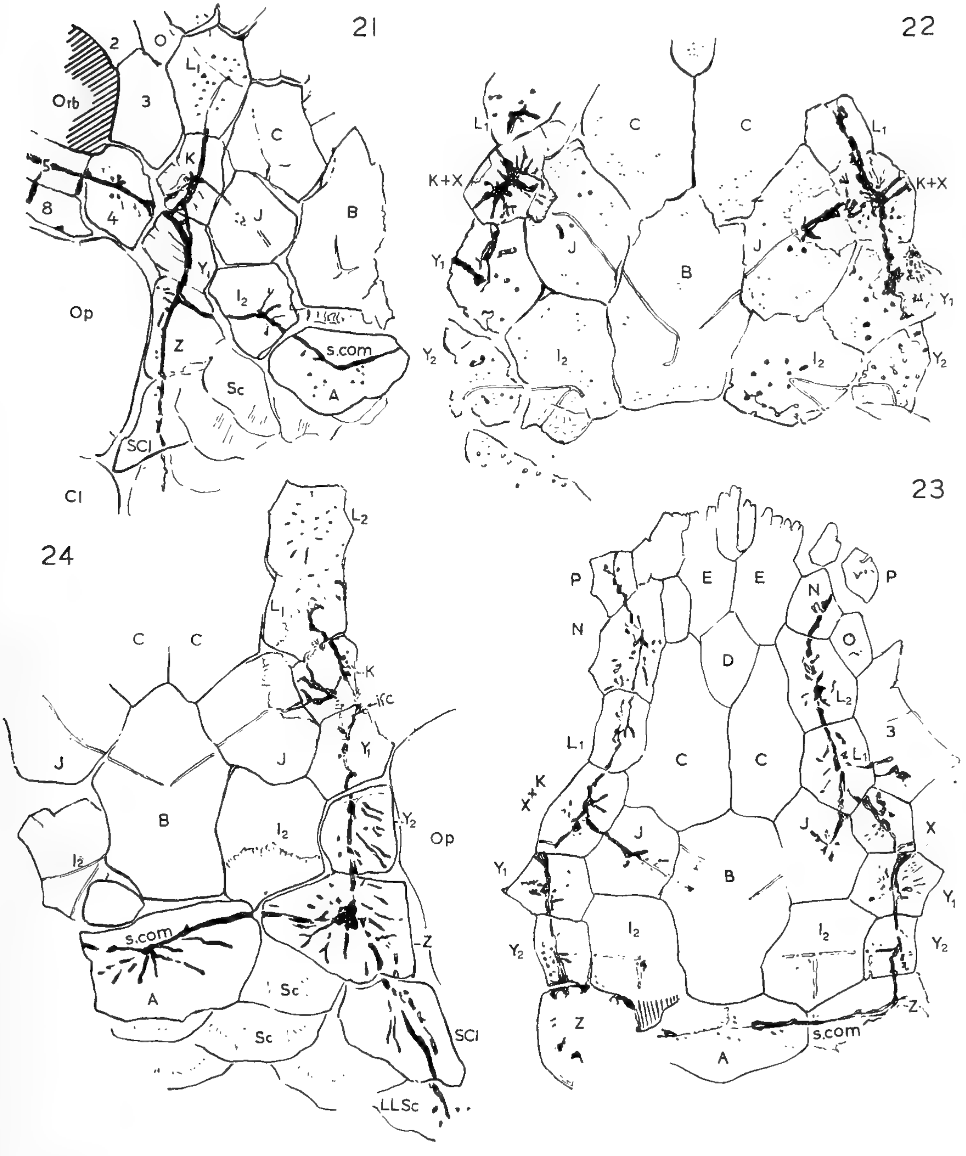
Of the two " brachypygopterus " types from Banniskirk illustrated (42480, R.S.M. 1859.33.624, Text-figs. 5, 6), the first shows a fairly obvious X and K fusion and the L_1–L_2, M and possibly N area is occupied by a single plate. The second shows a large N and on the left side only one small plate (labelled L_1) between N and K, also a large Y_1 and no Y_2. The naturally exposed sensory canals are standard as far as they may be traced.

Attempts to Identify the Head-plates

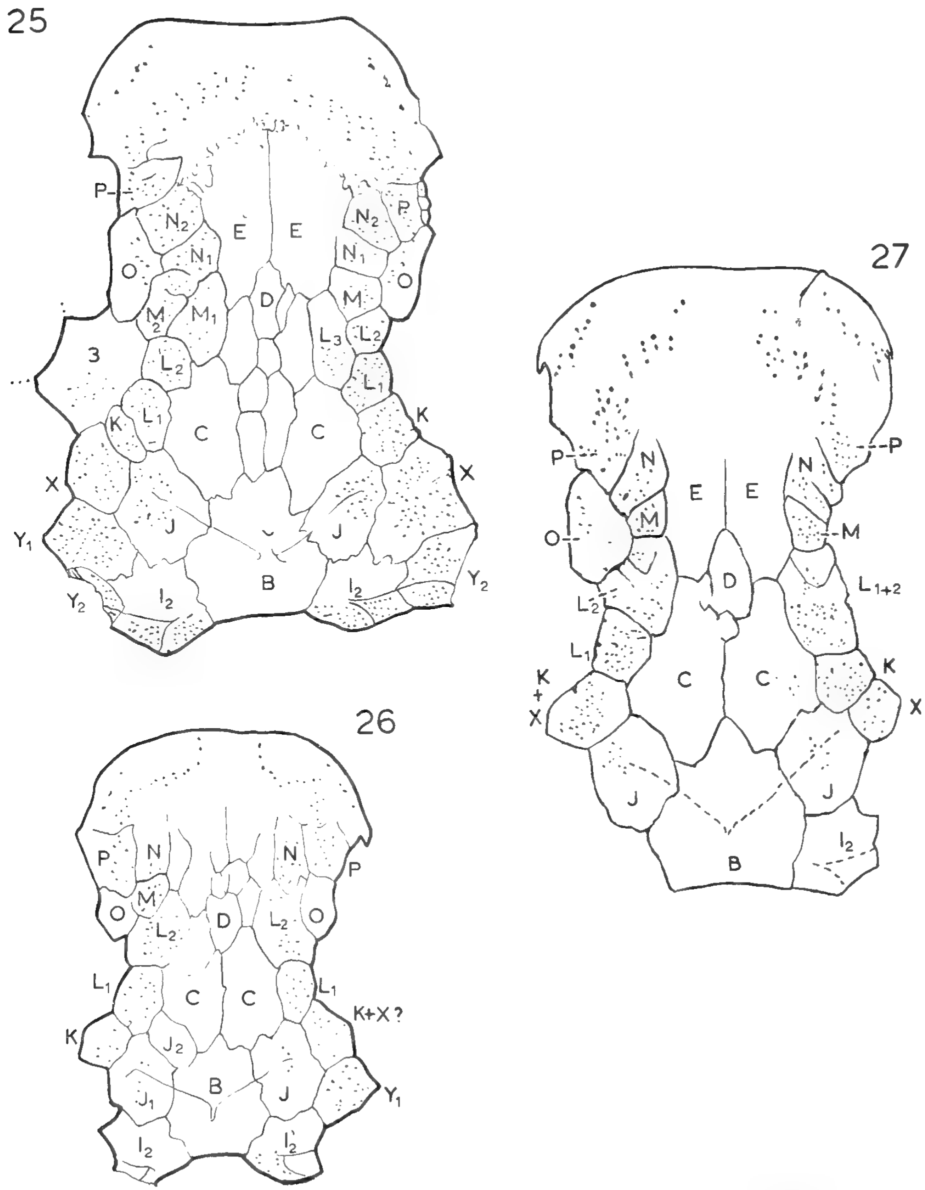
The difficulty of tracing the canals by the pores led Stensiö (*in* Holmgren & Stensiö 1936 : 366, text-fig. 280*A–C*) to misplace the connection between the supraorbital canal and the main canal in the three rather difficult Edinburgh skulls on which he based his nomenclature (Text-figs. 25–27).

Stensiö's choice of a key-specimen (R.S.M. 1878.5.164) on which to base his identifications was not altogether fortunate, for it suffers very much from multiplication of plates in the central area and in the front lateral line series. His figure (Text-fig. 28), was formalized and partly restored, cf. Text-figs. 25, 29.

Neither of Stensiö's supraorbital bones (SO_1, SO_2) belongs to the circumorbital series, but his " dermosphenotic + postorbital " (*Dsph* + *Po*) does, and the orbit is farther out and certainly smaller. This bone is not compound but is the circum-orbital 3 of Forster-Cooper's notation. In the original specimen it is preserved only



FIGS. 21–24. *Dipterus valenciennesi* S. & M. Fig. 21, Left posterior part of skull-roof and cheek with sensory canals dissected out (cf. Forster-Cooper 1937, pl. 5, fig. 9). Achanarras, Caithness. P.17642. ×<4. *Cl*, cleithrum. *Op*, operculum. *Orb*, orbit. *Sc*, scale (Forster-Cooper's " G "). *SCl*, supracleithrum. *s.com*, occipital cross-commissure. Fig. 22, Posterior half of much resorbed skull-roof with sensory canals partly dissected out to show probable fusion of plates K and X on each side. Killimster, near Wick, Caithness. 42403. ×4. Fig. 23, Skull-roof with sensory canals dissected out (cf. Forster-Cooper 1937, pl. 6, fig. 11; Westoll 1949, text-fig. 2E). Achanarras, Caithness. P.17641. ×2·5. *s.com*, occipital cross-commissure. Fig. 24, Right posterior part of skull-roof with sensory canals dissected out (cf. Forster-Cooper 1937, pl. 4, fig. 8). Achanarras, Caithness. P.17643. ×2. *ifc*, infraorbital canal. *LLSc*, lateral line scale. *Sc*, body scale. *SCl*, supracleithrum. *s.com*, occipital cross-commissure.



FIGS. 25–27. *Dipterus valenciennesi* S. & M. Camera lucida drawings of originals of skull-roofs of "platycephalus" type, sketched by Stensiö (*in* Holmgren & Stensiö 1936 : 366, text-figs. 280A–C). Fig. 25, Large head (6·1 cm. long) with median mosaic and unusually numerous plates (6) between K and P. Locality unknown. R.S.M. 1878.5.164. ×1·3. Fig. 26, Medium sized head (4–6 cm. long) with anterior mosaic and only three plates between K and P on right side. Firth, Orkney. R.S.M. 1898.163.6. ×1·3. Fig. 27, Large head (6·3 cm. long) showing tendency to subdivision of plates between K and P. Locality unknown. R.S.M. 1859.33.32. ×1·3.

on the left side and carries an unusually large branch of the supraorbital canal, for as a rule the pores are few, often absent. This skull-roof, in spite of its oddities, is reasonably reduced to order under Parringtonian influence with Forster-Cooper's amended lettering (Text-fig. 25). The only point of real importance is that Y_1, normal on the left side, has most exceptionally not developed at all on the right side, where its place has been covered very largely by a much expanded X, and only to a small degree by the advance of Y_2.

Both of Stensiö's other two specimens show peculiar features. The small broad head (R.S.M. 1898.163.6, Text-fig. 26) shows division of J on the left, and no M and a possible fusion of K and X on the right; the larger head (R.S.M. 1859.33.32, Text-fig. 27) shows fusion of K and X on the left side, fusion of L_1 and L_2 and imperfect subdivision of N on the right.

Lehman (1959) in his work on the Upper Devonian Dipnoans from Greenland followed Stensiö in endeavouring to name the plates of the skull-roof, although by no means agreeing on the terms to be used, nor for that matter on the homologies when he did.

Comparison of Text-figs. 28–30 well illustrates the confusion that can be caused by efforts to identify these head-plates with the bones of other fishes.

Stensiö's supposedly compound " dermosphenotic and postorbital " (*Dsph* + *Po*, Text-fig. 28) is not the homologue even in part of Lehman's " Dermosphénotique " (*Dsph*, Text-fig. 30), as a glance at Text-fig. 29 will show, for Stensiö's plate is a simple circumorbital, no. 3 of Forster-Cooper. Lehman's " Dermosphénotique " is a single-centred plate (Lehman 1959, pls. 1–14, 16) and represents the survivor of K or X, probably K, which has taken over the other's territory and acquired all the canals (cf. Text-figs. 19, 20, 24). It is therefore strictly homologous with the most posterior member of Stensiö's " laterale Frontalserie " (*Fr. l*, Text-fig. 28) of which Lehman's " Nasaux " are the front members.

Again, Stensiö's supposedly compound " Supratemporo-Intertemporale " (It + St, Text-fig. 28) is also a simple bone, the X of Text-figs. 25, 29, which has invaded Y_1's territory, and Y_1, the equivalent of Lehman's " Dermoptérotique antérieur " (*Dpt.* 1) has most exceptionally not developed at all. But Lehman's " Dermoptérotique postérieur" (*Dpt.* 2) is the Y_2 of Text-fig. 29, and thus the homologue of Stensiö's " laterale freie Extraskapularplatte " (*Ext.* l_2, Text-fig. 28). This last plate, which is laterally imperfect in the original (Text-fig. 25) does not show any part of the supratemporal cross-commissure as indicated by Stensiö (Text-fig. 28); it would have been present on the plate behind (Z), which is missing.

Stensiö's " hintere laterale Parietalplatte + einer lateralen Extraskapularplatte " (*Pa.* l_2 + *Ext.* l_1, Text-fig. 28) which is identical with Lehman's " pariétolatero-extrascapulaire " (*PalExSc*, Text-fig. 30; Lehman, 1959 : 18, pls. 1–21, text-figs. 2, 4, 5, 7–13, 21–23, 26), presents a very different problem, and indeed provides the key to the homologies of the plates of the earlier Dipnoi. These paired plates are the I_2 of Text-fig. 29 and show in the available material of *Dipterus* and Lehman's illustrations a single growth centre; nevertheless the suggestion that there is an extrascapular element is supported by Westoll (1947 : 134, text-fig. 3*I*) who states that " it is likely that at least bone I also arose from more than one rudiment since a few specimens show ossicles enclosing the appropriate section of the canal ". And

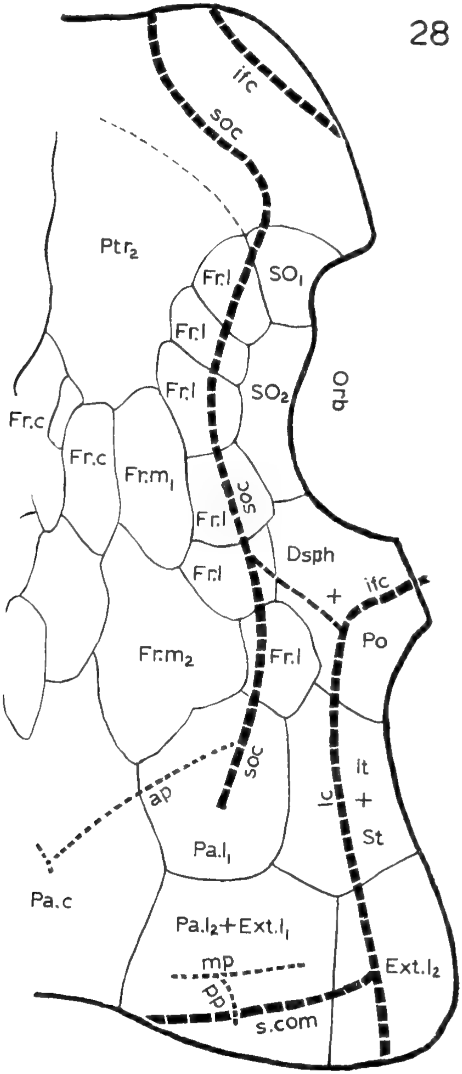
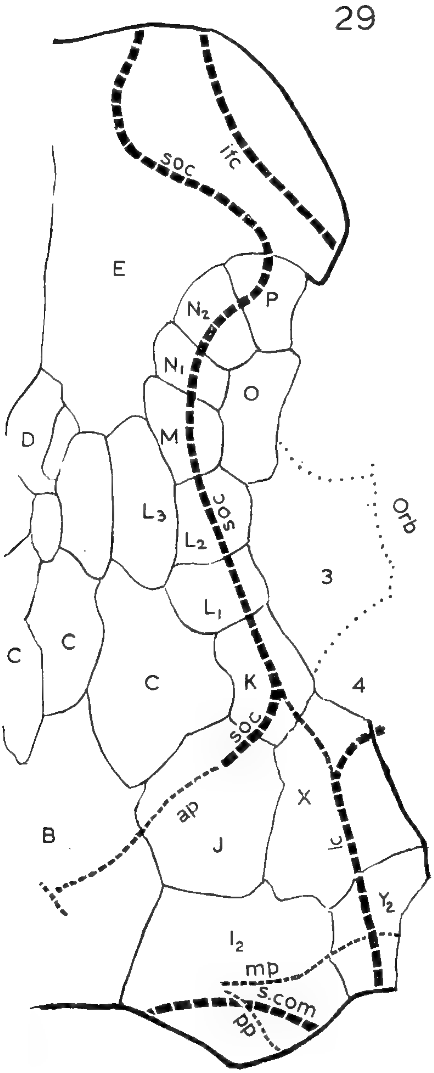


FIG. 28. *Dipterus valenciennesi* S. & M. Right side of Stensiö's diagram, text-fig. 280A (see Fig. 25), with original lettering.

Dsph + *Po*, Dermosphenotiko-Postorbitale ; *Ext.* l_2, laterale freie Extraskapularplatte ; *Fr.c*, zentrale Frontalserie ; *Fr.l*, laterale Frontalserie ; *Fr.*m_1, *Fr.*m_2, Platten der medialen Frontalserie ; *It*, Intertemporale ; *It* + *St*, Supratemporo-Intertemporale ; *Pa.c*, zentrales Parietale ; *Pa.*l_1, vordere Platte der lateralen Parietalserie ; *Pa.*l_2 + *Ext.*l_1, laterale Parietalplatte + einer lateralen Extraskapularplatte ; *Ptr*$_2$, hintere Postrostralia ; SO_1, SO_2, Platten der Supraorbitalserie (S.O. (=3) is omitted in Fig. 30) ; *ap*, vordere " Pitlinie " ; *ifc*, Infraorbitalkanal ; *mp*, mittlere " Pitlinie " ; *pp*, hintere " Pitlinie " ; *s.com*, Supratemporalkommissur ; *soc*, Supraorbitalkanal.



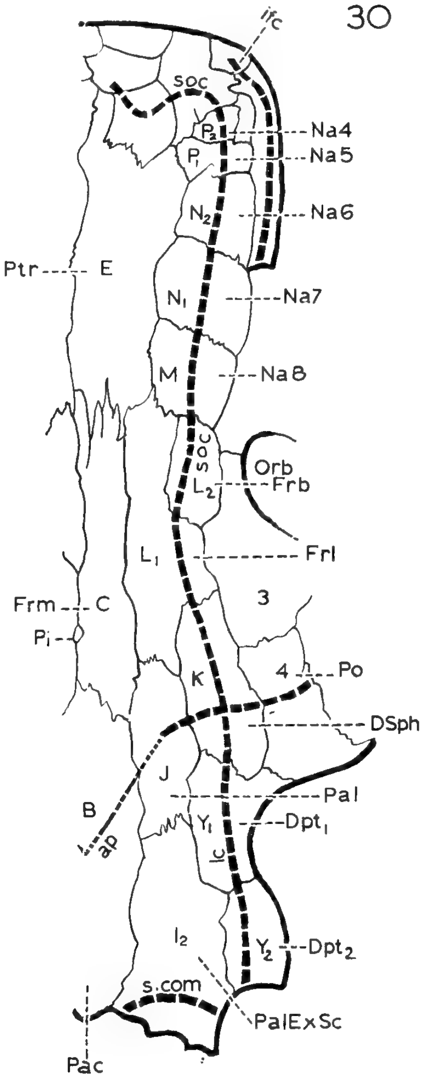


FIG. 29. *Dipterus valenciennesi* S. & M. Right side of same diagram (Fig. 28) partly redrawn from original specimen (cf. Fig. 25), with new interpretation of sensory canals and plates re-lettered according to modified FCAN. Other lettering as in Fig. 28.

FIG. 30. *Soederberghia groenlandica* Lehman. Right side of diagram of skull-roof by Lehman (1959, text-fig. 2) showing original lettering (with broken indication lines) and also modified FCAN.

Dpt_1, dermoptérotique antérieur; *Dpt_2*, dermoptérotique postérieur; *DSph*, dermosphénotique; *Frb*, composant antérieur distinct du frontal latéral; *Frl*, frontal latéral; *Frm*, frontal médian; *Na_1*–Na_8, nasaux; *Orb*, orbite; *Pac*, pariétal central; *Pal*, pariétal latéral; *PalExSc*, pariéto-latéroextrascapulaire; *Pi*, plaque pinéale; *Po*, postorbitaux; *Ptr*, postrostral; *So*, supraorbital. Sensory canals as in Fig. 28.

indeed the Belgian specimen of *Rhinodipterus secans* (White 1962 : 3, pl. 1, text-fig. 1) shows a similar " extra " plate enclosing the canal. Subdivision or proliferation of lateral line and general plates is not necessarily significant except that perhaps it points to the ancestral mosaic, and is of common occurrence in *Dipterus*, as the front of Stensiö's specimen shows. But in this instance it throws light on the presence of part of the commissure on I_2 which is anomalous, for it is clearly out of line. This points to the former presence of a plate on each side between A and Z, now lost, and that the section of the cross-commissure belonging to it has been captured by I_2, that is, usually, for as noted above (p. 18, Text-figs. 23, 24) the commissure does sometimes go straight across through Z–A–Z, as it must have done when there were five plates in the " extrascapular " series, even as Säve-Söderbergh (1932 : 98, text-figs. 18, 20) postulated for his " common ancestor " of the ichthyostegids and crossopterygians ; but it was not the bone I_2 (Säve-Söderbergh's and Stensiö's $Pa.l_2 + Ext.l_1$) that belonged to that row and originally bore the commissure, but a plate behind it, represented rarely by the little plate I_1, noted by Westoll, and seen also in *Rhinodipterus*.

The above correlations may be summarized as follows :

Stensiö 1936 (Text-fig. 28)	Forster-Cooper 1937 emend. (Text-fig. 29)	Lehman 1959 (Text-fig. 30)
Dsph + Po	(CO) 3	*SO* (omitted)
(*Posterior*) *Fr. l*	K	*DSph*
It + St	X	absent
absent	absent (Y_1)	Dpt_1
$Ext.\ l_2$	Y_2	Dpt_2
$Pa.l_2 + Ext.\ l_1$	I_2	*PalExSc*

To trace back the homologues of the skull-plates of *Dipterus* in the earlier genera of dipnoans, the two species of *Dipnorhynchus* from the Lower Devonian (Siegenian)[1], presents considerable difficulties. The roof-patterns of *D. süssmilchi* and *D. lehmanni* are reasonably well known, thanks to E. S. Hills (1941, pl. 9, text-fig. 5 ; 1943, text-fig. 1*B*), Westoll (1949 : 140–143, text-fig. 5) and Lehmann & Westoll (1952, pl. 24, fig. A, text-figs. 4*A*, 5*A*).

The most obvious points about the pattern of these skull-roofs (Text-figs. 31, 34) is the presence of a pineal foramen and the separateness of the supraorbital and infraorbital sensory canals. The back row of plates, presumably the extrascapulars, were finally shown in *D. lehmanni* (Text-fig. 31) to consist of two pairs of plates identified as H(Z), the smaller outside pair, and I, the large median pair, instead of the Z–A–Z arrangement of *Dipterus*. The occipital cross-commissure, apparently not seen in either specimen is assumed to run across H(Z)–I–I–(Z)H. There is no A plate but that immediately in front, a smallish median element, is considered to be B, and in front of that again a pair of larger plates completely separate in the German species, but partly attached to one another in the Australian. Westoll (1949 : 141) has resisted the temptation to label these as the " C " pair, as at first sight would seem obvious, on the grounds of their posterior relationship to the orbits and then to bones of the X–K area. This pair is labelled B_2 and along side the B

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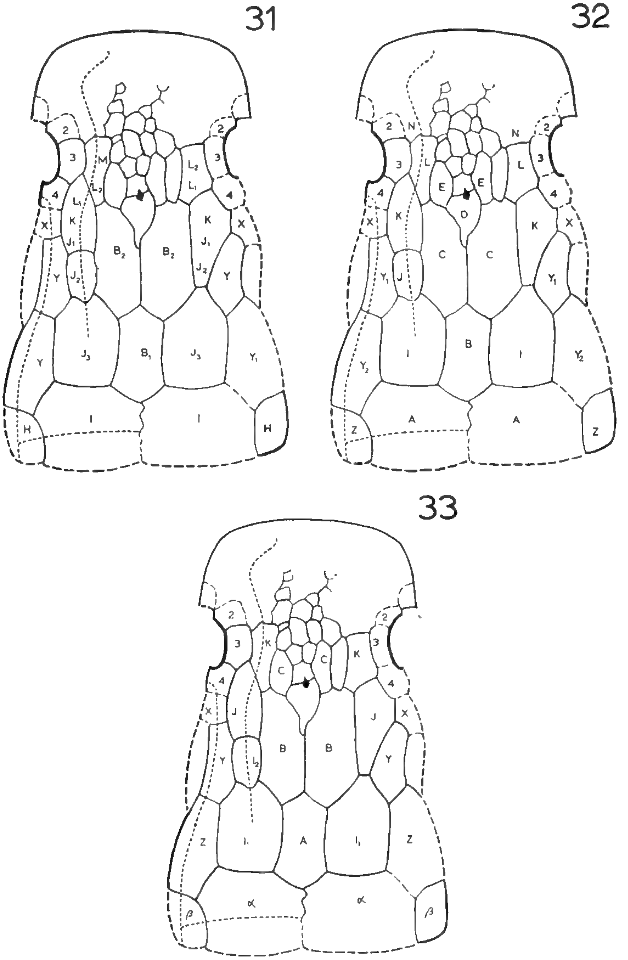
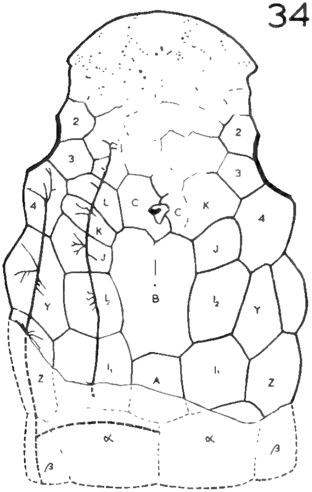
[1] G. M. Philip & A. E. H. Pedder (1964 : 1323).

plates and bearing the supraobrital canal are L, K and three J plates on each side, separate in *D. süssmilchi*, or partly fused in *D. lehmanni*, the most posterior of the J plates being very large (Lehmann 1956, text-figs. 1, 2). It is unexpected that B should be in three parts, two paired, and at least two other arrangements seem possible.

Taking first the obvious one rejected by Westoll (Text-fig. 32) one might consider that in the later *Dipterus* the orbits had moved backwards from their position in *Dipnorhynchus*, bringing them opposite the anterior ends of the C plates (Text-fig. 35), and this would account for the difference in the relative position of K, X etc. in the two genera; and their movements outside of J might have been a factor



FIGS. 31–33. *Dipnorhynchus lehmanni* Westoll. Fig. 31, Reconstruction of skull-roof after Lehmann & Westoll (1952 : 411, text-fig. 5A) with the original lettering (anterior Y-plates should be Y_2, posterior, Y_1). Fig. 32, The same, but re-lettered according to first alternative. Fig. 33, the same, but re-lettered according to second alternative.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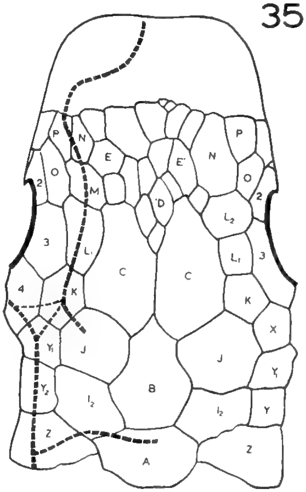
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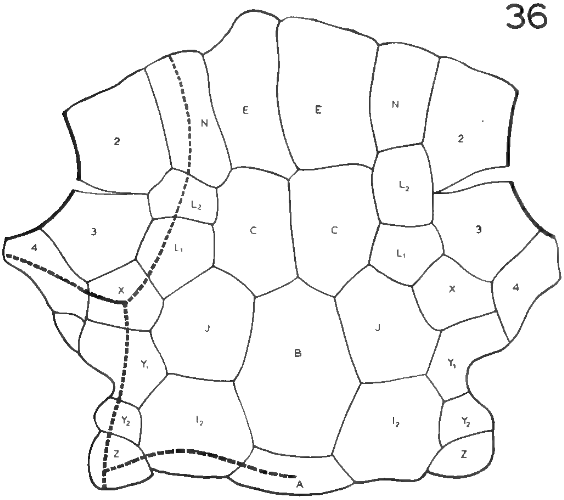
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FIG. 34. *Dipnorhynchus süssmilchi* (Etheridge). Outline reconstruction of skull-roof, after Hills (1933 : 637, text-fig. 2) with addition of the sensory canals from Hills (1941 : 646, text-fig. 1) and the back of the skull-roof restored in outline, after Westoll (1949 : 142). The lettering according to second alternative (cf. Fig. 33).

FIG. 35. *Dipterus valenciennesi* S. & M. Reconstruction of skull-roof, after Graham-Smith & Westoll (1937, text-fig. 2*a*) and Westoll (1949, text-fig. 1A), the lettering modified after Fig. 18.

FIG. 36. *Scaumenacia curta* (Whiteaves). Reconstruction of skull-roof, after Westoll (1949, text-fig. 6D) with the lettering modified.

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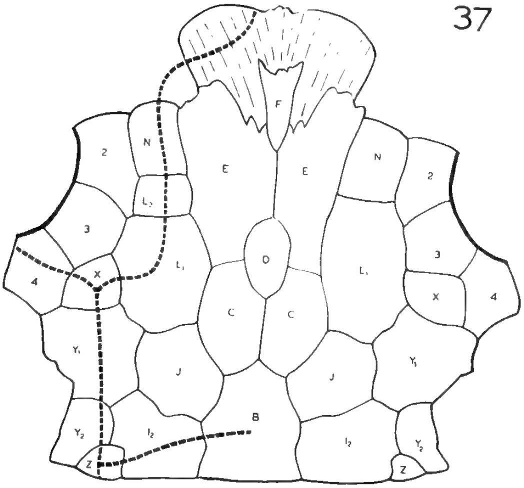

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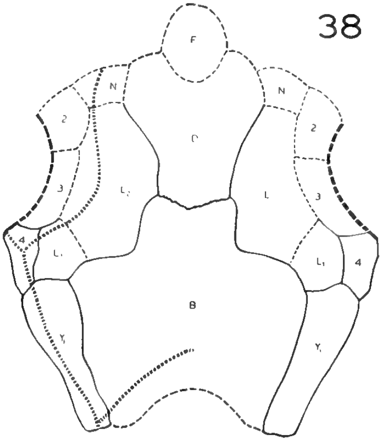

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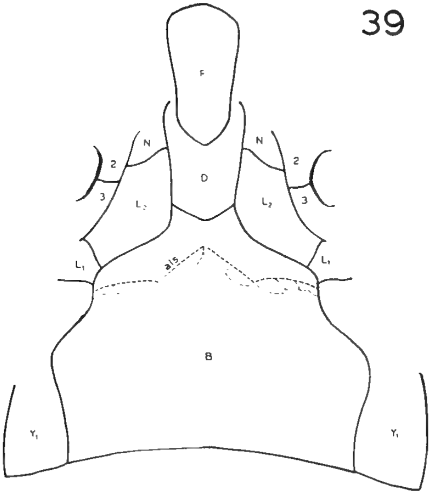

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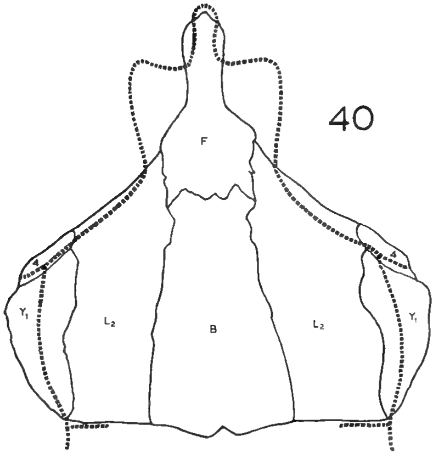

FIG. 37. *Ctenodus cristatus* Agassiz. Reconstruction of skull-roof, after Westoll (1949, text-fig. B) with the lettering modified, and Watson & Gill (1923, text-fig. 21).

FIG. 38. *Ceratodus sturi* Teller. Reconstruction of skull-roof, after Westoll (1949, text-fig. 9A), with lettering modified.

FIG. 39. *Ceratodus formosus* Wade. Reconstruction of skull-roof. *als*, approximate anterior limit of scale covering.

FIG. 40. *Neoceratodus forsteri* (Krefft). Skull-roof, after Holmgren & Stensiö (1936, text-fig. 288B), re-lettered.

contributory to the anastomosing of the infraorbital and supraorbital canals. The paired " B_2 " plates would then be C plates and instead of a proliferation of J plates we would have a more normal series of K, J and I. B would be small and A unaccounted for, unless it was the result of fusion of the very large paired plates labelled I by Westoll, for it seems unlikely in any event that the supposed I plates would later move forwards from the " extrascapular " row to embed themselves in the skull-roof between B and Y as in *Dipterus*.

On the other hand, if we accept the possibility that the two anterior B_2 plates of Westoll's interpretation did fuse to form the B of *Dipterus*, as seems indicated in *Dipnorhynchus süssmilchi* (Text-fig. 34), then an even more interesting situation could have held (Text-fig. 33). B, of Westoll, would be A and J_2 would be I_2 (missing on the right side) with J_3 as I_1, the plate that is still occasionally preserved as a small entity carrying part of the occipital cross-commissure in *Rhinodipterus* (White 1962, pl. 1, text-figs. 1, 2) and *Dipterus* (Westoll 1949, text-fig. 3*I*). On the outside of it is Z(H).

At this level of development, which Westoll (1942 : 142) claims is a fair approximation to the hypothetical ancestral condition, this row did not carry the cross-commissure, which was supposedly borne by the row behind, H–I–I–H of Westoll (Text-fig. 31), but here supposed to be a row of plates (β–α–α–β, Text-figs. 33, 34) that has now disappeared in other known fishes. This is in keeping with the important point shown by Westoll (1938, text-fig. 2) in his brief paper on the ancestry of the Tetrapods, that in vertebrates there is a movement backwards of the bones of the skull roof with additions at the anterior end by orderly development from the variables, and a loss of those behind with a shortening of the occipital region, features shown in some degree by *Dipterus* relatively to *Dipnorhynchus*.

Between *Dipnorhynchus* and *Dipterus* there must have been a stage when the hindmost row β–α–α–β was lost and the cross-commissure had been taken over by the full " extrascapular " row Z–I_1–A–I_1–Z, before the two I_1 plates lost their territory to their neighbours and their remnants fused with I_2 in front taking with them a segment of the commissure—as noted above, only rarely does this remnant of I_1 ever show itself as a minute independent plate.

From *Dipterus* one can move forward in time through a perfect morphological series based on Westoll's (1949, text-figs. 6*D*, 8*B*, 9*A*) outline restorations of the later dipnoans *Scaumenacia*, *Ctenodus* and *Ceratodus*, which show progressive diminution and final loss of the " extrascapular " Z–A–Z row, with the cross-commissure being finally captured by Y_1–B–Y_1 (Text-figs. 35–39). At the same time the series shows one other powerful trend coupled with the relative movement back of the head plates, and that is on simplification of the pattern, by invasion and loss rather than by fusion as Westoll indicates by his lettering. This trend is after all a continuation of the process seen in passing from *Dipnorhynchus* to *Dipterus*. The apparently unstable many plated mosaic inherited from the ancestral form persists in the CDE area in *Dipnorhynchus* ; in *Dipterus* the C area generally, and that of D and E quite often, has settled down in a more constant pattern of a few large plates, which is characteristic of the later terms in the series. It is interesting to note that in *C. formosus* Wade (1935 : 1, pl. 1 ; see also Text-fig. 39) the dermal skull pattern can be reasonably interpreted in a form comparable with that of *C. sturi* Teller from slightly earlier beds in the Austrian Alps (Text-fig. 38), the most striking difference being that F has increased in size at the expense of D, which in the living *Neoceratodus* has disappeared altogether (Text-fig. 40).

The various trends in this morphological series may be summarized as follows :

	Age	Posterior row of plates	Centre plates front to rear	Lateral line plates, β–X, α–P
Dipnorhynchus lehmanni	late Lower Devonian	αββα	Ant. mosaic BAα	4, 4
D. süssmilchi	do.	αββα	Ant. mosaic BAα	3, 7 +
Dipterus	Upper M.O.R.S.	ZAZ	Ant. mosaic CBA or FEDCBA	4, 7
Scaumenacia	Early U.O.R.S.	ZI_2AI_2Z	ECBA	4, 3
Ctenodus	U. Carbo-niferous	$Y_2ZI_2BI_2ZY_2$	FEDCB	4, 3
Ceratodus sturi	M. Trias	Y_1BY_1	FDB	1, 3
C. formosus	M. Trias	Y_1BY_1	FDB	1, 3
Neoceratodus	Living		FB	1, 1

The Endocranium

The undersurface of the skull of *Dipterus* has been tolerably well known since the days of Hugh Miller (1849 : 62, text-fig. 20). Pander (1858 : 10, pl. 3, figs. 11, 13, 14) was the first to deal seriously with this part ; Traquair (1878 : 5, pl. 3, fig. 1) established that the suspension was autostylic ; then Woodward (1891 : 234, text-fig. 36(i)) gave a restoration of the upper and lower jaws, and Goodrich (1909 : 242, text-fig. 210*A*) one of the whole palate. Finally Watson & Day (1916 : 29, text-fig. 6) published a general description of the palatal aspect of the head with an unlettered restoration which has been freely copied by later authors, either as originally published (Holmgren & Stensiö 1936 : 365, text-fig. 279) or somewhat modified (Graham-Smith & Westoll 1937 : 251, text-fig. 8*D*). Säve-Söderbergh (1952 : 22) noted further details ". . . similar canals [to those of *Chirodipterus*] for the efferent pseudobranchial arteries, grooves for the lateral dorsal aortae and orbital arteries, canals for occipital arteries, and grooves for the internal jugular veins ", but he gave no figures. Two years later Jarvik (1954 : 69, text-fig. 36B) figured a fine specimen in which he labelled the foramen for the occipital artery, a large paired fossa on the lower side of the otic region, and the groove for the lateral dorsal aorta.

Kesteven (1951 : 108) has given a clear warning against the too positive identification of foramina and other features in fossil skulls. The force of this warning is proportional to the distance in the relationship between the fossil and a living species. In the case of the Dipnoi, it can be shown that the endocranium of *Dipterus* is sufficiently close to the only other described fossil Dipnoan skull, that of the Upper

Devonian *Chirodipterus* (Säve-Söderbergh 1952)[1] and to that of the living *Neoceratodus* (Günther 1871; Huxley 1876; Kesteven 1931; Holmgren & Stensiö 1936 : 372) that comparisons may be reasonably made.

The most important specimen of *Dipterus* is an incomplete but uncrushed skull from "Caithness", P.17410, with a curiously asymmetrical pattern to its roof-plates (Text-figs. 42–47). This has lost the snout and most of the right side of the skull roof and endocranium, but the left side is reasonably well preserved, although the perichondral bone has flaked off in places and intractable matrix obscured others. The articular head of the left palatoquadrate is displaced upwards. This

FIG. 41. *Dipterus valenciennesi* S. & M. Head of small specimen showing part of lower dentition of each side. Achanarras, Caithness. P.22194. ×5. *AG*, anterior gular; *Br*, branchiostegal ray; *Cl*, cleithrum; *LatL*, lateral line; *Op*, operculum; *PG*, posterior gular; *SOp*, suboperculum.

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[1] Säve-Söderbergh pointed out (p. 8) that the snout of *Chirodipterus* if broken off would be identical with the fossils described as *Ganorhynchus*. The locality and formation of the unique holotype (44627) of the type-species, *G. woodwardi* Traquair (1873 : 555, pl. 14) are unrecorded, but Mr. H. A. Toombs has established that the matrix is so similar to that of Middle Devonian (Couvinian) fossils from the neighbourhood of Gerolstein in the Eifel as to leave little doubt as to its source.

skull was most probably developed by Säve-Söderbergh and formed the basis of his brief remarks on the endocranium of *Dipterus* (1952 : 22) in his classical description of the skull of *Chirodipterus*.

The bony structure of the endocranium is exactly as that described in *Chirodipterus* (Säve-Söderbergh 1952 : 6) consisting of inner and outer shells of thin laminar perichondral bone which also lined the vascular and nerve canals connecting the two capsules. The space between is largely filled by cancellar bone. The latter is frequently exposed in this specimen owing to the loss of the perichondral layer, and it is not always a simple matter to determine whether the supposed foramina are genuine or not. As often observed in this genus and noted in *Chirodipterus* the neurocranium is undivided and forms a single unit with the palatoquadrates which

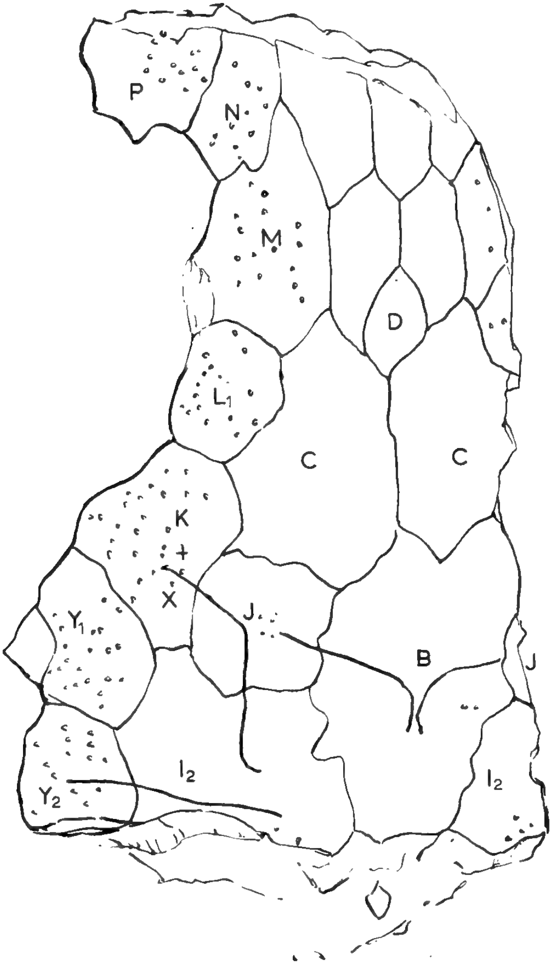
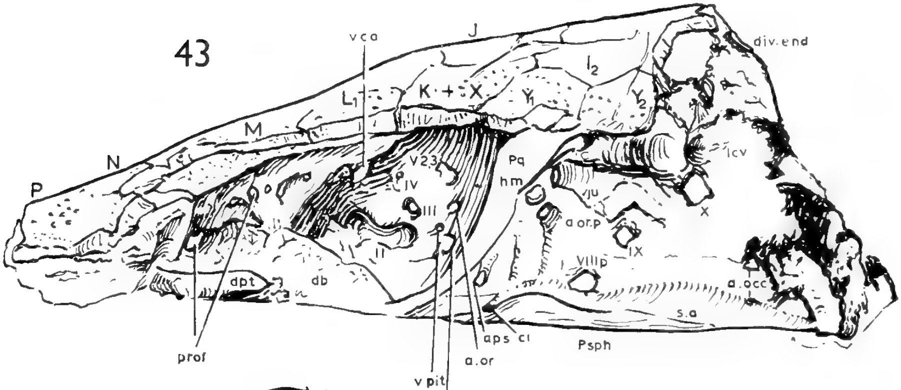
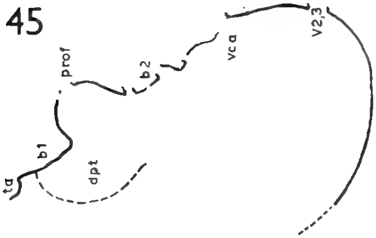
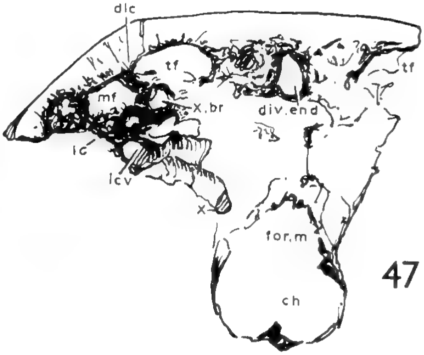
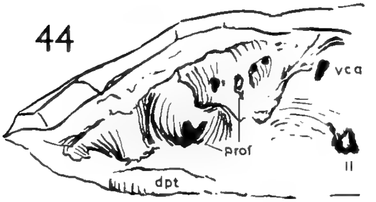


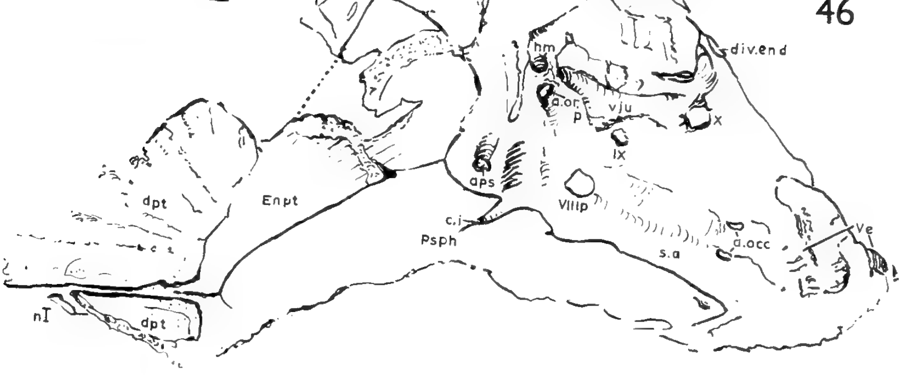
FIG. 42. *Dipterus valenciennesi* S. & M. Imperfect and irregular skull-roof. Same specimen (P.17410) as in Figs. 43–47. ×2·5.











FIGS. 43–47. *Dipterus valenciennesi* S. & M. Imperfect skull. Locality in Caithness unknown. P.17410. Fig. 43, Left side view. Palatoquadrate removed. ×2·5. Fig. 44, Planum antorbitale. ×<4. Fig. 45, Outline of left orbitotemporal space. ×2·5. Fig. 46, Three-quarters ventral view. ×2·5. Fig. 47, Back of skull. ×2.5. *a.occ*, foramen for occipital artery; *a.or*, foramen for orbital artery; *a.or.p*, posterior opening for orbital artery; *aps*, posterior opening of efferent pseudobranchial artery;

form on each side a high transverse lamina, in this specimen with a forward slope of about 45°. A major difference between the skulls of *Dipterus* and *Chirodipterus* is that in the former the neurocranium is in contact with the cranial roof throughout its length, so there is no median fossa or crest over the otic and occipital regions, the fossa for the temporal muscle (*tf*) on each side being bounded by the neurocranial wall medially and by the thin dorso-lateral crest (*dlc*) on the outer side (P.17410, Text-fig. 47). This crest is probably continued backwards under the " tabular horn " which is a projection of plate I_2 itself and seems to comprise all three layers (P.46761, Pl. 3, figs. 1, 2).

The lateral crest (*lc*), in continuation of the palatoquadrate, forms the outer wall of the masseter fossa (*mf*) on the inside and the roof of the branchial cavity on the outer.

Of the ethmoid region in front of the planum antorbitale there remains only a short length and cross-section of the perichondral lining of the right olfactory canal (*nI*, Text-fig. 46), through the post-nasal wall, and it is clear that, as in *Chirodipterus*, ossification was in this part only perichondral. The anterior ramifications of the profundus in the roof of the nasal capsules along with other canals and vessels, are well displayed in R.S.M. 1859.33.612, and to a lesser extent in P.46693.

The ethmoidal part of the orbital space, preserved only on the left side, is very different from that of *Chirodipterus* or *Neoceratodus* (Text-figs. 43–45), for it is much longer, occupying as much of the space as the orbito-temporal region. The posterior face of the planum antorbitale is completely ossified and runs diagonally from the outer margin backwards and inwards to the neurocranial wall. The outermost part is formed by a very large buttress (b_1) which joined the entopterygoid to support the dental plate. Narrow at the base it had a wide triangular section dorsally and a small space-filling talon (*ta*) outside it. Separated from it by a deep cavity containing the main profundus foramen (*prof*) was an even larger multiple buttress (b_2) forming the neurocranial wall and pierced by two or three small foramina for branches of the profundus. The lower half of this region, which is probably a little crushed downwards, is obscured by débris (*de*), but a diagonal fracture in P.755, apparently through the second buttress immediately above the inner posterior angle of the left tooth-plate shows the buttress passing below into a horizontal lateral shelf above the entopterygoid.

These buttresses provide a necessary support, from the skull-roof, to massive

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art.s, articular surface of palatoquadrate ; b_1, b_2, buttresses ; *ch*, notochord ; *c.i*, groove for internal carotid ; *db*, débris ; *div.end*, diverticulum of endolymphatic duct ; *dlc*, dorso-lateral crest ; *dpt*, tooth-plate ; *Enpt*, entopterygoid ; *for.m*, foramen magnum ; *hm*, exit of truncus hyomandibularis *VII* ; *l.c*, lateral crest ; *lcv*, foramen for lateral cerebral vein; *mf*, masseter fossa ; *Pq*, palatoquadrate (cut away in Fig. 43) ; *prof*, main profundus foramen ; *prof* + *vju*, foramen for profundus nerve and jugular vein ; *Psph*, parasphenoid ; *s.a*, groove for lateral dorsal aorta ; *ta*, talon of buttress ; *tf*, temporal fossa ; *vca*, foramen for anterior cerebral vein ; *Ve*, fused vertebra ; *vju*, groove for internal jugular vein ; *v.pit*, groove and foramen for pituitary vein.
nI, olfactory nerve ; *II* ; *III* ; *IV* ; $V_{2,3}$, opening for mandibular and maxillary branches of trigeminal nerve ; *VIIIp*, posterior branch of acoustic nerve ; *IX* ; *X* ; *Xbr*, branches of vagus.

dental plates, which with their strongly denticulated surfaces, were clearly capable of dealing with very rough food. Mollusca are not very evident in these beds, and such denticulated plates usually with no obvious facets of wear, speak rather for gripping and crushing struggling animal prey than for cutting inert vegetable matter, so arthropods, worms and perhaps other fishes suggest themselves. That *Chirodipterus* had feebly sculptured plates and rudimentary buttresses—Säve-Söderbergh (1952 : 11, pl. 3, fig. 2) speaks only of " a vertically elongated prominent area "—suggests that it fed on softer unresisting matter such as carrion. On the other hand the earlier Australian marine *Dipnorhynchus* had a large free buttress at the outer margin of the entopterygoid in the middle of the orbito-temporal space (P.33699) to support its large massive dental plates for holding and crushing shelly prey, such as the numerous brachiopods with which its remains are associated.

Only the outer face of the left wall of the orbito-temporal region of the neurocranium of *Dipterus* is reasonably preserved (P.17410, Text-fig. 43). The brain-case is short and narrow, and the wall, as preserved, curves gently inwards towards the skull roof. There is a wide subocular shelf, a continuation of that already noted, and this passes imperceptibly into the processes of the palatoquadrate. In front high up and just behind the second buttress is a large foramen for the anterior cerebral vein (*v.ca*). Below and behind this is a very large dumb-bell shaped aperture for the optic nerve (*II*). Whether this is its true shape is not quite certain, but if so, it is unlike what is found in either *Chirodipterus* or *Neoceratodus*. As in *Chirodipterus*, above and behind in a slanting line are three foramina, the topmost for the fourth nerve (*IV*), the middle and largest for the oculomotor (*III*) ; and on a level with the foramen for the optic nerve, a groove and foramen for the pituitary vein (*v.pit*). Immediately behind and below this vein is the large foramen for the profundus nerve and the internal jugular vein (*prof+v.ju*). This foramen lies at the junction of the endocranium and the fused processes of the palatoquadrate and faces forwards. High above this foramen is a large opening corresponding to that identified in *Chirodipterus* for the mandibular and maxillary branches of the trigeminal nerve (*V*2,3), but it is relatively farther back, and below it, instead of at the side, is the smaller foramen for the orbital artery (*a.or*).

Behind the palatoquadrate on the left side the ventro-lateral surface of the otic and occipital regions is reasonably well preserved (Text-figs. 43, 46, 47), although the upper part formed by the lateral crest (*lc*) is possibly a little distorted by crushing. Below it the wall of the endocranium is almost straight and vertical except for the slight swelling over the saccular division of the labyrinth cavity.

The back of the skull slopes somewhat irregularly at an average angle of 60° to the base of the occipital region as preserved, but although two vertebral elements (*Ve*) are seen to be incorporated in this part it is clearly imperfect.

A number of features are readily identifiable with those recognised in *Chirodipterus*.

Immediately above the labyrinth swelling lies the groove for the internal jugular vein (*vju*) which leads to the foramen piercing the palatoquadrate, and just in front of this foramen is another, almost as large, probably for the exit of the truncus hyomandibularis *VII*(*hm*), and below it the posterior opening of the canal for the orbital artery (*a.or.p*) to which a groove leads from that of the dorsal aorta (*s.a*).

Where these two grooves meet a third groove, for the internal carotid artery, passes slightly medially into a notch (*ci*) and then under the parasphenoid. Above it is the posterior opening of the efferent pseudobranchial artery (*aps*). All these features are little more than a paraphrase of what has been found in *Chirodipterus*, but not seen in that genus is a very large opening, possibly enlarged by fracture, just behind the junction of these same three grooves, probably for a posterior branch of the acoustic nerve (*VIIIp*). Above and behind this is the foramen for the glossopharyngeal nerve (*IX*).

The short occipital region is continuous with the otic but the sides are flatter and more nearly vertical. Owing to the slope of the back of the head, about 60° but exaggerated by breakage, the dorsal flange formed by the lateral crest is present only in the anterior part.

At least two vertebrae are fused on to the basioccipital region, and in other specimens (DMSW.P.149, Pl. 1, fig. 2; also P.755 and R.S.M. 1859.33.617) it seems evident there are three.

The main features of the otic region, the internal jugular groove (*vju*) above and that of the lateral dorsal aorta (*s.a*) below, are continued on to the occipital region. The vagus foramen (*X*) is in the jugular groove in much the same position as in *Chirodipterus* (Säve-Söderbergh 1952 : 19, text-fig. 8). Immediately above and at right angles to it is a large foramen running into the back of the skull, presumably for the lateral cerebral vein (*lcv*, Text-figs. 43, 47), and above this are two smaller openings for branches of the vagus (*Xbr*). However, the most conspicuous feature in the back of the skull is a pear-shaped opening in the centre near the skull-roof, presumably a cross-section of a median diverticulum of the endolymphatic duct, (*div. end*) as in *Eusthenopteron* (Stensiö 1963 : 97, 100, text-figs. 50A, 51A).

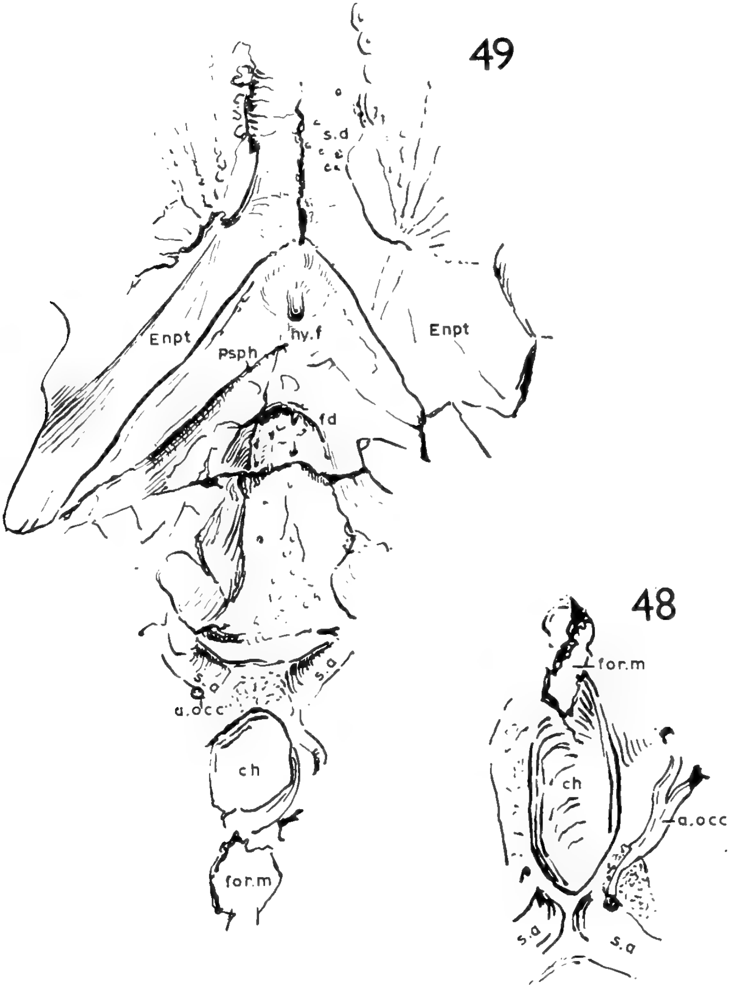
The groove of the lateral dorsal aorta (*s.a*) widens to the rear and joins that of the right side behind the parasphenoid (P.34549, Text-fig. 49 ; *cf.* Jarvik 1954, text-fig. 36B). Just before it does so, it is pierced at its upper margin by a foramen for the occipital artery (*a.occ*), which is nearly horizontal owing to the swelling out of the bone. It penetrates the bone for almost 3 mm. by a somewhat sinuous course, and re-emerges above and slightly behind by a similar foramen above, then continues upwards by a well-marked groove (P.34544 ; also DMSW.P.149) which apparently bifurcates before the vessel re-enters the skull through two distinct foramina (Text-fig. 48).

The right side of the occipital region of P.17410 is too imperfect to show these features, but the vagus foramen, much enlarged, is present and a little below and behind it, as in *Chirodipterus*, two or three foramina for spino-occipital nerves.

Of the dermal bones of the palate in this specimen, only the right half of the parasphenoid and part of the right entopterygoid is preserved. The former is sunk into the endocranium so that the surfaces are level, and they give the impression of being joined by a suture ; and the entopterygoid, to which the parasphenoid is truly sutured, has the same appearance in regard to the palatoquadrate.

The features of the palate are better seen in other specimens, in particular P.34549, a specimen collected by Dr. D. L. Dineley in Clardon Haven, near Thurso (Text-fig. 49, Pl. 1, fig. 1). It is a crushed head with very well preserved, but flattened palate.

The anterior angle of the parasphenoid in this specimen shows a very well marked hypophysial foramen (*hy. f*) which runs inwards (upwards) and somewhat backwards. There is a broad, flat or slightly concave selvage along the antero-lateral sides which is widest in front medially and decreases laterally to vanish at the greatest breadth. On the medial side of this selvage the parasphenoid shows a complementary depression or groove, narrowest medially in front and widest behind at the lateral angle. Between these grooves the parasphenoid is gently convex. Near the front of this



FIGS. 48, 49. *Dipterus valenciennesi* S. & M. Fig. 48, Basioccipital region to show course, partly excavated, of occipital artery (*a.occ*). Clardon Haven, near Thurso, Caithness. P.34544. ×2·25. Fig. 49, Palatal view. See also Pl. 1, fig. 1. Clardon Haven, near Thurso, Caithness. P.34549. ×2·25. Both specimens colld. D. L. Dineley, 1957. *fd*, fold; *hy.f*, hypophysial foramen; *s.d*, secondary denticles. Other lettering as in Figs. 43–47.

median area and some distance behind the hypophysial foramen there is a very conspicuous crescentic, transverse slit or infolding of the surface of the parasphenoid directed forwards (*fd*) with a corresponding broad and shallow depression behind it in which are four or five well marked denticles on low ridges. The depth of the pocket cannot be seen, but probably it does not extend far in. It is seen in a few other specimens, in varying degrees of development ; well developed although partly masked by transverse cracks in P.755, P.34556 and M.M. no. L.11577 ; irregular in R.S.M. 1859.33.614 ; replaced by a number of smaller shallow tucks in M.M. no. L.10861, and absent in R.S.M. 1859.33.33 (Traquair 1878, pl. 3, fig. 1) and other specimens. This feature is therefore no more than an individual defect, possibly based on an atrophied organ, in the laminar surface layer of the parasphenoid, which is frequently wrinkled or irregular when worn (P.34549 and DMSW.P.149, Pl. 1, figs. 1, 2) and possibly was denticulated over much of the palatal surface (M.M. no. L.11577).

The hypophysial foramen varies quite obviously in its development, being conspicuous in some specimens (Pl. 1, fig. 1) but in others reduced to a very small size and accompanied by other diminutive foramina (P.34556). It was figured without comment by both Pander (1858, pl. 3, figs. 11, 13) and Günther (1871, pl. 34, fig. 4) and has been noted by Westoll (1949, text-fig. 1*D*). It is also present in one of the specimens of *Rhinodipterus secans*, but Gross (1956 : 28, text-fig. 21*c*) dismissed it as " vielleicht sekundär entstanden ". No such foramen has been recorded from Upper Devonian dipnoans.

The dental plates are continuous with the entopterygoids and appear as mere outgrowths of the supporting bones. Fine new specimens of the mandible of the earlier *Dipnorhynchus* from New South Wales (P.33714, P.46773) clearly show that the rather formless swellings that do duty as dental plates are in fact just thickenings of the vascular and cosmine layers of the bone of the jaw, and it is evident the more definitely patterned " plates " of *Dipterus* and later dipnoans are of like origin. In well preserved specimens they are clearly differentiated by their thick surface layer, which has much the same appearance as the cosmine of the external head-bones but with rather fewer openings of the fine tubuli, well marked in the low flat longitudinal medial areas along which the two plates meet (P.34543, Pl. 2, figs. 1, 2; R.S.M. 1859.33.33, Traquair 1878, pl. 3, fig. 1). In P.755 and 33166 (Pl. 2, figs. 3, 4) there is irregularity along the symphysial margin due to resorption and in P.34556 (Pl. 2, fig. 5) as in P.46691 and R.S.M. 1859.33.612, much of the thick cosmine layer has disappeared showing underlying trabecular layer. In extreme cases not only has the whole of the surface between the dental plates gone, as in the relatively small original of Pl. 1, fig. 2 (DMSW, P.149), but secondary tubercles (*s.d.*) may be developed on the rough trabecular bone, and an unusual number of denticles appear between the regular rows on the biting surfaces (P.34549, Pl. 1, fig. 1, Text-fig. 49). In this specimen small irregular areas of the right dental plate (left of figure) have disappeared, but this degree of resorption is not seen in any other specimen and must be due to decay in an old specimen. Resorption of the plate is not correlated with size for the completely resorbed originals of Pl. 1, figs. 1 and 2 are respectively larger and smaller than Traquair's specimen which is almost perfect.

The vomerine dentition is not well displayed in any of the available specimens, although some show parts of the supporting bone, but one seems to show remains of the dentition that can be reasonably interpreted (33166, Pl. 2, fig. 4). Watson & Day (1916 : 33, text-fig. 6) and others following them showed a pair of elongated plates with three transverse rows of small denticles and a narrow hinder end inserted medially between the front of the entopterygoid tooth-plates. None of the available specimens shows evidence to support this arrangement, which may be based on the uneven resorption of the surface of the entopterygoid tooth-plates, as this tends to start along the mid-line and in front (P.34543, P.755, 33166, Pl. 2, figs. 2–4) and the narrow extension of these plates is usually broken away. The last of these specimens shows a very different arrangement : on each vomer there are two or perhaps three

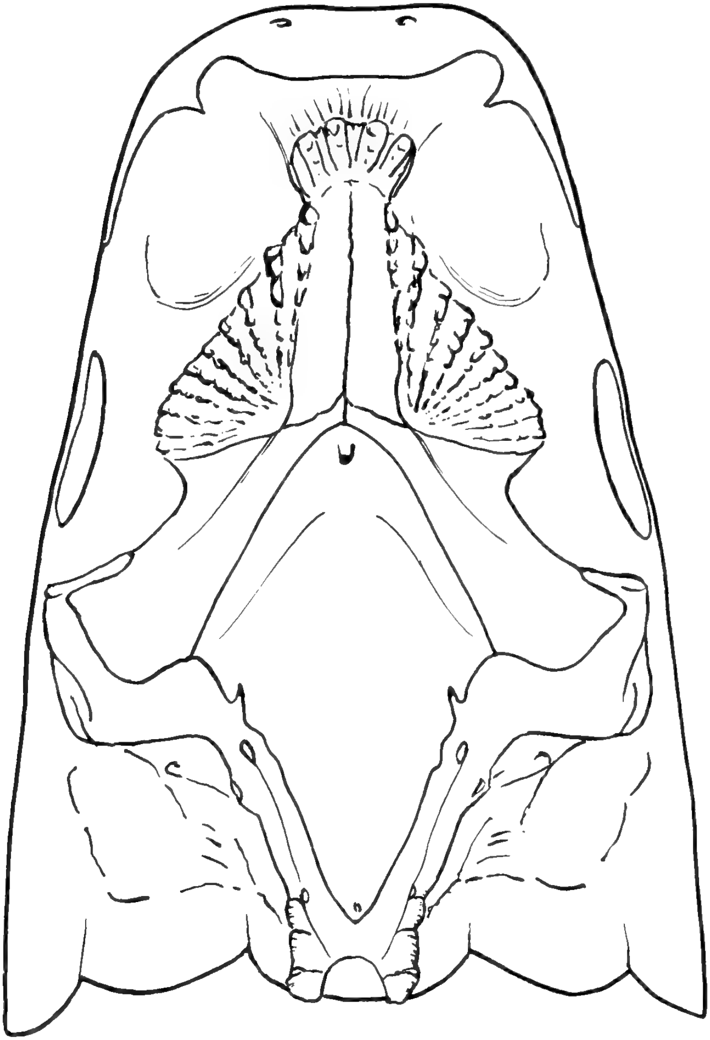


Fig. 50. *Dipterus valenciennesi* S. & M. Restoration of Skull, palatal view.

slightly diverging longitudinal ridges which most probably bore denticles, as Watson noted, although there is little evidence of these now. The vomers are well separated from the hard " lip " and must have bitten against a cartilage pad in the front of the much shorter lower jaw—Günther's (1871 : 525, pl. 35, figs. 1–3, *l.a.*) " lower labial cartilage " in *Neoceratodus*—and their function could have been merely to hold before gulping. Günther (1871 : 518) refers to the " double kind of action " that the main upper and lower tooth-plates have to perform, crushing or grinding food on the " flat surfaces " and cutting food with the " sharp lateral ridges " which " fit into the notches of the opposite tooth like the shells of a *Cardium* ". So very nicely do they fit that there can have been no grinding action involving any degree of lateral displacement, so that the movement must be a simple up and down champing, not quite vertical, for the lower plate is set at a small angle to the horizontal, sloping inwards. And the tooth-plates in *Dipterus*, with their highly denticulated ridges, must have functioned in much the same restricted manner, and such few facets of wear as the denticles show bear this out (P.34549). Generally speaking the wear is due to friction with the food and just blunts the tubercles which fit into pits of their own making between the radiating rows of denticles on the opposing plate (*e.g.*, 33166, Pl. 2, fig. 4), and in the lower jaw (P.46692).[1] In old worn dentitions, action was much more irregular and new denticles were sometimes developed between the ridges (P.34549, Pl. 1, fig. 1).

A restoration of the palatal aspect of *Dipterus* is given in Text-fig. 50.

SUMMARY

1. The pattern of the dipnoan skull-roof has developed from an ancestral mosaic principally by loss and invasion of roofing plates ; fusion occurs for the most part as an individual aberration.
2. The dipnoi were already widely separated from the Crossopterygii (Jarvik 1960 : 32) at their first appearance, and this separation took place when the skull-roof was in a mosaic stage. It is therefore not possible to correlate the plates of the dipnoan skull-roof meaningfully, and attempts to do so must result only in geographical approximations for which compound names have no validity.
3. The use of nomenclature based on that of the skulls of higher vertebrates is therefore both misleading and undesirable : a special notation is required and a modified edition of Forster-Cooper's alphabetical scheme, properly related to the standard sensory canal pattern adequately serves the purpose.

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[1] Dr. Gwynne Vevers' observations on the feeding of *Neoceratodus* at the Zoological Gardens in London (*in lit.* 25 Nov. 64) are very much to the point—" We feed the present specimen on strips of raw horse meat or fish approximately 3 × ½ × ¾ inches. The previous specimens here have all eaten a great deal of lettuce, but the present specimen does not appear to enjoy this at all . . . There is no lateral movement of the jaws in chewing but a very pronounced up and down nibbling movement along the length of the meat strip or fish. The food is then extruded from the mouth and the operation repeated. This may happen several times before the food is finally swallowed. These are straight observations. I suppose the nibbling movement would be a very suitable way of dealing with fresh water crayfish or a similar object."

In a film recently shown by Mr. I. R. Bishop at the Linnean Society of London (20 Feb. 1965) *Lepidosiren* is seen feeding on live worms with exactly the same action as that described above in *Neoceratodus*. *Dipterus* may very well have eaten in a similar fashion once food was obtained, but its heterocercal tail suggests less sluggish movement than in the living lung-fishes and therefore the possibility at times of livelier prey.

4. In the early Dipnoi there was an additional row of plates behind the " extrascapular " row of *Dipterus* (Z–A–Z) which bore the occipital cross commissure and was later lost.
5. Parallel with the relative movement of the roof-bones in Crossopterygii and higher vertebrates demonstrated by Westoll (1938), there was a movement backwards of the roofing bones of the Dipnoi ; while standard plates were developed from the primitive mosaic in front, presumably by loss and invasion, rows of plates were successively lost at the back of the skull-roof, the occipital cross-commissure being in turn captured by the row in front until in Triassic times it was established in Y_1BY_1. After the Devonian period there was also an *overall* reduction in the number of the plates, by invasion rather than fusion, a process continued to the present day.
6. The effect of §2 is further to emphasize the difference between the lung-fishes on the one hand and the rhipidistians and coelacanths on the other. It seems, indeed, on the evidence of the skull-roof patterns that the Dipnoi split off from all the other Osteichthyes at the skull-mosaic stage and developed an independent pattern of dermal bones in the skull-roof which has little relevance to that of the " Teleostomi " in spite of Westoll's ingenious arguments to the contrary and his bold assertion (1949 : 159, text-fig. 10) that " The evidence of Devonian forms shows very clearly that the early Dipnoi were very closely related to the contemporaneous Rhipidistia " ; my reading of the evidence favours very much Jarvik's (1960 : 31–35, text-figs. 28, 30) interpretation of their relationships as an isolated offshoot from " Preteleostomi ", and there is a lively expectation that the resemblances that they appear to show towards the contemporary Rhipidistia will prove of decreasing systematic significance. This supposed isolated position is supported by the development of the tooth-plates.
7. In regard to the classification of the Osteichthyes, we are forced back to the ideas of the early years of this century, as expressed by Goodrich (1909) when the first major cleft in the group was placed between the Dipnoi (without, of course, the Arthrodires) and the Teleostomi, equally rated as sub-classes. Lehman (1959 : 8) rates the Dipnoi as a Class, but whatever their evaluation, they are an isolated group, and the somewhat heated argument as to the significance of the term " Crossopterygii " and the appropriate label to cover all the Dipnoi Rhipidistia and Coelacanthini (Romer 1955 ; Trewavas, White, Marshall & Tucker 1955) is so much beating of the air—the Dipnoi stand apart, and the term Crossopterygii covers only the rhipidistians and the coelacanths.

ACKNOWLEDGMENTS

Most of the material studied is in the British Museum (Natural History), and to the collections there substantial and important additions have been made lately by Dr. D. L. Dineley and Mr. John Saxon and his son Alan ; and Mr. Saxon has also been able to send valuable information regarding a number of older localities. As usual, ready and patient help with invaluable material on loan from the Royal Scottish Museum was given by Dr. Charles Waterston, and a number of important fossils

from the Manchester Museum were generously lent by Dr. R. M. Eagar. These last were from the D.M.S. Watson collection, and one from Professor Watson's own collection was made available for study as well. Dr. F. R. Parrington also kindly sent me material on loan from Cambridge.

In the Department I had my usual full backing by Mr. Harry Toombs, well supported in the development of the fossil heads by Mr. Ian Macadie, who also influenced the offer of a number of valuable donations from his native Caithness to the right quarter.

The photographs were dexterously taken by Dr. W. T. Dean and Mr. John Ferguson, while in putting the final touches to this document Mr. R. H. Spires, Mr. F. M. Wonnacott and Mr. R. Baker exercised their respective skills.

To all these I offer my sincere thanks.

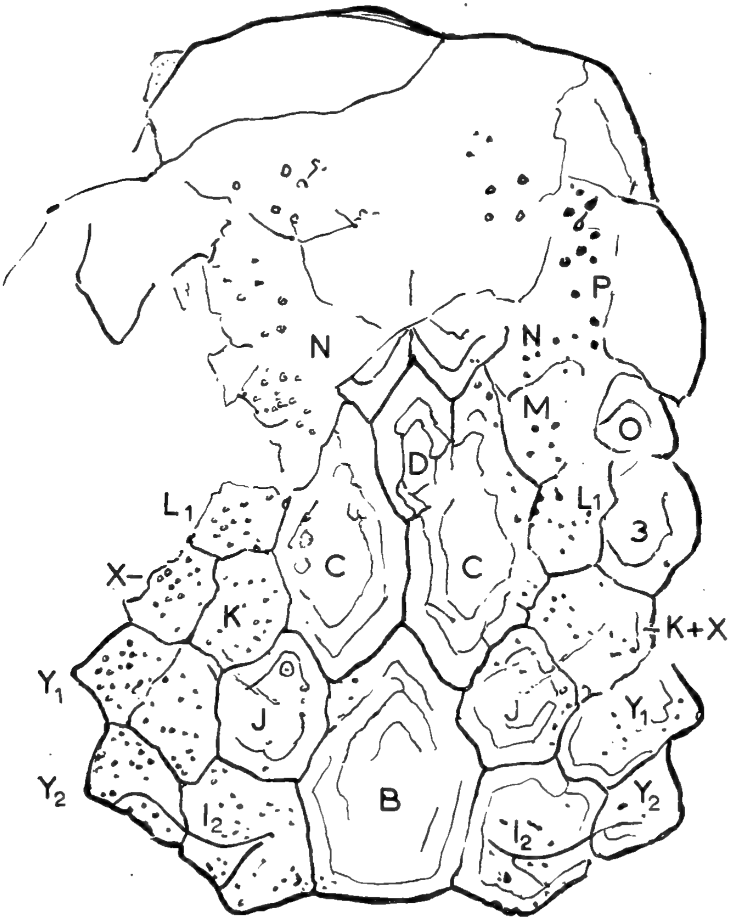

FIG. 51. *Dipterus valenciennesi* S. & M. Skull-roof of small but aged specimen. Lectotype of "*Polyphractus platycephalus*" Agassiz (1844 : 5, 29, pl. 27, fig. 1). Orkney. P.3373*a*. × 1·5.

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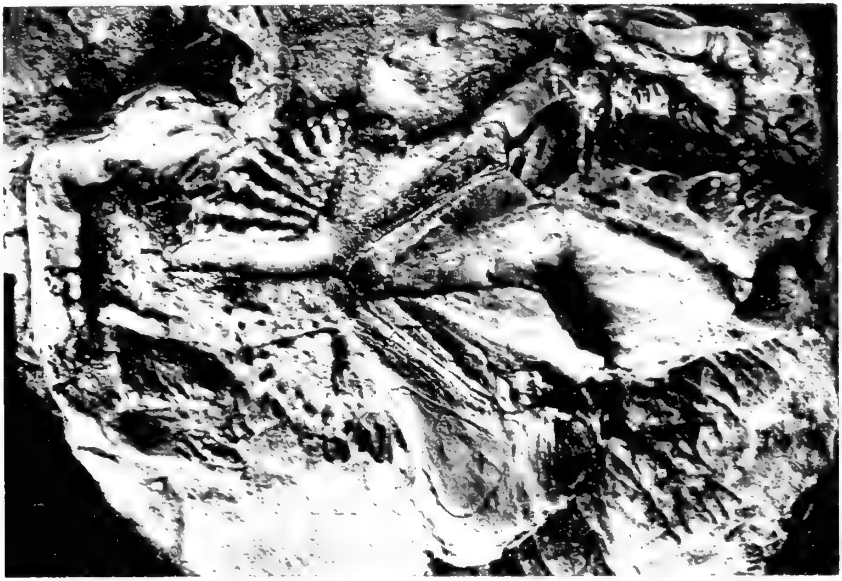
PLATE 1

Dipterus valenciennesi S. & M.

FIG. 1. Undersurface of skull of old specimen showing decay (or irregular resorption) of right tooth-plate (left of figure) and complete resorption of surface of entopterygoid between tooth-plates with formation of secondary denticles. Colld., D. L. Dineley 1957. Clardon Haven, Caithness. P.34549. × 2. See also Text-fig. 49.

FIG. 2. Undersurface of skull showing vertebral elements fused to basioccipital region. Loc. unknown, Caithness. DMSW.P.149. × 2.



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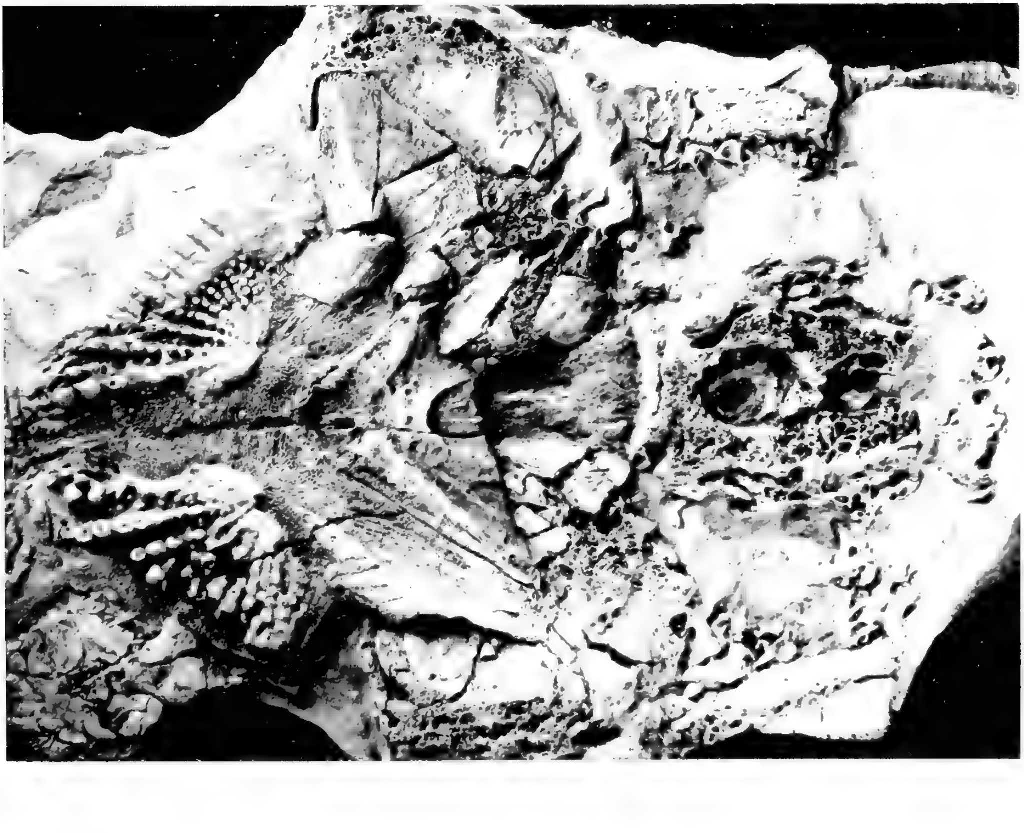

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PLATE 2

Dipterus valenciennesi S. & M.

FIG. 1. Imperfect entopterygoid tooth-plates showing cosmine surface and hypophysial foramen. Colld., D. L. Dineley, 1957. Clardon Haven, Caithness. P.34543. ×3.

FIG. 2. Same specimen powdered to show initial resorption along median suture. ×1·5.

FIG 3. Another specimen showing increased resorption along median suture. Orkney. P. 755. × 1·5

FIG. 4. Specimen showing advanced and irregular resorption along median suture and worn vomerine dentition in front. Near Thurso, Caithness. 33166. ×1·5.

FIG. 5. Palatal view of skull. The median area of the entopterygoid tooth-plates has lost the cosmine surface completely, and only the base of the vomerine dentition remains. Colld., D. L.Dineley, 1957. Clardon Haven, Caithness. P.34556. ×1·5.


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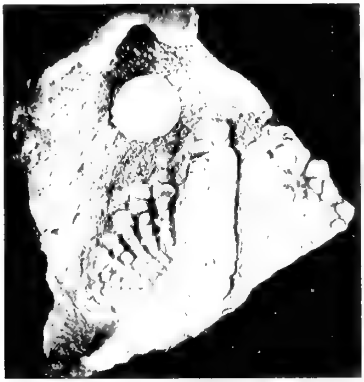
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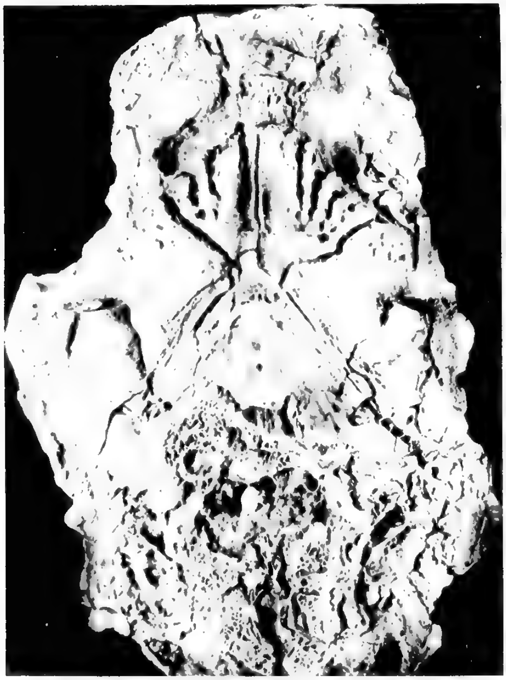
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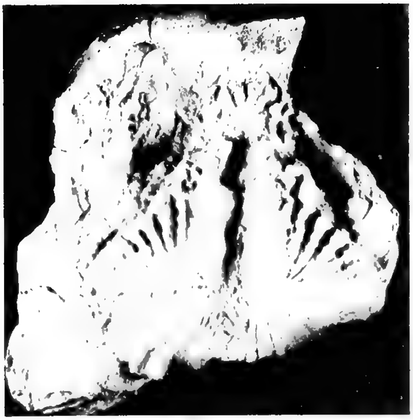
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PLATE 3

Dipterus valenciennesi S. & M.

FIG. 1. Skull-roof showing pores of sensory canals enlarged by resorption and the post-cranial processes (" tabular horns "). Colld. J. Saxon, 1964. Weydale Quarry, Caithness. P.46761. ×2.

FIG. 2. Hinder end of same specimen. The left post-cranial process and plate I_2 have lost outer and part of middle layers exposing section of occipital cross-commissure with short branch forwards. ×4·5.

FIG. 3. End of snout showing pores of supraoccipital canal enlarged by resorption. (See also Text-fig. 19) Colld. R. V. Collier, 1964. Clardon Haven, Caithness. P.46690. ×4·3.

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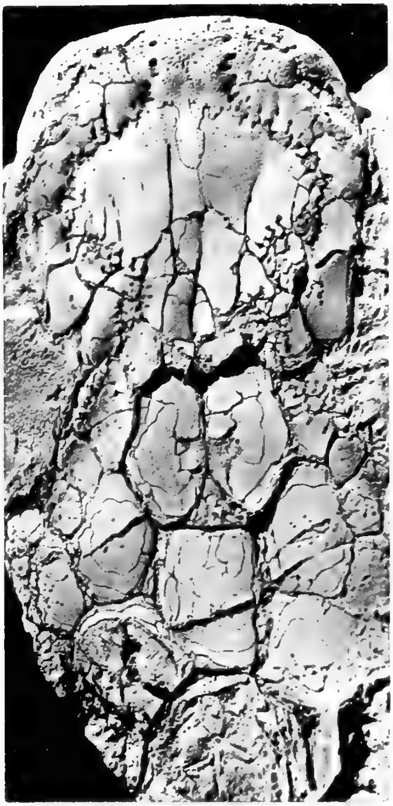

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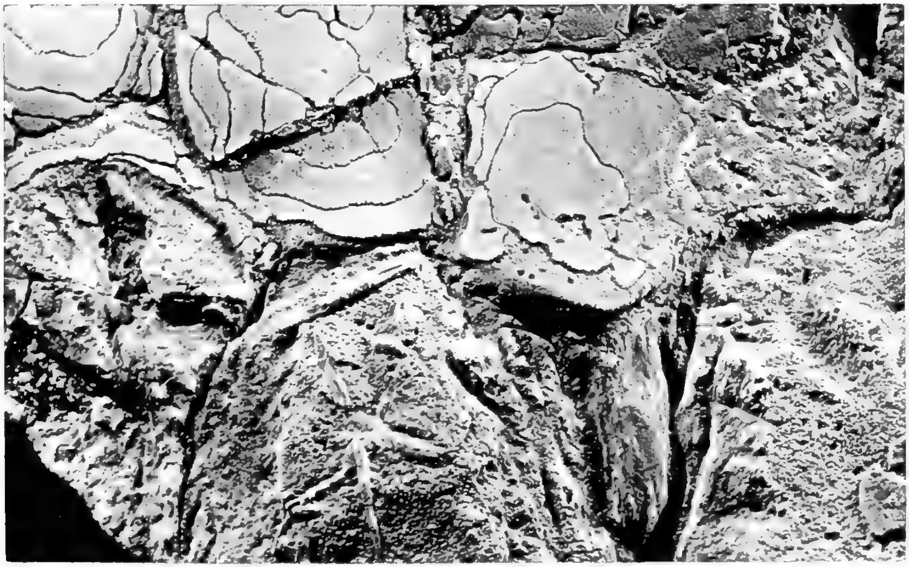

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E. F. OWEN

BULLETIN OF
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GEOLOGY Vol. 11 No. 2
LONDON: 1965

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BY

ELLIS FREDERIC OWEN

Pp. 47–72 ; 3 *Plates* ; 13 *Text-figures*

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SOME LOWER CRETACEOUS TEREBRATELLOIDEA

By ELLIS FREDERIC OWEN

SYNOPSIS

Several Lower Cretaceous species previously described by Walker, Davidson, Meyer and Keeping are revised and referred to *Tamarella* gen. nov. or *Vectella* gen. nov. Serial sections of representative species of these forms are shown for the first time. In addition, two new species of *Rugitela* from the Neocomian of Lincolnshire and Yorkshire are described and related to forms previously recorded from North Germany and France.

INTRODUCTION

Representative genera of the Mesozoic brachiopod family Zeilleriidae have been recorded from the Trias to the Lower Cretaceous but few of the early records have been further investigated, and the Jurassic genus *Zeilleria* has often been quoted from the Neocomian and, more recently, with those of *Aulacothyris* and *Ornithella* by Middlemiss (1959) and Casey (1961), from Aptian and Albian beds of the Lower Greensand. Some of these Cretaceous brachiopods, while possibly belonging to the same families as Jurassic species, have characters which merit generic distinction.

Until the researches of Muir-Wood (1934, 1936) the internal structures of the British Jurassic Terebratelloidea had been known only from dissections or by chance exposure of brachial loops and cardinalia in damaged specimens. Minor differences in loop development had previously escaped critical investigation and no real advance had been made in their further classification. It is not the purpose of this paper to add to or further discuss the classification of the terebratelloid brachiopods. However, a systematic study has been made of some of the Lower Cretaceous species within this suborder together with comparisons of genera already described by Muir-Wood (1934, 1936) and Cooper (1955).

Some of the early Cretaceous terebratelloid species formerly described by Walker (1867, 1868, 1870) from the Lower Greensand of Upware (Cambridgeshire), Brickhill (Buckinghamshire) and Potton (Bedfordshire) have been revised and referred to *Tamarella* gen. nov. Others, which had been broadly interpreted as *Waldheimia, Zeilleria, Aulacothyris* and *Ornithella* are placed in *Vectella* gen. nov.

Keeping (1883 : 24) suggested a possible line of evolution of some of Walker's species and related them to others described by Morris (1854) and J. de C. Sowerby (1836) from the Lower Greensand of the Isle of Wight. His suggestions were, however, based mainly on a comparison of external morphology, and an examination of the species listed by him has revealed a degree of homoeomorphy. Information obtained from transverse serial sections of these forms has now made possible a revision of his ideas regarding their relationships.

In a description of a brachiopod fauna from the Mural Limestone (Middle Albian) of Arizona, Cooper (1955 : 10) referred *Terebratula tamarindus* J. de C. Sowerby to his new genus *Psilothyris*. He figured a series of etched specimens showing (pl. 3) what he described as precampagiform, terebrataliform and dalliniform stages in the development of the brachial loop of certain specimens. On the same plate, for comparison, he figured the cardinalia without brachial loop of a dissected specimen which he identified as *T. tamarindus* from the Lower Greensand of Faringdon, Berkshire. If, as he suggested, the etched loops of his specimens exhibit dallinoid development stages, then *Psilothyris* would appear to belong with the Dallinidae.

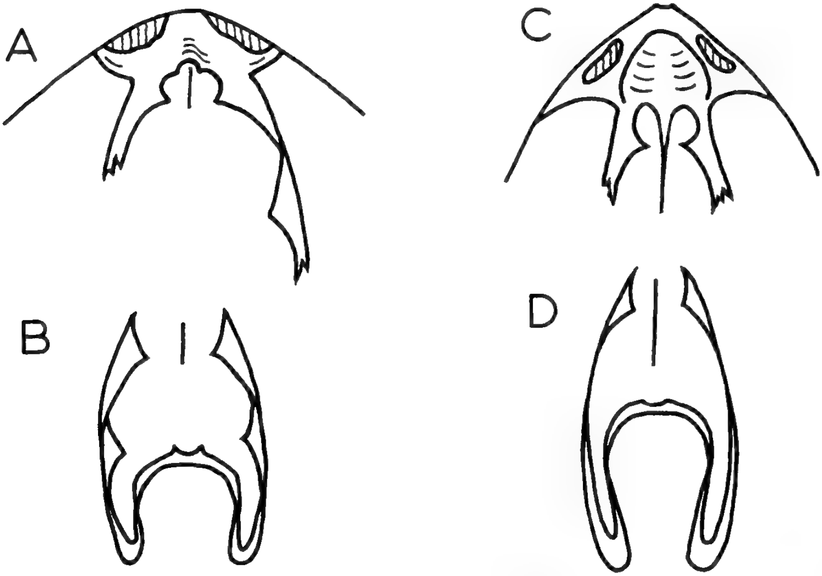

Fig. 1. Diagram illustrating the cardinalia of (A) *Tamarella*, showing the broad hinge-plates with the anterior plication, and (B) a reconstruction of the brachial loop showing the thickening of the descending branches. (C) *Vectella*, showing the deep hinge-trough and long dorsal septum, and (D) reconstruction of the brachial loop.

Although many young specimens of *T. tamarindus* have been examined from the Lower Greensand of Faringdon, Berkshire, no dallinoid stages in loop development have been found, but a remarkable specimen of *T. tamarindus* from Faringdon (Pl. 1, fig. 8*c*) shows what appears to be a thickening of the descending branches some 6 mm. below the dorsal umbo in a brachial valve, 15 mm. long. It is possible that this thickening may be the remains of an early connecting band or attachment. A similar thickening is seen on the descending branches of the brachial loops of specimens of *Psilothyris* figured by Cooper (1955, pl. 3, figs. 18, 19).

The lack of serial sections of the genus *Psilothyris* make absolute comparison with British Upper Aptian species of *Tamarella* impossible and the absence of any evidence of early loop attachment in even very young specimens of *Tamarella* means that any attempt to relate the two genera is purely conjecture. However, the two genera have much in common and it may be necessary at some future date to emend the present study.

The varied brachiopod fauna contained in the condensed Neocomian beds represented in the Claxby Ironstone of Lincolnshire and the Speeton Clay of Yorkshire is comparable to that described by Roemer (1836–1840) from the Hilsconglomerat of the Hanover district, north-west Germany. Species of zeilleriid brachiopods described as *Terebratula hippopus* and *T. longa* by Roemer are revised here and assigned to the genus *Rugitela* Muir-Wood from the Fuller's Earth Rock of Somerset and said at the time to have a probable range of ? Inferior Oolite to ? Upper Jurassic.

Judd (1868) was the first to recognize Roemer's species *T. hippopus* in Lincolnshire where it occurs fairly abundantly in the Claxby Ironstone. Davidson (1874) erected a varietal name for the British form on the grounds of its larger dimensions, but these are directly proportionate to specimens from the type locality at Berklingen and from Saltzgitter, near Hanover. Furthermore, the pattern of variation in outline, width of shell and depth of dorsal sulcus is identical in both forms and there seems no point in upholding Davidson's varietal name.

SYSTEMATIC DESCRIPTIONS

Family **ZEILLERIIDAE** Allan, 1940

Genus ***VECTELLA*** nov.

Diagnosis. Shell elongate-oval, sulco-carinate to biconvex, rectimarginate to uniplicate or sulcate. Umbo massive, beak suberect. Foramen circular. Beak-ridges sharp, mesothyrid; interarea short. Test smooth, finely punctate. Deltidial plates conjunct. Short, subparallel dental lamellae embedded in callus; in mature individuals these lamellae support massive, peg-like, inwardly directed hinge-teeth. Cardinal process poorly developed. Acute septalium forms broad V-shaped hinge-trough supported by short, thick, persistent dorsal median septum. Crural bases triangular, giving rise to zeilleriiform brachial loop developed ventrally.

Type species. *Waldheimia celtica* Morris 1854 : 158.

Locality and horizon. In addition to the type-species, which comes from the Upper Aptian, *Parahoplites nutfieldensis* Zone, Shanklin, Isle of Wight, *Vectella* is represented at an equivalent horizon at Upware (Cambridgeshire) by *V. woodwardi* (Walker) and *V. angusta* (Walker) and by *V. morrisi* (Meyer) from the Bargate Beds of Surrey, from Brickhill (Buckinghamshire) and from Shanklin, Isle of Wight.

Remarks. *Vectella* is probably a further development of the Jurassic genus *Ornithella* but differs in its more acute septalium and deeper hinge-trough, more acutely triangular hinge-plates and crural bases, and more extensive inner socket-ridges. It differs from *Tamarella* nov. and *Rugitela* in its thicker shell, fused dental lamellae and narrower, anteriorly plane, septalium.

Vectella celtica (Morris)

(Pl. 1, figs. 4*a–c*; Text-fig. 2)

1847 *Terebratula longa* Roemer; Davidson & Morris : 255, pl. 19, figs. 1 & 1*a–d*.
1854 *Waldheimia celtica* Morris : 158.
1855 *Waldheimia* (*Terebratula*) *celtica* Morris; Davidson : 73, pl. 9, figs. 32–35.
1874 *Waldheimia celtica* Morris; Davidson : 47, pl. 6, fig. 15.

Description. Biconvex, elongate-oval zeilleriid brachiopod, approximately

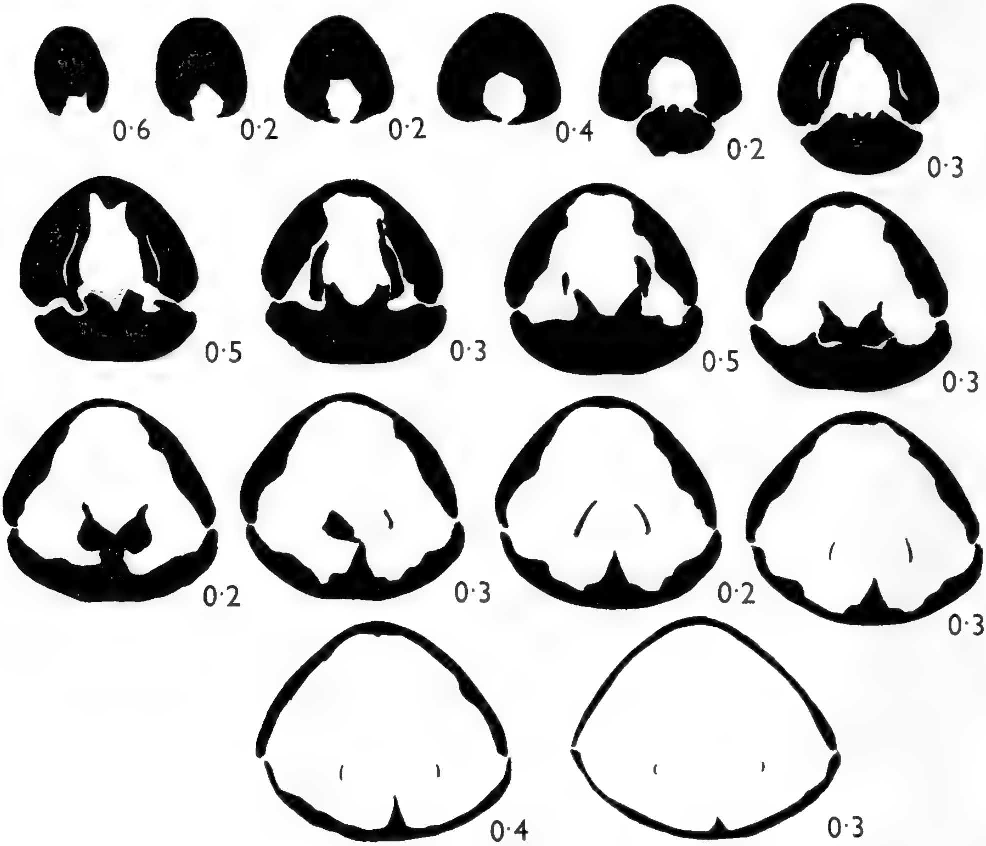

FIG. 2. A series of sixteen transverse sections through the umbonal part of *Vectella celtica* (Morris) from the Upper Aptian, Shanklin, Isle of Wight. BM. B.25801. ×2.

30 mm. long, 19 mm. wide and 18 mm. thick. It has a short, massive umbo, suberect beak and well exposed symphytium. The circular foramen is fairly large with mesothyrid beak-ridges bordering a short interarea. In young forms a marked sulcus is developed posteriorly in the brachial valve and may still be seen in some specimens of mature forms.

LECTOTYPE. Morris was the first to use the specific name *Waldheimia celtica* for a brachiopod from the Lower Greensand of Great Britain and listed it in the second edition of his catalogue (Morris 1854 : 158). He illustrated the species by indicating specimens in Davidson's Cretaceous Monograph which was not, in fact, published until a year later (Davidson 1855 : 73, pl. 9, figs. 32–35). One of these specimens had certainly been taken from a series of four given to Davidson by Morris and now in the Davidson Collection at the British Museum (Natural History), registered number B.6757. The specimens are here regarded as syntypes of *V. celtica* (Morris) and one, figured by Davidson (1855, pl. 9, fig. 33) is chosen as lectotype and has been re-registered BB.42915.

MATERIAL. The lectotype and numerous specimens in the Davidson Collection and general collection of the British Museum (Natural History) from the Upper Aptian, *Parahoplites nutfieldensis* Zone of Shanklin, Isle of Wight, registered as B.6757, B.25800, B.25802–25810. A specimen, B.14728, in the Sedgwick Museum, Cambridge shows the brachial loop and cardinalia in an almost perfect state of preservation.

REMARKS. This species probably illustrates an evolutionary link with some species of the Jurassic genus *Ornithella*. Externally, the long tapering oval outline, massive umbo and carinate pedicle valve suggest such species as *O. ornithocephala* (J. Sowerby) and *O. bathonica* (Rollier). Internally the thickened valve walls and callus embedded dental lamellae in the pedicle valve and the thick septum, supporting short, stout hinge-plates, have much in common with those of *O. bathonica* as shown in transverse serial sections by Muir-Wood (1934 : 544). It can be distinguished from either of the two Jurassic species in its shorter umbo, larger foramen and less acutely tapering valves. It is distinguished from other Lower Cretaceous forms, such as *V. woodwardi* (Walker), by its more regular oval outline, more incurved beak, smaller foramen and absence of anterior sulcation of the brachial valve. It differs from *V. morrisi* (Meyer) in its greater dimensions, stronger biconvexity and lack of uniplication of the anterior margin. It bears a superficial resemblance to *V. angusta* (Walker) from Upware and Brickhill but differs in having a more incurved beak and more robust general outlines. It is nevertheless very near this species.

Vectella angusta (Walker)

(Pl. 1, figs. 5*a–c*)

1868 *Waldheimia mutabilis* var. *angusta* Walker : 400, pl. 19, fig. 5, 5*a*.
1870 *Waldheimia mutabilis* var. *angusta* Walker ; Walker : 562.
1874 *Waldheimia wanklyni* var. *angusta* Walker ; Davidson : 51, pl. 7, figs. 26–28.

DESCRIPTION. Elongate-oval to fusiform *Vectella* about 34 mm. long, 18 mm. wide and 12 mm. thick. Maximum width midway between umbo and anterior margin. Biconvex with acute carination of pedicle valve. Large foramen dominating a slightly produced suberect umbo with wide interarea and well exposed symphitium. Extensive beak-ridges are well defined. Anterior commissure plane.

HOLOTYPE. British Museum (Natural History) no. 67601, figured by Walker (1868, pl. 19, figs. 5, 5*a*) as *Waldheimia mutabilis* var. *augusta*. From the Lower Greensand of Upware, Cambridgeshire.

MATERIAL. In addition to the holotype, eight specimens from Upware, registered no. B.2712 and seventeen specimens from Brickhill, Buckinghamshire, registered no. B.25503, all in the British Museum (Natural History).

REMARKS. As in the case of *Tamarella elliptica* (Walker), this species was originally described as a variety of *Waldheimia mutabilis*, a name already used by Oppel (1861 : 538) for a Liassic species. On Walker's instructions the name *W. wanklyni* was substituted by Davidson (1874 : 51) for *W. mutabilis* Walker.

Walker neither selected nor indicated a type specimen for *W. mutabilis* [= *W. wanklyni*] and the species is, therefore, in doubt. The variety *augusta*, however, is easily recognizable as a form from the Lower Greensand of Upware and Brickhill. It is in no way related to the species *Tamarella elliptica* and is here promoted to specific rank.

Somewhat resembling *V. celtica* (Morris) in general outline, *V. augusta* differs in less clearly defined features, more acutely convex brachial valve and produced umbo. The form from Brickhill has a shorter umbo and is more regularly elongate-oval in outline than the typical form. It also has a slight depression or sulcus visible on the brachial umbonal region. This depression is more marked in younger specimens.

Vectella woodwardi (Walker)

(Pl. 1, fig. 1*a–c* ; Text-fig. 3)

1867 *Waldheimia woodwardi* Walker ; 455, pl. 19, fig. 3.
1868 *Waldheimia woodwardi* Walker ; Walker : 404.
1874 *Waldheimia woodwardi* Walker ; Davidson : 52, pl. 6, figs. 1–5*a*.
1883 *Waldheimia woodwardi* Walker ; Keeping : 21.

DESCRIPTION. Elongate-oval *Vectella*, about 37 mm. long, 20 mm. wide and 19 mm. thick. The pedicle valve is acutely carinate with steep flanks. It has a short, suberect umbo truncated by a large, circular foramen. Sharp mesothyrid beak-ridges border a short, flat interarea. The finely punctate shell surface is covered by numerous fine growth-lines. A shallow sulcus originating from the umbo in the brachial valve broadens anteriorly. The internal characters are as described for the genus.

LECTOTYPE. The original specimen described and figured by Walker (1867) is one of the two syntypes originally registered with the Walker Collection in the British Museum (Natural History) as 62202. It has been re-registered as BB.42910 and is here selected as lectotype.

MATERIAL. Eighteen specimens in the general collection of the British Museum (Natural History) nos. B.25717, B.25801, 62202, BB.21130–38, BB.42922, all from the type locality at Upware, and several internal moulds from Potton.

REMARKS. *Vectella woodwardi* is known from the type locality at Upware (Cambridgeshire) and from Potton (Bedfordshire), where it occurs in the *Parahoplites nutfieldensis* Zone of the Upper Aptian. In many respects it resembles *V. celtica* (Morris) which occurs at the same horizon at Shanklin, Isle of Wight but differs in shell convexity and beak characters. These differences in morphology may be due merely to change of environment.

The broad sulcation of the brachial valve in *V. woodwardi* and the shorter, more massive umbo and larger foramen distinguish the species from *V. morrisi* (Meyer) and *V. angusta* (Walker).

Vectella morrisi (Meyer)

(Pl. 1, fig. 7 ; Text-fig. 4)

(Pl. 3, figs. 7–9)

1863 *Terebratula moutoniana* Lankester : 414, pl. 19, figs. 1–3. (non d'Orbigny 1848).
1864 *Waldheimia moutoniana* Lankester ; Meyer : 251, figs. 12–14.
1868 *Waldheimia morrisi* Meyer : 269.
1874 *Waldheimia morrisi* Meyer ; Davidson : 47.

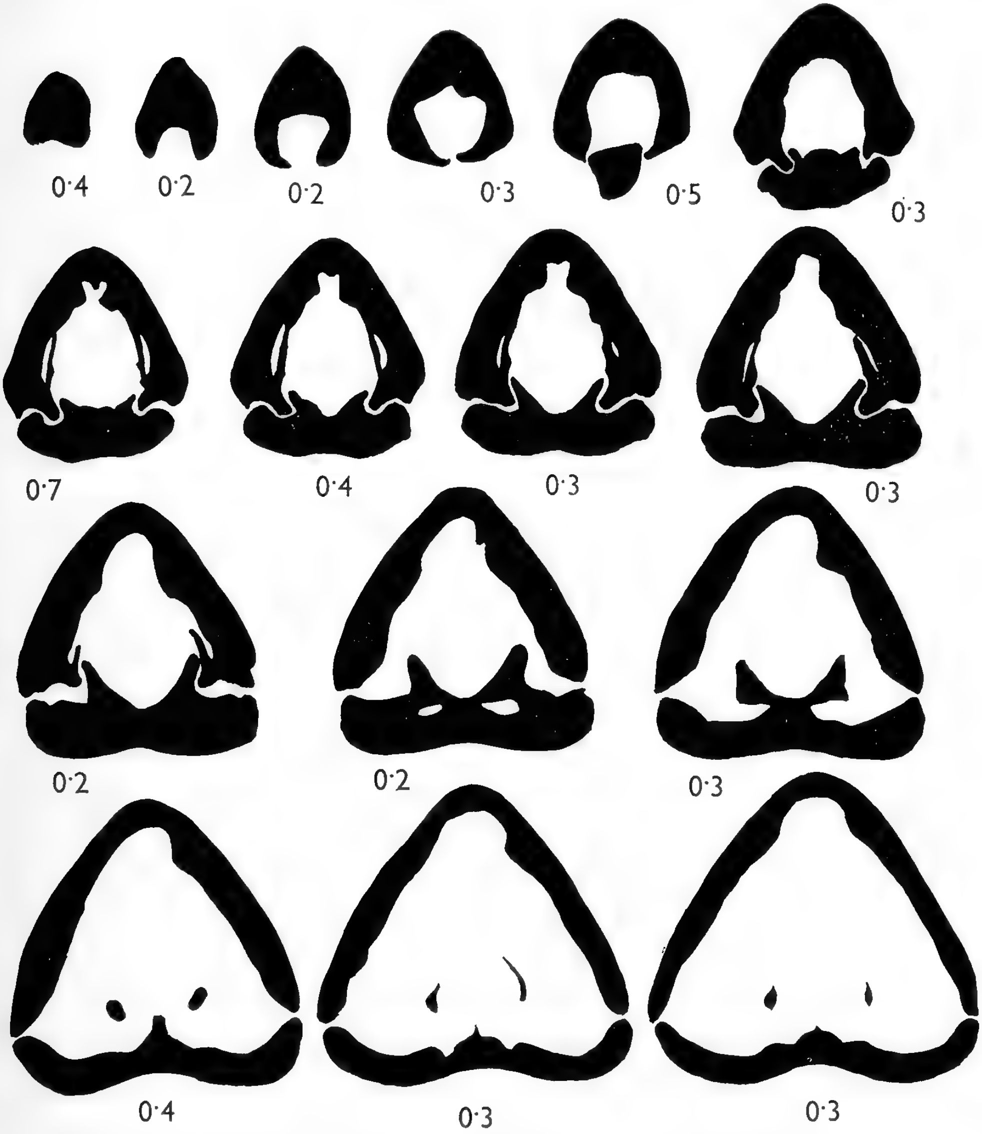

FIG. 3. Sixteen transverse serial sections through the umbo of *Vectella woodwardi* (Walker) from the Upper Aptian, Upware, Cambridgeshire. BM. B.42922. ×2.

DESCRIPTION. Although somewhat terebratulid in general aspect, *Vectella morrisi* is characteristically oval in outline with a shorter, more incurved umbo than other described species of *Vectella*. Both valves are comparatively flat but the brachial valve has a marked median ridge extending two-thirds of the shell length and giving rise to fairly steep flanks. The pedicle valve remains gently convex. The anterior commissure is marked by a faint uniplication distinguishing it from

V. celtica (Morris) which it somewhat resembles. The typical form occurring at Shanklin, Isle of Wight reaches a maximum length of 23 mm., a width of 17 mm. and attains an average thickness of 11 mm.

LECTOTYPE. Meyer (1864 : 249) first described the species as *Terebratula moutoniana* Lancaster and later (1868 : 269) re-described it under the binomen *Waldheimia morrisi* referring to the figured specimens (1864 : figs. 12–14) of his earlier work. Two of the specimens figured by Meyer (figs. 12, 13) were stated to have been collected from the Pebble-bed of Shanklin, while the other (fig. 14) was said to have come from the Pebble-bed of Godalming, Surrey.

These specimens, here regarded as syntypes of *V. morrisi*, are in the Sedgwick Museum, Cambridge and are registered as B.14770–71 and B.16785. The lectotype, here selected, is B.14771. It was originally figured by Meyer (1864, pl. 12, fig. 13) and was collected from the Pebble-bed, *Parahoplites nutfieldensis* Zone, Shanklin, Isle of Wight.

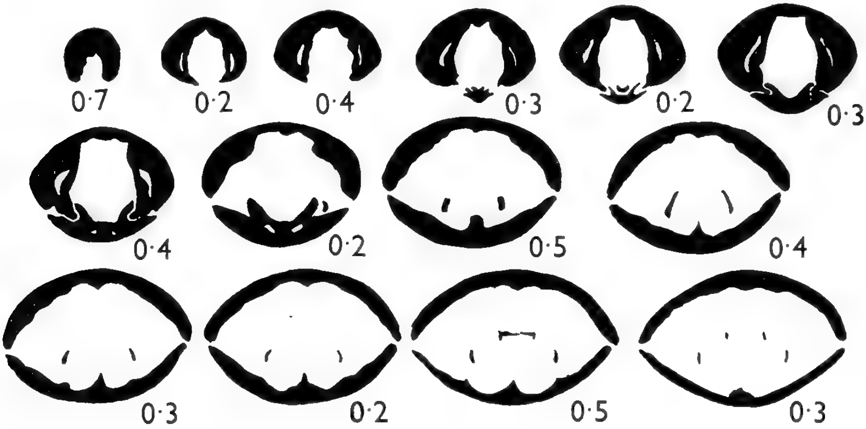

FIG. 4. Fourteen transverse serial sections through the umbo of *Vectella morrisi* (Meyer) from the Upper Aptian, Shanklin, Isle of Wight. BM. B.21937. ×2.

MATERIAL. Apart from the type specimens mentioned above, there are forty-two specimens in the Sedgwick Museum, Cambridge, twenty-nine from Shanklin and thirteen from the Bargate Pebble-bed of Godalming, Surrey, registered B.16838–50, B.14761–69, B.14776–89. Also there are fifty-four specimens in the general collection and Davidson Collection of the British Museum (Natural History) registered B.25506–9, B.6740, B.25815–16, BB.42914, BB.42916–18.

REMARKS. A smaller form of *V. morrisi*, though with similar proportions, occurs in the Bargate Pebble-beds of Surrey and beds of equivalent age at Brickhill, Buckinghamshire. The latter has often been confused with *Tamarella juddi* (Walker) but differs from this species in its more regular oval outline, less acutely convex valves, steeper flanks, shorter umbo, less extensive interarea, rounded beak-ridges and simpler zeilleriform brachial loop. It is approximately 17 mm. long, 11 mm. wide and 8 mm. thick.

Genus *TAMARELLA* nov.

DIAGNOSIS. Shell biconvex. Circular to elongate-oval to pentagonal in outline. Folding rectimarginate to incipiently uniplicate to ligate. Umbo massive, suberect; beak-ridges sharp. Deltidial plates conjunct. Foramen large, mesothyrid. Shell surface often with marked concentric growth-lines. Median septum short, extending less than one third the length of brachial valve. Septalium broad, shallow, anteriorly arched. Hinge-plates fused, overlapping. Long brachial loop unattached to median septum in adult stage, given off ventrally.

TYPE SPECIES. *Terebratula tamarindus* J. de C. Sowerby 1836.

RANGE. Upper Aptian.

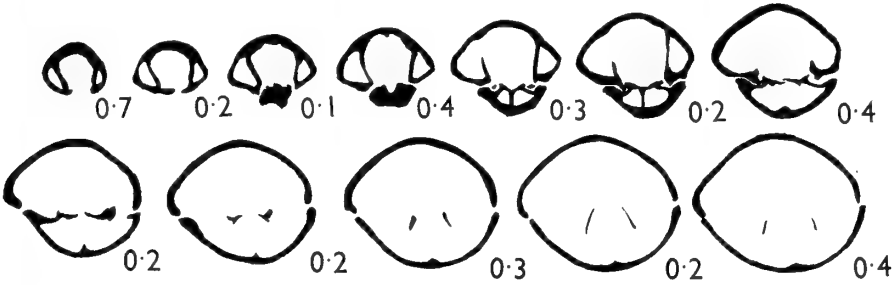

FIG. 5. Twelve transverse serial sections through the umbonal part of *Tamarella tamarindus* (J. de C. Sowerby) from the Upper Aptian, Shanklin, Isle of Wight. BM. B.506. ×2.

Tamarella tamarindus (J. de C. Sowerby)

(Pl. 1, figs. 2*a*–*c*, 8*a*–*c*, 10*a*–*c*, Pl. 3, figs. 5*a*–*c*, 6*a*–*c*; Text-figs. 5, 6)

1836	*Terebratula tamarindus* J. de C. Sowerby : 338, pl. 14, fig. 8.
1843	*Terabratula tamarindus* Sowerby ; Morris : 137.
1855	*Waldheimia tamarindus* (J. de. C. Sowerby), Davidson : 74, pl. 9, figs. 26–31.
1868	*Terebratula tamarindus* var. *magna* Walker : 465, pl. 19, fig. 10.
1874	*Waldheimia tamarindus* var. *magna* (Walker) Davidson : 49, pl. 6, figs. 16–19*a*.
1955	*Psilothyris tamarinda* (Sowerby) Cooper : 14, pl. 3, fig. 25.

DESCRIPTION. *Tamarella* subcircular to elongate-oval in general outline. Acutely biconvex to almost orbicular. Approximately 11 mm. long, 10 mm. wide and 8 mm. thick. The massive umbo is truncated by a large foramen. Well marked mesothyrid beak-ridges border extensive interarea. Shell surface evenly punctate and ornamented by fine concentric growth-lines. The anterior commissure is rectimarginate to incipiently uniplicate. There is sometimes a shallow anterior depression or sulcus bordered by faint carinae noticeable on the pedicle valve. Shell margins show a tendency to gerontic thickening.

NEOTYPE. J. de C. Sowerby *in* Fitton (1836 : 338) described a zeilleriid brachiopod from the Lower Greensand near Hythe, Kent, under the name *Terebratula tamarindus*. No type material was indicated but a specimen, stated to belong to the Sowerby

Collection, was figured (pl. 14, fig. 8) and is now lost. Sowerby's description refers to a specimen with an orbicular outline and with beak-ridges extending some distance down the sides of the valves. The figured specimen appears flattened in lateral profile and with short beak-ridges which are not clearly defined. Although its geo-

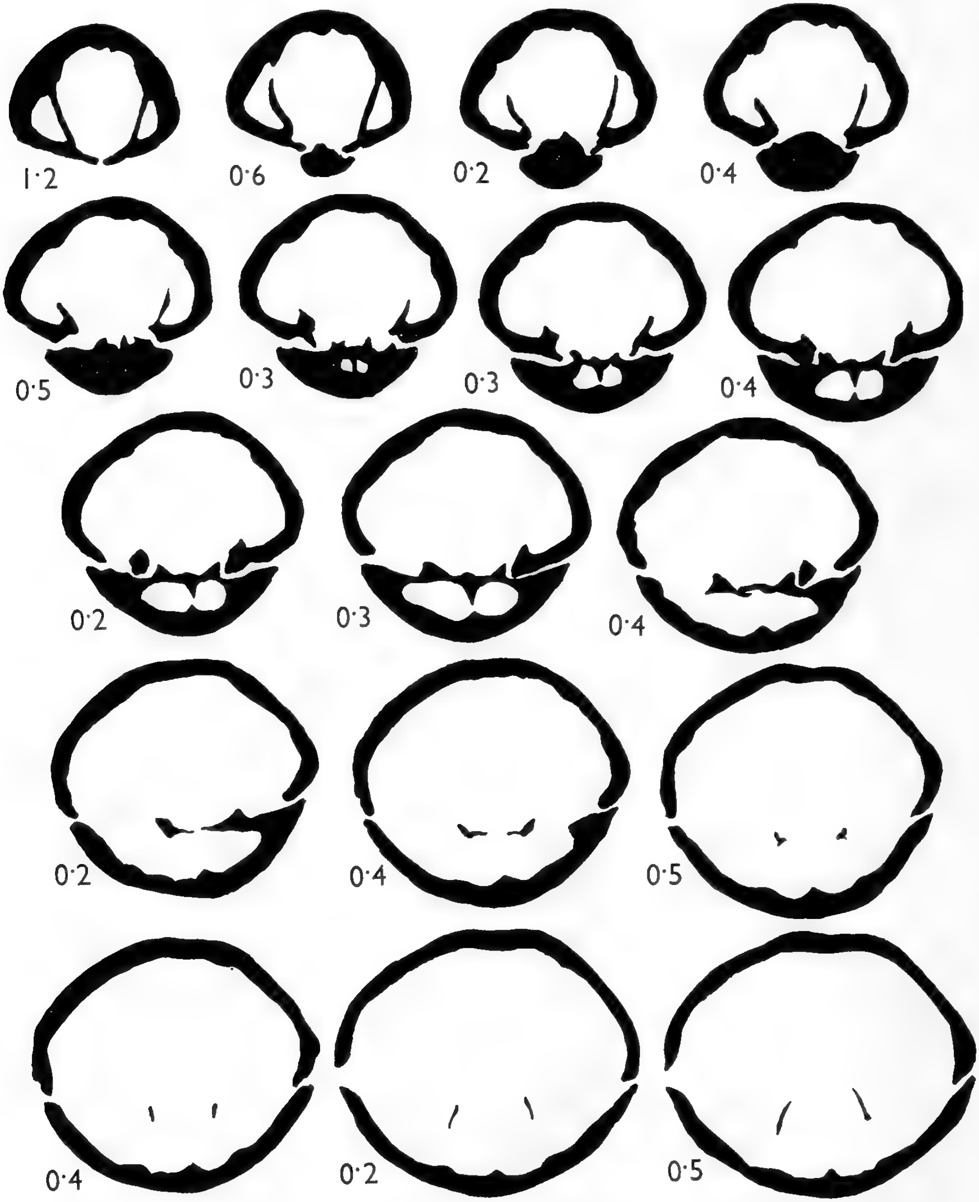

FIG. 6. Seventeen transverse serial sections through the umbo of *Tamarella tamarindus* (J. de C. Sowerby) from the Upper Aptian, Upware, Cambridgeshire. BM. B.25693. ×2.

logical age was stated to be Lower Greensand, no precise beds were mentioned within this horizon nor was any associated fauna listed. Its geological age must, therefore, remain broadly defined. Furthermore, the type locality, said to be "near Hythe, Kent ", although suggesting a Hythe Beds origin, might alternatively have indicated the Sandgate Beds (Upper Aptian) or even an Albian horizon.

The present widely accepted connotation of a brachiopod under the specific name *tamarindus* is Davidson's description (1855 : 74) under the binomen *Waldheimia tamarindus* (J. de C. Sowerby). Davidson figured six specimens from various localities of Lower Greensand age, including one specimen (pl. 9, fig. 26) stated to have been collected from between Hythe and Sandgate, Kent. Unfortunately none of the six specimens figured by Davidson is available in the Davidson Collection and they cannot be traced elsewhere.

Although Sowerby's definition of *Terebratula tamarindus* was vague, the name is so entrenched in literature that it would seem a pity not to preserve it. The preservation of the name, however, depends on the erection of a neotype to replace Sowerby's original figured specimen.

The Lower Greensand includes, among other horizons, the Sandgate Beds (Upper Aptian), which crop out between Hythe and Sandgate, Kent, and from which Sowerby's specimen is likely to have been collected. It is no longer possible to collect brachiopod specimens from the Sandgate Beds exposed in this area but beds of an equivalent age falling within the *Parahoplites nutfieldensis* Zone occur at Shanklin, Isle of Wight and occasionally contain specimens which agree with the original description of *Terebratula tamarindus* J. de C. Sowerby. They also compare favourably with specimens figured by Davidson (1855) from " near Sandgate " and from the Isle of Wight.

A specimen probably used by Davidson (1855 : 74) in his description of the species is figured here (Pl. 3, fig. 5) and proposed as neotype. This specimen, originally registered as B.6724, forms part of the Davidson Collection in the British Museum (Natural History) and was collected from the Upper Aptian beds of Shanklin, Isle of Wight. It has been re-registered as BB.42907.

MATERIAL. A further sixty-one specimens of *Tamarella tamarindus* (J. de C. Sowerby), all from the Isle of Wight, are contain in the general collection and the Davidson Collection at the British Museum (Natural History) and are registered as B.506, B.6724, B.25820, B.25187, BB.42905, BB.42906, BB.42919, BB.42920.

REMARKS. A larger form of this species approximately 24 mm. long, 21 mm. wide and 15 mm. thick occurs in the Upper Aptian at Upware and Potton. It was originally described and figured as *Terebratula tamarindus* var. *magna* by Walker (1868 : 465, pl. 19, fig. 10) but agrees in every detail with the typical form and has proportionately similar dimensions. *T. tamarindus* is distinguished from other described species of *Tamarella* by its acute biconvexity and almost circular general outline.

Tamarella bonneyi (Keeping)

(Pl. 1, figs. 3*a–c* ; Text-fig. 7)

1883 *Waldheimia bonneyi* Keeping : 129, pl. 7, fig. 4.

DESCRIPTION. Oval to pentagonal, somewhat cinctiform in outline, this species attains an approximate length of 32 mm. with a maximum width of 24 mm. and thickness of 17 mm. Each broad, flattened valve has a shallow anterior sulcation and is ornamented by numerous distinct or clearly defined concentric growth-lines. The umbo is not so produced as in other species of *Tamarella* but shows the same broad, flat interarea bordered by sharp beak-ridges. Although constantly biconvex, the degree of convexity of each valve varies considerably in *T. bonneyi*. Some forms have an almost flat pedicle valve with an acutely convex brachial valve. Others are almost equally biconvex and, apart from their greater length, resemble *T. tamarindus* from Upware.

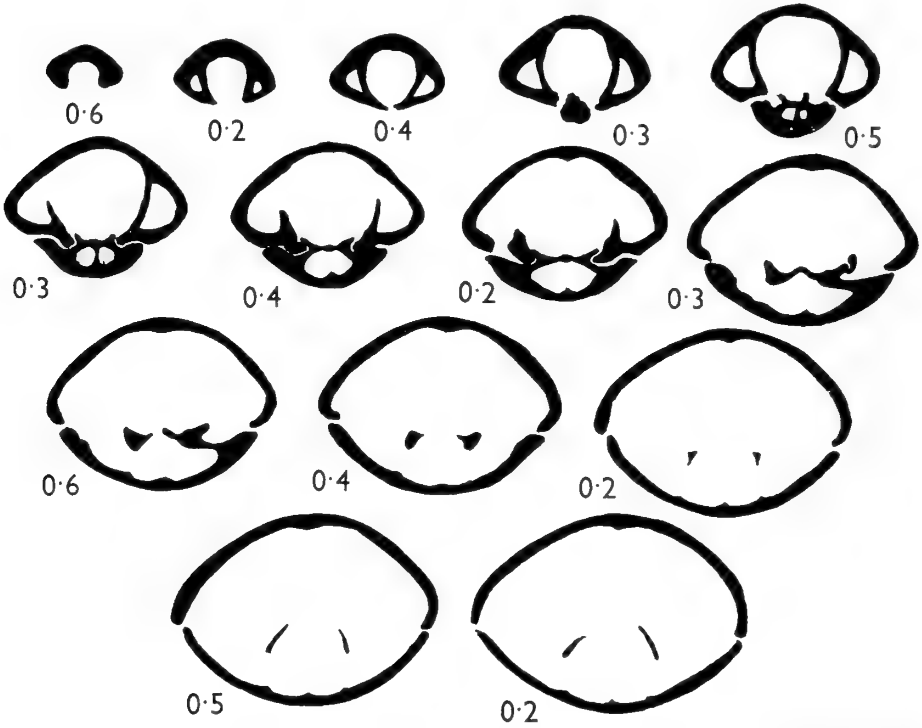

FIG. 7. A series of fourteen transverse serial sections through the umbo of *Tamarella bonneyi* (Keeping) from the Upper Aptian of Brickhill, Buckinghamshire. BM. B.25493. × 2.

HOLOTYPE. B.26803 from the Lower Greensand, Upper Aptian of Brickhill, Buckinghamshire in the collections of the Sedgwick Museum, Cambridge.

MATERIAL. In addition to the holotype, thirty-eight specimens from Brickhill are in the Sedgwick Museum registered as B.80836–39, B.26509–19, B.25490–513 and thirty-six specimens in the general collections of the British Museum (Natural History) registered as B.25492–93, B.25499.

REMARKS. There is a marked similarity between this species and *Tamarella vesta* sp. nov. and attempts have been made to illustrate gradation from one species to another. A series registered B.25490–531 in the Sedgwick Museum illustrates this variation. *T. bonneyi*, however, appears to be confined to the deposits at Brickhill and *T. vesta* is only rarely found at this locality while it is abundant at Upware.

Tamarella bonneyi is distinguished from *T. vesta* and other species of *Tamarella* mainly by its larger dimensions, broad cinctiform outline and more marked concentric growth-lines.

Tamarella juddi (Walker)

(Pl. 1, figs. 11*a–c*; Text-fig. 8)

1868 *Waldheimia rhomboidea* Walker : 400, pl. 18, figs. 3, 4.
1870 *Waldheimia juddi* Walker : 562.
1874 *Waldheimia juddi* Walker ; Davidson : 50, pl. 7, figs. 15–18.

DESCRIPTION. *Tamarella* about 19 mm. long, 14 mm. wide and 12 mm. thick. Elongate-oval in outline with a maximum width just less than half the distance from the umbo to the anterior margin. Acutely biconvex in lateral profile with marked marginal growth-lines. Short massive umbo and suberect beak with large foramen and sharp mesothyrid beak-ridges. An extensive interarea exposes conjunct deltidial plates. Anterior margin laterally compressed and incipiently uniplicate.

LECTOTYPE. Although the species was originally described by Walker (1868 : 400) as *Waldheimia rhomboidea*, it has never been referred to under this name. Walker mistakenly thought the name to be preoccupied by *Terebratula rhomboidea* Barondi 1855, from the Tertiary of Italy and subsequently changed the name (1870 : 562) to *Waldheimia juddi*. As a junior synonym of *W. rhomboidea*, *W. juddi* has

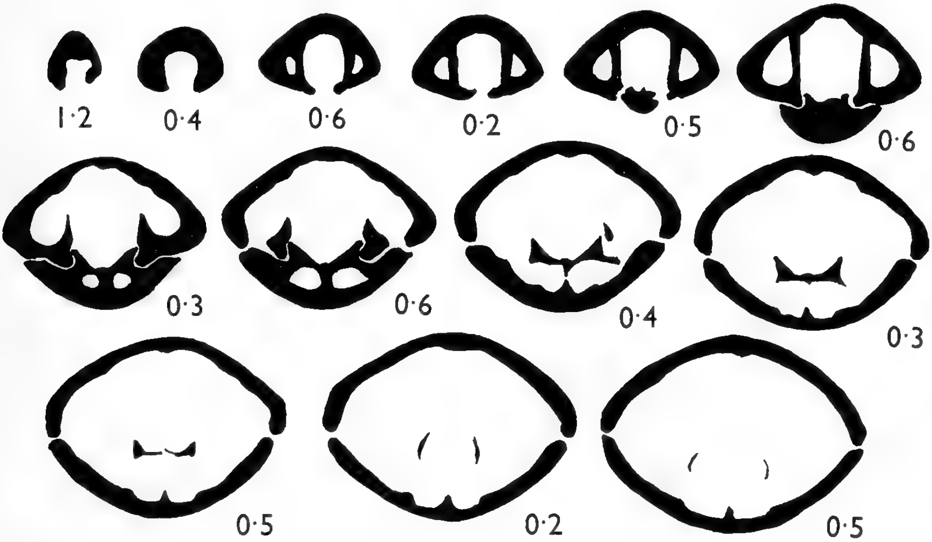

FIG. 8. Thirteen transverse serial sections through the umbo of *Tamarella juddi* (Walker) from the Upper Aptian of Upware, Cambridgeshire. BM. B.25681. × 2.

since become entrenched in literature as the name of a well known fossil brachiopod and is maintained here. Walker's (1868) original description was accompanied by figures of two specimens from the type locality at Upware which are in the general collections at the British Museum (Natural History) registered as 67602. The larger has been re-registered as BB.42929 and is here selected as lectotype (Pl. 1, figs. 11*a–c*).

MATERIAL AND LOCALITY. In addition to the type material, there are fifty-eight specimens in the British Museum (Natural History) registered as B.25681 and B.25682. Among seven specimens in the Sedgwick Museum from the Upper Aptian of Faringdon, registered as B.18400–06, one specimen, B.18400, shows a well exposed brachial loop and cardinalia which appear to be very similar to Cooper's figure of *Psilothyris* (Cooper 1955, pl. 3, fig. 19). The thickened portion of the descending branches can be clearly seen.

REMARKS. *Tamarella juddi* is distinguished from other species of *Tamarella* by its acute biconvexity, extensive interarea, laterally compressed and tapering anterior and smaller foramen.

Tamarella vesta sp. n.

(Pl. 1, figs. 9*a–c* ; Text-fig. 9)

1868 *Waldheimia pseudojurensis* (Leymerie) ; Walker : 405, pl. 18, figs. 8–11.
1874 *Waldheimia pseudojurensis* (Leymerie) : Davidson : 48, pl. 7, figs. 12–14.

DIAGNOSIS. *Tamarella* about 22 mm. long, 15 mm. wide and 10 mm. thick. Shell biconvex, elongate-oval to pentagonal in outline. Anterior commissure plane. Folding ligate. Test smooth with prominent growth-lines. Umbo slightly produced, suberect. Deltidial plates conjunct, well exposed. Beak-ridges sharp.

DESCRIPTION. Although characteristically elongate with steep flanks and slightly produced umbo, the range of variation within this species includes forms which are broader and, in some cases, more inflated than the typical. Marked gerontic thickening of the shell margins tends to accentuate the anterior sulcation of each valve.

The generic characters seen in transverse serial sections (Text-fig. 9) show very clearly the overlapping hinge-plates which appear to be more marked in *T. vesta* than in the type-species *T. tamarindus* (J. de C. Sowerby).

HOLOTYPE. This was originally one of four specimens in the Walker Collection, British Museum (Natural History) which were used in Walker's description of the species under the name *Waldheimia pseudojurensis* Leymerie. The holotype was figured by Walker (1868, pl. 18, fig. 8) and was collected from the Upper Aptian of Upware, Cambridgeshire. It has been re-registered as BB.42904.

MATERIAL AND LOCALITY. In addition to the holotype, forty-eight specimens from Upware registered as B.25498, B.25699, B.25701, B.25703. In the Davidson Collection there are nine specimens from Upware registered as B.6754 and three from Brickhill registered as B.6755, all in the British Museum (Natural History).

REMARKS. Often confused with *Terebratula pseudojurensis* Leymerie from the Middle Neocomian of Marolles, Aube, France, *Tamarella vesta* nevertheless bears a superficial resemblance to this species. It differs fundamentally in its internal

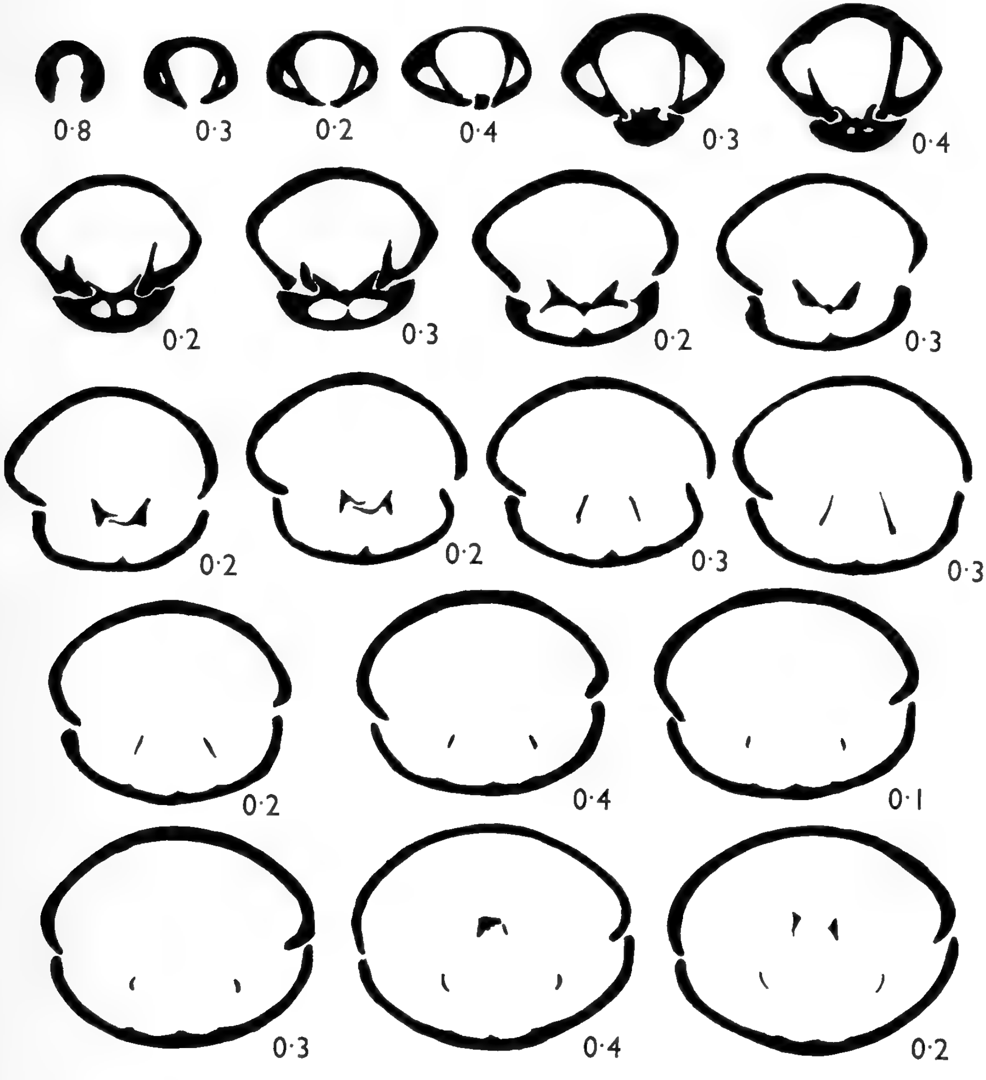

FIG. 9. Twenty transverse serial sections through the umbo of *Tamarella vesta* sp. n. from the Upper Aptian of Upware, Cambridgeshire. BM. B.25700. ×2.

generic characters which can be seen in serial section (Text-fig. 9). It is distinguished from *T. bonneyi* (Keeping) by its more elongate outline, steeper flanks, more produced umbo and less prominent concentric growth-lines. It differs from *T. juddi* and *T. tamarindus* in having flatter or less convex valves and ligate anterior margin.

A common fossil in the Upper Aptian beds of Upware, *T. vesta* occurs, though less commonly, in beds of equivalent age at Brickhill, Buckinghamshire and at Potton, Bedfordshire.

Tamarella elliptica (Walker)

(Pl. 1, figs. 6*a*–*c*)

1868 *Waldheimia mutabilis* var. *elliptica* Walker : 400, pl. 19, fig. 4.
1870 *Waldheimia mutabilis* var. *elliptica* Walker ; Walker : 562.
1874 *Waldheimia wanklyni* var. *elliptica* Walker ; Davidson : 51, pl. 7, figs. 22–25.

DESCRIPTION. Large oval *Tamarella* approximately 35 mm. long, 26 mm. wide and 15 mm. thick. Both valves are equiconvex and the lateral commissure is almost straight. Somewhat resembling *T. bonneyi* (Keeping) in general outline and convexity, *T. elliptica* lacks the ligation of the anterior margin noted in the former species. A large circular foramen truncates a broad, flattened umbo. Sharp beak-ridges border a fairly extensive interarea. The shell surface is smooth apart from a trace of concentric growth-lines which become more prominent at the margins.

HOLOTYPE. In the British Museum (Natural History) registered number 67600, and figured by Walker (1868, pl. 19, fig. 4) as *Waldheimia mutabilis* var. *elliptica*. It was collected from the Upper Aptian of Upware.

REMARKS. Walker (1868 : 400) used the name *Waldheimia mutabilis* for a brachiopod from the Lower Greensand of Upware. No specimen was figured nor was any type material indicated. Instead, two forms which Walker called " varieties or sub-species " were erected and named *W. mutabilis elliptica* and *W. mutabilis angusta*. The descriptions of these were accompanied by illustrations (1868, pl. 19, figs. 4, 5) of two specimens now in the British Museum (Natural History) and registered as 67600 and 67601 respectively.

Walker's conception of the species *W. mutabilis* having been established on the description of the two " varieties or sub-species ", is, therefore, indefinable. In any case, the name *Waldheimia mutabilis* had already been used by Oppel (1861) for a zeilleriid brachiopod from the Lower Lias of Germany, and it was for this reason that Walker asked Davidson (1874 : 51) to correct the name to *wankylni* in his Cretaceous monograph.

The varietal name *elliptica* is here raised to specific rank and referred to *Tamarella* gen. nov. The varietal name *angusta* has also been raised to specific rank and referred to *Vectella* gen. nov. on p. 53. Both species are common members of collections of brachiopods from Upware and are easily recognizable.

Genus ***RUGITELA*** Muir-Wood, 1936

Rugitela roemeri sp. n.

(Pl. 2, figs. 1*a*–*c*, 3*a*–*c*, 6*a*–*c*, 8*a*–*c*, 9*a*–*c* ; Text-fig. 10)

1836 *Terebratula longa* Roemer : 50, pl. 2, fig. 11.
1839 *Terebratula longa* Roemer ; Roemer : 22, pl. 18, fig. 12.
1840 *Terebratula longa* Roemer ; Roemer : 44, No. 50.
1847 *Terebratula faba* Sowerby ; d'Orbigny : 77, pl. 506, figs. 8, 9, 11, 12.
1864 *Terebratula* (*Waldheimia*) *faba* Sowerby ; Credner : 561, pl. 21, figs. 3, 4, 5.
1868 *Terebratula longa* Roemer ; Quenstedt : 338, pl. 4,6 fig. 99.

DIAGNOSIS. *Rugitela* about 28 mm. long, 18 mm. wide and 14 mm. thick. Shell biconvex, oval to subtriangular in outline. Umbo short, massive, suberect. Extensive interarea bordered by sharp, mesothyrid beak-ridges. Foramen large, circular. Deltidial plates well exposed, conjunct. Anterior margin rectimarginate to sulcate.

HOLOTYPE. British Museum (Natural History) no. BB.42912, from the Neocomian, Hilsconglomerat of Elligser Brinke, near Hanover, North Germany. According to Judd (1870 : 331) the " Elligser Brinke Schist " has its English equivalent in the *Acanthodiscus speetonensis* Zone at Speeton, Yorkshire and in Lincolnshire.

DESCRIPTION. This species is characteristically elongate-oval in outline with marked growth-lines becoming still more prominent at the margins. Gerontic thickening of the anterior and lateral margins is a common feature. Some variants show a tendency to broad anterior sulcation of the brachial valve.

Internal characters. Short, slightly curved, divergent dental lamellae are embedded in thick callus and support inwardly curving hinge-teeth. Cardinal process not developed. A short septalium develops with long, fused hinge-plates which are deflected ventrally forming a small anterior plication. A long median septum extending two-thirds the length of the shell supports the hinge-plates. Inner and outer socket-ridges are extensive and well marked. Triangular crural bases give rise to thick descending branches of the brachial loop with dorsal development and short crural processes. Fairly broad transverse band developed from ascending branches of the loop. A thickening of the descending branches at a point about one-third the distance from the hinge-plates has been noted in mature forms so far sectioned and may be due to resorption of the attachment branches to the median septum in the dorsal valve. No attachment of brachial loop to septum has been noted in any sections of either young or mature forms.

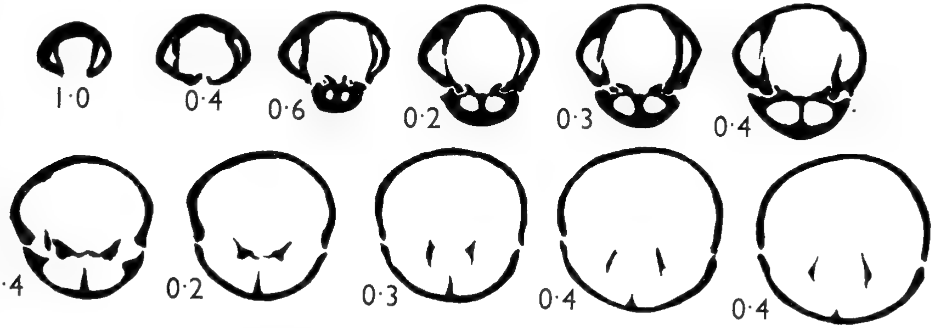

FIG. 10. Eleven transverse serial sections through the umbo of *Rugitela roemeri* sp. n. from the Neocomian of Berklingen, North Germany, showing the characteristic W-shaped hinge-plates and thickened area of the descending branches of the brachial loop. BM. B.35656. ×2.

REMARKS. Zieten (1830 : 52) was the first to use the binomen *Terebratula longa* for a terebratelloid brachiopod which he figured (pl. 39, fig. 7) from the " calcaire jurassique " [Upper Jurassic] of Donzdorf, North Germany. Roemer's description of *Terebratula longa* (1836 : 50, pl. 2, fig. 11) from the Neocomian of Hanover was, therefore, invalid.

D'Orbigny (1847 : 77, pl. 506, figs. 8–12) described and figured a brachiopod from the Neocomian of St. Dizier, Haute Marne, France, and assigned it to *Terebratula faba* Sowerby, a name which J. de C. Sowerby (1836 : 338) had originally used in a description of a brachiopod from the Lower Greensand beds between Folkestone and Sandgate, Kent. Specimens collected from the Lower Albian beds of Folkestone in the Sedgwick Museum (B.17633–17650), have been matched with others collected from the *Leymeriella tardefurcata* Zone of Folkestone by Dr. R. Casey and compare favourably in size, general outline and convexity with *Terebratula faba* as figured by J. de C. Sowerby (1836, pl. 14, fig. 10). A duplicate specimen (Brit. Mus (N.H.) no. B.25994) has been sectioned (Text-fig. 12) and is shown to belong to the genus *Modestella* Owen (1961 : 573) described from the Lower Albian of Folkestone.

D'Orbigny's illustrations (1847, pl. 506, figs. 8–12) were probably an idealization of eight specimens which were collectively numbered 5159 in the d'Orbigny Collection, Laboratoire de Paléontologie, Muséum National d'Histore Naturelle, Paris. Unfortunately only four of these specimens can be traced. One has been identified as a specimen of *Vectella celtica* (Morris) from the Lower Greensand of the Isle of Wight, and another (see Pl. 2, figs. 8*a–c*) is almost identical with the specimen figured by Roemer (1839, pl. 18, fig. 12) from the Neocomian of Hanover.

Rugitela roemeri occurs rarely in Britain, being found in the upper part of the Claxby Ironstone, Lincolnshire and in the Speeton Clay of Yorkshire. A fine, well preserved specimen (Pl. 2, figs. 1*a–c*) from the Claxby Ironstone of Nettleton, Lincolnshire, collected by Mr. Peter Rawson of Hull University, is the only example known from these beds which compares exactly with Roemer's original illustration (1836, pl. 2, fig. 11). The dimensions of this specimen are : 40 mm. long, 20 mm. wide and 16 mm. thick.

A form described here as *Rugitela rugosa* sp. n. resembles *R. roemeri* but is shorter, more gibbous and oval in outline with no marked sulcation of the anterior portion of the brachial valve. It is found in the same beds of the Claxby Ironstone and is probably present in the Speeton Clay, although specimens collected from beds within the range C6 to C3 of Swinnerton (1936–55) and which may belong to this species are too crushed for accurate determination. *R. rugosa* also occurs in the Hauterivian at Salins-les-Bains in the French Jura Mountains. A well preserved example is figured here (Pl. 2, figs. 5*a–d*) for comparison.

The reference of this species to the genus *Rugitela* has been made after careful comparison with transverse serial sections of the type-species *R. bullata* Muir-Wood and extends the range of the genus from ? Inferior Oolite to the Lower Cretaceous. It is possible that the final range may include species from the Inferior Oolite at present under review by Dr. H. M. Muir-Wood.

MATERIAL AND LOCALITY. Well preserved material from the German Neocomian is rare but there are, in addition to the holotype metioned above, nine other specimens in the Davidson Collection, Brit. Mus. (Nat. Hist.) B.6759, BB.41911, from the " Elligser Brinke Schist " of Delligsen near Hanover.

A specimen from the Neocomian of St. Dizier in the Haute-Marne is also in the Davidson Collection (B.6736). It is accompanied by the note in Davidson handwriting which reads : " . . . given to me by d'Orbigny . . . from the d'Orbigny Coll . . . "

Seven specimens, British Museum (Natural History) (BB.42925–31), from the *Acanthodiscus speetonensis* Zone of the Speeton Clay, Yorkshire. Although crushed they compare favourably with the North German forms.

Rugitela rugosa sp. n.

(Pl. 2, figs. *2a–c*, *4a–c*, *5a–c* ; Text-fig. 11)

1874 *Waldheimia faba* d'Orbigny ; Davidson : pl. 6, figs. 12–14.

Diagnosis. Biconvex *Rugitela* about 29 mm. long, 17 mm. wide and 17 mm. thick. Oval to sub-circular in outline. Shell surface covered with pronounced growth-lines. Anterior and lateral margins thickened. Umbo short, slightly incurved. Interarea extensive. Deltidial plates conjunct. Beak-ridges sharp. Anterior commissure, rectimarginate.

Holotype. Davidson Collection, British Museum (Natural History) no. B.6734 from the Claxby Ironstone (Lower Hauterivian) of Acre House, Tealby, Lincolnshire.

Material. In addition to the holotype, four specimens from the Claxby Iron-

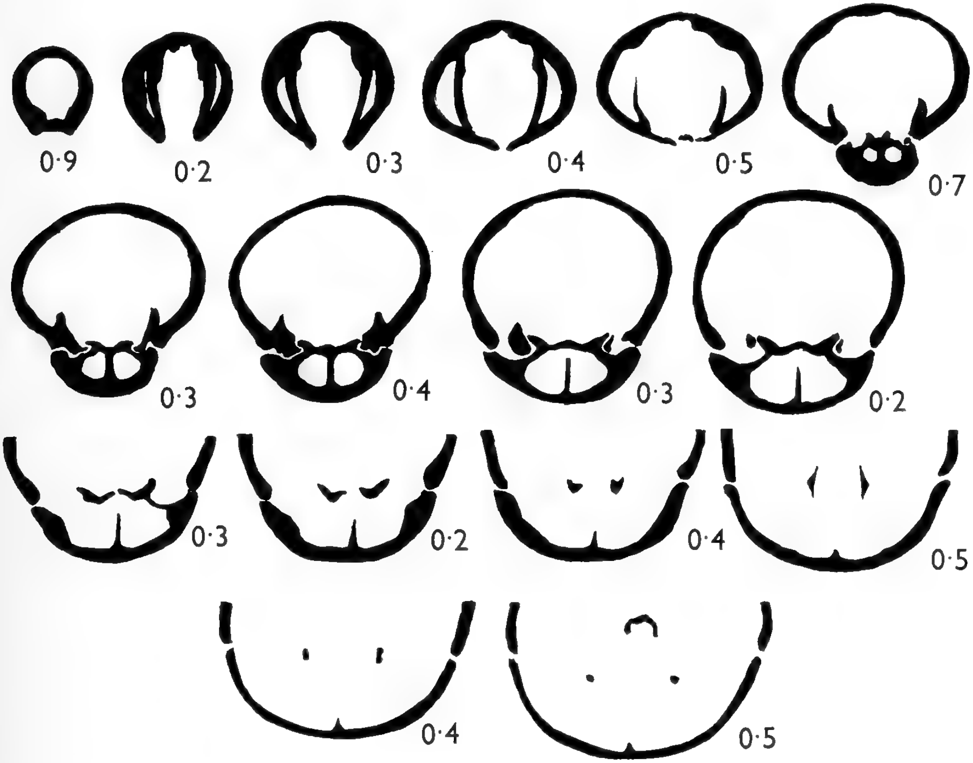

Fig. 11. A series of sixteen transverse sections through the umbonal part of *Rugitela rugosa* sp. n. from the Neocomian, Claxby Ironstone, Acre House, Tealby, Lincolnshire. BM. B.50359. × 2.

stone, British Museum (Natural History) nos. B.6734, B.50358–59, B.50324 and two well preserved specimens from Salins-les-Bains, nos. 33984 and BB.42913. There are two specimens from the Claxby Ironstone in the Sedgwick Museum (B.11400 and B.12278).

DESCRIPTION. In general outline this is a shorter, more gibbous species than

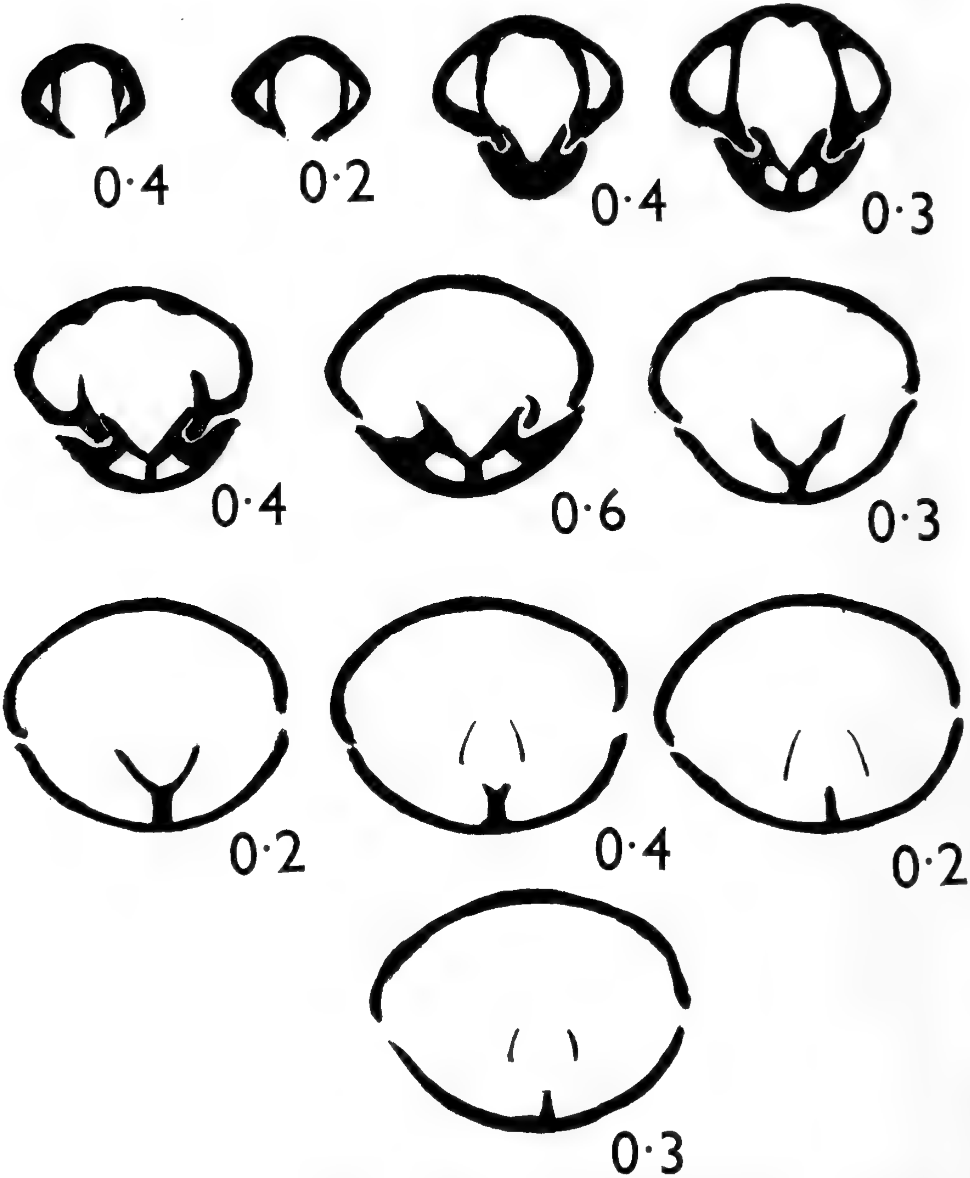

FIG. 12. Eleven transverse serial sections through the umbo of *Modestella faba* (J. de C. Sowerby) from the Lower Albian, Folkestone, Kent. BM. B.25994. ×4.

Rugitela roemeri. It has more acutely convex valves with an absence of any marked sulcation of the brachial valve, although some mature forms exhibit a faint depression in this part of the shell. The surface of the valves is ornamented by numerous concentric growth-lines which give it a rugose appearance. Marginal thickening of the valves is a common feature in more mature forms. The umbo is less produced and more incurved than in *R. roemeri.* Well defined, sharp beak-ridges border an extensive interarea.

LOCALITY AND HORIZON. This species enjoys the same lateral range as *Rugitela roemeri*, occurring in the Lower Hauterivian at Salins-les-Bains in the French Jura Mountains; a similar horizon at Brunswick, North Germany, and in the Claxby Ironstone of Lincolnshire, as well as the *Acanthodiscus speetonensis* Zone of the Speeton Clay of Yorkshire.

Rugitela hippopus (Roemer)

(Pl. 3, figs. 1*a–c*, 2*a–c*, 3*a–c*, 4*a–c*; Text-fig. 13)

1840 *Terebratula hippopus* Roemer: 114, pl. 16, fig. 28.
1842 *Terebratula hippopus* Roemer; Geinitz: 87.
1864 *Terebratula (Waldheimia) hippopus* Roemer; Credner: 565, pl. 21, figs. 17, 18, 19.
1866 *Terebratula hippopus* Roemer; Schloenbach: 33.
1868 *Terebratula ? defluxa* Schloenbach: 31, pl. 2, figs. 10–12.
1868 *Terebratula hippopus* Roemer; Judd: 245.
1874 *Waldheimia hippopus* ? Roemer var. *tilbyensis* Davidson: 53, pl. 6, figs. 10, 11.
1884 *Terebratula (Waldheimia) hippopus* Roemer; Weerth: 62, pl. 11, figs. 5, 6.

DESCRIPTION. This well established species is characterized by its almost circular outline, sulcate brachial valve, slightly incurved beak and acutely carinate pedicle valve. It is 12 mm. long, 10 mm. wide and 8 mm. thick. Because of the similarity of external form it has often been assigned to the Liassic genus.

Aulacothyris. It differs from this genus, however, in having a less elongate outline, smaller dimensions, larger foramen and longer brachial loop.

Internal characters. From the transverse serial section of the species (Text-fig. 13) it is possible to compare the internal characters of *R. hippopus* with sections of species of *Rugitela* figured by Muir-Wood (1936: 124, 128, 131). While agreeing basically with sections of the type-species *Rugitela bullata* from the Fuller's Earth Rock of Somerset, it appears to have closer morphological affinities with *R. emarginata* from the same horizon and locality.

NEOTYPE. Dr. R. G. Thurrell of H.M. Geological Survey has kindly given me permission to publish some of the notes he prepared in a revision of this species which he included in his thesis for the degree of Ph.D of London University, 1957. The following is a quotation from p. 320 of his thesis:

"Owing to war damage, the Roemer Collection in Hildesheim Museum was partly destroyed. Dr. Friedrich Smid of the German Geological Survey has undertaken to search for the type material, but nothing has so far come to light."

In spite of renewed enquiry no specimens have been forthcoming.

A specimen in the British Museum (Natural History) no. 32313 from the Hilsconglomerat of Berklingen, North Germany (Pl. 3, figs. 2*a–c*) appears to be the only

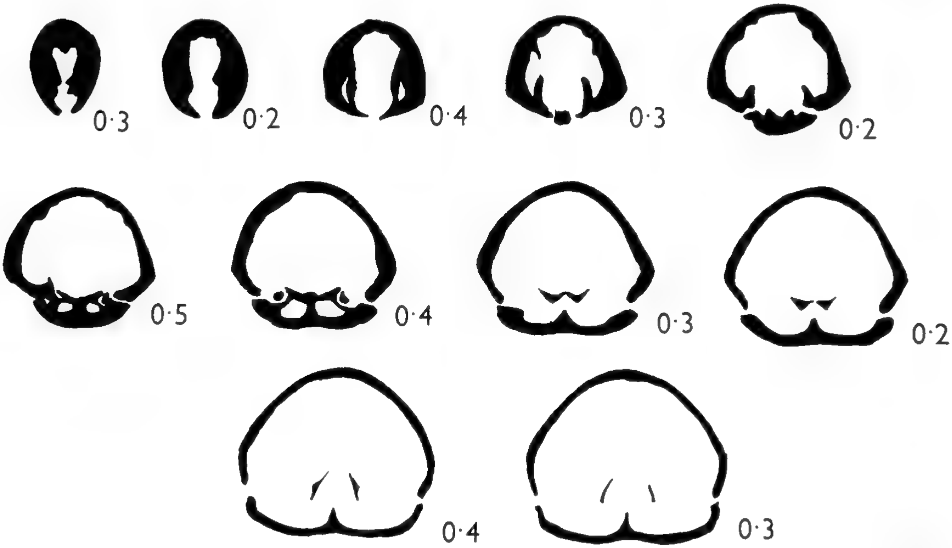

FIG. 13. A series of eleven transverse serial sections through the umbo of *Rugitela hippopus* (Roemer) from the Neocomian, Claxby Ironstone, Acre House, Tealby, Lincolnshire. BM. BB.42934. × 2.

available specimen from the type locality, and is here proposed as neotype. It departs from the original illustration (Roemer 1840, pl. 16, fig. 28) in having less clearly defined beak-ridges and less extensive interarea but, after examination of some 150 specimens from both English and North German localities, these features appear to vary within the species.

MATERIAL AND LOCALITY. Numerous specimens from the Claxby Ironstone from Acre House, Tealby and from Nettleton, Lincolnshire. Ten specimens from the Neocomian of Saltzgitter, Hanover (B.6748, BB.42921, BB.42932), a single specimen from the Speeton Clay of Yorkshire (BB.42923), and one specimen from Marolles, Aube, France (B.6742), all in the British Museum (Natural History).

REMARKS. Differing only in size from the North German form, the British species, originally described as *Waldheimia hippopus* var. *tilbyensis* by Davidson (1874), attains an average length of 15 mm., a width of 13 mm., and a thickness of 10 mm.

The specimen from the Lower Hauterivian of Marolles, France, differs slightly in beak characters. It has less prominent beak-ridges and less extensive interarea.

CONCLUSION

Owing to the lack of recent exposures of the Lower Greensand at Upware, Brickhill and Potton, it is impossible to draw any real conclusions about the distribution of species. All information regarding these localities has been obtained from research on museum collections and the results recorded here.

Critical examination of transverse serial sections of species of *Tamarella* gen. nov. has revealed that they have many characters in common with those of *Rugitela*. For example, the divergent dental lamellae, broad, shallow septalium, anteriorly arched and fused hinge-plates, triangular crural bases and thickened portion of the descending branches of the brachial loop. The dorsal median septum of *Rugitela* is, however, more strongly developed and considerably longer than that of *Tamarella.*

Prozorovskaya (1962 : 111) described *Gusarella* from the Upper Jurassic of Turkmenistan as a subgenus of *Zeilleria.* Serial sections of the type species *Z.* (*Gusarella*) *gusarensis* have much in common with those of *Tamarella* particularly *T. bonneyi* (Text-fig. 7). The hinge-plates show the anterior arching or plication, and the crural bases, brachial loop and general outline are similar to those of *Tamarella.* In *Gusarella,* however, the dorsal median septum appears to be absent.

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PLATE 1

a. Dorsal view. b. Lateral view. c. Anterior view.

FIGS. 1a, b, c. *Vectella woodwardi* (Walker), Upper Aptian of Upware, Cambridgeshire. BM. BB.42922.

FIGS. 2a, b, c. *Tamarella tamarindus* (J. de C. Sowerby), Upper Aptian, Upware, Cambridgeshire. BM. BB.42905.

FIGS. 3a, b, c. *Tamarella bonneyi* (Keeping), Upper Aptian, Brickhill, Buckinghamshire. BM. BB.42935.

FIGS. 4a, b, c. *Vectella celtica* (Morris), Upper Aptian, Shanklin, Isle of Wight. BM. BB.42915. Lectotype.

FIGS. 5a, b, c. *Vectella angusta* (Walker), Upper Aptian, Upware, Cambridgeshire. BM. no. 67601. Holotype.

FIGS. 6a, b, c. *Tamarella elliptica* (Walker), Upper Aptian, Upware, Cambridgeshire. BM. no. 67600. Holotype.

FIG. 7. *Vectella morrisi* (Meyer), Upper Aptian, Bargate Pebble-bed, Compton, Surrey. Internal of brachial valve showing the broad, deep hinge-trough and extensive dorsal median septum. BM. BB.42918.

FIGS. 8a, b, c. *Tamarella tamarindus* (J. de C. Sowerby). Dissected specimen showing relatively shallow hinge-trough in brachial valve 8a, with anterior plication and 8b. pedicle valve of the same specimen. BM BB.42920. 8c. Dissected specimen of a brachial valve of a specimen from the Upper Aptian of Faringdon. BM. BB.42919, showing cardinalia and remains of brachial loop with thickened portion of descending branch.

FIGS. 9a, b, c. *Tamarella vesta* sp. n., Upper Aptian, Upware, Cambridgeshire. BM. BB.42904. Holotype.

FIGS. 10a, b, c. *Tamarella tamarindus* (J. de C. Sowerby), Upper Aptian, Shanklin, Isle of Wight. BM. BB.42906.

FIGS. 11a, b, c. *Tamarella juddi* (Walker), Upper Aptian, Upware, Cambridgeshire. BM. BB.42909. Lectotype.


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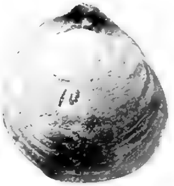
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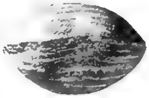
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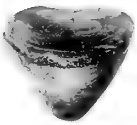
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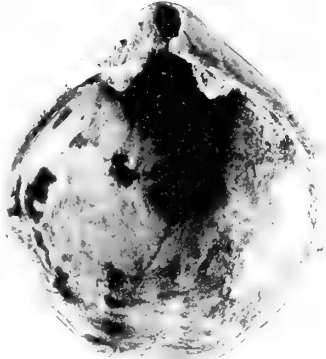
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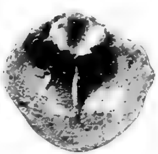
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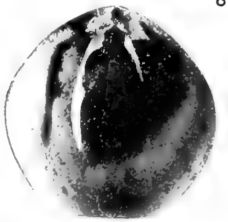
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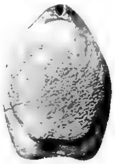
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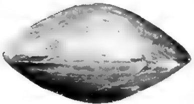
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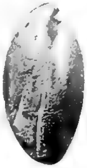
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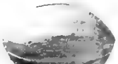
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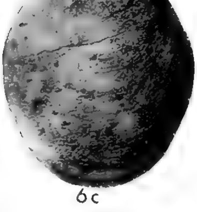
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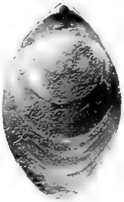
11a


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PLATE 2

a. Dorsal view. b. Lateral view. c. Anterior view.

FIGS. 1a, b, c. *Rugitela roemeri* sp. n. from the Neocomian (Hauterivian), Nettleton, Lincolnshire. Hull University Collection H.U.C/Rn. 317.

FIGS. 2a, b, c. *Rugitela rugosa* sp. n., Neocomian, Claxby Ironstone, Acre House, Tealby, Lincolnshire. BM. B.50324.

FIGS. 3a, b, c. *Rugitela roemeri* sp. n., Neocomian, St. Dizier, Haute-Marne, France. BM. B.6736.

FIGS. 4a, b, c. *Rugitela rugosa* sp. n., Neocomian, Claxby Ironstone, Acre House, Tealby, Lincolnshire. BM. B.6734. Holotype.

FIGS. 5a, b, c. *Rugitela rugosa* sp. n., Neocomian, Salins-les-Bains, Jura Mountains, France. BM. BB.42913.

FIG. 5d. Enlarged portion of above specimen showing incurved beak, sharp beak-ridges and wide interarea.

FIGS. 6a, b, c. *Rugitela roemeri* sp. n., Neocomian, Elligser Brinke, Hanover, North Germany. BM. BB.42912. Holotype.

FIGS. 7a, b, c. *Modestella faba* (J. de C. Sowerby), Lower Albian, Folkestone, Kent. SM. B.17642.

FIGS. 8a, b, c. *Rugitella roemeri* sp. n., Neocomian, St. Dizier, Haute-Marne, France. d'Orbigny Collection no. 5159.

FIGS. 9a, b, c. *Rugitela roemeri* sp. n., Neocomian, Elligser Brinke, Hanover, North Germany. BM. BB.42911.


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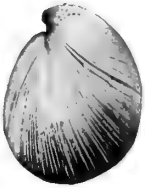
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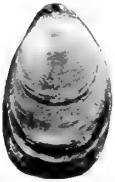
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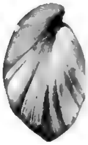
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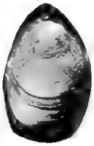
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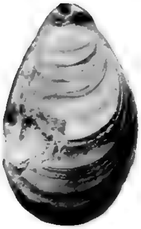
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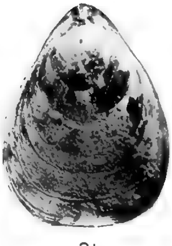
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PLATE 3

a. Dorsal view. b. lateral view. c. Anterior view.

FIGS. 1a, b, c. *Rugitela hippopus* (Roemer), Neocomian, Speeton Clay, Speeton, Yorkshire. P. Rawson Coll. BM. BB.42923. × 2.

FIGS. 2a, b, c. *Rugitela hippopus* (Roemer), Neocomian, Berklingen, near Hanover, North Germany. BM. no. 32313. Neotype. × 2.

FIGS. 3a, b, c. *Rugitela hippopus* (Roemer), Neocomian, Saltzgitter, North Germany. BM. BB.42921. × 2.

FIGS. 4a, b, c. *Rugitela hippopus* (Roemer), Neocomian, Saltzgitter, North Germany. BM. BB.42932. × 2.

FIGS. 5a, b, c. *Tamarella tamarindus* (J. de C. Sowerby), Upper Aptian, Isle of Wight, BM. BB.42907. Neotype. × 2.

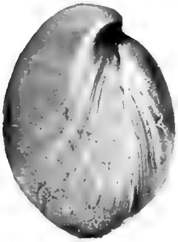
FIGS. 6a, b, c. *Tamarella tamarindus* (J. de C. Sowerby), Upper Aptian, Faringdon, Berkshire. BM. B.6723.

FIGS. 7a, b, c. *Vectella morrisi* (Meyer), Upper Aptian, Brickhill, Buckinghamshire. BM. BB.42916. × 2.

FIGS. 8a, b, c. *Vectella morrisi* (Meyer), Upper Aptian, Godalming, Surrey. BM. BB.42917. × 2.

FIGS. 9a, b, c. *Vectella morrisi* (Meyer), Upper Aptian, Shanklin, Isle of Wight, BM. BB.42914.

FIG. 9d. *Vectella morrisi* (Meyer), Upper Aptian, Shanklin, Isle of Wight. SM. B.14770. Lectotype.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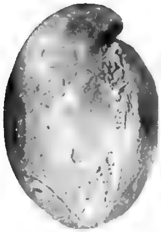
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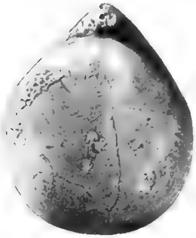
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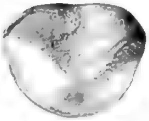
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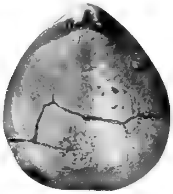
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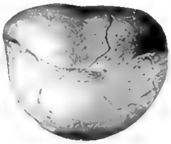
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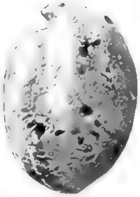
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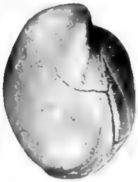
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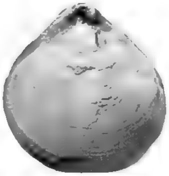
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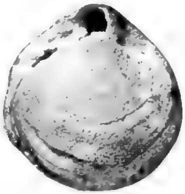
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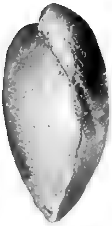
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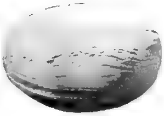
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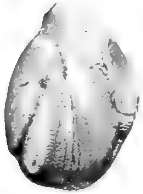
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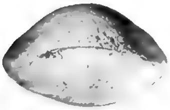
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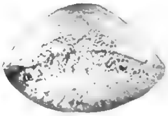
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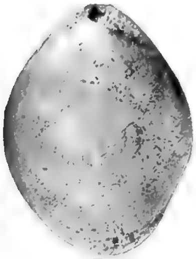
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MIDDLE JURASSIC OSTRACODA FROM THE GREY LIMESTONE SERIES, YORKSHIRE

R. H. BATE

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 11 No. 3
LONDON: 1965

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BY

R. H. BATE

Pp. 73–133 ; 21 *Plates* ; 24 *Text-figures*

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MIDDLE JURASSIC OSTRACODA FROM THE GREY LIMESTONE SERIES, YORKSHIRE

By RAYMOND HOLMES BATE

CONTENTS

SYNOPSIS

The Middle Jurassic (Bajocian) Grey Limestone Series of Yorkshire is shown to have been deposited in a broad embayment, transgressing deltaic sediments of Bajocian age, and is here divided into two ostracod faunal zones : a lower zone of *Glyptocythere polita* and an upper zone of *G. scitula*, the type section being at Hundale Point. The zone of *G. polita* is present only towards the centre of the basin and represents the first phase of the marine transgression. The facies changes within the Series are produced by intermittently rising sea-level and the repeated southward extension of the northern delta. Shore-line sediments are also identified. Fourteen stratigraphical sections are described in detail. The period of marine deposition is considered to have taken place approximately during *sauzei* to *blagdeni* times and is thus in part at least equivalent to the Coronaten-Schichten of N.W. Germany. The ostracod fauna of the Grey Limestone Series is described for the first time. Four genera : *Caytonidea, Cloughtonella, Malzia* and *Mesocytheridea* are new. Sixteen new species and one new subspecies are also described. The palaeoecology of the ostracod fauna is briefly mentioned.

I INTRODUCTION AND ACKNOWLEDGEMENTS

IN north-eastern England, the uppermost marine horizon of Bajocian age consists of a well developed succession of calcareous shales and sandy limestones known as the Grey Limestone Series or Scarborough Beds. The maximum thickness of this sequence occurs in the neighbourhood of Cloughton Wyke (62 feet) and Ravenscar (62 feet), the beds thinning to the north, south and west where they eventually pass

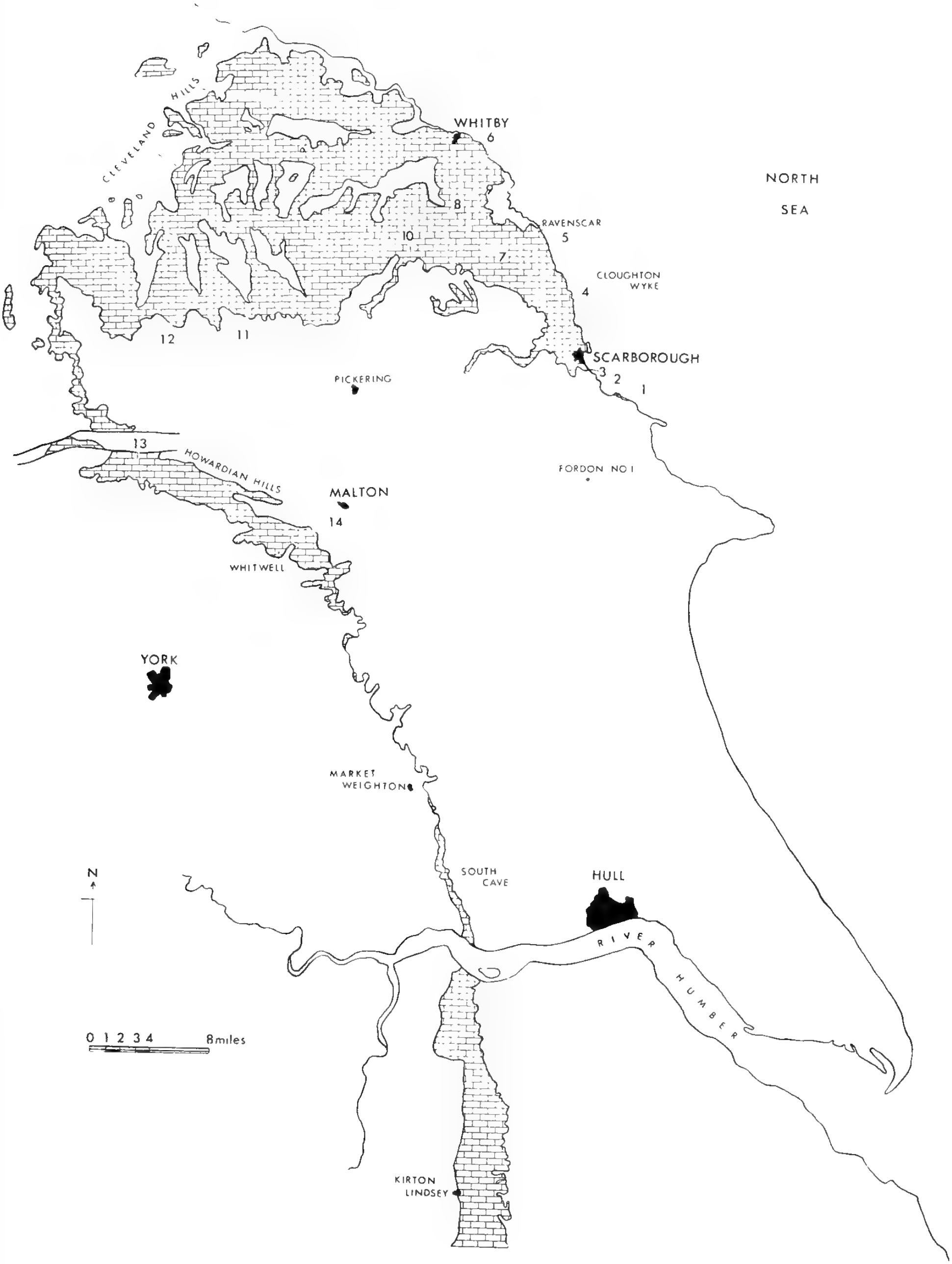

FIG. 1. Outcrop of Middle Jurassic Strata in N.E. England, with the localities and sections (1–14) mentioned in the text.

into arenaceous shore-line deposits. The open sea during this period lay to the east, occupying the site of the present day North Sea, whilst a delta lay to the north. Sediments equivalent in age to the Grey Limestone Series were also deposited in north-western Germany.

The dating of the Grey Limestone Series is difficult owing to the almost complete absence of ammonites : those which have been recorded (Fox-Strangways 1892 : 231 ; Buckman 1911 : 205–208 ; and Hemingway 1951 : 119)[1] indicate that part of the sequence at least belongs to the *Teloceras blagdeni* Subzone. As the ammonite zones are well known in north-western Germany, comparison of the ostracod faunas of the two regions should eventually offer a solution to this problem. At the moment, however, only two ostracods, present in the Grey Limestone Series have also been, recorded from Germany ; these are *Ljubimovella piriformis* Malz (1961 : 165, pl. 2, figs. 15–25) and *Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida* Brand & Malz (1962 : 19, pl. 4, figs. 33–37 ; pl. 5, fig. 46).

Ljubimovella piriformis has a range in Germany of *sauzei* to *blagdeni* Zones, with the type horizon being in the *sauzei* Zone. In Yorkshire this ostracod is restricted to the zone of *Glyptocythere scitula*, the upper zone from which the ammonites recorded from the Grey Limestone Series were most probably obtained. The ostracod *Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida* is recorded from the upper part of the Coronaten-Schichten (*romani* to *blagdeni* Zones) in Germany, whilst in Yorkshire it is

TABLE 1

Generalised table of the Middle Jurassic stata in Yorkshire, north of Market Weighton

Strata	*Stage*
CORNBRASH (UPPER)	CALLOVIAN
UPPER DELTAIC SERIES	BATHONIAN
GREY LIMESTONE SERIES	BAJOCIAN
MIDDLE DELTAIC SERIES (UPPER)	
MILLEPORE SERIES	
MIDDLE DELTAIC SERIES (LOWER)	
ELLER BECK BED/HYDRAULIC LIMESTONE	
LOWER DELTAIC SERIES	
DOGGER	
LIAS	TOARCIAN

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[1] The map reference for Monk's Walk Wood, Sneaton has been given with a misprint, and should read NZ/896086 (personal communication, Prof. Sylvester-Bradley).

FIG. 2. Sections 1-6 across the Yorkshire Basin.

largely restricted to the *G. scitula* zone, being found at only one locality in the *G. polita* Zone.

The Grey Limestone Series represents a period of deposition which appears to approximate with the Coronaten-Schichten of Germany although there is insufficient evidence to say how many of the German ammonite zones are represented in the Yorkshire sediments. It should be possible, however, to correlate the Grey Limestone Series with the German succession more precisely at a future date when the ostracod faunas are more fully known.

Fox-Strangways (1892 : 223) recorded the presence of lamellibranch casts within a 15 ft. bed of sandstone at Ravenscar. This is bed 17 of Section 5 (Text-fig. 2), which is the lower part of the Moor Grit (basal Upper Deltaic Series). The period of marine deposition was thus brought to a close by the infilling of the Yorkshire basin with deltaic sediments. The next marine transgression did not occur until Callovian times, it is, therefore, evident that the end of the Bajocian and the whole of the Bathonian is represented in Yorkshire by deltaic sediments of the Upper Deltaic Series.

The localities listed below are those at which the Grey Limestone Series has been examined at outcrop, the numbers corresponding with those in Text-fig. 1. Map references refer to the one-inch Ordnance Survey map of Great Britain (seventh series).

Coastal Exposures

1. Gristhorpe Bay, cliff section and foreshore, map reference TA/085842. A complete section, maximum thickness 15 ft. 6 in.
2. Cayton Bay, cliff section, map reference TA/082843. A complete section, maximum thickness 10 ft. 7 in.
3. White Nab, Scarborough, foreshore section, map reference TA/058865. Base below Low Water Mark, seen to 25 ft. 6 in.
4. Hundale Point, Cloughton Wyke, cliff and foreshore section, map reference TA/024949 to TA/027943. A complete section, maximum thickness 62 ft. 4 in.
5. Ravenscar, cliff section, map reference NZ/988012. A complete section, maximum thickness 62 ft. 4 in.

Inland Exposures

6. Hawsker, stream section at Hawsker Bottoms, map reference NZ/937079. Top of section not seen, 22 ft. 5 in.
7. Bloody Beck, stream section, map reference SE/945981 to SE/947982. A complete section, 29 ft. 4 in.
8. May Beck, stream section, map reference NZ/890015 to NZ/891019. Isolated exposures, base not seen, 14 ft. 9 in.
9. Ramsdale Beck, stream section NZ/925034. Upper part of Series only exposed, seen to 9 ft. 6 in.

10. Eller Beck, just downstream of road bridge, map reference SE/856984. Upper part of Series only, seen to 6 ft. 5 in.
11. Harland Beck, stream section, map reference SE/684914 to SE/686913. Incomplete section seen to 14 ft. 4 in.
12. Bogmire Gill, stream section, map reference SE/608905 to SE/609909. Almost a complete section, seen to 40 ft. 3 in.
13. Yearsley Moor, map reference SE/579754. A small quarry by the side of the Yearsley-Ampleforth road. Fauna indicates position of beds high up in the Grey Limestone Series, seen to 8 ft. 3 in.
14. Stonecliff Wood, Crambeck, map reference SE/744676, a small gully exposing 12 ft. 2 in. of sediment. Map reference SE/743676, section higher up the bank, above the York–Scarborough railway-line, exposing 5 ft. 8 in. of limestone. Map reference SE/740675 a 9 inch bed of limestone is exposed. All strata high up in the Grey Limestone Series.

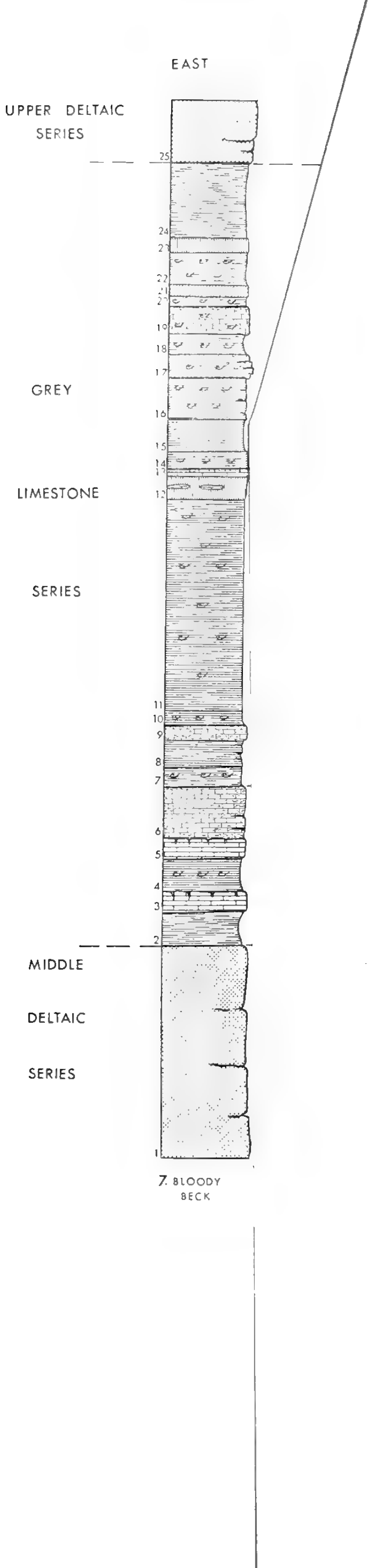
Morphological terms used in the text are those introduced in vol. Q of the American Invertebrate Paleontology Treatise (Moore 1961), Sylvester-Bradley (1956) and Bate (1963).

The work embodied in this paper was largely conducted in the Geology Departments of Sheffield University and Leicester University. My sincere thanks go to Professors L. R. Moore and P. C. Sylvester-Bradley respectively, for the use of their departmental facilities. Grateful thanks are also due to the Department of Industrial and Scientific Research for a grant to finance this work. Dr. H. Malz, Senckenberg Museum, Frankfurt-am-Main and Dr. H. J. Oertli, S.N.P.A., Centre de Recherches, Pau (Basses-Pyr) also assisted with the loan of type and/or comparative material, for which they are gratefully acknowledged.

II STRATIGRAPHICAL SECTIONS

Section No. 1. Gristhorpe Bay (Text-fig. 2), exposure in south face of Yons Nab headland and on the foreshore at low tide. The section is complete and exposes 15 ft. 6 in. of sediment (G.L.S.).

	ft.	*in.*
Upper Deltaic Series		
10. Yellow-grey sandstone (Moor Grit) with coaly lenses and grey sulphurous shale	30–40	0
Grey Limestone Series		
9. Black, sulphur stained shale	4	0
8. Dark grey, ironstained shale	4	9
7. Mudstone	0	9
6. Black shale with indet. ostracods	1	4


EAST
UPPER DELTAIC SERIES
GREY LIMESTONE SERIES
MIDDLE DELTAIC SERIES
25
24
23
22
21
20
19
18
17
16
15
14
13
12
11
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9
8
7
6
5
4
3
2
1
7. BLOODY BECK

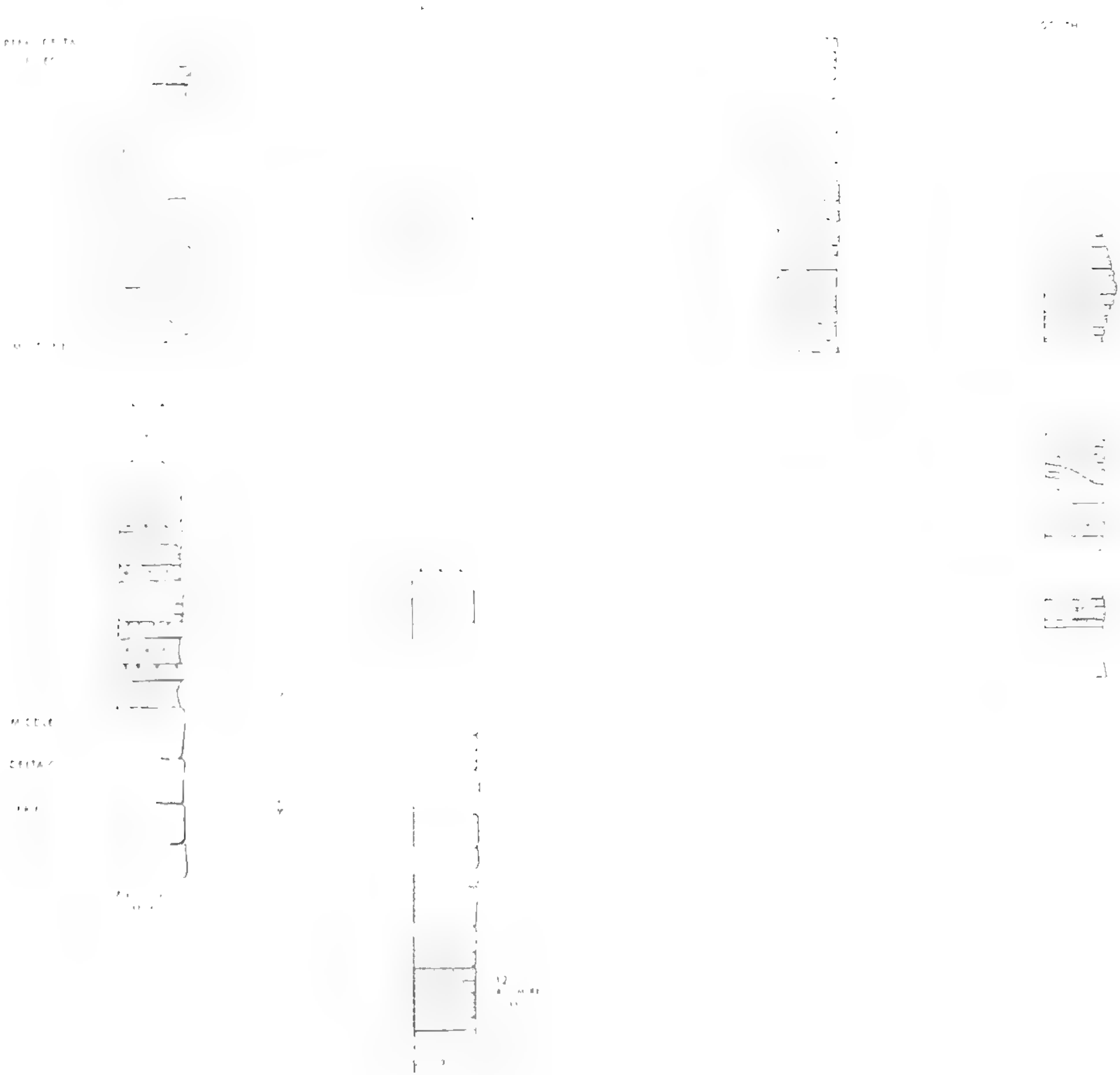


Fig. 3. Sections 7 and 12–14.

	ft.	*in.*
5. Fossiliferous mudstone with *Glyptocythere scitula*; *Vernoniella bajociana* and *Monoceratina scarboroughensis*	0	6
4. Black fossiliferous shale with a compact limy band at base. Lamillibranch *Gervillia scarburgensis* and Belemnites common. *Glyptocythere scitula*; *Praeschuleridea subtrigona intermedia*; *Vernoniella bajociana*; *Vernoniella* ? *caytonensis*; *Systenocythere ovata*; *Paracypris bajociana*; *Caytonidea faveolata*; *Fuhrbergiella* (*Praefurbergiella*) *horrida horrida* and *Pleurocythere* sp.	4	6

Middle Deltaic Series

3. Yellow sandstone, flaggy in part with carbonaceous bands	4	10
2. Black Shale	0	5
1. Grey shale	7	0

Section No. 2. Cayton Bay (Text-fig. 2), exposure in north face of Yons Nab headland. This section is complete, but like Section No. 1 is liable to be cut into by washouts infilled with deltaic sandstone (Moor Grit). Up to 10 ft. 7 ins. of sediment (G.L.S.) exposed.

Upper Deltaic Series

8. Moor Grit.

Grey Limestone Series

7. Chocolate-brown to grey coloured shale with fragmentary shells	1	5
6. Fossiliferous, chocolate-brown mudstone, variable in thickness. *Glyptocythere scitula*; *Vernoniella bajociana*; *Vernoniella* ? *caytonensis*; *Systenocythere ovata*; *Paracytheridea* ? *caytonensis*; *Progonocythere acuminata*; *Progonocythere yonsnabensis and Praeschuleridea subtrigona intermedia*	2 to 0	0 9
5. Grey fossiliferous shale with: *Glyptocythere scitula*; *Vernoniella bajociana*; *Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida*; *Monoceratina scarboroughensis*; *Praeschuleridea subtrigona intermedia*; *Progonocythere yonsnabensis* and *Caytonidea faveolata*	2	0
4. Brown fossiliferous mudstone with: *Glyptocythere scitula* and *Vernoniella bajociana*	0	4
3. Grey shelly shale with: *Glyptocythere scitula*; *Vernoniella bajociana* and *Praeschuleridea subtrigona intermedia*.	2	9
2. Grey-black sulphurous shale	2	1

Middle Deltaic Series

1. Flaggy yellow sandstone.

SECTION No. 3. White Nab (Text-fig. 2), Scarborough. Exposure largely along the foreshore, cut out as a series of steps by the sea —well exposed and possibly almost complete, lowermost beds below Low Water Mark. 25 ft. 6 in. of marine sediment exposed.

Upper Deltaic Series

18. Massive deltaic sandstone (Moor Grit) forming base of high cliffs.

Grey Limestone Series

	ft.	in.
17. Sandy shale passing into base of Moor Grit above	1	0
16. Fossiliferous, grey calcareous shale, partly ironstained. *Fuhrbergiella (Praefuhrbergiella) horrida horrida*	0	7
15. Fossiliferous shale with mudstone nodules. Internal casts, possibly of *Glyptocythere scitula* and *Praeschuleridea subtrigona intermedia*	0	8
14. Mudstone with *Glyptocythere scitula ; Vernoniella bajociana* and *Praeschuleridea subtrigona intermedia*	0	4
13. Grey shale with ooliths	0	2
12. Grey to chocolate-brown fossiliferous shale with *Glyptocythere scitula ; Vernoniella bajociana* and *Praeschuleridea subtrigona intermedia*	1	0
11. Ironstained mudstone crowded with the lamellibranch *Gervillia scarburgensis*	0	5
10. Sandy limestone containing large specimens of *Gervillia scarburgensis Glyptocythere scitula* and *Praeschuleridea subtrigona intermedia*	1	5
9. Purplish-brown calcareous shale with *Glyptocythere scitula ; Vernoniella bajociana* and *Praeschuleridea subtrigona intermedia*	1	0
8. Ironstained, sandy limestone. *Vernoniella bajociana*	1	6
7. Fossiliferous grey shale with *Glyptocythere scitula ; Vernoniella bajociana ; Monoceratina scarboroughensis* and *Praeschuleridea subtrigona intermedia*	1	2
6. Calcareous shale with mudstone bed at top which varies from 0 in. to 9 in. in thickness	1	5
5. Massive, well bedded sandy limestone, fossiliferous though no microfauna so far obtained	6	7
4. Hard calcareous shale, almost an argillaceous limestone	1	6
3. Soft, grey fossiliferous shale. *Glyptocythere scitula ; Monoceratina scarboroughensis ; Fuhrbergiella (Praefuhrbergiella) horrida horrida* and *Praeschuleridea subtrigona intermedia*	1	0
2. Ironstained limestone	1	0
1. Grey sandy shale with large belemnites. *Glyptocythere scitula ; Vernoniella bajociana* and *Praeschuleridea subtrigona intermedia* seen to	4	0

SECTION No. 4. Hundale point (Text-fig. 2). A complete succession of these beds is exposed in the cliff face and along the foreshore, with a maximum thickness of 62 ft. 4 in.

	ft.	in.
Upper Deltaic Series		
32. Moor Grit—carbonaceous and more thinly bedded at base.		
Grey Limestone Series		
31. Grey, sandy and micaceous shale, ironstained	3	8
30. Dark grey sulphurous shale	1	7
29. Fossiliferous mudstone, variable in thickness, maximum	0	4
28. Grey shale, ironstained at base	0 to 0	7 10
27. Chocolate-brown, fossiliferous shale	0	10
26. Grey calcareous shale, almost an argillaceous limestone. *Glyptocythere scitula ; Vernoniella bajociana ; Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida ; Praeschuleridea subtrigona intermedia*.	0	9
25. Chocolate-brown mudstone, shelly. *Glyptocythere scitula ; Vernoniella bajociana* and *Monoceratina scarboroughensis*	0	4
24. Purplish brown, fossiliferous shale grading into bed 25. *Glyptocythere scitula ; Vernoniella bajociana ; Monoceratina scarboroughensis* and *Praeschuleridea subtrigona intermedia*	0	11
23. Grey shale becoming less fissile towards base. *Glyptocythere scitula ; Vernoniella bajociana ; Monoceratina scarboroughensis* and *Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida*	4	0
22. Grey-black, very fossiliferous shale. Ostracod fauna at top of sequence : —*Glyptocythere scitula ; Monoceratina scarboroughensis ; Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida* and *Praeschuleridea subtrigona intermedia.* Fauna 7 ft. from base :— ostracods indet. Fauna 6 ft. from base :— *Ljubimovella piriformis.* Fauna 5 ft. from base :— *Glyptocythere scitula* and *Vernoniella bajociana.* Fauna 2 ft. from base :— *Monoceratina scarboroughensis ; Cloughtonella rugosa* and *Praeschuleridea subtrigona intermedia.* Fauna at base :— *Glyptocythere scitula ; Ljubimovella piriformis* and *Praeschuleridea subtrigona intermedia*	11	1
21. Calcareous shale. *Cloughtonella rugosa ; Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida ; Praeschuleridea subtrigona intermedia ; Monoceratina scarboroughensis ; Systenocythere ovata* and *Ljubimovella piriformis*.	1	0

	ft.	*in.*
20. Sandy limestone, very fossiliferous (*Trigona* sp. *Pholadomya* sp. etc.). *Glyptocythere scitula*	0	8
19. Calcareous, grey shale with macrofossils as for bed 20. *Glyptocythere scitula ; Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida ; Praeschuleridea subtrigona intermedia* and *Systenocythere ovata*	4	9
18. Grey sandy shale. *Systenocythere ovata*	1	11
17. Calcareous sandstone	1	5
16. Dark grey shale extensively burrowed by marine organisms—the burrows infilled with sand. Belemnites present—no microfossils	2 to 3	10 to 0
15. Hard calcareous shale. *Pentacrinus* ossicles common	1	2
14. Grey sandstone with *Pentacrinus* ossicles. The Crinoid Grit. Current bedded with ripple markings along the bedding planes. Worm burrows common. This bed grades upwards into bed 15. Foraminifera but no ostracods have been obtained from this bed	4 to 6	0 to 2
13. Grey shale	1	3
12. Purplish-brown mudstone with *Glyptocythere polita* and *Praeschuleridea subtrigona intermedia*	1	10
11. Limestone *Glyptocythere polita ; Malzia unicarinata* and *Praeschuleridea subtrigona intermedia*	1	3
10. Sandstone	0	9
9. Grey sandy shale. *Glyptocythere polita ; Malzia bicarinata* and *Praeschuleridea subtrigona intermedia*	2	2
8. Dark grey shale. *Glyptocythere polita ; Vernoniella bajociana ; Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida* and *Praeschuleridea subtrigona intermedia*	0	6
7. Grey mudstone. *Glyptocythere polita* in this bed, as in bed 12, occurs in extremely large numbers. Other members of the ostracod fauna are :— *Progonocythere acuminata ; Vernoniella bajociana* and *Praeschuleridea subtrigona intermedia*.	1	1
6. Grey shale. *Glyptocythere polita* and *Praeschuleridea subtrigona intermedia*	1	2
5. Grey calcareous sandstone. *Glyptocythere polita* and *Glyptocythere costata*	3	4
4. Sandy shale	2	0
3. Hard black shale	2	7
Middle Deltaic Series		
2. Massive sandstone	11	7

		ft.	*in.*
1. Black shale	seen to	0	2

SECTION No. 5. Ravenscar (Text-fig. 2). As in the previous section, a complete sequence of marine strata is exposed, although the junction between the Grey Limestone Series and the Upper Deltaic Series is obscured by talus. The beds crop out high up in the steep cliff face, the Moor Grit of the Deltaic Series above capping the cliffs.

Upper Deltaic Series

17. Soft yellow, false bedded sandstone, about 15 ft. of which cap the cliffs at this point.

Grey Limestone Series

	ft.	*in.*
16. Reddish-brown, rather soft sandstone above which there is 3–4 ft. of sediment obscured by talus	1	10
15. Ochre coloured sandy shale	3	5
14. Ironstone with fossil casts	0	4
13. Ochre coloured sandy shale	4	0
12. Dark grey calcareous shale, fossiliferous throughout with shelly bands and nodules. Fauna 27 ft. from base :— *Monoceratina scarboroughensis ; Ljubimovella piriformis ; Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida* and *Praeschuleridea subtrigona intermedia.* Fauna 25 ft. from base :— indeterminate ostracods. Fauna 21 ft. from base :— *Glyptocythere scitula ; Vernoniella bajociana* and *Monoceratina scarboroughensis.* Fauna 19 ft. from base :— indet. internal casts. Fauna 17 ft. from base :— indet. internal casts. Fauna 15 ft. from base :— *Glyptocythere scitula ; Praeschuleridea subtrigona intermedia* and *Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida.* Fauna 13 ft. from base in shelly band :— *Glyptocythere scitula.* Fauna 11 ft. from base in shelly bed :— *Glyptocythere scitula* and *Ljubimovella piriformis.* Fauna 6 ft. from base :— *Glyptocythere scitula ; Glyptocythere costata ? ; Ljubimovella piriformis ; Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida* and *Praeschuleridea subtrigona intermedia.* In the shale sampled within the basal 4 ft. of shale, no microfauna has been so far obtained	30	7
11. Fossiliferous yellow sandstone with *Pentacrinus* ossicles. The Crinoid Grit	4	3

	ft.	in.
10. Light-grey, calcareous shale with abundant *Gervillia scarburgensis.* Fauna at top of bed :— *Malzia unicarinata ; Praeschuleridea subtrigona intermedia ; Glyptocythere costata* and *Vernoniella bajociana.* Fauna at base :— *Malzia unicarinata ; Malzia bicarinata ; Glyptocythere costata* and *Progonocythere acuminata* ?	2	3
9. Dark-grey, fossiliferous shale. *Glyptocythere polita* and *Malzia unicarinata*	1	9
8. Fossiliferous argillaceous limestone with *Gervillia scarburgensis. Glyptocythere polita ; Glyptocythere costata ; Malzia unicarinata ; Malzia bicarinata* and *Praeschuleridea subtrigona intermedia* .	0	4
7. Grey sandy shale. Fauna at top :— *Glyptocythere polita ; Malzia bicarinata ; Progonocythere acuminata* and *Praeschuleridea subtrigona intermedia.* Fauna at Base :— *Glyptocythere polita ; Vernoniella bajociana* and *Praeschuleridea subtrigona intermedia.*	2	6
6. Calcareous mudstone, almost an argillaceous limestone. *Glyptocythere polita ; Progonocythere acuminata* and *Praeschuleridea subtrigona intermedia*	1	2
5. Rubbly bed—same lithology as bed 4. *Glyptocythere polita* and *Praeschuleridea subtrigona intermedia*	0	7
4. Dark grey, massive, sandy limestone. *Glyptocythere polita* and *Praeschuleridea subtrigona intermedia*	2	0
3. Dark-grey shale extensively burrowed by marine organisms—the whole bed being a mixture of shale and sandstone. Large specimens of *Gervillia scarburgensis* present. *Glyptocythere polita* and *Praeschuleridea subtrigona intermedia*	1	6
2. Grey-black, rather brittle shale—no microfauna	1	10

Middle Deltaic Series

	ft.	in.
1. Deltaic sandstone, massively bedded	6	10

SECTION No. 6. Hawsker (Text-fig. 2.). The thickness of the Grey Limestone Series has been considerably reduced and although the top of the succession is not exposed, the observed thickness of 22 ft. 5 in. cannot be far short of the total in this area.

Grey Limestone Series

	ft.	in.
13. Well bedded grey sandstone, rather coarse grained, virtually a grit, which grades down into a chocolate-brown sandstone shelly in parts. Ostracods (*Glyptocythere scitula* ? and *Praeschuleridea subtrigona intermedia*) present though somewhat decalcified . . . . seen to	5	2
12. Sandy limestone, crowded with shells towards the base—rather fissile on weathering. *Vernoniella ? caytonensis ; Systenocythere ovata* at base	2	5

	ft.	*in.*
11. Sandy and very fossiliferous chocolate-brown shale. *Southcavea microcellulosa*; *Praeschuleridea subtrigona intermedia*; *Eocytheropteron* ? sp.; *Glyptocythere scitula* ? and *Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida*	1	6
10. Chocolate-brown shale. *Glyptocythere scitula*; *Vernoniella bajociana* and *Praeschuleridea subtrigona intermedia*	1	8
9. Grey shale crowded with fossils at top. *Glyptocythere scitula* and *Vernoniella bajociana* at the top and *Glyptocythere scitula*; *Cloughtonella rugosa* and *Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida* at base	3	0
8. Grey shale with large nodules of limestone	2	0
7. Grey fossiliferous shale with *Glyptocythere scitula*; *Vernoniella bajociana*; *Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida*; *Ljubimovella piriformis*; *Systenocythere ovata*; *Progonocythere acuminata* and *Praeschuleridea subtrigona intermedia* . .	3	0
6. Calcareous sandstone, fossiliferous. No microfossils obtained. The Crinoid Grit of elsewhere	2	0
5. Dark-grey sandy shale, fossiliferous along bedding planes. Internal casts of *Glyptocythere* sp.	1	8

Middle Deltaic Series

4. Light-grey shale with sandstone lenses	0	8
3. Grey and white laminated sandy shale—sandstone lenses . .	2	1
2. Grey sandy shale with 1 ft. 1 in. lens of sandstone at top. Shale carbonaceous with plant remains	3	0
1. Grey sandstone . . . . seen to	4	6

Section No. 7. Bloody Beck (Text-fig. 3). Of the inland exposures of the Grey Limestone Series, this is by far the best—it is complete and all beds are accessible along the course of the stream. 29 ft. 4 in. of marine sediment are developed here.

Upper Deltaic Series

25. Moor Grit—massively bedded sandstone forming the base of the Deltaic Series—flaggy towards base, grading into bed below.

Grey Limestone Series

24. Sandy, micaceous, dark-grey shale	2	10
23. Clay ironstone with specks of pyrite	0	7
22. Fossiliferous grey, sandy shale, no microfossils	1	2
21. Light-grey mudstone, very fossiliferous. *Glyptocythere scitula* .	0	6

	ft.	*in.*
20. Fossiliferous grey sandy shale—internal casts of *Glyptocythere* ? sp. and *Vernoniella* ? sp. Beds 24–20 have suffered extensive decalcification—fresh material if possible to obtain would probably yield a larger fauna	0	4
19. Hard, grey, calcareous shale. Ostracods fragmentary and indeterminate	1	0
18. Grey calcareous shale, fossiliferous. *Glyptocythere scitula* and *Vernoniella bajociana*	0	9
17. Hard, grey, fossiliferous mudstone. *Glyptocythere scitula* and *Vernoniella bajociana*.	0	11
16. Hard, grey, calcareous shale—quite fossiliferous although the ostracod fauna appears to be restricted to the single species, *Vernoniella bajociana*	1	7
15. Grey, rather shelly shale, softer than bed 16. Ostracod fauna restricted to *Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida*	1	4
14. Fossiliferous calcarous shale—poor ostrocod fauna. *Glyptocythere scitula* and *Praeschuleridea subtrigona intermedia*	0	9
13. Hard, grey, calcareous shale/mudstone with sub-rounded quartz grains embedded particularly in upper part. *Glyptocythere scitula*	0	3
12. Sparsely fossiliferous shale with mudstone nodules. No ostracods recovered	0	10
11. Grey fossiliferous shale. Fauna at top :— indet. Fauna 3 ft. 8 in. from top :— *Glyptocythere scitula* ; *Systenocythere ovata* and a fragment of *Praeschuleridea subtrigona intermedia*. Fauna 6 ft. 6 in. from top :— *Glyptocythere scitula* ; *Vernoniella bajociana* and *Praeschuleridea subtrigona intermedia*	8	0
10. Grey, very fossiliferous shale. *Cloughtonella rugosa* and *Praeschuleridea subtrigona intermedia*	0	7
9. Calcareous shale grading upwards into bed 10. It is, however, a much more resistant bed to weathering—fossiliferous. *Glyptocythere scitula* ; *Progonocythere acuminata* and ? *Southcavea microcellulosa*	0	7
8. Hard, grey shale, sparsely fossiliferous. *Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida* and indet. ostracod fragments	1	0
7. Grey sandy shale, fossiliferous. *Mesocytheridea howardianensis* ; *Glyptocythere scitula* and *Malzia bicarinata*	0	10
6. Grey-black fossiliferous limestone becoming shaly towards base. Fauna at top in limestone :— *Glyptocythere polita* and *Glyptocythere scitula*. Fauna in shaly beds at the base consists entirely of *Glyptocythere polita* which occurs in enormous numbers	2	0

	ft.	in.
5. Well jointed, grey limestone. *Glyptocythere polita* and *Praeschuleridea subtrigona intermedia*	0	9
4. Grey, fossiliferous shale. *Glyptocythere polita*; *Malzia unicarinata*; *Progonocythere acuminata* and *Praeschuleridea subtrigona intermedia*.	1	4
3. Grey, well jointed, limestone. *Glyptocythere polita* and *Praeschuleridea subtrigona intermedia*	0	8
2. Grey sandy shale. *Glyptocythere polita* and *Praeschuleridea subtrigona intermedia*	1	3

Middle Deltaic Series

	ft.	in.
1. Massive sandstone, flaggy in places . . . . seen to	8	0

SECTION No. 8. May Beck, stream section. Exposures poor and discontinuous, the ostracod fauna being almost entirely leached out. Section at NZ/890015.

Upper Deltaic Series

	ft.	in.
10. Moor Grit—flaggy at base . . . . . seen to	12	0

Grey Limestone Series

	ft.	in.
9. Sandy limestone. *Glyptocythere scitula* and ? *Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida* . . . . . . seen to	2	9
8. Rubbly sandy bed with mudstone nodules	1	2
7. Grey, calcareous sandstone. *Praeschuleridea subtrigona intermedia*	1	1

Section at NZ/890017, about 100 yds. downstream.

	ft.	in.
6. Grey flaggy sandstone with fossil casts . . . . seen to	1	0

Section at NZ/891019, about 100 yds. downstream.

	ft.	in.
5. Grey calcareous sandstone with fossil casts. This bed is probably more correctly a sandy limestone, leaching of the $CaCO_3$ reducing the bed to a sandstone. *Praeschuleridea subtrigona intermedia*	3	3
4. Purplish-red siltstone with decalcified shells. *Glyptocythere scitula* and *Vernoniella bajociana*	0	4
3. Grey sandstone with fucoid markings	0	7
2. Grey, brittle shale—ostracod internal casts	1	7
1. Light-grey shale with plant remains . . . . . seen to	3	0

SECTION No. 9. Ramsdale Beck, stream section. Only 9 ft. 6 in. of marine shale exposed in the left bank of the stream (facing downstream). Although macrofossils are present within the shale, all the microfauna has been leached away except for the occasional indeterminate internal cast.

SECTION No. 10. Eller Beck, stream section, exposing 6 ft. 5 in. of marine sediment in the right bank of the stream, below road bridge.

Grey Limestone Series

	ft.	*in.*
5. Dark grey shale—sandy and ironstained. Internal casts of *Glyptocythere* ? sp.	2	4
4. Calcareous mudstone with macrofossils. *Glyptocythere scitula* and *Praeschuleridea subtrigona intermedia*	1	2
3. Grey, sandy shale with a few fossils	0	9
2. Calcareous grey shale. This bed has a good calcareous cement and has not been so extensively decalcified. *Glyptocythere scitula ; Vernoniella bajociana* and *Praeschuleridea subtrigona intermedia*.	1	2
1. Dark grey shale, internal casts of *Glyptocythere* ? sp., and *Vernoniella bajociana* seen to	1	0

SECTION No. 11. Harland Beck, stream section in left bank in a disused bend of the stream just above the junction of the Harland Beck with the river Dove : 14 ft. 4 in. exposed.

Grey Limestone Series

7. Sandy shale. *Glyptocythere scitula ; Vernoniella bajociana* and *Praeschuleridea subtrigona intermedia* seen to	0	6
6. Grey, sandy limestone, fossiliferous along the bedding planes. *Praeschuleridea subtrigona intermedia*	2	8
5. Grey sandy shale with calcareous nodules	1	7
4. Massive bedded sandstone almost a grit, flaggy at base	5	3
3. Sandy shale	0	7
2. Dark-grey shale, almost a mudstone in appearance. Lamellibranch *Gervillia scarburgensis* common. *Glyptocythere scitula* and *Praeschuleridea subtrigona intermedia*	1	6
1. Dark-grey mudstone. *Glyptocythere scitula* and *Praeschuleridea subtrigona intermedia* seen to	2	3

SECTION No. 12. Bogmire Gill (Text-fig. 3), an almost complete stream section exposing some 40 ft. 3 in. of the Grey Limestone Series.

Upper Deltaic Series

10. Moor Grit—flaggy at base seen to	6	0

Grey Limestone Series

9. Grey sandy shale	6	1

	ft.	*in.*
8. Dark-grey ironstained shale with fossils. *Glyptocythere scitula* and *Vernoniella bajociana*	1	6
7. Grey-brown mudstone. *Glyptocythere scitula ; Vernoniella bajociana ; Progonocythere acuminata* and *Praeschuleridea subtrigona intermedia*	0	9
6. Dark-grey, fossiliferous shale. *Glyptocythere scitula* and *Vernoniella bajociana*	3	4
unexposed section approx. 2 ft.		
5. Flaggy yellow sandstone with fossil casts	10	6
4. Grey sandy shale	2	1
3. Grey ironstained shale	1	0
unexposed section approx. 20 ft.		
2. Calcareous sandstone, known as the Crinoid Grit. Fossiliferous and false bedded. Ostracod internal casts, *Glyptocythere* ? sp. . .	10 to 12	0 0
1. Steel-grey, flinty limestone, ripple marked along bedded planes. Indeterminate ostracods . . . . . . seen to	3	0

SECTION No. 13. (Text-fig. 3). A small, disused quarry on Yearsley Moor, exposing 8 ft. 3 in. of marine sediment.

Upper Deltaic Series		
3. Yellow, rather soft, flaggy sandstone with plant remains along bedding planes . . . . . . seen to approx.	6	0
2. Yellow sandy bed with lenses of grey shale	1	0
Grey Limestone Series		
1. Buff coloured sandy limestone, weathers to a sandstone—fossiliferous. Fauna approx. 3 ft. 6 in. from the base :— *Glyptocythere scitula ; Praeschuleridea subtrigona intermedia ; Mesocytheridea howardianensis ; Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida* and *Systenocythere ovata.*	8	3

SECTION No. 14. (Text-fig. 3). Three isolated sections within the Grey Limestone Series, exposed in Stonecliff Wood, above the York–Scarborough railway-line. Altogether a maximum of 20 ft. 1 in. of sediment is exposed.

Grey Limestone Series

	ft.	*in.*
8. Sandy, fossiliferous limestone exposed at map reference SE/743676. Fauna at top of section :— *Eocytheropteron* ? sp. ; *Southcavea microcellulosa* and *Praeschuleridea subtrigona intermedia.* Fauna 3 ft. 8 in. from base :— *Southcavea microcellulosa ; Praeschuleridea subtrigona intermedia ; Glyptocythere scitula ; Mesocytheridea howardianensis and Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida.* Fauna 1 ft. 6 in. from base includes all those listed above, with the exception of *Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida*	5	8
Section at SE/744676 :—		
7. Grey limestone weathering to orange-red sandstone containing fossil casts. This bed is largely decalcified at outcrop . . .	1 to 2	4 to 6
6. Yellow sand, false bedded at top. Fossil casts	1	7
5. Limestone, impersistent laterally, being replaced by yellow sand. *Glyptocythere scitula ; Eocytheropteron* ? sp. ; *Praeschuleridea subtrigona intermedia* and *Southcavea microcellulosa* . . .	1	8
4. Soft yellow sandstone—easily weathers to a sand—fossil casts common in lower part	3	0
3. Shelly limestone, impersistent and replaced laterally by sand. *Glyptocythere scitula* and *Southcavea microcellulusa*	0	8
2. Reddish-brown sand with fossil casts	0	4
1. Coarse silver sand . . . . seen to	2	5
Section at SE/740675 :—		
2. Grey limestone. *Praeschuleridea subtrigona intermedia ; Mesocytheridea howardianensis ; Glyptocythere scitula* and *Vernoniella bajociana.* This bed is possibly at a slightly lower horizon than those listed in the two sections above	0	9
1. Yellow sandstone . . . . seen to	1	6

III STRATIGRAPHY

During Middle Jurassic times an important axis of downwarping, the Cleveland Axis, extended approximately east-west through the centre of the Yorkshire Basin, cutting the present coastline somewhere about Ravenscar (Text-fig. 1). This axis of movement played an important role during the deposition of the Grey Limestone Series.

The Grey Limestone Series or Scarborough Beds are well exposed along the coast as far north as Whitby where the outcrop turns inland. In the northern part of the Yorkshire basin, the Cleveland Hills (Text-fig. 4), the outcrops are generally represented by expanses of coarse calcareous grit known as the Crinoid Grit. Down the western part of the outcrop, exposures are sometimes good but incomplete ; the most complete inland exposures are found towards the centre of the basin in stream sections.

Fox-Strangways (1892 : 236) was the first to subdivide this marine series on lithological terms. His divisions consisted of an upper shale division, a middle sandstone division and a lower limestone division. This arrangement was continued by Richardson (1911). However, the subdivision of the Grey Limestone Series in this way, although basically correct, is a simplification of what really takes place. In fact failure to recognize facies changes resulted in Arkell (1933 : 221) making the following statement " Although the exact horizons of the ammonites recorded from the Scarborough or Grey Limestone are not known, it may be presumed that most if not all came from the lowest or limestone division ". The impure limestones developed in the Scarborough district belong to the upper shale division. The lower so called limestone division is not exposed at Scarborough and may not, in fact, extend as far south. As many of the ammonites recorded come from Scarborough, it is clear that they must come from the upper division. The examination of the ostracod faunas brought out this fact and at the same time made it possible to correlate the various sections more precisely than would have been possible on purely lithological evidence.

The division of the Grey Limestone Series on lithological evidence is here abandoned, instead two ostracod zones are recognized : a lower zone of *Glyptocythere polita* and an upper zone of *Glyptocythere scitula*, the type section for both being taken at Hundale Point—see Section 4.

Glyptocythere scitula Zone

The ostracod fauna associated with the index ostracod of this zone is more varied than that of the lower zone and possesses several species which are restricted in their geographical distribution. The typical faunal assemblage of this zone is as follows:—

> *Glyptocythere scitula ; Vernoniella bajociana ; Monoceratina scarboroughensis ; Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida ; Ljubimovella piriformis ; Systenocythere ovata* and *Praeschuleridea subtrigona intermedia.*

Of this fauna *P. subtrigona intermedia* ranges throughout the entire Grey Limestone strata and is not indicative of either zone. The two ostracods *Vernoniella bajociana* and *Fuhrbergiella* (*P.*) *horrida horrida* are similarly found to occur in sediments below this zone, but they are relatively uncommon at the lower horizon and are not considered to be characteristic there.

A number of ostracods, restricted to this zone, have a limited geographic distribution, the palaeoecological considerations of which will be dealt with later. These are :— *Cloughtonella rugosa ; Cytheropteron* ? *yonsnabensis ; Caytonidea faveolata ;*

Mesocytheridea howardianensis ; Vernoniella ? caytonensis ; Paracytheridea ? caytonensis ; Progonocythere yonsnabensis and *Southcavea microcellulosa.*

The ostracod *Progonocythere acuminata* is present in this zone, but is equally, if not more so, as common in the lower zone of *G. polita* and is of little value stratigraphically.

Glyptocythere polita Zone

The diagnostic fauna of this zone is :— *G. polita, G. costata ; Malzia unicarinata* and *M. bicarinata.* As mentioned above (see also Text-fig. 24), several ostracods are present in both zones and need not be listed again. The above assemblage is characteristic of and restricted to this lower part of the Grey Limestone Series.

In all cases the junction between the zone of *G. polita* and *G. scitula* is clear-cut. There is a very slight overlap of one or two species in some cases, but this is relatively insignificant, and where observed limited to a few feet of strata only. A few species, however, as mentioned above are not restricted to either zone, but range throughout the complete succession (Text-fig. 24).

Along the coast the most southerly exposure of the Grey Limestone Series is in Gristhorpe Bay. Here the beds rapidly thicken to the observed maximum of 15 ft. 6 in. at the north of the Bay in Yons Nab headland (Section 1, Text-fig. 2). The marine sediments consist entirely of calcareous shales and mudstones both here and on the other side of the headland in Cayton Bay (Section 2, Text-fig. 2) where a maximum of 10 ft. 7 in. was observed. In this area the basal sandstone of the Upper Deltaic Series (here a rather incipient lateral equivalent of the massive Moor Grit further north) cuts down into the marine sediments as a number of well exposed washouts. These have been described and figured by Black (1928).

At White Nab, Scarborough, the Series is again exposed (Section 3, Text-fig. 2) and has increased to an exposed maximum of 25 ft. 6 in. The shales are rather more strongly calcareous, and impure sandy limestones are developed. The ostracod fauna throughout the sequence, as in the previous two sections, is indicative of the *G. scitula* zone. It is possible that the lower zone of *G. polita* may be present under the sea. However this part of the section is never exposed even at low tide and must remain not proven for the present.

North of Scarborough, at Hundale Point, Cloughton, the marine strata attain their maximum development of 62 ft. 4 in. (Section 4, Text-fig. 2). This is exactly the same thickness of sediment as measured for the Grey Limestone Series a few miles further north at Ravenscar (Section 5, Text-fig. 2). In both cases there is a very thick development of calcareous shale in the upper part, tending to be arenaceous at the top of Hundale, whilst at Ravenscar a bed of sandstone is developed. At Hundale there is still a remnant of the sandy limestone of the White Nab succession, present towards the lower part of the shale sequence. This limestone is not represented at Ravenscar. At both localities the shale beds are followed by a thick bed of calcareous sandstone in which *Pentacrinus* ossicles are plentiful. This is the Crinoid Grit which is more typically developed further north. The ostracod fauna of the shale beds is indicative of the *G. scitula* Zone. No ostracods have been obtained from the calcareous sandstone (Crinoid Grit) and it is taken to belong to the *G. scitula* Zone. As all the sediments below this bed at Hundale and Ravenscar belong to the *G. polita* Zone, the bed is here, a good marker horizon.

The strata belonging to the *G. polita* Zone here reach their maximum development and consist of calcareous and sandy shales, some impure limestones and calcareous sandstones. Some mudstones are also present and these invariably are crowded with the ostracod *Glyptocythere polita*.

Just south of Whitby the outcrop of the Grey Limestone Series turns inland away from the coast. However, an excellent exposure has been obtained in a stream section at Hawsker, or more precisely, Hawsker Bottoms (Section 6, Text-fig. 2). According to the section described by Fox-Strangways (1892 : 237) only 6 ft. 4 in. of sediment at the top of the section is unexposed at the present time. In this section the upper shale horizon, so well developed at Hundale and Ravenscar, is much thinner and a thick bed of fossiliferous sandstone and a bed of sandy limestone are introduced at the top. The sandstone is almost certainly laterally equivalent to bed 16 present at the top of the shale horizon at Ravenscar, but here much more massive in character. The lateral equivalent of the Crinoid Grit (bed 6) is not very strongly developed here and beds possibly belonging to the *G. polita* Zone are very much reduced in thickness. The shale bed which probably represents this horizon (bed 5) has only produced extensively decalcified internal casts of *Glyptocythere* sp., so that conclusive evidence is at the moment lacking. Stratigraphically, however, there is good reason to consider bed 5 as representing the *G. polita* Zone with beds 6–13 belonging to the *G. scitula* Zone.

To the north and west of Whitby the marine sediments of the Series are poorly exposed and appear to consist almost entirely of coarse grained fossiliferous grits in which *Pentacrinus* ossicles are common. This lithofacies has been named the Crinoid Grit (Richardson 1911 : 195 and 197) and is laterally equivalent not only to the calcareous sandstone containing *Pentacrinus* ossicles at Hundale and Ravenscar but to practically the whole of the *G. scitula* Zone. However, shale and limestone horizons are still to be found in this northern area but are definitely subordinate to the arenaceous facies.

Towards the centre of the depositional basin the Grey Limestone Series continues to exhibit a wide variety of lithofacies. At the Bloody Beck stream section (Section 7, Text-fig. 3) calcareous shales and mudstones predominate with some impure limestones coming in towards the base in the zone of *G. polita*. The Crinoid Grit appears to be absent here and the junction of the two ostracod zones falls between beds 6 and 7. Only a few miles to the north-west the majority of the sediments exposed in the May Beck section (Section 8) are quite arenaceous. In the west at Bogmire Gill (Section 12, Text-fig. 3) a large part of the section is again arenaceous and the Crinoid Grit (bed 2) is well developed and shows strong false bedding. The sediments in the Harland Beck section (Section 11) are also predominantly arenaceous. Apart from the Bloody Beck section where beds of *G. polita* age definitely occur, the only possible exposure of these beds is at Bogmire Gill where a flinty ripple marked limestone is probably to be correlated with this zone. So far no ostracods have been extracted from this lithology in a recognizable form. The basal limestone at Bogmire Gill was seen to be 3 feet, and is probably not very much thicker. The *G. polita* Zone at Bloody Beck is 6 feet in thickness. Not only does this zone diminish considerably in thickness north and south away from the Hundale/Ravenscar area but it also thins westwards. The probable area covered by sediments of the *G. polita* Zone is shown in Text-fig 4.

The most westerly outcrop of the Grey Limestone Series runs north/south through the Howardian Hills and consists of strongly arenaceous limestones interbedded with pure sand. In many cases decalcification of the limestone has resulted in the production of beds of sand. No complete section is exposed. Section 13 (Text-fig. 3) on Yearsley Moor exposes 8 ft. 3 in. of sandy limestone overlain by yellow sandstone of the Upper Deltaic Series. Further south at Stonecliff Wood, near Whitwell a

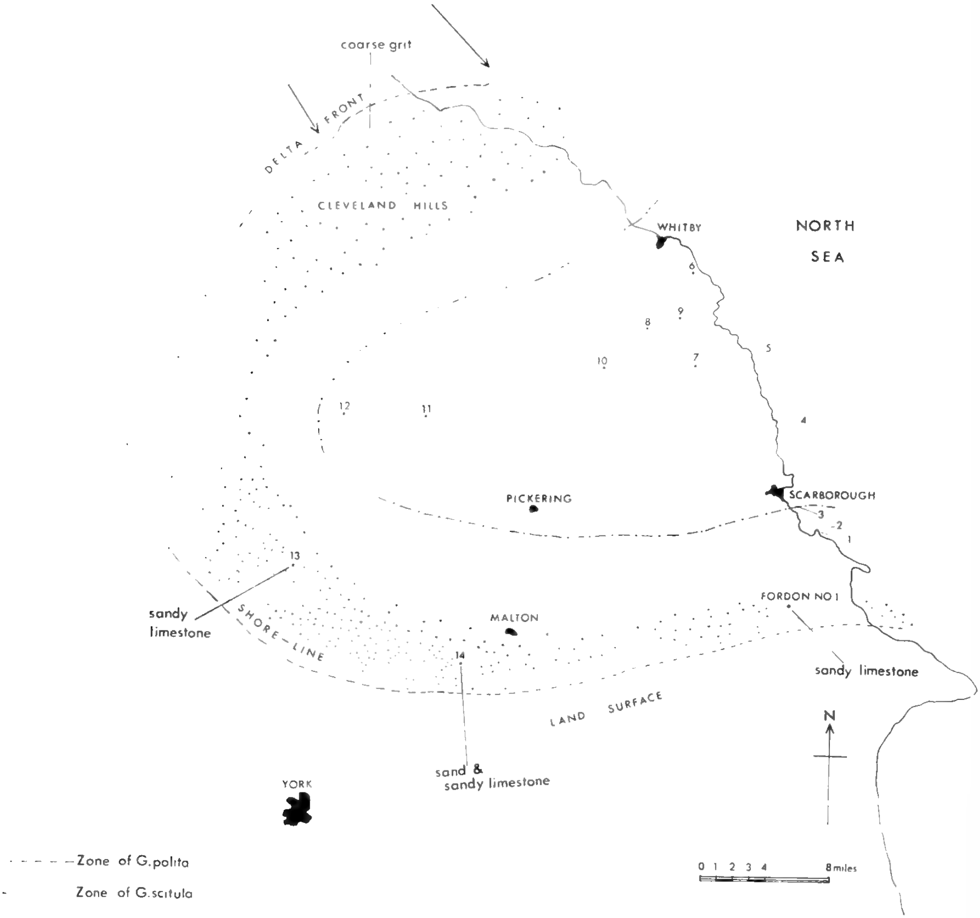


FIG. 4. Plan view of the marine basin during the deposition of the Grey Limestone Series, showing the probable maximum extent of the two faunal zones.

rather more complete section is exposed (Section 14, Text-fig. 3). Here sandy limestones are seen to be not only interbedded with false-bedded sand but are also observed to pass laterally into red sandstone or sand. This strongly arenaceous facies of the Grey Limestone Series is also present in the east, south of Gristhorpe Bay. Here, however, not exposed at the surface. The Fordon No. 1 borehole proved 5 feet of sandy limestone with belemnites (Falcon & Kent 1960 : 27). This facies is, therefore, continued around the western and southern perimeters of the Yorkshire basin whilst coarse grits are present along the northern edge. The shales and impure limestones are the major development towards the east and centre of the basin.

IV CONCLUSIONS

The Grey Limestone Series of north-east England is considered to represent the marine deposits of a broad embayment which cut into the deltaic sediments in Middle Jurassic times.

The transgression of the sea at this point was the result of downwarping along the Cleveland Axis, the lowermost beds of the Series (zone of *Glyptocythere polita*) being deposited only towards the centre of the basin (Text-fig. 4). The higher beds (zone of *Glyptocythere scitula*) extend over a wider area and in part rest directly upon deltaic sediments. The probable maximum extent of these higher beds is indicated in Text-fig. 4.

That deposition of the marine sediments occurred in shallow water is evidenced by the presence of ripple markings, false bedding, worm burrows etc. The macrofauna is also generally indicative of shallow water conditions, which, together with a possible lowering of the salinity close to a delta may explain the almost complete absence of ammonites. The shore-line of the Series is indicated by the change in facies to a very sandy limestone and even to pure sand around the south and western boundaries of the outcrop. To the north, the whole series is more coarsely arenaceous, the detrital material being brought in by the delta. The present day perimeter of the Grey Limestone Series outcrop approximates closely to the original shore-line.

As shown in Text-fig. 5, there are two prominent sandstone horizons which extend across the basin. Each reflects the influence of the northern delta. A third sandstone, the deltaic Moor Grit brings the period of marine deposition to a close. This type of sedimentation with marine shales and limestones interfingered by marine deposited deltaic sandstones is suggestive of intermittently rising sea-level, see Dunbar & Rodgers (1958 : 85, text-fig. 35*c*).

The ostracod fauna is typically shallow water benthos and in the majority of species present, appears to be largely independent of bottom facies. There is, however, a typical shore-line fauna consisting of :— *Southcavea microcellulosa ; Mesocytheridea howardianensis ; Praeschuleridea subtrigona intermedia* and *Glyptocythere scitula*. A number of other species such as *Vernoniella bajociana ; Systenocythere ovata* and *Fuhrbergiella* (*P.*) *horrida horrida* also occur in this very sandy shore-line facies, although they are only poorly represented. Towards the centre of the basin in slightly deeper water, the characteristic fauna consists of (in the *G. scitula* Zone) :— *Glyptocythere scitula ; Vernoniella bajociana ; Monoceratina scarboroughensis ;*

Ljubimovella piriformis; Praeschuleridea subtrigona intermedia; Cloughtonella rugosa; Systenocythere ovata and *Fuhrbergiella* (*P.*) *horrida horrida*. A number of other species such as *Caytonidea faveolata; Vernoniella ? caytonensis; Paracytheridea ? caytonensis* and *Progonocythere yonsnabensis* also occur but are rather restricted in their geographical range, reflecting an environment most probably restricted to the Cayton Bay region. The ostracod *Progonocythere acuminata* is only sporadically present at this horizon. In the *G. polita* Zone the fauna appears to have lived in a similar environment, with regard to bottom sediment and depth of water, as the above and consists of the following :— *Glyptocythere polita; G. costata; Malzia bicarinata; M. unicarinata; Progonocythere acuminata* and *Praeschuleridea subtrigona intermedia*. *Vernoniella bajociana* occurs in the upper part of this zone whilst *Fuhrbergiella* (*P.*) *horrida horrida* has only been recorded from a single locality. No definite shore-line fauna has been identified in this lower zone, due, no doubt to lack of exposures, although the ostracod *Mesocytheridea howardianensis* occurs in sandy shale at the base of the *G. scitula* Zone in the Bloody Beck section, whilst a little higher up in the same section there is a single specimen possibly belonging to *Southcavea microcellulosa*. The presence of these ostracods here may indicate a shallowing of the water or a change in environment to their liking. It is not possible, however, to draw any further conclusions at this stage.

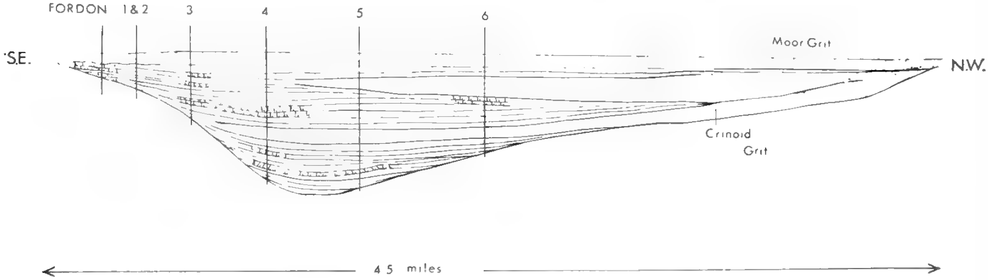


FIG. 5. Section across the Yorkshire Basin showing the facies changes of the Grey Limestone Series. Sections 1–6 are indicated together with information from the Fordon bore-hole. Vertical scale exaggerated.

V SYSTEMATIC DESCRIPTIONS

Subclass *OSTRACODA* Latreille 1806
Order PODOCOPIDA Müller 1894
Suborder PODOCOPINA Sars 1866
Superfamily **CYPRIDACEA** Baird 1845
Family **PARACYPRIDIDAE** Sars, 1923
Genus ***PARACYPRIS*** Sars 1866

Paracypris bajociana Bate

For complete synonymy see Bate 1964 : 9.

REMARKS. *Paracypris bajociana* has been recorded from the Lincolnshire Limestone and from the Cave, Whitwell and Millepore Oolites of N.E. England (Bate 1963, 1963*a* and 1964). Plumhoff (1963 : 18) records this species from beds of *discites* age and younger from North Germany.

The only occurrence within the Grey Limestone Series is at the base of the Gristhorpe Bay sequence where two specimens have been found.

Superfamily **CYTHERACEA** Baird 1850
Family **BYTHOCYTHERIDAE** Sars 1926
Genus ***MONOCERATINA*** Roth 1928

Monoceratina scarboroughensis sp. nov.

(Pl. 1, figs. 1–12)

DIAGNOSIS. *Monoceratina*, with finely punctate, subquadrate to elongate carapace, slightly constricted just anterior of mid-dorsal region.

HOLOTYPE. Io.1711, top of bed 22, Hundale Point, Cloughton.

PARATYPES. Io.1712–23, from top and base of bed 22 and bed 25, Hundale Point ; bed 5, Cayton Bay and bed 12 (21 ft. and 27 ft. from base), Ravenscar.

DESCRIPTION. *Carapace* subquadrate in outline, slightly constricted just anterior of mid-dorsal region, the more elongate dimorphs are considered to be the males. Greatest length of carapace through mid-point ; greatest height in anterior or posterior third ; greatest width in posterior third. The shallow constriction (sulcus) does not extend below mid-point, the ventro-lateral part of the carapace being noticeably swollen, particularly postero-ventrally. Dorsal margin straight with distinct, rounded cardinal angles. Ventral margin incurved medially ; anterior rounded ; posterior triangular with a short, straight or slightly concave postero-dorsal slope and a long, convex postero-ventral slope. Shell surface finely ornamented with small, round puncta, arranged in longitudinal rows in the male dimorph. Valves almost equivalve : mid-ventrally the left valve slightly overlaps the right, whilst dorsally the right valve overlaps the left, the degree of overlap increasing towards the posterior cardinal angle. *Muscle scars* consist of a subvertical row of four rectangular adductor scars and two antero-dorsal scars situated below mid-length and below the shallow sulcus. *Hinge* in the left valve consists of the slightly downset mid-dorsal edge of the valve acting as a hinge-bar ; not seen in the right valve, but presumably consisting of a simple dorsal groove for the articulation of the left valve hinge. *Duplicature* not clearly seen, though there appears to be a narrow anterior vestibule developed in one paratype (Io.1716).

Dimensions

Holotype Io.1711, female carapace (Pl. 1, figs. 1–3), length 0·61 mm. ; height 0·32 mm. ; width 0·25 mm.

Io.1719, female right valve, length 0·60 mm.; height 0·35 mm. Io.1720, female left valve (Pl. 1, fig. 12), length 0·55 mm.; height 0·33 mm. Io.1721, male carapace (Pl. 1, figs. 9–11), length 0·70 mm.; height 0·32 mm.; width 0·27 mm. Io.1722, female carapace, length 0·52 mm.; height 0·27 mm.; width 0·22 mm. Io.1723, female carapace (Pl. 1, figs. 4–8), length 0·57 mm.; height 0·31 mm.; width 0·23 mm.

REMARKS. *Monoceratina scarboroughensis* differs from all previously named species in outline (greatest length being through mid-point and not dorsal of mid-point as in the majority of cases), surface ornamentation of fine puncta coupled with the presence of dimorphism.

Family **PROGONOCYTHERIDAE** Sylvester-Bradley 1948

Subfamily **PROGONOCYTHERINAE** Sylvester-Bradley 1948

Genus ***CAYTONIDEA*** nov.

DIAGNOSIS. Progonocytherinae, oval-rectangular in outline with well rounded anterior and posterior margins. Low eye swelling situated at anterior cardinal angle. Cardinal angles prominent, broadly rounded. Hinge antimerodont. Muscle scars consist of subvertical row of four adductor scars, rounded antero-dorsal antennal scar and rounded antero-ventral mandibular scar. Radial pore canals long, straight, few in number. Left valve larger than right.

TYPE SPECIES. *Caytonidea faveolata* sp. nov.

REMARKS. Only a single species can be placed in the genus at the present time and this is typified by a strongly reticulate ornament. The possession of a well rounded oval-rectangular carapace with an antimerodont hinge, type A muscle scar arrangement and a distinct eye swelling identifies the genus *Caytonidea* from all other cytheracean genera. The genus (feminine) is named after the type locality, Cayton Bay.

Caytonidea faveolata sp. nov.

(Pl. 1, figs. 13–14; Pl. 2, figs. 1–10; Text-figs. 6, 7)

DIAGNOSIS. *Caytonidea*, with strongly reticulate ornament of 5–6 sided pits.

HOLOTYPE. Io. 1831, bed 5, Cayton Bay.

PARATYPES. Io.1832–35, horizon and locality as above and from bed 4, Gristhorpe Bay.

FIG. 6. Hinge of right valve, *Caytonidea faveolata* sp. nov. Paratype, Io.1832, approx. × 190.

Description. *Carapace* oval-subrectangular in outline with well rounded anterior and posterior margins, slightly concave mid-dorsal margin and antero-medially incurved ventral margin. The carapace is constricted slightly in the mid-dorsal region, and is noticeably swollen in the postero-dorsal region. Greatest length of carpace through mid-point, greatest height in the anterior third, greatest width in the posterior third. Shell surface ornamented by prominent 5–6 sided pits. Ventrally the reticulate ornament is somewhat subdued and is dominated by a series of longitudinal ridges. A low, smooth, *eye swelling* is situated at the anterior cardinal angle. *Left valve* larger than the right which it over-laps along the ventral margin and slightly in the region of the anterior cardinal angle. *Hinge* antimerodont, seen only in the right valve: 4 anterior and 5 posterior teeth observed; median groove long and locellate. *Duplicature* of moderate width, the inner margin and line of concrescence coinciding. *Radial pore canals* long, straight and widely spaced, 7 observed anteriorly. *Muscle scars* with rounded antero-dorsal antennal scar (Type A).

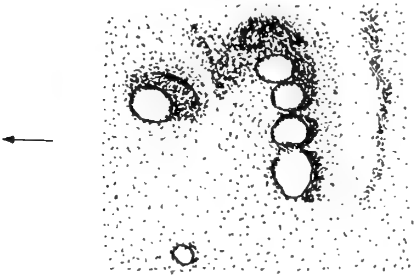


Fig. 7. Muscle scars, *Caytonidea faveolata* sp. nov. Paratype, Io.1833, approx. ×250.

Dimensions

Holotype Io.1831, carapace (Pl. 2, figs. 1–4), length 0·56 mm.; height 0·33 mm.; width 0·30 mm.

Io.1834, carapace (Pl. 1, figs. 13, 14; Pl. 2, figs. 5, 6), length 0·65 mm.; height 0·37 mm.; width 0·33 mm. Io.1835, carapace length 0·56 mm.; height 0·34 mm.; width 0·27 mm.

Remarks. Externally similar to *Southcavea reticulata* Bate (1964 : 27, pl. 10, figs. 3–14; pl. 11, figs. 1–4), *Caytonidea faveolata* differs in the presence of an eye swelling, type A muscle scar arrangement as against type D, and in being less convex in dorsal view. The reticulate ornament of *S. reticulata* differs markedly from that of *C. faveolata* in the presence of strong punctation inside the shallow pits.

Genus *CLOUGHTONELLA* nov.

Diagnosis. Progonocytherinae with subquadrate carapace, virtually parallel-sided in dorsal view. Ventero-lateral border convex projecting downwards and outwards in type species. Dorsal margin of larger left valve concave with upstanding cardinal angles. Posterior traingular; anterior rounded with narrow marginal border. Hinge antimerodont. Duplicature of moderate width, inner margin and line of concrescence coinciding. Radial pore canals straight, few in number, widely spaced. Muscle scars not observed.

Type species. *Cloughtonella rugosa* sp. nov.

Remarks. *Cloughtonella* is very close to *Aulacocythere* Bate (1963 : 198) from which it probably evolved. The general morphological features of these two genera suggest a very close relationship. However, *Cloughtonella* can be distinguished by the absence of the horseshoe-shaped swelling of *Aulacocythere* and does not possess an eye swelling.

At present only a single species can be definitely assigned to the genus : *Cloughtonella rugosa* sp. nov. However, the ostracod *Procytheridea hoffmani* Brand (1961 : 159, pl. 1, figs. 1–8) is possibly congeneric although tending to be more oval in side view, with the dorsal margin of the left valve broadly convex, passing down to the extreme posterior without any break at the cardinal angle. The dorsal margin of the left valve, male dimorph, may be slightly concave, however. *P. hoffmanni* does not appear to belong to the genus *Micropneumatocythere* Bate (1963*a* : 29), to which many of the European procytherids belong, nor is it a true *Procytheridea* Peterson (1954 : 171) which is a much more posteriorly acuminate genus. It is here tentatively considered to be congeneric with *C. rugosa.* The specimens of *Procytheridea hoffmanni* examined here were obtained from a sample of the *romani* Schichten, South Hannover, sent to me by Dr. F. Plumhoff, Erdöl A. G., Wietze krs. Celle. The known range of *P. hoffmanni* is *romani* to *blagdeni* Zones, that of *C. rugosa* uncertain because of the almost complete absence of an ammonite fauna, but probably just below *blagdeni* Zone.

The genus *Cloughtonella* (feminine) is named after the type locality Hundale Point, Cloughton Wyke.

Cloughtonella rugosa sp. nov.

(Pl. 3, figs. 1–13 ; Text-figs. 8, 9)

Diagnosis. *Cloughtonella,* with small subquadrate carapace. Dorsal margin medially concave in left valve. Ornamentation consists of prominent diagonal, rather irregular median ridge extending from postero-dorsal to antero-ventral region. Weak longitudinal ridges occur on either side of diagonal ridge. Ventro-lateral border of valves project slightly outwards and downwards, with longitudinal groove above, particularly prominent in male dimorphs. Hinge antimerodont. Muscle scars and radial pore canals not seen.

Holotype. Io.2118, base bed 22, Hunsdale Point, Cloughton Wyke.

Paratypes. Io.2119–36, horizon and locality as above and from horizon 2 ft. from base of bed 22, Hundale Point ; from bed 10, Bloody Beck and from base of bed 10, Hawsker.

DESCRIPTION. *Carapace* subquadrate in outline, more elongate in the male dimorphs. Greatest length of carapace extends through mid-point whilst the greatest height is in the anterior third. Greatest width in the posterior third, although there is only a slight increase in width posteriorly when compared with the width in the anterior part of the carapace. This is clearly seen in dorsal view, the carapace tending to be almost parallel-sided. Anterior broadly rounded, posterior triangular. Posterior marginal border narrow ; anterior border broad, directed obliquely back towards anterior cardinal angle. Dorsal margin concave in the left valve, convex in the right. Cardinal angles prominent in both valves. Ventral margin tends to be straight, the central part of the ventral surface being flattened, overhung on either side by the convex ventro-lateral margins, which in some specimens tend to project slightly outwards although not sufficiently developed to be termed alate. Left valve larger than the right which it overlaps along the ventral margin and strongly overreaches along the dorsal margin. Terminally the left slightly overreaches the right with the possible exception of at the extreme posterior where there is no overreach or overlap. Shell surface ornamented by a series of low ridges, the dominant ridge running obliquely across the carapace from the postero-dorsal region to the antero-ventral region. This oblique ridge is rather irregular in outline and is bounded on either side by short, also irregular ridges which tend to be lateral below the main diagonal ridge and vertical above. Just above the ventro-lateral margin, which in some specimens also bears lateral ridges, there appears to be a shallow groove which gives the ventro-lateral extension of the carapace a pinched-up appearance particularly noticeable in the male dimorphs. The intensity of the ornamentation varies in each specimen but generally the impression given is of a wrinkled carapace. The ventral surface is ornamented by 3–4 longitudinal ridges on each valve. *Hinge* antimerodont. In the left valve the terminal sockets are separated by a short median ridge above which the shell slopes upwards to the dorsal margin. As a result there is virtually no accommodation groove developed. In the right valve only the anterior dentate element has been observed, bearing some 5–6 teeth. The median groove is poorly developed in the material examined but appears to be loculate. Inner margin and line of concrescence coincide, the *duplicature* being of moderate width. Radial pore canals almost imperceptible but can be made out as being short, straight and few in number. *Muscle scars* not observed.

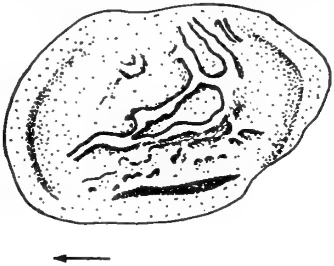


FIG. 8. Left side, female carapace, *Cloughtonella rugosa* sp. nov. Holotype, Io.2118, approx. ×85.

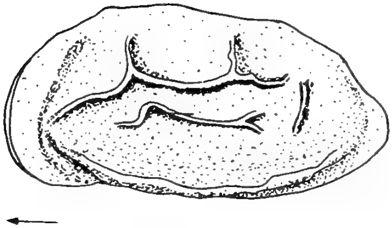


FIG. 9. Left side, male carapace, *Cloughtonella rugosa* sp. nov. Paratype, Io.2119, approx. ×95.

Dimensions

Holotype, Io.2118, female carapace (Pl. 3, figs. 1–4; Text-fig. 8), length 0·53 mm.; height 0·34 mm.; width 0·28 mm.

Io.2119, male carapace (Pl. 3, figs. 5–7; Text-fig. 9), length 0·55 mm.; height 0·28 mm.; width 0·26 mm. Io.2120, male carapace (Pl. 3, figs. 12, 13), length 0·61 mm.; height 0·33 mm.; width 0·26 mm. Io.2121, female left valve (Pl. 3, fig. 11), length 0·48 mm.; height 0·32 mm. Io.2134, male carapace (Pl. 3, fig. 10), length 0·54 mm.; height 0·29 mm.; width 0·22 mm. Io.2135, female carapace (Pl. 3, figs. 8, 9), length 0·51 mm.; height 0·32 mm.; width 0·26 mm. Io.2136, male right valve, length 0·60 mm.; height 0·29 mm.

REMARKS. *Cloughtonella rugosa* is close to the genus *Aulacocythere* in outline but as mentioned under remarks for the genus does not possess the generic characters of the latter. The present species is also close to *Procytheridea hoffmanni* Brand, which can, however, be distinguished by the strongly arched dorsal margin in the left valve; presence of a definite accommodation groove and in the more positive ornamentation. The two species are probably congeneric however.

Genus ***FUHRBERGIELLA*** Brand & Malz 1962.

Subgenus ***PRAEFUHRBERGIELLA*** Brand & Malz 1962

Fuhrbergiella (*Praefuhrbergiella*) *horrida* Brand & Malz.

REMARKS. Brand & Malz (1962 : 19) described a new subgenus *Praefuhrbergiella* with *Fuhrbergiella* (*P.*) *horrida* as type species. Two subspecies were introduced: *Fuhrbergiella* (*P.*) *horrida horrida* having a range of *romani* to *blagdeni* Zones and *Fuhrbergiella* (*P.*) *horrida bicostata* typically developed in the Sonninien-Schichten (*sowerbyi* to *grandis* Zones) but also occurring in the Coronaten-Schichten (*pinguis* Zone). The subspecies recorded here from the Grey Limestone Series is *Fuhrbergiella* (*P.*) *horrida horrida*.

Fuhrbergiella (***Praefuhrbergiella***) ***horrida horrida*** Brand & Malz

(Pl. 4, figs. 1–12)

1962. *Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida* Brand & Malz: 19, pl. 4, figs. 33–37; pl. 5, fig. 46.

1962. *Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida* Brand & Malz: Simon & Bartenstein: 141, pl. 20, fig. 32; table 9.

MATERIAL. Seventy-two specimens examined from the Grey Limestone Series, of which the following have been registered in the British Museum collections: Io.2109–17.

DESCRIPTION. *Carapace* subquadrate narrowing towards the posterior. Sexual dimorphism indicated by the presence of more elongate dimorphs, considered to be the males. Greatest length through mid-point; greatest height in the anterior third; greatest width in the posterior third. Shell surface strongly reticulate, the reticulae in adults being extended into thin lamellae. Postero-dorsally a keel-like extension of the carapace projects above the dorsal margin of the valve bending down at about mid-point to die out close to the anterior margin below mid-length. Along the ventral surface a ridge is developed which turns upwards anteriorly towards an anterior vertical ridge which bounds the broad, flattened anterior border, to die out below the prominent *eye node*. The latter is situated just below the prominent, well rounded anterior cardinal angle. A short ventro-lateral ridge may be present above the ventral ridge in some specimens. Posterior marginal border also well developed. Anterior and posterior margins may possess short spines. Left valve larger than the right which it overlaps along the ventral margin and over-reaches along the antero-dorsal and postero-dorsal slopes. *Hinge* antimerodont with strongly loculate terminal sockets in the left valve and a long denticulate median bar. Accommodation groove poorly developed. In the right valve the hinge consists of some 8 anterior teeth and approximately 7 posterior teeth. Median groove poorly preserved in the present material. Inner margin and line of concrescence coincide, the *duplicature* both anteriorly and posteriorly being quite broad. *Radial pore canals* long, straight and widely spaced; 8–9 anteriorly and 4 posteriorly. The *selvage* forms a prominent ridge around the free margin, outside of which there is a narrow *flange* developed around the anterior margin and along the ventral margin. Only the 4 oval adductor scars have been seen in the present material, the anterior muscle scars not being preserved.

Dimensions

Io.2109, female left valve (Pl. 4, figs. 1–3), length 0·78 mm.; height 0·45 mm. Io.2110, female carapace (Pl. 4, figs. 11, 12), length 0·68 mm.; height 0·37 mm.; width 0·38 mm. Io.2111, male carapace (Pl. 4, figs. 6–9), length 0·74 mm.; height 0·37 mm.; width 0·37 mm. Io.2115, female left valve, length 0·61 mm.; height 0·35 mm. Io.2116, female right valve (Pl. 4, figs. 4, 5), length 0·75 mm.; height 0·40 mm. Io.2217, female right valve (Pl. 4, fig. 10), length 0·73 mm.; height 0·38 mm.

REMARKS. All the specimens of *Fuhrbergiella* present within the Grey Limestone Series are here referred to *Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida* although in some cases the presence of a short ventro-lateral ridge indicates some affinity with the subspecies *F.* (*P.*) *horrida bicostata* Brand & Malz (1962: 21, pl. 4, figs. 38–40). The variation observed is here, however, restricted to the subspecies *F.* (*P.*) *horrida horrida*.

Genus *GLYPTOCYTHERE* Brand & Malz 1962

Glyptocythere costata sp. nov.

(Pl. 5, figs. 1–7)

DIAGNOSIS. *Glyptocythere* with subquadrate, posteriorly tapered carapace. Ornamented medially by branching transverse ridges radiating outwards from dorsal margin; ventro-laterally by single longitudinal ridge and ventrally by second longitudinal ridge.

HOLOTYPE. Io.1775, base bed 10, Ravenscar.

PARATYPES. Io.1776–82, from top and base of bed 10, and from bed 8, Ravenscar.

DESCRIPTION. *Carapace* subquadrate, tapering towards the narrowly triangular posterior. Elongate dimorphs indicate the presence of males within the population. The shell surface is strongly ornamented by irregular, branching transverse ridges which radiate downwards from the dorsal margin of the valve and by two prominent longitudinal ridges. The uppermost ridge extends along the ventro-lateral part of the carapace whilst the lower ridge, being an increased development of one of the finer longitudinal ridges which occur on the ventro-lateral and ventral surfaces, is ventral in position and in some specimens forms a prominent ventral keel. Anterior and posterior with narrow marginal border. Left valve larger than the right which it overlaps along the ventral margin and overreaches around the anterior margin, in the region of the anterior cardinal angle and along the postero-dorsal slope. Greatest length through mid-point; greatest height in the anterior third; greatest width in the posterior third. Anterior broadly rounded, posterior narrow, triangular, with short, concave, postero-dorsal slope and convex postero-ventral slope. Ventral margin incurved medially. Dorsal margin strongly convex in the right valve concave in the left. A low *eye swelling* is suggested in the right valve only, elongate in outline and situated below the anterior cardinal angle. Internal characters not observed.

Dimensions

Holotype, Io.1775, female carapace (Pl. 5, figs. 1–4), length 0·65 mm.; height 0·40 mm.; width 0·37 mm.

Io.1776, female right valve (Pl. 5, fig. 7), length 0·62 mm.; height 0·35 mm. Io.1777, female carapace, length 0·60 mm.; height 0·38 mm.; width 0·36 mm. Io.1780, male carapace, length 0·80 mm.; height 0·43 mm.; width 0·42 mm. Io.1782, male carapace (Pl. 5, figs. 5, 6), length (broken) 0·59 mm.; height 0·34 mm.; width 0·32 mm.

REMARKS. So far this species has only been found in sediments of the Grey Limestone Series as exposed at Ravenscar. *Glyptocythere costata* resembles *Glyptocythere dorsicostata* Brand & Malz (1962*a*: 145, pl. 21, fig. 10, table 9) although it differs in being smaller with a more pronounced posterior taper and in the absence of the dorso-median ridge which characterizes the latter. *G. costata* is also close to

Progonocythere juglandica (Jones, 1884), Sylvester-Bradley (1948 : 193, pl. 12, figs. 5, 6, pl. 13, fig. 8 ; text-fig. 4) to which it could be ancestral. *G. costata*, however, differs in being smaller and in the possession of strong longitudinal ridges in the ventral and ventro-lateral regions. [It is here considered that the species *Progonocythere juglandica* should be assigned to the genus *Glyptocythere*, to which it bears greater relationship than to *Progonocythere*. This will, however, be discussed in more detail in a subsequent paper.]

Glyptocythere polita sp. nov.

(Pl. 5, figs. 8–11 ; Pl. 6, figs. 1–9)

DIAGNOSIS. *Glyptocythere* with subquadrate/subtriangular carapace. Shell surface smooth with occasional wrinkles in dorso-median part. Downwardly projected ventro-lateral margin may be extended into thin keel, particularly in female dimorph.

HOLOTYPE. Io.1724, bed 7, Hundale Point, Cloughton.

PARATYPES. Io.1725–49 and Io.2210, beds, 7 and 8, Hundale Point, Cloughton ; beds 6, 7 and 9 Ravenscar and bed 6 Bloody Beck.

DESCRIPTION. *Carapace* subquadrate to subtriangular in outline with strong sexual dimorphism : the males being much more elongate in outline and quite strongly convex in dorsal view. Greatest length of carapace through mid-point with the greatest height in the anterior third. Greatest width just behind valve middle. Left valve larger than the right which it overlaps along the ventral margin and overreaches in the region of the antero-, and postero-dorsal slopes and slightly around the anterior margin. Shell surface smooth with a shallow median sulcus marking the position of the adductor muscle scars. Occasionally there is apparent a slight wrinkling of the dorso-median part of the carapace, but this is rarely well developed. *Normal pore canals* are large, circular and prominently displayed over the valve surface. The ventral surface of each valve is strongly ornamented with longitudinal ridges some of which may be bifurcate, about 4–6 per valve, the outermost being situated along the convex ventro-lateral extension of the carapace and may be developed as a thin, blade-like keel. One or two weaker longitudinal ridges may occur outside this keel on the ventro-lateral part of the carapace. The keel, when developed appears to be restricted to the female dimorphs, being little more than a well developed ridge in the males. Anterior margin of carapace broadly rounded with flattened marginal border. Posterior triangular with marginal border, concave postero-dorsal slope, almost straight in the male, and convex postero-ventral slope. Ventral margin medially incurved, sweeping upwards posteriorly in female dimorph. Ventro-lateral margin extended below ventral surface, also sweeping strongly upwards posteriorly in the female dimorph. Dorsal margin medially concave in the left valve with prominent cardinal angles ; in the right valve medially convex, although the strong median convexity noticeable here is really dorso-median in position. *Hinge* entomodont : left valve with terminal loculate sockets and a strongly dentate median bar, especially so antero-medially. Accommodation groove virtually absent. Right valve hinge complementary to the left. Hinge in juveniles antimerodont. *Muscle scars* consist of a subvertical row of 4 oval adductor scars with (as seen in a single specimen) a crescent-shaped antero-dorsal antennal scar. Mandibular scar not observed. This muscle scar type is placed in type A (Bate 1963 : 181) rather than type B. Inner margin and line of concrescence coincide the *duplicature* being of moderate width. *Radial pore canals* straight and widely spaced, approximately 9 anteriorly and 4 posteriorly. Anteriorly a narrow *flange* may be developed outside the *selvage* but is rarely preserved.

Dimensions

Holotype, Io.1724, female carapace (Pl. 6, figs. 1–4), length 0·84 mm. height 0·52 mm. ; width 0·47 mm.

Io.1725, male carapace (Pl. 6, figs. 5–8), length 1·18 mm. ; height 0·53 mm. ; width 0·55 mm. Io.1736, female carapace (Pl. 5, fig. 10), length 0·71 mm. ; height 0·46 mm. ; width 43 mm. Io.1737, female carapace (Pl. 6, fig. 9), length 0·85 mm. ; height 0·54 mm. ; width 0·45 mm. Io.1738, female left valve (Pl. 5, fig. 9), length 0·82 mm. ; height 0·49 mm. Io.1739, female right valve, length 0·77 mm. ; height 0·46 mm. Io.1741, female left valve (Pl. 5, fig. 11), length 0·72 mm. ; height 0·46 mm. Io.1742, male carapace, length 1·00 mm. ; height 0·50 mm. ; width 0·51 mm. Io.1743, female carapace (Pl. 5, fig. 8), length 0·93 mm. ; height 0·56 mm. ; width 0·48 mm. Io.1744, female carapace, length 0·71 mm. ; height 0·45 mm. ; width 0·37 mm.

REMARKS. In general appearance *Glyptocythere polita* is similar to *Progonocythere acuminata* sp. nov., although it is not so strongly tapered posteriorly. The main differences between these two species are to be found in the dorsal margin, that of *P. acuminata* being straight and not convex as in *G. polita*. The dorsal margin of the left valve is also almost straight, or may be slightly concave, but not strongly so as in the present species. The much straighter dorsal margin of species of *Progonocythere* and the strongly convex dorsal development of the right valve in species of *Glyptocythere* serve to distinguish the species of these respective genera.

Glyptocythere scitula sp. nov.

(Pl. 7, figs. 1–13 ; Pl. 8, figs. 1–9 ; Pl. 9, figs. 1–4 ; Text-fig. 10)

DIAGNOSIS. Squat, subquadrate to elongate *Glyptocythere* with strong branching and anastomosing ridges, radiating from dorsal margin. Ventro-lateral and ventral surfaces ornamented with longitudinal ridges, some of which bend upwards antero-ventrally. All ridges with rounded surfaces. Internal characters as for genus.

HOLOTYPE. Io.1750, bed 5, Cayton Bay section.

PARATYPES. Io.1751–74, from bed 5 Cayton Bay ; bed 5, Gristhorpe Bay ; beds 17 and 18, Bloody Beck ; 6 ft. from base and 15 ft. from base bed 12, Ravenscar and from bed 10, Hawsker.

DESCRIPTION. *Carapace* subquadrate in the female dimorph, elongate in the male.

Greatest length through mid-point ; greatest height in the anterior third. Greatest width in the posterior third. Carapace strongly convex in dorsal view, slightly constricted medially. Anterior and posterior with flattened marginal borders. Left valve larger than the right which it overlaps most strongly mid-ventrally and overreaches along the anterior, posterior and dorsal margins. The degree of overreach is most strongly developed mid-dorsally. Anterior margin broadly rounded ; posterior triangular with concave postero-dorsal slope and convex postero-ventral slope. Ventral margin medially incurved ; dorsal margin strongly concave in the left valve convex in the right. The dorsal margin in the left valve besides projecting above that of the right valve is also very much thicker, almost keel-like. Ornamentation of carapace strongly developed and consists of transverse ridges which radiate outwards and downward from the dorsal margin, branching and anastomosing to produce a coarse reticulate pattern. The ridges are rounded and not lamellate. Ventrolateral part of carapace strongly convex and ornamented by approximately 4 longitudinal ridges. The same number of longitudinal ridges also occur along the ventral surface of each valve. The ventro-lateral ridges tend to turn upwards antero-ventrally. In some specimens the ornament is only poorly developed, here the very large, circular *normal pore canals* are particularly evident, widely scattered over the shell surface. *Hinge* entomodont : left valve with terminal loculate sockets and a strongly dentate median bar of which the anterior part is more coarsely dentate. Accommodation groove virtually absent, the valve sloping upwards to the dorsal margin from the base of the median bar. In the right valve 6 anterior and 6 posterior teeth are developed. Median groove expanded anteriorly, strongly loculate. *Muscle scars* (Type A) consist of a subvertical row of 4 oval adductor scars, a small round, antero-dorsal antennal scar and a much larger rounded antero-ventral mandibular scar which appears as a rosette of several smaller scars. Inner margin and line of concrescence coincide the *duplicature* being of moderate width. *Radial pore canals* long, straight, 9 anteriorly and 4 posteriorly. A narrow *flange* may be present around the anterior margin outside the *selvage*, whilst in the right valve a short ventral " lip " occurs just below the ventral incurvature of the valve.

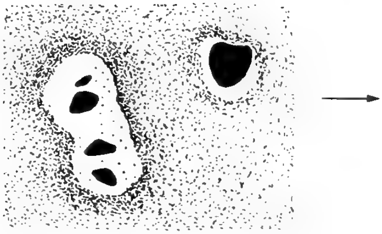


FIG. 10. Muscle scars, *Glyptocythere scitula* sp. nov. Female paratype, Io.1770, approx. ×300.

Dimensions

Holotype, Io.1750, female carapace (Pl. 8, figs. 1–4), length 0·72 mm. ; height 0·47 mm. ; width 0·43 mm.

Io. 1751, male left valve (Pl. 7, figs. 11, 12), length 0·82 mm. ; height 0·45 mm. Io. 1752, female carapace (Pl. 8, figs. 6–9), length 0·77 mm. ; height 0·50 mm. ; width 0·47 mm. Io.1753, male carapace (Pl. 9, figs. 1–4), length 0·93 mm. ; height 0·54 mm. ; width 0·52 mm. Io.1754, female left valve (Pl. 8, fig. 5), length 0·75 mm. ; height 0·48 mm. Io.1756, female right valve, length 0·63 mm. ; height 0·36 mm. Io. 1760, female right valve (Pl. 7, figs. 1, 7), length (broken) 0·72 mm. ; height 0·40 mm. Io.1768, female right valve (Pl. 7, figs. 4, 6, 10), length 0·60 mm. ; height 0·35 mm. Io.1769, female left valve (Pl. 7, figs. 5, 9), length 0·61 mm. ; height 0·37 mm. Io.1771, female right valve (Pl. 7, figs. 3, 8), length 0·68 mm. ; height 0·37 mm. Io.1772, male right valve (Pl. 7, fig. 13), length 0·82 mm. ; height 0·40 mm. Io.1773, female left valve, length 0·82 mm. ; height 0·48 mm.

REMARKS. *Glyptocythere scitula* although smaller than *Glyptocythere tuberodentina* Brand & Malz (1962*a* : 143, pl. 21, figs. 11, 12 ; table 9) is similar in general appearance. The two species may, however, be distinguished by the ornamentation which in *G. tuberodentina* consists essentially of a reticulate ornament on the lateral surface with prominent longitudinal ridges ventrolaterally. Both the longitudinal ridges and the ridges which comprise the reticulations are thin and lamellate. In *G. scitula* the ornament as described consists of radiating transverse ridges which produce a coarse reticulation on branching and anastomosing. In this species the longitudinal ridges and the transverse ridges are rounded, contrasting strongly with the lamellate ridges of *G. tuberodentina.*

The known range of *G. tuberodentina* is from the middle of the *acris* Zone to the top of the *friederici-augusti* Zone of the Parkinsoni-Schichten. The range of *G. scitula* is more difficult to give precisely but probably does not occur higher than the *blagdeni* Zone of the Coronaten-Schichten.

Genus ***MALZIA*** nov.

Named after Dr. Heinz Malz of the Senckenberg Museum, Frankfurt-am-Main, Germany.

DIAGNOSIS. Progonocytherinae with subquadrate carapace, tapering to posterior. Anterior and posterior with flattened marginal borders. Ventro-lateral part of carapace extended into one or two keel-like projections. Low eye swelling developed at anterior cardinal angle. Species may be dimorphic. Hinge entomodont. Radial pore canals long and straight, approximately 8 anteriorly, 3 posteriorly. Muscle scars as for subfamily (Type A).

TYPE SPECIES. *Malzia bicarinata* sp. nov.

REMARKS. The genus *Malzia* (feminine) is erected here with two species : *M. bicarinata* having two ventro-lateral keel-like extensions and *M. unicarinata* sp. nov., having but a single valvular extension. It is considered that *Malzia* has a position transitory between *Progonocythere* Sylvester-Bradley (1948 : 189) and *Marslatourella* Malz (1959: 19). This is suggested by the general similarity of carapace outline, muscle scars and radial pore canals present in all three. *Progonocythere* has a strong entomodont hinge and only a faint suggestion of an eye swelling. In *Marslatourella* the hinge is antimerodont and a strong eye tubercle is developed. At the same time prominent ventro-lateral outgrowths of the carapace occur. *Malzia* possesses a hinge which can be considered as entomodont, a low eye swelling and ventro-lateral outgrowths of the carapace. It appears, therefore, that the development of ventro-lateral outgrowths coupled with a change from an entomodont to an antimerodont hinge and the development of an eye tubercle results in the appearance in the Bathonian of the genus *Marslatourella*. This evolutionary series commences in the Bajocian with the genus *Progonocythere* an offshoot of which produces *Malzia*. This second lineage then continues giving rise to *Marslatourella*.

The genus *Marslatourella* described by Malz from the Bathonian of France (Mars-la Tour and Boulonnais) and Germany (Eichberg) is also common in the Bathonian sediments of England. Species of this genus will be described in forthcoming publications.

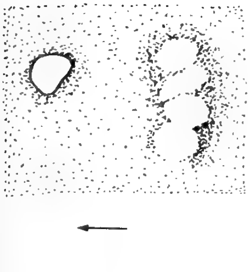
Malzia bicarinata sp. nov.

(Pl. 9, figs. 5–8 ; Pl. 10, figs. 1–3 ; Text-figs. 11–14)

Diagnosis. *Malzia* with two, short, well developed ventro-lateral keels. Internal details as for genus.

Holotype. Io.1797, bed 9, Ravenscar section.

Paratypes. Io.1798–1800, beds 7 and 8, Ravenscar and bed 7, Bloody Beck.



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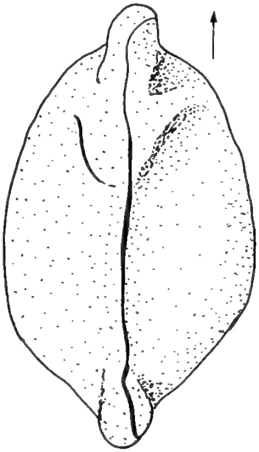

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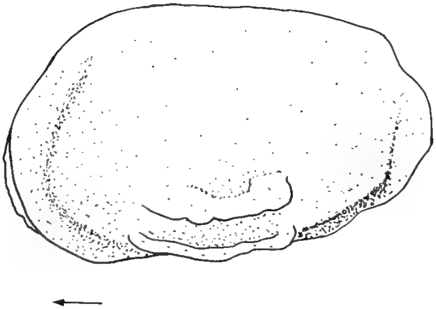

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Fig. 11. Muscle scars. *Malzia bicarinata* sp. nov. Paratype, Io.1800, approx. ×290.

Figs. 12–13. Dorsal and left views, complete carapace *Malzia bicarinata* sp. nov. Holotype, Io.1797, approx. ×85.

DESCRIPTION. *Carapace* subquadrate in outline with straight or very slightly convex dorsal margin. Cardinal angles well developed. Anterior rounded; posterior triangular with concave postero-dorsal slope and convex postero-ventral slope. Ventral margin medially incurved. Anterior and posterior with flattened marginal borders. Shell surface laterally smooth with two, stubby keels developed, the uppermost of which tends to project slightly outwards, particularly noticeable in dorsal view. Ventral surface may be smooth or possess two longitudinal ridges on each valve. A low *eye swelling* is situated just below the anterior cardinal angle, particularly noticeable in the right valve. Greatest length of carapace through mid-point; greatest height in the anterior third; greatest width in the posterior third. Left valve larger than the right which it overlaps mid-ventrally and slightly over-reaches around the posterior and along the dorsal margin. *Hinge* entomodont, only seen in the left valve where the terminal loculate sockets are separated by a dentate median bar the dentition of which increases in coarseness towards the anterior. Accommodation groove narrow, elongate. *Muscle scars* (Type A), the antennal scar being round and antero-dorsal in position. Mandibular scar not seen. *Radial pore canals* straight and simple: approximately 8 anteriorly and 3 posteriorly. *Duplicature* in completely seen in present material. *Selvage* prominent external to which there is a narrow *flange* developed around the anterior margin and along the ventral margin.

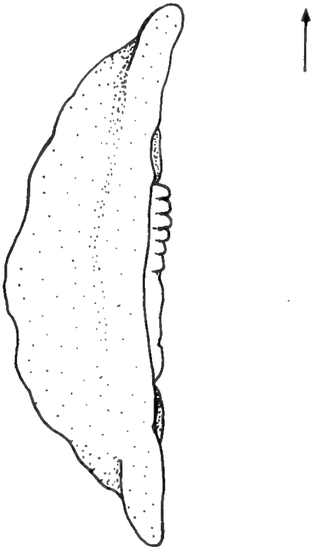


FIG. 14. Dorsal view, left valve hinge, *Malzia bicarinata* sp. nov. Paratype, Io.1799, approx. ×105.

Dimensions

Holotype, Io.1797, carapace (Pl. 9, figs. 5–8; Text-figs. 12–13), length 0·70 mm.; height 0·43 mm.; width 0·41 mm.

Io.1798, carapace (Pl. 10, fig. 1), length 0·69 mm.; height 0·43 mm.; width 0·38 mm. Io.1799, left valve (Pl. 10, figs. 2, 3; Text-fig. 14), length 0·70 mm.; height 0·43 mm.

REMARKS. *Malzia bicarinata* cannot easily be confused with *Marslatourella exposita* Malz (1959 : 20, text-figs. 1–4), lacking the prominent eye tubercle and antimerodont type hinge of the latter. It is, however, sufficiently close as to be considered ancestral to *M. exposita*. The present species differs from species of *Progonocythere* in the development of ventro-lateral outgrowths of the carapace and in the development of an eye swelling. Although some species of *Progonocythere* may show the development of an eye swelling it is not so prominent as in *Malzia* although even here it is hardly a dominant feature of the carapace.

Malzia unicarinata sp. nov.

(Pl. 10, figs. 4–10; Pl. 11, fig. 1–4; Text-fig. 15)

DIAGNOSIS. *Malzia*, with single ventro-lateral keel. Dimorphic.

HOLOTYPE. Io.1801, bed 9, Ravenscar section.

PARATYPES. Io.1802–6, beds 8 and 10, Ravenscar and bed 4, Bloody Beck.

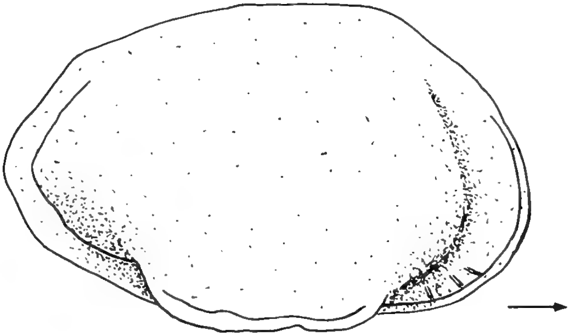


FIG. 15. Right side, female carapace, *Malzia unicarinata* sp. nov. Holotype, Io.1801, approx. ×105.

DESCRIPTION. *Carapace* subquadrate in outline in the female dimorphs, elongate in the male. Ventro-lateral part of carapace convex, extended as a short, rather stubby keel. Greatest length through mid-point; greatest height in the anterior third; greatest width in the posterior third. Shell surface punctate. Anterior broadly rounded; posterior broadly triangular with concave postero-dorsal slope and convex postero-ventral slope. Ventral margin medially incurved. Dorsal margin very slightly convex in the female, straight in the male although slightly concave just behind the anterior cardinal angle. Cardinal angles prominent, the anterior angle being broadly rounded with the posterior angle tending to be more acute. Anterior and posterior margins with well defined borders. *Eye swelling* elongate in outline situated below the anterior cardinal angle, more prominently developed in the male dimorph. Left valve larger than the right which it overlaps mid-ventrally and overreaches along the remaining part of the ventral margin and along the dorsal margin. Internal details not seen. *Radial pore canals* as seen from the exterior straight and widely spaced, approximately 8 anteriorly and 3 posteriorly. A narrow *flange* extends around the anterior margin and although not clearly seen probably also along the ventral margin.

Dimensions

Holotype Io.1801, female carapace (Pl. 10, figs. 4–8 ; Text-fig. 15), length 0·71 mm. ; height 0·42 mm. ; width 0·41 mm.

Io.1802, female carapace (Pl. 10, figs. 9, 10), length 0·73 mm. ; height 0·44 mm. ; width 0·43 mm. Io.1804, female carapace, length 0·75 mm. ; height 0·46 mm. ; width 0·43 mm. Io.1806, male carapace (Pl. 11, figs. 1–4), length 0·85 mm. ; height 0·45 mm. ; width 0·44 mm.

REMARKS. *Malzia unicarinata* is distinguished easily from *M. bicarinata* by the possession of but a single ventro-lateral keel. The male dimorph of *M. unicarinata* is, however, similar to *Progonocythere acuminata* sp. nov., from which it can be identified by the mid-laterally swollen, strongly convex carapace, a feature which characterizes species of this genus, and by the possession of a short stubby keel.

Genus ***PROGONOCYTHERE*** Sylvester-Bradley 1948

Progonocythere acuminata sp. nov.

(Pl. 11, figs. 5–10 ; Pl. 12, figs. 1–4)

DIAGNOSIS. *Progonocythere* with posteriorly acuminate carapace. Ventro-lateral margin convex with knife-edge keel developed in some specimens. Lateral surface smooth, though may possess faint transverse furrows medially. Low eye swelling at anterior cardinal angle. Ventral surface with longitudinal ridges in region of ventro-lateral overhang. Anterior with well developed border.

HOLOTYPE. Io.1783, bed 7, Hundale Point, Cloughton.

PARATYPES. Io.1784–91, bed 7, Hundale Point ; bed 6, Cayton Bay ; bed 7, Bogmire Gill ; top bed 7, Ravenscar and bed 10, Hawsker.

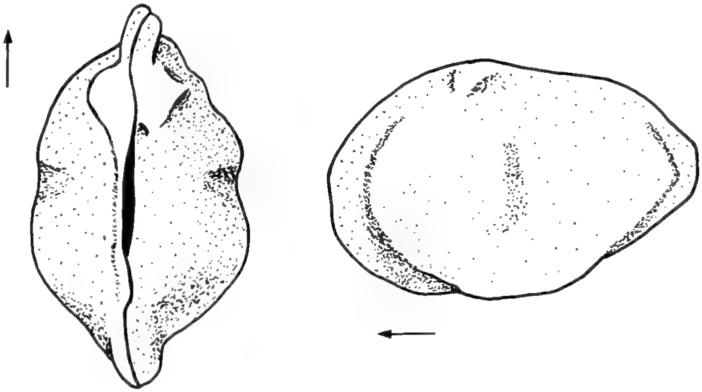
DESCRIPTION. *Carapace* elongate, tapering strongly towards the sharply acuminate posterior. Sexual dimorphism not apparent. The ventro-lateral border of the carapace is extended below the ventral surface and generally possesses a thin, knife-edge keel, developed from one of the longitudinal ridges which extend along the undersurface of the ventro-lateral part of the carapace, remainder of ventral surface smooth. The ventro-lateral margin of the carapace sweeps obliquely upwards just behind valve middle. Shell surface smooth, although weak transverse furrows may be observed in some specimens in the mid-lateral area. *Normal pore canals* often well developed, large and circular, widely scattered over the carapace. Greatest length through mid-point ; greatest height in the anterior third ; greatest width at or just behind middle. A shallow, indistinct sulcus, medially situated marks the position of the adductor *muscle scars*. Anterior broadly rounded with a distinct marginal border ; posterior narrow, acuminate with a short, concave postero-dorsal slope and a convex postero-ventral slope. Ventral margin broadly concave. Dorsal margin slightly convex in the right valve slightly concave medially in the left. Cardinal angles prominent. Below the anterior cardinal angle an oblique swelling, separated off from the convex part of the carapace below by an oblique groove, is suggestive of an eye swelling. Left valve larger than the right which it overlaps along the ventral margin and overreaches along the dorsal margin and around the anterior. The left valve may also overreach the right along the postero-dorsal slope but not at the extreme posterior. *Hinge* poorly seen in a single individual (left valve) where the terminal sockets are separated by a median groove which can be made out as dentate. Accommodation groove elongate, deep. *Duplicature* appears to be of moderate width, but imperfectly seen. Other internal details not observed.

Dimensions

Holotype, Io.1783, carapace (Pl. 12, figs. 1–4), length 0·80 mm. ; height 0·49 mm. ; width 0·38 mm.

Io.1784, left valve, length 0·71 mm. ; height 0·41 mm. Io.1786, left valve (Pl. 11, figs. 7, 8), length 0·60 mm. ; height 0·36 mm. Io.1787, carapace (Pl. 11, figs. 9, 10), length 0·69 mm. ; height 0·41 mm. ; width 0·34 mm. Io.1789, carapace (Pl. 11, figs. 5, 6), length 0·73 mm. ; height 0·41 mm. ; width 0·36 mm. Io.1791, right valve, length 0·71 mm. ; height 0·36 mm.

REMARKS. The similarity of *P. acuminata* to the male dimorph of *Malzia unicarinata* has already been discussed and need not be gone into again. The male dimorph of *Progonocythere yonsnabensis* sp. nov. also bears some resemblance to the



FIGS. 16–17. Dorsal and left views, female carapace, *Progonocythere yonsnabensis* sp. nov. Holotype, Io. 1792, approx. ×95.

present species although it can be readily distinguished by its much smaller size and by the distinct median sulcus not present to such an extent here.

Progonocythere yonsnabensis sp. nov.

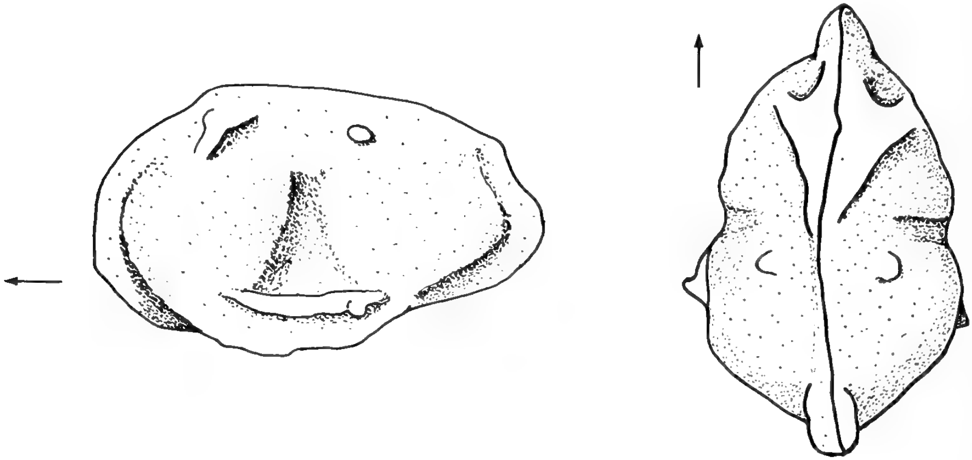
(Pl. 12, figs. 5–14; Pl. 13, figs. 1–4; Text-figs. 16–19)

DIAGNOSIS. Small progonocytherid with distinct median sulcus. Eye swelling prominent. Ventro-lateral margin extended into ventral keel. Shell surface punctate.

HOLOTYPE. Io.1792, bed 5, Cayton Bay section.

PARATYPES. Io.1793–96, horizon and locality as above.

DESCRIPTION. *Carapace* small, subquadrate; elongate in the male dimorph. Greatest length through mid-point; greatest height in the anterior third; greatest width in the posterior third. As seen in dorsal view a shallow sulcus divides the carapace into an anterior and a posterior half. This sulcus is more strongly developed in the female. Ventro-lateral margin strongly convex, extended ventrally into a prominent keel. In a single male specimen there is a second, short keel dorsal to the first and terminating in a small node. Almost directly above this node a second node is situated dorso-medially on each valve of the carapace posterior to the median sulcus. In all other respects this specimen is identical to the others. Dorsal margin strongly convex in the left valve, slightly convex in the right. Anterior rounded with a short, obliquely convex antero-dorsal slope. Posterior triangular: postero-dorsal slope concave; postero-ventral slope convex. Ventral margin medially incurved. Cardinal angles prominent, the posterior angle being the more strongly angled of the two, anterior angle tending to be broadly rounded. A prominent oval



FIGS. 18–19. Left and dorsal views, male carapace, *Progonocythere yonsnabensis* sp. nov., showing development of second keel and tubercles. Paratype, Io.1795, approx. ×95.

eye swelling is situated below the anterior cardinal angle. Anterior and posterior marginal borders distinct. Shell surface punctate. Left valve larger than the right which it overlaps mid-ventrally and overreaches postero-ventrally, postero-dorsally and antero-dorsally. Mid-dorsally the left valve is strongly projected above the right. There is little or no overreach around the anterior margin. Internal characters not observed for this species.

Dimensions

Holotype, Io.1792, female carapace (Pl. 12, figs. 5–8 ; Text-figs. 16–17), length 0·54 mm. ; height 0·32 mm. ; width 0·30 mm.

Io.1793, male carapace (Pl. 12, figs. 11–14), length 0·57 mm. ; height 0·34 mm. ; width 0·31 mm. Io.1794, female carapace (Pl. 12, figs. 9, 10), length 0·60 mm. ; height 0·36 mm. ; width 0·35 mm. Io.1795, male carapace (Pl. 13, figs. 1–4 ; Text-figs. 18–19), length 0·63 mm. ; height 0·36 mm. ; width 0·35 mm.

REMARKS. The single specimen (Io.1795) mentioned in the description, possessing two ventro-lateral keels and two lateral nodes is considered to be simply an extreme variant of the present species. Possibly this morphological variation may have been brought about by changes in the salinity of the water. Morphologically the possession of two lateral keels results in this specimen having some resemblance to *Malzia bicarinata*, although it can be distinguished by the possession of a prominent median sulcus and a very much smaller adult size.

The species *Progonocythere yonsnabensis* more closely resembles *Progonocythere cristata* Bate (1963 : 191, pl. 4, figs. 5–15 ; pl. 5, figs. 1–6) than any other ostracod. It is, however more strongly sulcate, possesses a more prominent eye swelling and is very much smaller.

Subfamily **PLEUROCYTHERINAE** Mandelstam 1960

Genus ***PLEUROCYTHERE*** Triebel 1951

Pleurocythere sp.

(Pl. 13, fig. 5)

REMARKS. A single left valve belonging to the genus *Pleurocythere* but not readily assignable to any known species is here recorded from the Gristhorpe Bay section, bed 4. The ornamentation of the valve consists of a longitudinal ventro-lateral ridge, an oblique median ridge and a short diagonal ridge which is situated below the anterior cardinal angle. This short ridge V's downwards, connected by a short ridge at the apex of the V to the median ridge. The dorsal end of the diagonal ridge terminates in an eye swelling. Shell surface between the ridges strongly reticulate.

Dimensions. Io.1836, left valve (Pl. 13, fig. 5), length 0·80 mm. ; height 0·35 mm.

Family **CYTHERIDEIDAE** Sars 1925

Subfamily **CYTHERIDEINAE** Sars 1925

Genus ***VERNONIELLA*** Oertli 1957

Remarks. The genus as diagnosed by Oertli (1957 : 659) possesses either a hemimerodont or antimerodont type hinge, and is considered to be without any strong ornamentation. Two species are here placed in *Vernoniella* : *V. bajociana* sp. nov., a smooth form possessing an antimerodont hinge and the strongly ornamented *V.* ? *caytonensis* sp. nov. There is, however, some uncertainty concerning the generic designation of the last named species.

Vernoniella bajociana sp. nov.

(Pl. 13, figs. 6–11 ; Pl. 14, figs. 1–13)

Diagnosis. *Vernoniella* with subquadrate carapace, elongate in male dimorphs. Shell surface finely punctate. Anterior and posterior margins with narrow marginal borders. Hinge antimerodont. Radial pore canals long, straight, approximately 10–11 anteriorly, 4–5 posteriorly.

Holotype. Io.1807, bed 23, Hundale Point, Cloughton.

Paratypes. Io.1808–30 and Io.2988, bed 5, Cayton Bay ; beds 7, 8, 23 and 25, Hundale Point ; bed 12, Ravenscar and beds 9 and 10, Hawsker.

Description. *Carapace* subquadrate to subtriangular in the female dimorph, elongate in the male. Shell surface punctate. Ventral surface may possess weak longitudinal ridges. In the dorso-median part of the carapace the valve is slightly constricted and here may exhibit weak, transverse furrowing. Greatest length of carapace through mid-point ; greatest height in the anterior third ; greatest width in the posterior third, although there is here only a slight increase over the width in the anterior third. Carapace appears compressed in dorsal view, almost parallel-sided. Dorsal margin medially concave in the left valve (both dimorphs), convex in the right. Cardinal angles in both valves prominent : anterior angle broadly rounded, posterior angle sharply angled and situated at extreme posterior of the carapace. Ventral margin medially incurved. Ventral surface overhung slightly by the convex ventrolateral margin. The incurving of the ventral surface produces, particularly in the male, an enlarged anterior portion of the carapace as seen in lateral view. Anterior broadly rounded with marginal border which is separated off from the convex lateral part of the carapace by a marginal groove. Posterior broadly triangular with a steeply angled, straight or slightly convex postero-dorsal slope and a convex postero-ventral slope. Left valve larger than the right which it overlaps along the ventral and postero-ventral margins and overreaches around the anterior margin and along the postero-dorsal slope. Mid-dorsally the convex dorsal margin of the right valve projects above the left. *Hinge* antimerodont : left valve with terminal loculate sockets and a strong denticulate median bar. No accommodation groove. Right valve with 6 terminal teeth, dorsally bifid and an elongate, finely locellate median groove. *Muscle scars* (Type B?) with a subvertical row of 4 oval adductor scars, a rounded antero-ventral mandibular scar which as seen in one individual is composed of a rosette of several small scars and an antero-dorsal antennal scar which is cloverleaf in shape. The antennal scar appears to be formed by the fusion of at least three scars which together form a clover-leaf pattern, or may appear rounded. Between the antennal scar and the dorsal adductor scar there is a large depression which is the mandibular support spot. This muscle scar arrangement is tentatively placed as Type B. Inner margin and line of concrescence coincide, the *duplicature* being of moderate width. Radial pore canals straight, approximately 10–11 anteriorly and 4–5 posteriorly. Outside the *selvage* in the right valve a *flange* is developed around the anterior margin, extending back along the ventral margin, where it expands opposite the ventral incurvature into a broad " lip ".

Dimensions

Holotype, Io.1807, female carapace (Pl. 13, figs. 6–9), length 0·67 mm. ; height 0·38 mm. ; width 0·30 mm.

Io. 1808, female carapace (Pl. 13, figs. 10, 11), length 0·66 mm. ; height 0·37 mm. width 0·26 mm. Io.1812, female left valve, length 0·69 mm. ; height 0·44 mm. Io.1814, male carapace (Pl. 14, figs. 1–4), length 0·84 mm. ; height 0·43 mm. ; width 0·29 mm. Io.1816, female carapace, length 0·61 mm. ; height 0·34 mm. ; width 0·28 mm. Io.1818, female left valve (Pl. 14, figs. 5–9), length 0·48 mm. ; height 0·31 mm. Io.1819, female right valve (Pl. 14, figs. 10, 12, 13), length 0·65 mm. ; height 0·37 mm. Io.1821, male carapace, length 0·68 mm. ; height 0·37 mm. ; width 0·28.

REMARKS. *Vernoniella bajociana* is similar in general external appearance to *V. sequana* Oertli (1957 : 659, pl. 3, figs. 70–85) but has an antimerodont instead of a hemimerodont hinge, and also lacks the accommodation groove which is present in *V. sequana*. *V. bajociana* has a distinct marginal border, a feature not present in Oertli's species.

***Vernoniella* ? *caytonensis* sp. nov.**

(Pl. 15, figs. 1–9)

DIAGNOSIS. *Vernoniella* ? with elongate, posteriorly acuminate carapace. Shell surface strongly ornamented by 4–5 longitudinal ridges arranged in broad, inverted V. Two to three obliquely transverse ridges occur anterior to these. Anterior and posterior with distinct marginal borders. Normal pore canals prominent.

HOLOTYPE. Io.1855, bed 6, Cayton Bay section.

PARATYPES. Io.1856–69, bed 4, Gristhorpe Bay ; bed 6 Cayton Bay and bed 11, Hawsker.

DESCRIPTION. *Carapace* elongate tapering towards the narrowly rounded posterior. Greatest length through mid-point ; greatest height in the anterior third ; greatest width in the posterior third. In dorsal view the carapace is slightly constricted medially. Anterior broadly rounded ; posterior narrowly rounded with steeply angled, convex postero-dorsal slope and convex postero-ventral slope. Dorsal margin in the right valve medially convex, in the left valve thickened and medially concave. Cardinal angles prominent ; the anterior angle being broadly rounded, posterior angle more acute, situated at extreme posterior of carapace. Anterior and posterior with distinct marginal borders. Ventral margin medially incurved. Shell surface strongly ornamented by 4–5 longitudinal ridges arranged in a broad inverted V, the lowermost being almost straight. These ridges are situated on the strongly convex part of the carapace which is cut off posteriorly by the posterior border and anteriorly by an oblique groove running just behind and below the anterior cardinal angle. In front of this groove there are 2–3 obliquely transverse ridges which antero-ventrally bend back to extend along the ventro-lateral and ventral surfaces where weak longitudinal ridges may be made out. *Normal pore canals* distinctly seen along the ventral surface where they are large and circular, elsewhere tending to be masked by lateral ornamentation. Left valve larger than the right which it overlaps along the ventral margin and overreaches in the region of the antero-dorsal and postero-dorsal slope. *Hinge* incompletely seen: right valve with the terminal elements consisting of approximately 6 dorsally bifid teeth. Median groove obscured by matrix. Left valve hinge not seen. Inner margin and line of concrescence appear to coincide. *Radial pore canals* long, straight and widely spaced, approximately 8 anteriorly and 3–4 posteriorly. Below the ventral incurvature in the right valve an elongate " lip " is developed.

Dimensions

Holotype, Io.1855, carapace (Pl. 15, figs. 1–4), length 0·63 mm. ; height 0·33 mm. ; width 0·30 mm.

Io.1857, right valve (Pl. 15, figs. 8, 9), length 0·66 mm. ; height 0·33 mm. Io.1858, carapace (Pl. 15, figs. 5–7), length 0·66 mm. ; height 0·37 mm. ; width 0·32 mm.

REMARKS. In outline this species approaches *Vernoniella* and as a result has been placed tentatively in that genus. It is, however, a strongly ornamented form whose hinge and muscle scars are as yet unknown.

Vernoniella ? caytonensis resembles the male dimorph of *Eocytheridea carinata* Bate (1964 : 18, pl. 5, figs. 5–8) primarily because of the similarity of ornament although it is easily distinguishable by the more prominent posterior cardinal angle, the not so strongly tapered carapace, and by the more strongly pronounced marginal borders.

Genus ***LJUBIMOVELLA*** Malz 1961

Ljubimovella piriformis Malz

(Pl. 15, figs. 10–13 ; Pl. 16, figs. 1, 2)

1949. Ostracod 96 Brand : 337, pl. 10 (fauna 2), fig. 4, pl. 14.
1961. *Ljubimovella piriformis* Malz : 165, pl. 2, figs. 15–25 ; text-figs. 2–3.
1962. *Ljubimovella piriformis* Malz : Brand & Fahrion : 134, pl. 20, fig. 33 ; table 9.

MATERIAL. Twenty-three specimens examined from the Grey Limestone Series, of which the following have been registered in the British Museum collections: Io.2103–08.

Description. *Carapace* piriform, very much enlarged in the anterior third, in which region it attains maximum height. Greatest length below mid-point; greatest width at, or in front of valve centre. A strong, downwardly projected spine is developed at the postero-ventral angle whilst a much shorter spine may also be present on the lower half of the anterior margin. Shell surface smooth except for the ventral surface where a number of fine longitudinal striae occur. *Normal pore canals* circular and widely scattered over the surface. Dorsal margin slightly concave medially; cardinal angles broadly rounded, although the posterior angle may be acute. Ventral margin with a strong median incurvature. Anterior broadly rounded; posterior obliquely rounded with a relatively long, convex postero-dorsal slope and a short, almost vertical but slightly convex postero-ventral slope which terminates in the prominent posterior spine. Left valve larger than the right which it overlaps along the ventral margin. Along the antero-dorsal and postero-dorsal slopes the left valve tends to overreach the right, whilst mid-dorsally the right valve overreaches the left. *Hinge* hemimerodont: left valve without an accommodation groove; right valve with smooth median groove and terminal dentate elements. *Muscle scars* not clearly seen. Inner margin and line of concrescence coincide. *Radial pore canals* short and widest at their base, 5 in number antero-ventrally and 5 postero-ventrally, of which the lowermost passes down through the centre of the posterior spine. A well developed *flange* extends around the anterior margin and along the ventral margin in the right valve, not observed in the left valve probably because of the preservation of the material.

Dimensions

Io.2103, carapace, length 0·69 mm.; height 0·34 mm.; width 0·31 mm. Io.2106, carapace (Pl. 16, figs. 1, 2), length 0·75 mm.; height 0·40 mm.; width 0·32 mm. Io.2107, juv, carapace (Pl. 15, figs. 10, 11), length 0·44 mm.; height 0·25 mm.; width 0·22 mm. Io.2108, right valve (Pl. 15, figs. 12, 13), length 0·72 mm.; height 0·37 mm.

Remarks. The single juvenile specimen observed of this species exhibits a much enlarged anterior half of the carapace. It would appear that in subsequent instars of the species there is a proportionately greater increase in the posterior part of the carapace, a process almost certainly related to the development of the reproductive organs as the animal reaches maturity.

Family **SCHULERIDEIDAE** Mandelstam 1959

Subfamily **SCHULERIDEINAE** Mandelstam 1959

Genus ***MESOCYTHERIDEA*** nov.

Diagnosis. Schulerideinae with oval/subquadrate carapace. Central part of valve strongly cut off from remainder of carapace by oblique groove below the anterior and posterior cardinal angles, particularly well developed in right valve. Dorso-median part of right valve strongly projected above dorsal margin. Hinge antimerodont with anterior socket of left valve cutting back into median bar. Radial pore canals long, slightly curved, 10 anteriorly, 4 posteriorly. Inner margin and line of concrescence coincident. Muscle scars (Type C) as for family. Left valve larger than right.

TYPE SPECIES. *Mesocytheridea howardianensis* sp. nov.

REMARKS. The genus (feminine) is close to *Eocytheridea* Bate (1963*a* : 35) from which it has probably evolved. *Mesocytheridea* is distinguishable from *Eocytheridea* by the presence of a strongly antimerodont hinge and a slight reduction in the number of anterior radial pore canals (10 as against 14) which tend to be straighter. The species *Eocytheridea carinata* Bate (1964 : 18, pl. 4, figs. 6–11 ; pl. 5, figs. 1–8) is very close to this genus but has a hemimerodont hinge and the radial pore canals are slightly more curved.

Mesocytheridea howardianensis sp. nov.

(Pl. 16, figs. 3–11 ; Pl. 17, figs. 1–3 ; Text-figs. 20, 21)

DIAGNOSIS. *Mesocytheridea* with oval/subquadrate carapace, convex in dorsal view. Ornamentation consists of some 5–6 low, broad ridges arranged in an inverted V. The lowermost, ventro-lateral ridges are longitudinal, thereby forming base to V. Ornamentation never strong, may be almost completely lacking, when shell appears smooth. Shell surface with prominent, circular, normal pore canals. Hinge, muscle scars, radial pore canals as for genus. Left valve larger than right. Species dimorphic.

HOLOTYPE. Io.1870, bed 2, Stonecliff Wood, locality SE/740675.

PARATYPES. Io.1871–81, horizon and locality as above and 1 ft. 6 in. and 3 ft. 8 in. from base bed 8, Stonecliff Wood, locality SE/743676.

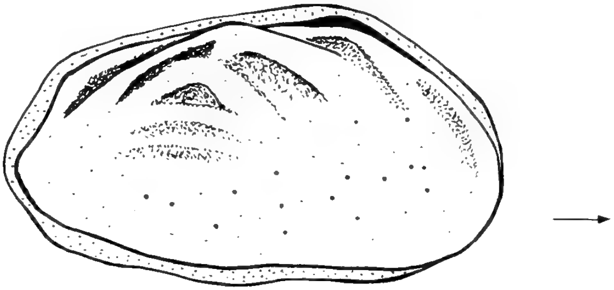


FIG. 20. Right view, female carapace, *Mesocytheridea howardianensis* sp. nov. Holotype, Io.1870, approx. ×93.

DESCRIPTION. *Carapace* oval/subquadrate, the male dimorphs being more elongate in outline. Greatest length through mid-point ; greatest height in the anterior third ; greatest width in the posterior third. Dorsal margin medially concave in the left valve with well rounded cardinal angles. In the male dimorph the dorso-median part of the left valve tends to project slightly above the dorsal margin, but not so strongly as in the right valve. Cardinal angles in the right valve more acute than in the left. Ventral margin medially incurved, convex in the posterior half where the carapace appears to be noticeably swollen. Anterior rounded with oblique, straight or slightly convex antero-dorsal slope. Posterior narrowly rounded with convex postero-dorsal and postero-ventral slopes. Narrow, convex, anterior and posterior marginal borders are separated from the lateral part of the carapace by a marginal groove. Dorsal margin of the left valve noticeably thickened. Shell surface with something like 5–6 low, rather poorly developed ridges which are arranged in the form of an inverted V, the apex of which reaches the dorsal margin, more noticeably developed in the right valve. Several of the lower, ventro-lateral ridges are straight and form a base to the inverted V. A strong diagonal groove separates the central part of the valve from the terminal parts, particularly in the right valve. The anterior groove extends diagonally below the anterior cardinal angle whilst the posterior groove extends below the posterior angle. A transverse ridge extends from the anterior cardinal angle towards the antero-ventral angle. Remainder of shell surface punctate, although a few very minor ridges may connect some of the antero-dorsal ridges. The degree with which the ornamentation is developed varies with each individual, but is often so poorly represented that the specimen appears smooth.

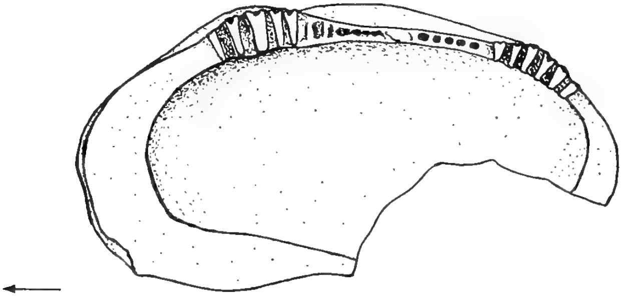


FIG. 21. Internal view, right valve showing hinge, *Mesocytheridea howardianensis* sp. nov. Paratype, Io. 1879, approx. ×95.

In all cases the *normal pore canals* which are large and circular, are prominently displayed over the shell surface. Left valve larger than the right which it overlaps along the ventral margin and overreaches practically everywhere else apart from mid-dorsally where the two valves are drawn apart. *Hinge* antimerodont: left valve with elongate terminal loculate sockets separated by a strong, denticulate median bar. The anterior socket, and to some extent the posterior socket also, tends to cut back into the median bar. There is virtually no accommodation groove. In the right valve the median groove is quite strongly locellate, whilst terminally there are 5 anterior and 7 posterior teeth, all dorsally bifid and well developed. *Muscle scars* (Type C) consist of a slightly crescentic row of 4 oval adductor scars with an antero-median, round, antennal scar. No mandibular scar observed. Inner margin and line of concrescence coincide, *duplicature* being quite broad. *Radial pore canals* long and widely spaced, some straight others slightly curved ; 10 anteriorly and 4 posteriorly.

Dimensions

Holotype, Io.1870, female carapace (Pl. 16, figs. 3–6 ; Text-fig. 20), length 0·73 mm. ; height 0·43 mm. ; width 0·38 mm.

Io.1871, female right valve (Pl. 16, fig. 9, Pl. 17, figs. 2, 3), length 0·71 mm. ; height 0·37 mm. Io.1872, male left valve (Pl. 17, fig. 1), length 0·93 mm. ; height 0·47 mm. Io.1875, female left valve (Pl. 16, fig. 11), length 0·76 mm. ; height 0·44 mm. Io.1877, male right valve, length 0·71 mm. ; height 0·36 mm. Io.1879, male right valve (Pl. 16, figs. 8, 10), length 0·78 mm. ; height 0·41 mm. Io.1881, female left valve (Pl. 16, fig. 7), length 0·71 mm. ; height 0·41 mm.

REMARKS. This is a much larger species than *Eocytheridea carinata* with which it bears some resemblance, although in *M. howardianensis* the ornamentation tends to be much weaker and the presence of a strong antimerodont hinge and a slight reduction in the number of radial pore canals help to distinguish the two species. The majority of the specimens examined come from the uppermost beds of the Grey Limestone Series as exposed along the western shore-line. However a population belonging to this species has been found at the base of the Series in the Bloody Beck section. The specimens here are generally smaller, no males having been found and are very poorly ornamented. They are not, however, considered to be sufficiently distinct as to be separated specifically.

Genus ***PRAESCHULERIDEA*** Bate 1963

Praeschuleridea subtrigona (Jones & Sherborn 1888)

SYNONYMY. See Bate (1964 : 22).

REMARKS. Two subspecies of *P. subtrigona* have been recognized : *P. subtrigona subtrigona* having a size range of up to 0·56 mm. in the female dimorph and 0·58 mm. in the male ; and *P. subtrigona magna* where the range extends to 0·73 mm. for the female and 0·83 mm. for the male. Within the Grey Limestone Series, however, there is a third subspecies having a maximum size of about 0·68 mm. for the female and 0·77 mm.–0·82 mm. for the male. There are also a number of minor morphological details which help to distinguish this third subspecies. As all the specimens examined from the Grey Limestone Series fall into this intermediate range the subspecies *Praeschuleridea subtrigona intermedia* subsp. nov. has been erected to account for them.

Praeschuleridea subtrigona intermedia subsp. nov.

(Pl. 17, figs. 4–10 ; Pl. 18, figs. 1–9)

DIAGNOSIS. A subspecies of *Praeschuleridea subtrigona* in which adult female is of the order of 0·68 mm. and male is 0·77 mm. to 0·82 mm. Carapace subtrigonal, punctate. Posterior dorsal margin virtually straight, sloping strongly to posterior. Anterior dorsal margin long, obliquely convex. Posterior with steeply inclined, convex postero-ventral slope. Anterior with narrow marginal border ; posterior border poorly developed.

HOLOTYPE. Io.1837, bed 7, Hundale Point, Cloughton.

PARATYPES. Io.1838–54, bed 4, Gristhorpe Bay ; bed 12, White Nab, Scarborough ; bed 7 & base bed 22, Hundale Point and bed 2 Stonecliff Wood, locality SE/740675.

DESCRIPTION. *Carapace* subtrigonal in outline, more elongate in the male dimorph. Shell surface finely punctate. *Normal pore canals* fairly large, circular, evenly scattered over carapace. A very low *eye swelling* may be seen on the right valve, female dimorph and slightly more strongly developed in the right valve of the male, situated below the anterior cardinal angle, not observed in the left valve of either dimorph. Greatest length passes through mid-point ; greatest height and width approximately at centre of carapace. A narrow marginal border delimited along its inner side by a marginal groove extends around the anterior margin, only poorly developed around the posterior. Left valve larger than the right which it overlaps along the ventral margin and overreaches elsewhere around the carapace. Dorsal margin " umbonate " the highest point being just about at valve centre, the dorsal margin sloping steeply away from this point to the anterior and posterior. Anteriorly the dorsal margin is broadly convex and passes into the anterior margin without a break. Posteriorly the dorsal margin is steeply angled, straight or very slightly convex. Posterior cardinal angle more prominently developed than the anterior angle. Posterior rounded-triangular with a short postero-dorsal slope which is convex in the left valve and straight in the right. Postero-ventral slope longer, convex and tending to be obliquely angled away from the ventral margin. Anterior uniformly rounded. Ventral margin antero-medially incurved, medially convex. *Hinge* paleohemimerodont ; left valve with terminal loculate sockets and a short median bar (longer in the male dimorph) across which there is a narrow groove connecting the terminal sockets. Accommodation groove broad and shelf-like. Right valve with strongly dentate terminal elements, not clearly seen in the present material. *Muscle scars* (Type C) with rounded anteromedian antennal scar. Inner margin and line of concrescence coincide ; *duplicature* of moderate width. Anterior *radial pore canals* slightly curved and in some specimens appearing to thicken slightly towards the outer termination ; 12–16 observed in the present material.

Dimensions

Holotype, Io.1837, female carapace (Pl. 17, figs. 4–6), length 0·64 mm. ; height 0·40 mm. ; width 0·32 mm.

Io.1838, male carapace, length 0·82 mm. ; height 0·45 mm. ; width 0·37 mm. Io.1839, male carapace (Pl. 18, figs. 1–3), length 0·77 mm. ; height 0·43 mm. ; width 0·33 mm. Io.1840, female carapace (Pl. 17, figs. 7–10), length 0·62 mm. ; height 0·41 mm. ; width 0·32 mm. Io.1843, female right valve (Pl. 18, fig. 9), length 0·60 mm. ; height 0·34 mm. Io.1846, female left valve (Pl. 18, figs. 6, 7), length 0·61 mm. ; height 0·43 mm.

Remarks. Apart from the variations in size range between the three subspecies of *Praeschuleridea subtrigona* there are also a number of additional characters by which the subspecies may be distinguished. The first of these characters concerns the angularity of the carapace which in the female dimorph of *intermedia* is very close to that of the type subspecies, the dorsal margin sloping strongly away from the region of greatest height. If anything, however, the posterior half of the dorsal margin is more elongate and not so steeply sloping as in *subtrigona subtrigona*. The dorsal margin in *magna* appears more uniformly convex on either side of the region of greatest height, contrasting with the almost straight posterior part in the other two subspecies. Posteriorly there are slight differences in all three : triangular in *subtrigona subtrigona* ; rounded in *magna* and bluntly flattened in *intermedia* where the postero-ventral slope although convex appears to flatten out slightly on approaching the extreme posterior. Actually the posterior margin of *intermedia* is closer to that of *magna* than to *subtrigona subtrigona*. The male dimorph of *intermedia* may be equivalent in size to that of *magna*—there however, it is the male of the last named species which shows the greater degree of angularity, being more noticeably " umbonate " than *intermedia*.

The conditions pertaining in north-eastern England during Middle Jurassic times appear to have offered a number of environments inhabited by a subspecies of *Praeschuleridea subtrigona* each population being characterized by a variation in size range. *Praeschuleridea subtrigona subtrigona* inhabited the marine waters of the shallow oolitic sea which covered Lincolnshire during Bajocian times. The northern extension of this sea lapped against the Yorkshire delta and provided a changed environment in which the subspecies *P. s. magna* developed. Higher up in the succession, the Yorkshire delta was still influencing the sedimentation of the Bajocian and throughout the entire marine embayment which spread over N.E. Yorkshire the population that existed was of *P. s. intermedia*.

Family **CYTHERURIDAE** Müller 1894

Genus ***EOCYTHEROPTERON*** Alexander 1933

Eocytheropteron ? sp.

(Pl. 18, figs. 10–13 ; Pl. 19, figs. 1–4)

Remarks. Four complete carapaces of a species externally resembling the genus *Eocytheropteron* have been obtained from beds high up in the Grey Limestone Series. Two male carapaces (Io.1910–11) have been obtained from bed 8, Stonecliff Wood section whilst a single female carapace (Io.2102) has been obtained from bed 5 of the same section. From bed 11, Hawsker, a further female carapace (Io.1909) has been found. The carapace is elongate-oval in side view with the ventro-lateral margin strongly convex and overhanging the ventral surface, especially so in the female dimorph. A short caudal process is developed and the greatest length of the carapace extends through mid-point. Shell surface with a very faint reticulation. A shallow sulcus is present at about valve centre in the female, slightly anterior to this in the male. Left valve larger than the right. Internal details not known although some radial pore canals can be made out externally in the antero-ventral area where they appear to be straight and widely spaced. This species is close to *Cytheropteron* (*Cytheropteron*) *purum* Schmidt (1954 : 88, pl. 6, figs. 3–6 ; pl. 7, figs. 25–29) although somewhat smaller and may be further distinguished by the more elongate and posteriorly tapering carapace of the female dimorph which in *C.* (*C.*) *purum* is shorter in comparison.

Io.1909, female carapace (Pl. 19, figs. 1–4), length 0·47 mm. ; height 0·26 mm. ; width 0·26 mm. Io.1911, male carapace (Pl. 18, figs. 10–13), length 0·53 mm. ; height 0·26 mm. width 0·28 mm.

Genus ***PARACYTHERIDEA*** Müller 1894

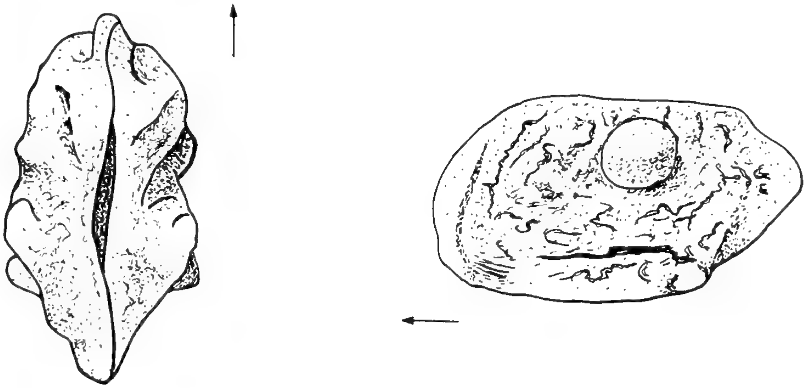
Paracytheridea*? *caytonensis sp. nov.

(Pl. 19, figs. 5–16 ; Text-figs. 22, 23)

DIAGNOSIS. *Paracytheridea* ? with backwardly projected ala terminating in prominent node. A second node is situated dorso-medially on lateral surface of valve, just behind median sulcus. Shell surface reticulate. Anterior and posterior with flattened marginal borders. Left valve larger than right. Species dimorphic.

HOLOTYPE. Io.2137, bed 6, Cayton Bay Section.

PARATYPES. Io.2138–42, horizon and locality as above.



FIGS. 22–23. Dorsal and left views, female carapace, *Paracytheridea* ? *caytonensis* sp. nov. Holotype, Io.2137, approx. ×105.

DESCRIPTION. *Carapace* subquadrate in side view with a prominent, backwardly projected ala at the tip of which is situated an oval node-like swelling. Above and slightly in front of this swelling a much larger node is situated on the lateral surface of the valve. In front of this circular node a transverse median sulcus is present which appears to curve under the lateral node. An oblique groove extending from the dorsal margin, below the anterior cardinal angle, extends down to the antero-ventral part of the valve where it turns back to extend along the dorsal side of the ventro-lateral ala. Shell surface rather coarsely reticulate, including the surface of the two nodes. An *eye swelling* is situated just below the anterior cardinal angle. Anteriorly and posteriorly the marginal borders are flattened, the convex lateral part of the carapace not extending right up to the margins. Ventral surface with approximately 5 longitudinal ridges to each valve. Sexual dimorphism indicated by the presence of an elongate specimen considered to be the male. Greatest length of carapace passes through mid-point ; greatest height in the anterior third ; greatest width in the posterior third. Dorsal margin slightly concave in the left valve, convex in the right. Anterior margin rounded with oblique, convex, antero-dorsal slope. Posterior triangular, extended into a caudal process, especially in the female. Postero-dorsal slope strongly concave, postero-ventral slope strongly convex. Ventral margin medially incurved. Cardinal angles prominent ; anterior angle broadly rounded ; posterior angle more acute. Left valve larger than the right which it overlaps along the ventral margin and slightly at the cardinal angles. Elsewhere the left valve overreaches the right, apart from along the dorsal margin where the valves diverge. Internal characters not seen.

Dimensions

Holotype, Io.2137, female carapace (Pl. 19, figs. 5–8 ; Text-figs. 22, 23), length 0·45 mm. ; height 0·26 mm. ; width 0·25 mm.

Io.2138, male carapace (Pl. 19, figs. 13–16), length 0·54 mm. ; height 0·25 mm. ; width 0·23 mm. Io.2140, female carapace (Pl. 19, figs. 9–12), length 0·43 mm. ; height 0·25 mm. ; width (broken) 0·22 mm.

Remarks. Only six specimens of this species have been found and these all occur in the same bed and represent a single population. Owing to the lack of knowledge concerning the internal details of this ostracod the generic designation is given with a query, although on general external morphology there is good reason to place this species into *Paracytheridea*. Superficially there is some resemblance between *P.* ? *caytonensis* and *Cytheropteron* (*Cytheropteron*) *bispinosum crassum* Schmidt (1954 : 87, pl. 7, figs. 23–24) although in the last named ostracod the ventro-lateral alar projection is not backwardly directed as in *P.* ? *caytonensis* and also lacks the characteristic nodes of that species.

Family **PROTOCYTHERIDAE** Ljubimova 1955

Subfamily **KIRTONELLINAE** Bate 1963

Genus ***SOUTHCAVEA*** Bate 1964

Southcavea microcellulosa sp. nov.

(Pl. 20, figs. 1–13 ; Pl. 21, figs. 1–4)

Diagnosis. *Southcavea* with oval-subquadrate carapace and coarse reticulate ornament. Pits produced by reticulate ornament 4–6 sided, internally strongly punctate. Hinge antimerodont. Species dimorphic.

HOLOTYPE. Io.1882, bed 5, Stonecliff Wood section.

PARATYPES. Io.1883–99, beds 3, 5 & 8, Stonecliff Wood and bed 11, Hawsker.

DESCRIPTION. *Carapace* oval-subquadrate in outline, more elongate in the male dimorph. Posteriorly tapered in the female. Greatest length through mid-point; greatest height in the anterior third; greatest width just behind valve centre. Dorsal margin in the left valve slightly concave medially with broadly rounded cardinal angles, in the right valve slightly convex, cardinal angles somewhat more acute. Anterior broadly rounded; posterior more narrowly rounded with convex postero-dorsal and postero-ventral slopes in the left valve, and a concave postero-dorsal and convex postero-ventral slope in the right. Ventral margin medially incurved. Ventro-lateral margin convex. Anterior without a marginal border, whilst posteriorly there is a very narrow, flattened border. Left valve larger than the right which it overlaps mid-ventrally, at the cardinal angles and along the postero-dorsal slope. Antero-ventrally, postero-ventrally and antero-dorsally the left valve overreaches the right. Shell surface strongly reticulate, the 4–6 sided pits produced being strongly punctate. This degree of punctation in many cases has resulted in the pits themselves being subdivided by secondary ridges—this development appears to be more characteristic of the ventro-lateral areas of the carapace. Ventral surface strongly ornamented by longitudinal ridges. *Normal pore canals* few in number and widely scattered over the carapace, although because of the ornamentation only clearly seen along the ventral surface. *Hinge* antimerodont: left valve with terminal sockets separated by a finely denticulate median bar. The accommodation groove is elongate and shelf-like. Right valve with 5 bifid, posterior teeth, exact number anteriorly not known but appears to be more than 5. Median groove elongate and finely locellate. Inner margin and line of concrescence coincide, *duplicature* of moderate width. *Radial pore canals* straight, simple and widely spaced, approximately 8 anteriorly, at least 4 posteriorly. *Muscle scars* (Type D?): adductor scars an oblique row of 4 scars with an antero-ventral mandibular scar and an antero-dorsal antennal scar which may be heart-shaped, but not so definitely V-shaped as in other species of this genus. A narrow *flange* has been observed in the right valve extending around the anterior margin and along the ventral margin.

Dimensions

Holotype, Io.1882, male carapace (Pl. 20, figs. 1–4), length 0·67 mm.; height 0·36 mm.; width 0·38 mm.

Io.1883, female carapace (Pl. 20, figs. 5–8), length 0·60 mm.; height 0·36 mm.; width 0·37 mm. Io. 1886, female right valve (Pl. 20, figs. 9, 10), length (broken) 0·60 mm.; height 0·34 mm. Io.1888, male carapace (Pl. 21, figs. 1–4), length 0·77 mm.; height 0·41 mm.; width 0·46 mm.; Io.1891, female carapace, length 0·65 mm.; height 0·36 mm.; width 0·36 mm. Io.1893, female carapace, length 0·54 mm.; height 0·30 mm.; width 0·31 mm.

REMARKS. *Southcavea microcellulosa* is a much more elongate ostracod than *Southcavea reticulata* Bate (1964 : 27, pl. 10, figs. 3–14 ; pl. 11, figs. 1–4) with which it might be confused, and also has a much finer ornamentation. *S. microcellulosa* appears to be virtually restricted to the sandy shore-line facies along the western outcrop of the Grey Limestone Series with the exception of a single female carapace found in bed 11, Hawsker. However, even at Hawsker in the east it is doubtful whether the northern coast-line was very far away.

Genus ***SYSTENOCYTHERE*** Bate 1963

Systenocythere ovata sp. nov.

(Pl. 21, figs. 5–12)

DIAGNOSIS. *Systenocythere* with ovoid carapace showing a strong reticulate ornamentation when well preserved, but generally only possessing ornamentation of longitudinal ridges on ventro-lateral and ventral surfaces. Internal characters as for genus.

HOLOTYPE. Io.1900, bed 7, Hawsker.

PARATYPES. Io.1901–8, bed 4, Gristhorpe Bay ; bed 6, Cayton Bay ; beds 19 and 22, Hundale Point, Cloughton ; beds 7 and 12, Hawsker and bed 1, Yearsley Moor.

DESCRIPTION. *Carapace* ovoid in side view, tapering posteriorly. Greatest length through mid-point ; greatest height in the anterior third ; greatest width in the posterior third. Dorsal margin convex in both valves ; cardinal angles rounded. Anterior rounded with oblique, convex, antero-dorsal slope. Posterior narrowly rounded with convex postero-dorsal and postero-ventral slopes in the left valve and concave postero-dorsal and convex postero-ventral slopes in the right valve. Ventral margin medially incurved. Ventro-lateral margin convex, overhanging the ventral surface in side view. Anterior and posterior with flattened marginal borders. Left valve larger than the right which it overlaps most strongly mid-ventrally, from which point, along the ventral margin the left valve progressively overreaches the right. The left valve also overreaches the right along the antero- and postero-dorsal slopes. Shell surface may be either strongly reticulate or only noticeably ornamented along the ventro-lateral and ventral surfaces with longitudinal ridges. Fairly large *normal pore canals* may be seen, depending on preservation, widely scattered over the carapace. *Hinge* merodont, not fully determinable. Right valve with 5 anterior teeth and possibly 5 posterior teeth ; median groove long and very narrow, it is difficult to state precisely whether this groove is smooth or locellate because of the preservation of the material. Hinge poorly preserved in the left valve : Accommodation groove of moderate width situated above the median bar which cannot be identified as being either smooth or denticulate. *Muscle scars* (Type D) consist of a subvertical row of 4 oval adductor scars with an oval anteroventral mandibular scar and a V-shaped antero-dorsal antennal scar. Inner margin and line of concrescence coincide, the *duplicature* being of moderate width. Approximately 8 anterior and 3 posterior *radial pore canals* may be distinguished, these appear to be straight and widely spaced. A narrow *flange* widening opposite the ventral incurvature, extends

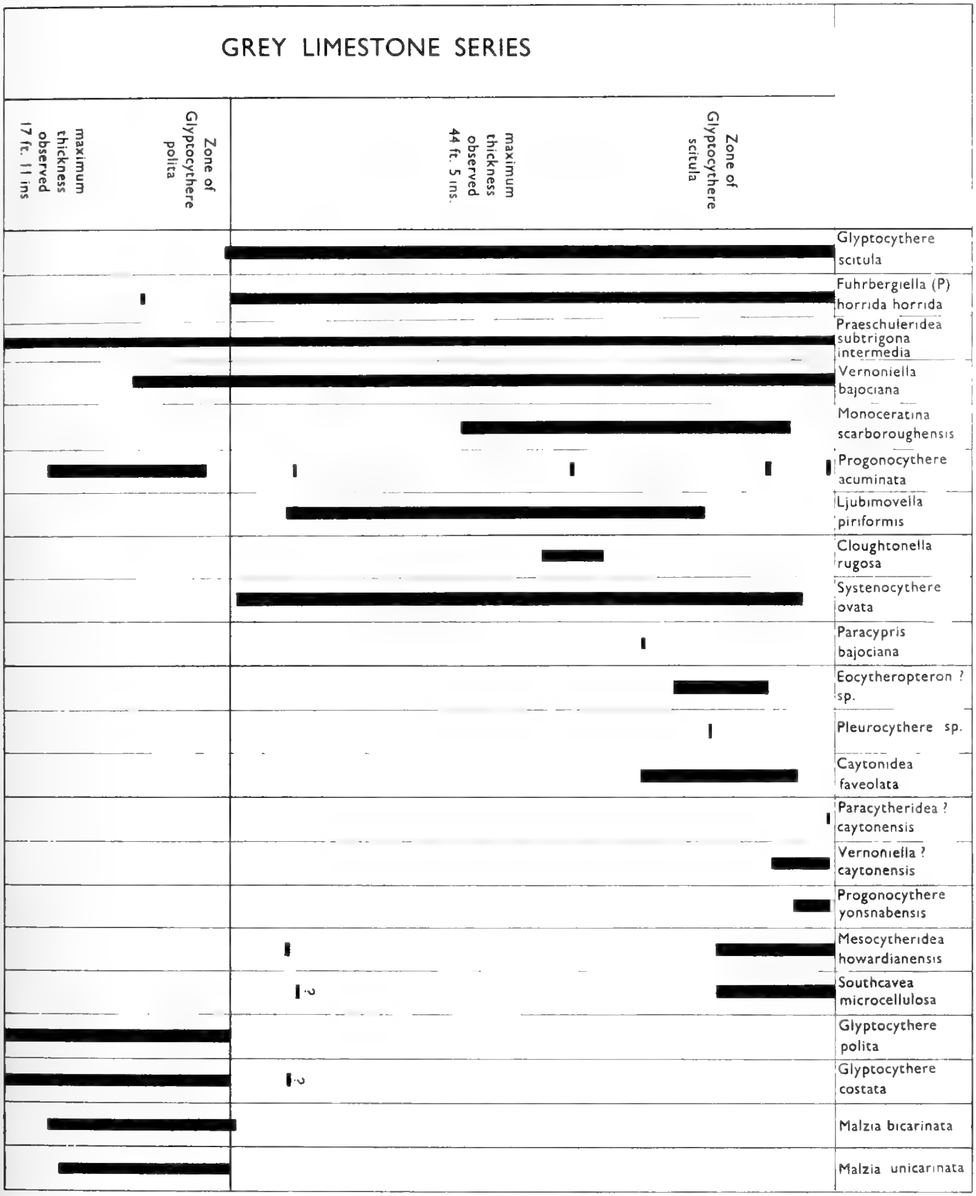


FIG. 24. Range table of the Grey Limestone Series Ostracoda.

along the ventral margin of the right valve and possibly also extends around the anterior margin. A flange has not been observed in the left valve.

Dimensions

Holotype, Io.1900, carapace (Pl. 21, figs. 5–8), length 0·70 mm.; height 0·44 mm.; width 0·37 mm.

Io.1901, left valve, length 0·66 mm.; height 0·39 mm. Io.1903, left valve (Pl. 21, fig. 12), length 0·60 mm.; height 0·36 mm. Io.1904, right valve, length 0·48 mm.; height 0·28 mm. Io.1907, right valve (Pl. 21, figs. 9–11), length 0·60 mm.; height 0·34 mm.

REMARKS. *Systenocythere ovata* is similar in outline to the female dimorph of *S. exilofasciata* Bate (1963 : 212, pl. 14, figs. 7–10; pl. 15, figs. 1–4), the type species, although it differs in not being so noticeably acuminate posteriorly and, when preservation permits, in being strongly reticulate.

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EXPLANATION OF PLATES

All the specimens illustrated are now in the Department of Palaeontology, British Museum (Natural History). All photographs, taken by the author, ×85 unless otherwise indicated.

PLATE 1

Monoceratina scarboroughensis sp. nov. p. 99.

FIGS. 1–3, 12. Bed 22, Hundale Point.

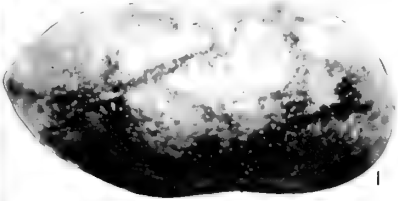
FIGS. 4–11. Bed 5, Cayton Bay.

FIGS. 1–3. Right, left and ventral views, female carapace. Holotype, Io.1711.
FIG. 4. Muscle scars, female carapace. Paratype, Io.1723, ×310.
FIGS. 5–8. Right, left, dorsal and ventral views, female carapace. Paratype, Io.1723.
FIGS. 9–11. Left, dorsal and ventral views, male carapace. Paratype, Io.1721.
FIG. 12. Internal view, female left valve. Paratype, Io.1720.

Caytonidea faveolata gen. et sp. nov. p. 100.

Specimen from bed 4, Gristhorpe Bay.

FIGS. 13, 14. Right, left, views, carapace. Paratype, Io.1834.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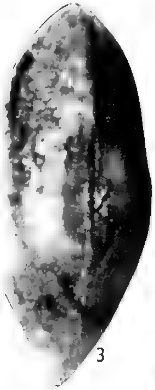
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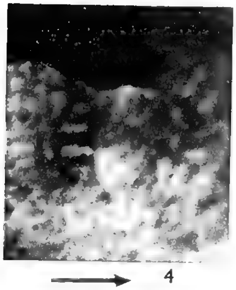
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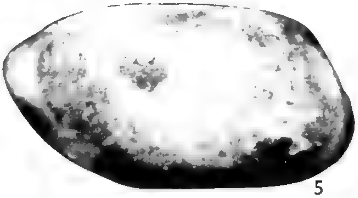
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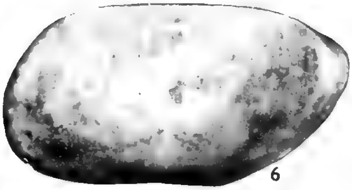
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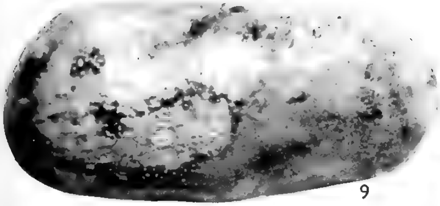
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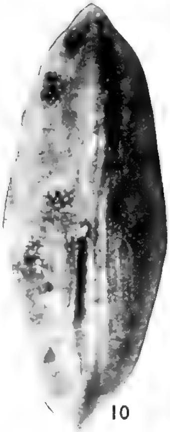
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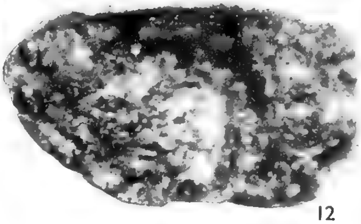
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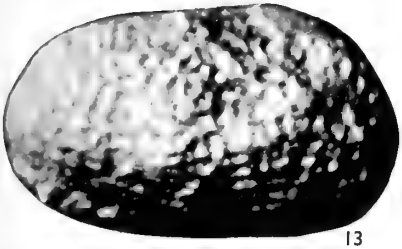
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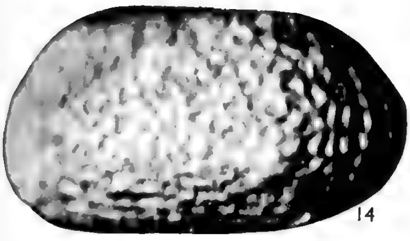
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PLATE 2

Caytonidea faveolata gen. et sp. nov. p. 100

FIGS. 1–4, 7–10. Bed 5, Cayton Bay.

FIGS. 5, 6. Bed 4, Gristhorpe Bay.

FIGS. 1–4. Right, left, dorsal and ventral views, carapace. Holotype, Io.1831.
FIGS. 5, 6. Dorsal and ventral views, carapace. Paratype, Io.1834.
FIGS. 7, 8. Dorsal and lateral views of right valve hinge.,Paratype, Io.1832, ×95.
FIGS. 9, 10. Internal views of right valve fragment to show muscle scars and anterior radial pore canals. Paratype, Io.1833.

PLATE 2


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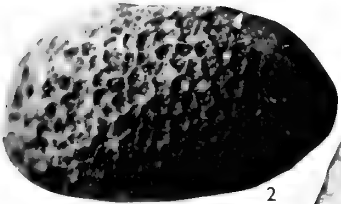
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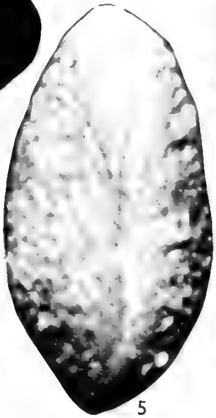
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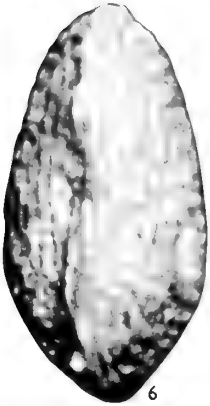
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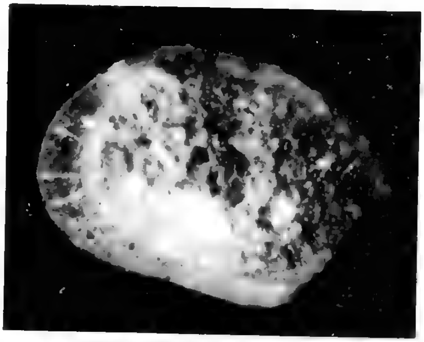
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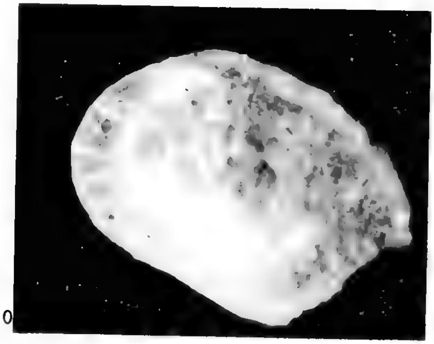
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PLATE 3

Cloughtonella rugosa gen. et sp. nov. p. 102

FIGS. 1–7, 11–13. Bed 22, Hundale Point, Cloughton.

FIGS. 8–10. Bed 10, Bloody Beck.

FIGS. 1–4. Right, left, dorsal and ventral views, female carapace. Holotype, Io.2118.
FIGS. 5–7. Ventral, right and left views, male carapace. Paratype, Io.2119.
FIGS. 8, 9. Left and right views, female carapace. Paratype, Io.2135.
FIG. 10. Left view, showing large normal pore canals, male carapace. Paratype, Io.2134.
FIG. 11. Dorsal view of hinge, female left valve. Paratype, Io.2121.
FIGS. 12, 13. Right and left views, male carapace. Paratype, Io.2120.


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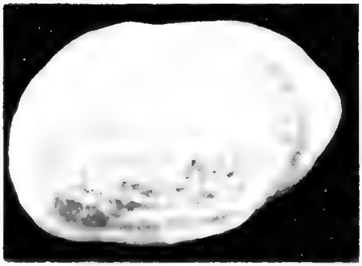
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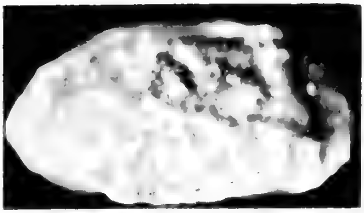
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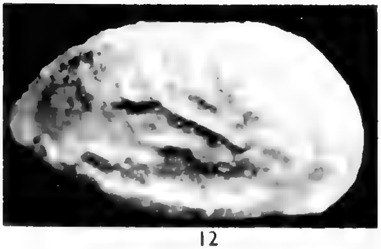
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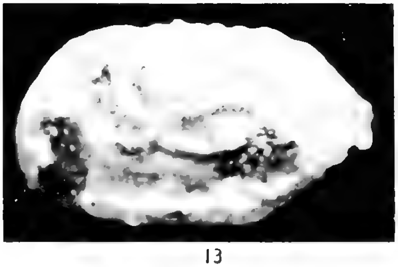
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PLATE 4

Fuhrbergiella (Praefuhrbergiella) horrida horrida Brand & Malz p. 104

FIGS. 1–3. Bed 5, Cayton Bay.

FIGS. 4, 5, 10. Bed 6, Cayton Bay.

FIGS. 6–9, 11, 12. Bed 23, Hundale Point, Cloughton.

FIGS. 1–3. Internal, external and dorsal views, female left valve, Io.2109.
FIGS. 4, 5. External and dorsal views, female right valve, Io.2116.
FIGS. 6–9. Dorsal, left, right and ventral views, male carapace, Io.2111.
FIG. 10. External view, female right valve showing anterior and posterior radial pore canals, Io.2117.
FIGS. 11, 12. Dorsal and right views, female carapace, Io. 2110.


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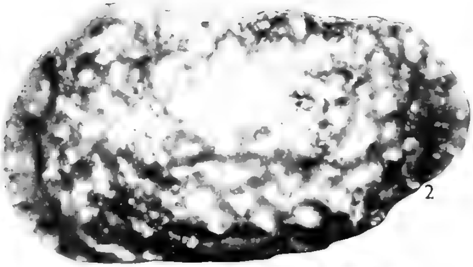
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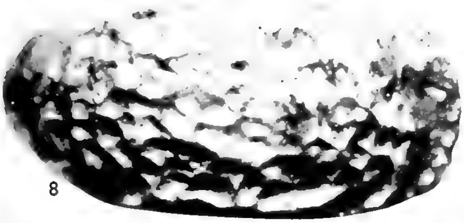
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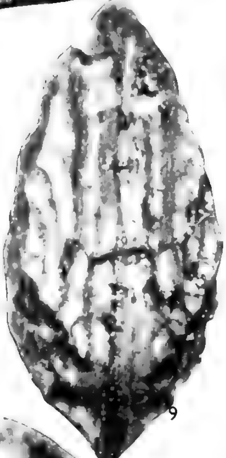
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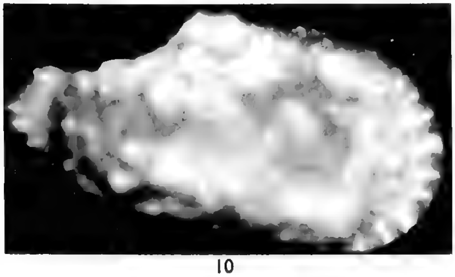
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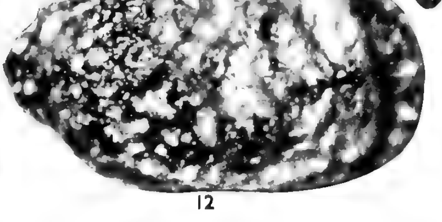
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PLATE 5

Glyptocythere costata sp. nov. p. 106

FIGS. 1–4, 7. Bed 10, Ravenscar.

FIGS. 5, 6. Bed 8, Ravenscar.

FIGS. 1–4. Right, left, dorsal and ventral views, female carapace. Holotype, Io.1775.
FIGS. 5, 6. Right and left views, male carapace. Paratype, Io.1782.
FIG. 7. Female right valve. Paratype, Io.1776.

Glyptocythere polita sp. nov. p. 107

FIG. 8. Bed 6, Bloody Beck.

FIG. 9. Bed 7, Ravenscar.

FIG. 10. Bed 7, Hundale Point, Cloughton.

FIG. 11. Bed 9, Ravenscar.

FIG. 8. Right view, female carapace. Paratype, Io.1743.
FIG. 9. Internal view, female left valve. Paratype, Io.1738, ×70.
FIG. 10. Right view, female carapace, showing normal pore canals. Paratype, Io.1736, ×70.
FIG. 11. Dorsal view of hinge, female left valve. Paratype, Io.1741.

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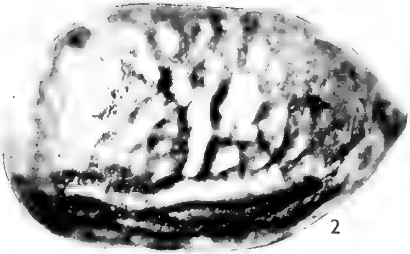

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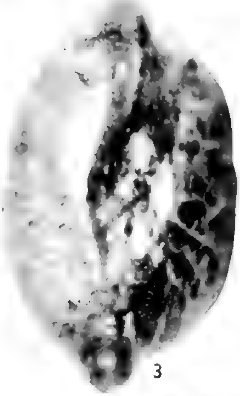

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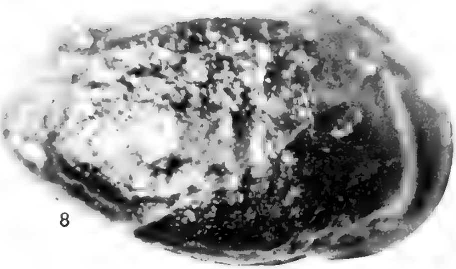

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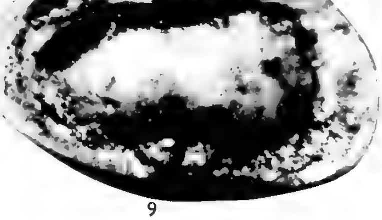

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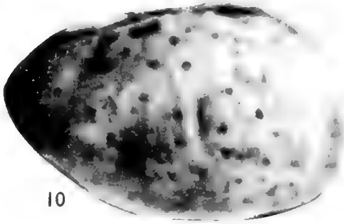

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PLATE 6

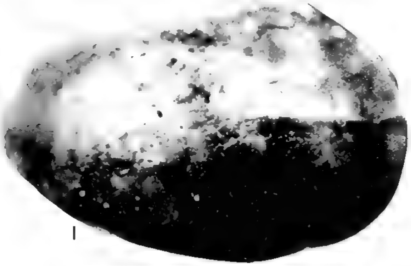
Glyptocythere polita sp. nov. p. 107

FIGS. 1–8. Bed 7, Hundale Point, Cloughton.

FIG. 9. Bed 8, Hundale Point, Cloughton.

FIGS. 1–4. Right, left, dorsal and ventral views, female carapace. Holotype, Io.1724, ×70.
FIGS. 5–8. Right, left, dorsal and ventral views, male carapace. Paratype, Io.1725, ×70.
FIG. 9. Muscle scars, female left valve. Paratype, Io.1737, ×150.

PLATE 6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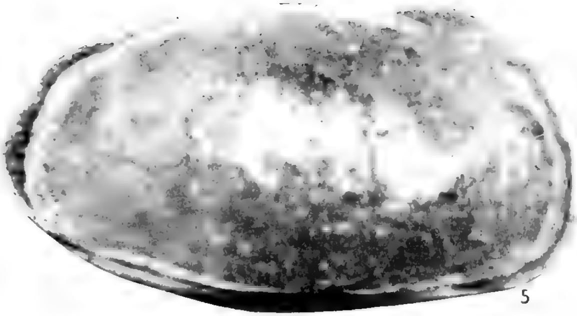
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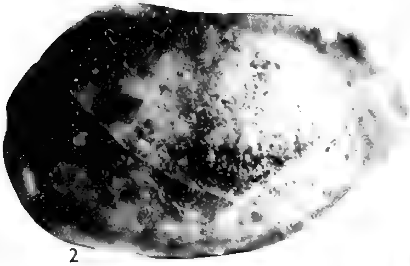
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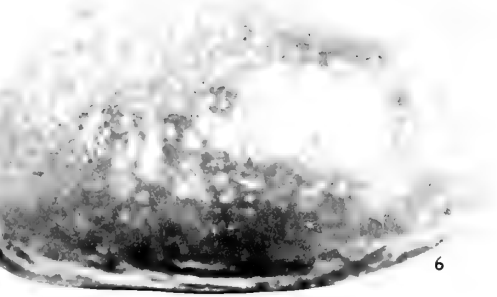
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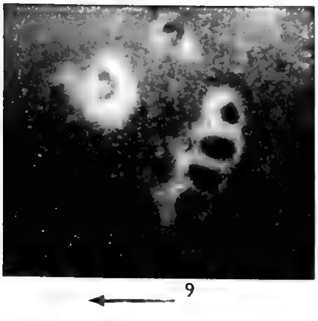
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PLATE 7

Glyptocythere scitula sp. nov. p. 108

FIGS. 1, 7. Bed 10, Hawsker.

FIGS. 2–6, 8–10. Bed 12, Ravenscar.

FIGS. 11, 12. Bed 5, Cayton Bay.

FIG. 13. Bed 5, Gristhorpe Bay.

FIGS. 1, 7. Internal and dorsal views, female right valve. Paratype, Io.1760.

FIG. 2. Muscle scars. Note antero-ventral mandibular scar, which is a rosette of several. smaller scars. Broken female right valve. Paratype, Io.1774, ×150.

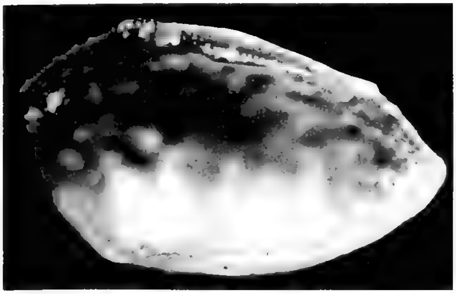
FIGS. 3, 8. Muscle scars (×125) and anterior radial pore canals (×90), female right valve. Paratype, Io. 1771.

FIGS. 4, 6, 10. Internal view, showing radial pore canals, and two dorsal views of hinge, female right valve. Paratype, Io.1768.

FIGS. 5, 9. Dorsal views of hinge, female left valve. Paratype, Io.1769.

FIGS. 11, 12. External and internal views, male left valve. Paratype, Io.1751.

FIG. 13. External view, male right valve. Paratype, Io.1772.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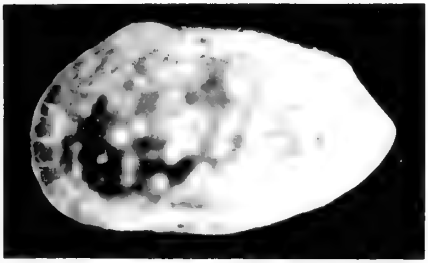
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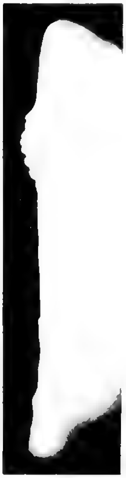
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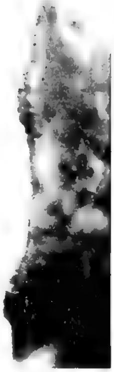
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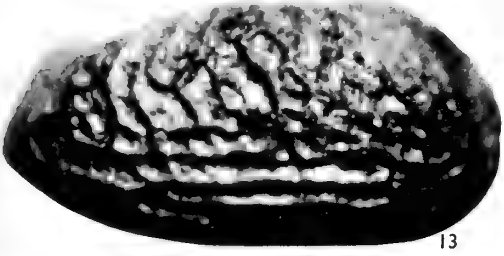
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PLATE 8

Glyptocythere scitula sp. nov. p. 108

FIGS. 1–5. Bed 5, Cayton Bay.

FIGS. 6–9. Bed 10, Hawsker.

FIGS. 1–4. Left, right, dorsal and ventral views, female carapace. Holotype, Io.1750.
FIG. 5. External view, female left valve. Paratype, Io.1754.
FIGS. 6–9. Left, right, dorsal and ventral views, female carapace. Paratype, Io.1752.


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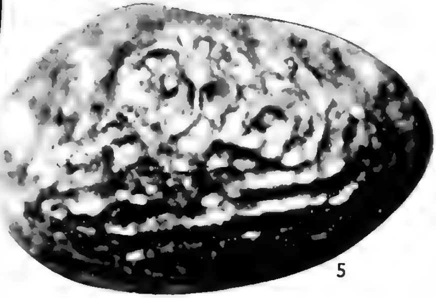
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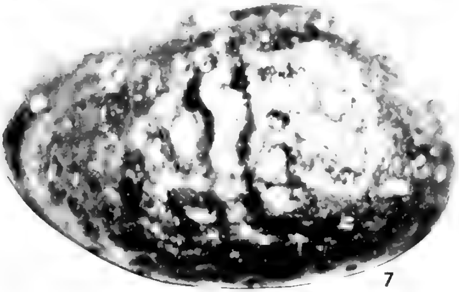
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PLATE 9

Glyptocythere scitula sp. nov. p. 108

Specimen from bed 10, Hawsker.

FIGS. 1–4. Left, right, dorsal and ventral views, male carapace. Paratype, Io.1753.

Malzia bicarinata gen. et sp. nov. p. 111

Specimen from bed 9, Ravenscar.

FIGS. 5–8. Left, right, dorsal and ventral views. Holotype, Io.1797.

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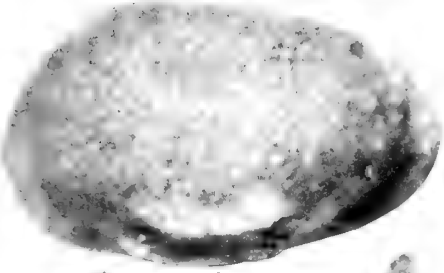

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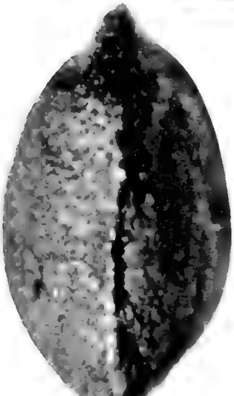

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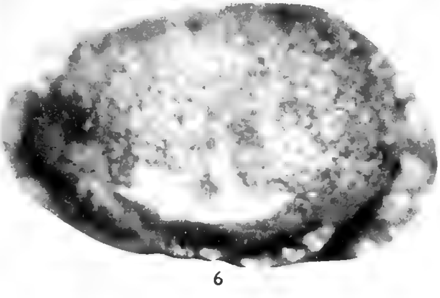

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PLATE 10

Malzia bicarinata gen. et sp. nov. p. 111.

FIG. 1. Bed 8, Ravenscar.

FIGS. 2, 3. Bed 7, Ravenscar.

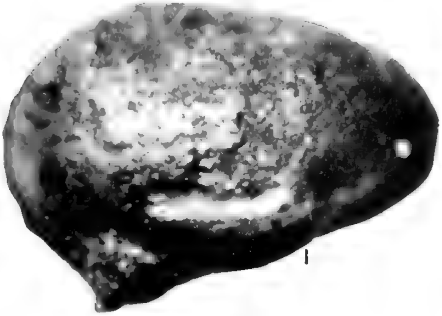
FIG. 1. Left side, carapace. Paratype, Io.1798.
FIGS. 2, 3. Internal view and dorsal view (× 100) left valve. Paratype, Io.1799.

Malzia unicarinata gen. et sp. nov. p. 113.

FIGS. 4–8. Bed 9, Ravenscar.

FIGS. 9, 10. Bed 8, Ravenscar.

FIGS. 4–7. Left, right, dorsal and ventral views, female carapace. Holotype, Io.1801.
FIG. 8. Right view of female carapace to show radial pore canals. Holotype, Io.1801.
FIGS. 9, 10. Left and right views, female carapace. Paratype, Io.1802.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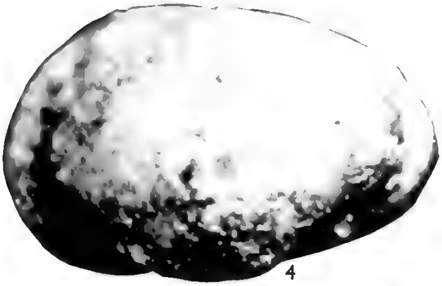
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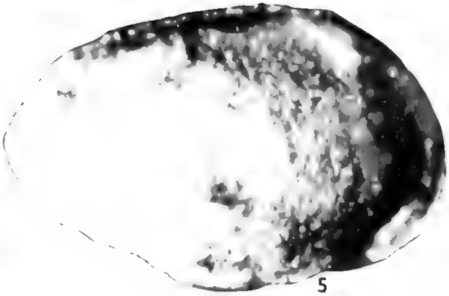
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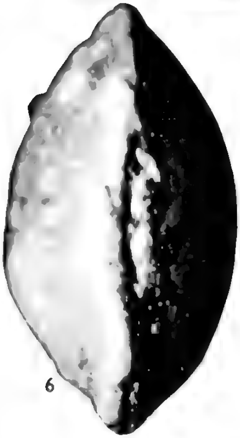
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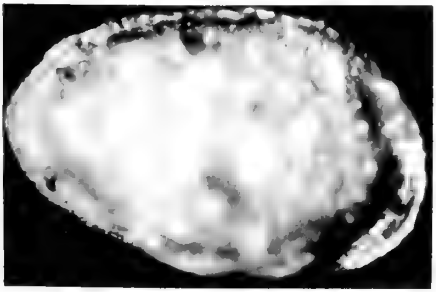
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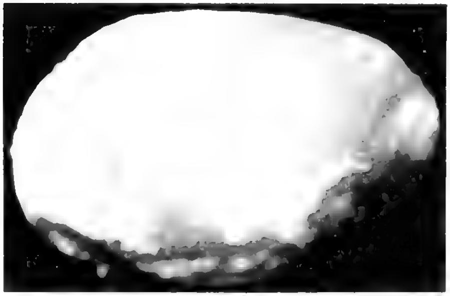
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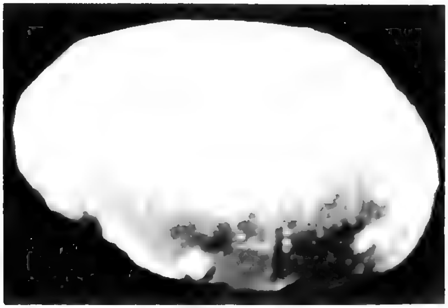
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PLATE 11

Malzia unicarinata gen. et sp. nov. p. 113.

Specimen from bed 10, Ravenscar.

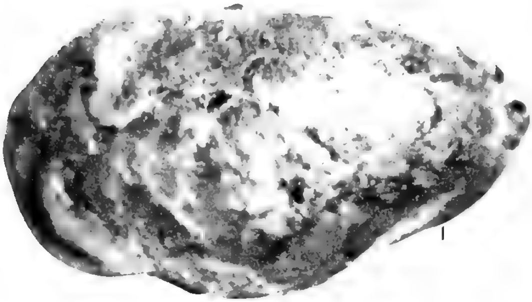
FIGS. 1–4. Left, right, dorsal and ventral views, male carapace. Paratype, Io.1806.

Progonocythere acuminata sp. nov. p. 114.

FIGS. 5, 6. Bed 7, Ravenscar.

FIGS. 7–10. Bed 6, Cayton Bay.

FIGS. 5, 6. Left and right views, carapace. Paratype, Io.1789.
FIGS. 7, 8. External and internal views, left valve. Paratype, Io.1786.
FIGS. 9, 10. Right and left views, carapace. Paratype, Io.1787.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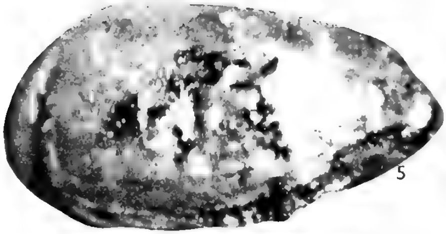
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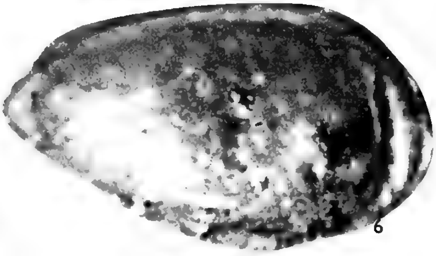
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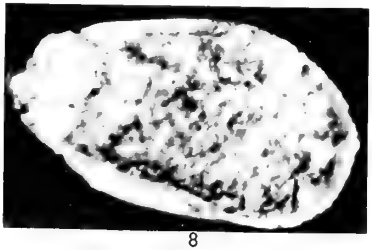
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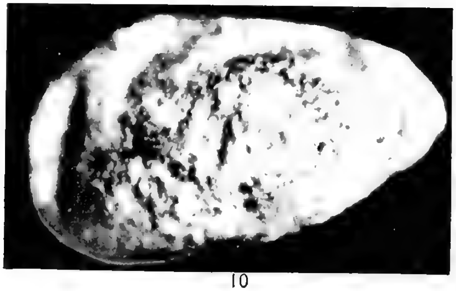
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PLATE 12

Progonocythere acuminata sp. nov. p. 114.

Specimen from bed 7, Hundale Point, Cloughton.

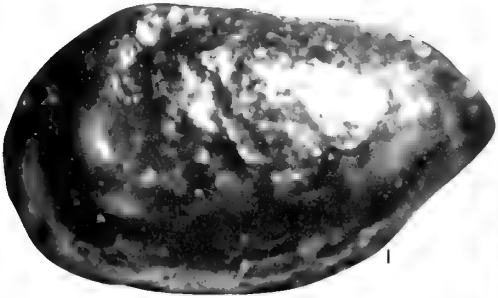
FIGS. 1–4. Left, right, dorsal and ventral views, carapace. Holotype, Io.1783.

Progonocythere yonsnabensis sp. nov. p. 116.

All specimens from bed 5, Cayton Bay.

FIGS. 5–8. Left, right, dorsal and ventral views, female carapace. Holotype, Io.1792.
FIGS. 9, 10. Left and right views, female carapace. Paratype, Io.1794.
FIGS. 11–14. Left, right, dorsal and ventral views, male carapace. Paratype, Io.1793.

PLATE 12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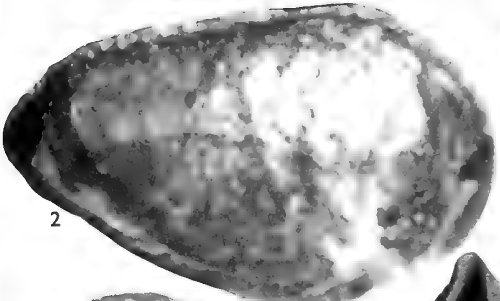
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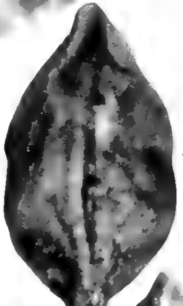
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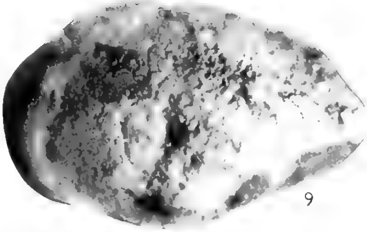
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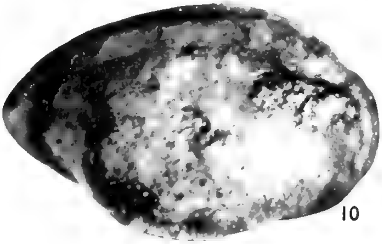
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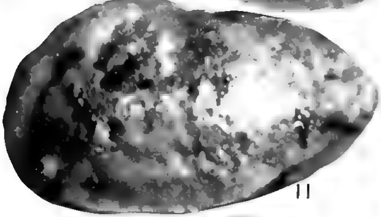
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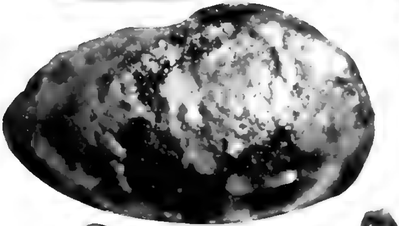
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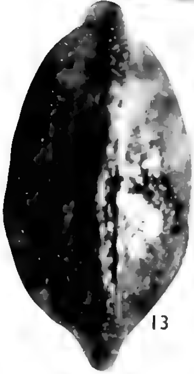
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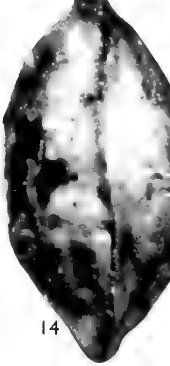
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PLATE 13

Progonocythere yonsnabensis sp. nov. p. 116.

Specimen from bed 5, Cayton Bay.

Figs. 1–4. Left, right, dorsal and ventral views, male carapace, showing development of two lateral keels and nodes. Paratype, Io.1795.

Pleurocythere sp. p. 117.

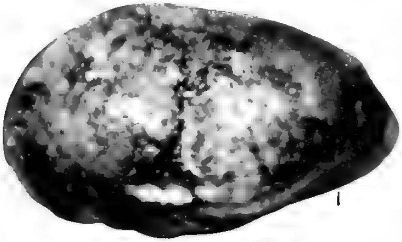
Specimen from bed 4, Gristhorpe Bay.

Fig. 5. External view, left valve, Io.1836.

Vernoniella bajociana sp. nov. p. 118.

Specimens from bed 23, Hundale Point, Cloughton.

Figs. 6–9. Left, right, dorsal and ventral views, female carapace. Holotype, Io.1807.
Figs. 10, 11. Right and left views, female carapace. Paratype, Io.1808.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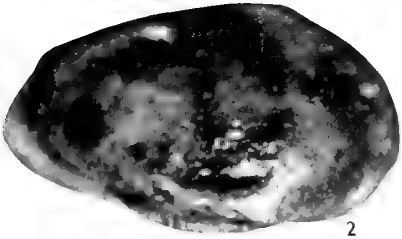
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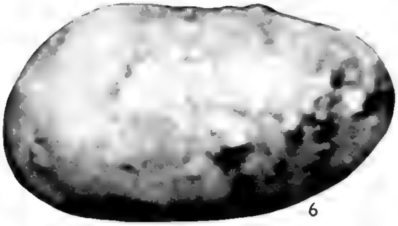
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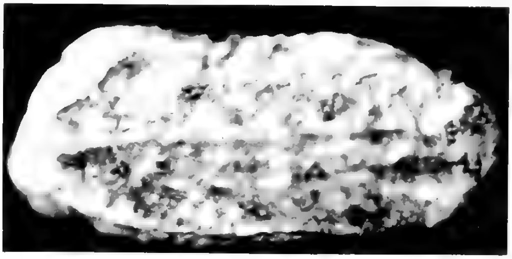
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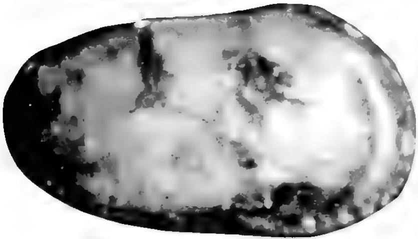
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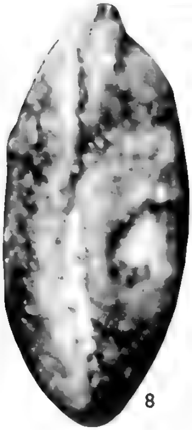
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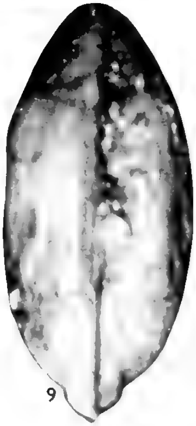
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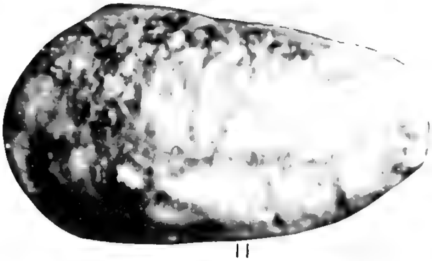
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PLATE 14

Vernoniella bajociana sp. nov. p. 118.

FIGS. 1–4. Bed 7, Hundale Point, Cloughton.

FIGS. 5–10, 12, 13. Bed 12, Ravenscar.

FIG. 11. Bed 9, Hawsker.

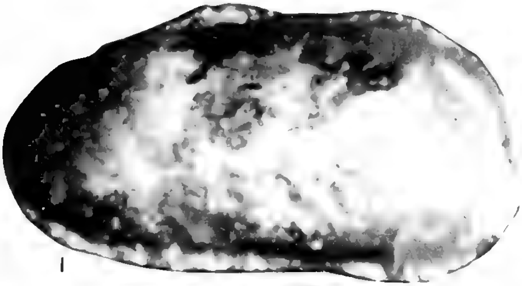
FIGS. 1–4. Right, left, dorsal and ventral views, male carapace. Paratype, Io.1814.

FIGS. 5–9. 5, anterior radial pore canals (×140); 6, dorsal view of hinge; 7, internal view to show boring of shell by marine organism; 8, lateral view of hinge; 9, internal view to show radial pore canals. Female left valve. Paratype Io.1818.

FIGS. 10, 12, 13. Muscle scars (×180) showing composite antennal scar, dorsal view of hinge (×95) and internal view of male right valve. Paratype, Io.1819.

FIG. 11. Muscle scars, fragment of female right valve. Paratype, Io.1813, ×110.

PLATE 14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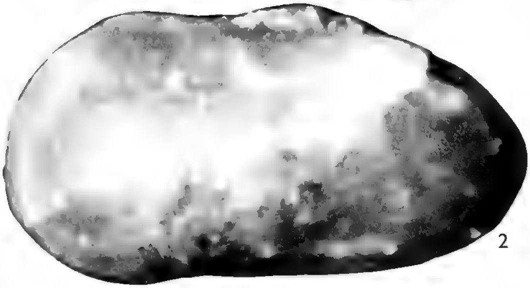
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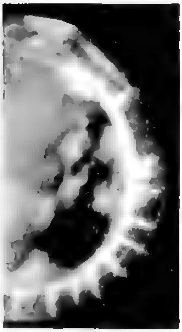
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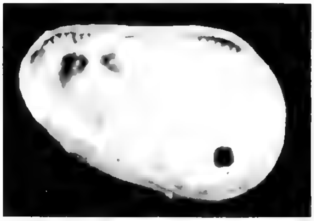
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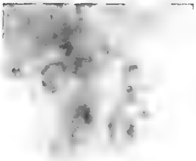
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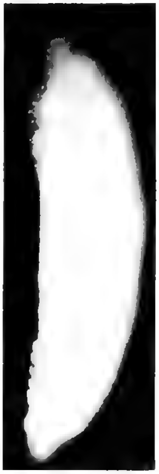
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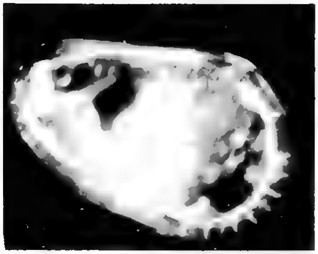
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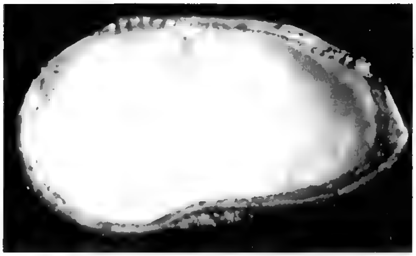
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PLATE 15

Vernoniella caytonensis sp. nov. p. 119.

All specimens from bed 6, Cayton Bay.

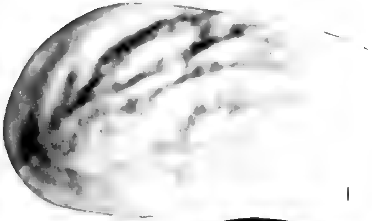
FIGS. 1–4. Left, right, dorsal and ventral views, carapace. Holotype, Io.1855.
FIGS. 5–7. Right, left and ventral views, carapace. Paratype, Io.1858.
FIGS. 8, 9. Dorsal and internal views, right valve. Paratype, Io.1857.

Ljubimovella piriformis Malz p. 120.

FIGS. 10, 11. Bed 22, Hundale Point, Cloughton.

FIGS. 12, 13. Bed 12, Ravenscar.

FIGS. 10, 11. Left and right sides, juvenile carapace. Io.2107.
FIGS. 12, 13. Internal and external views, right valve. Io.2108.



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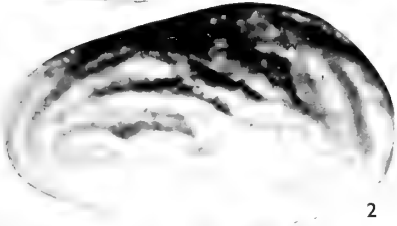

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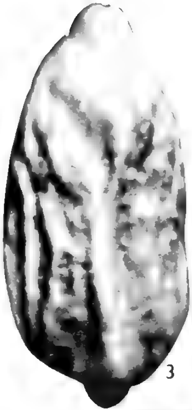

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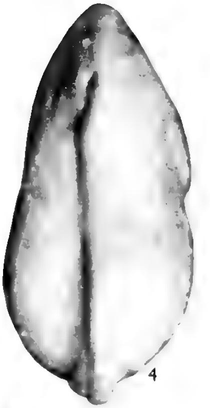

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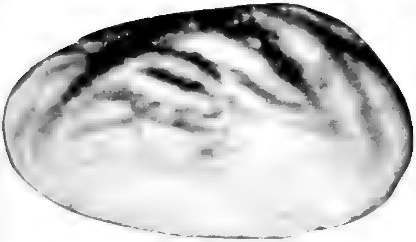

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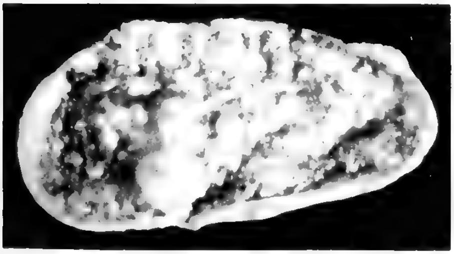

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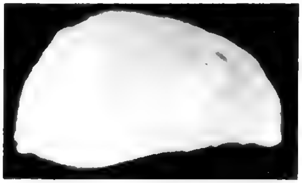

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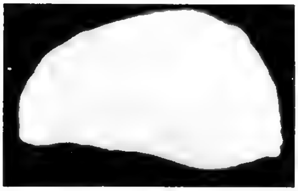

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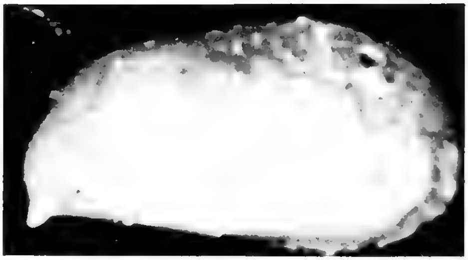

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PLATE 16

Ljubimovella piriformis Malz. p. 120.

Specimen from bed 7, Hawsker.

FIGS. 1, 2. Left and right sides, adult carapace. Io.2106.

Mesocytheridea howardianensis gen. et sp. nov. p. 122.

FIGS. 3–6, 9, 11. Bed 2, Stonecliff Wood.

FIG. 7. Bed 7, Bloody Beck.

FIGS. 8, 10. Bed 8, Stonecliff Wood.

FIGS. 3–6. Right, left, dorsal and ventral views, female carapace. Holotype, Io.1870.
FIG. 7. Dorsal view hinge, female left valve. Paratype, Io.1881.
FIGS. 8, 10. Dorsal and internal views, male right valve. Paratype, Io.1879.
FIG. 9. Dorsal view, female right valve. Paratype, Io.1871.
FIG. 11. Internal view, female left valve, showing anterior socket cutting back into the median bar. Paratype, Io.1875.


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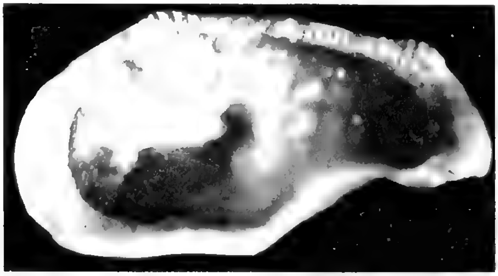
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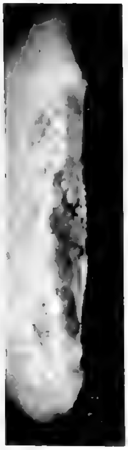
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PLATE 17

Mesocytheridea howardianensis gen. et sp. nov. p. 122.

Specimens from bed 2, Stonecliff Wood.

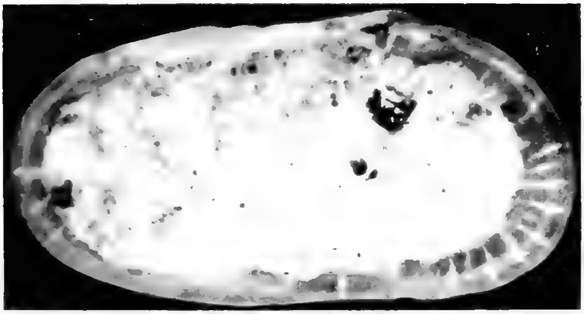
FIG. 1. Internal view, showing radial pore canals, male left valve. Paratype, Io. 1872.
FIGS. 2, 3. Internal views to show hinge and radial pore canals, female right valve. Paratype, Io.1871.

Praeschuleridea subtrigona intermedia subsp. nov. p. 124.

FIGS. 4–6. Bed 7, Hundale Point, Cloughton.

FIGS. 7–10. Bed 2, Stonecliff Wood.

FIGS. 4–6. Left, right and dorsal views, female carapace. Holotype, Io.1837.
FIGS. 7–10. Ventral, dorsal, right and left views, female carapace. Paratype, Io.1840.



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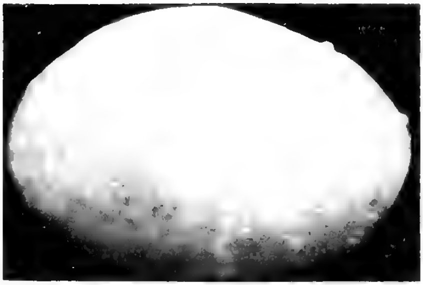

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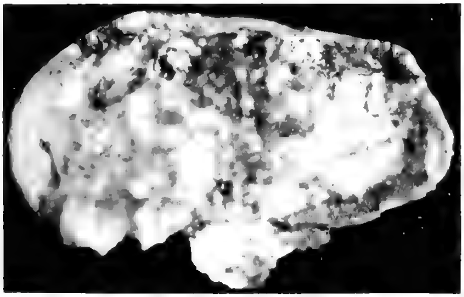

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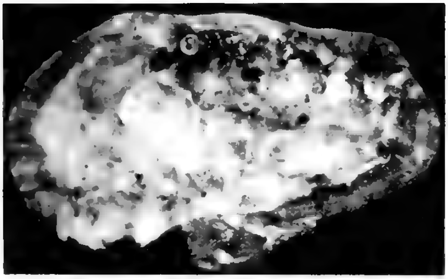

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PLATE 18

Praeschulerida subtrigona intermedia subsp. nov. p. 124.

FIGS. 1–3. Bed 7, Hundale Point, Cloughton.

FIGS. 4, 5, 8, 9. Bed 2, Stonecliff Wood.

FIGS. 6, 7. Bed 4, Gristhorpe Bay.

FIGS. 1–3. Left, right and ventral views, male carapace. Paratype, Io.1839.
FIG. 4. Muscle scars from internal cast. Paratype, Io.1844, × 180.
FIG. 5. Anterior radial pore canals, right valve fragment. Paratype, Io.1841, × 135.
FIGS. 6, 7. Dorsal and internal views to show hinge, female left valve. Paratype, Io.1846.
FIG. 8. Right side to show normal and radial pore canals, female carapace. Paratype, Io.1842.
FIG. 9. Dorsal view of hinge, female right valve. Paratype, Io.1843.

Eocytheropteron ? sp. p. 126.

Specimen from bed 8, Stonecliff Wood.

FIGS. 10–13. Ventral, left, right and dorsal views, male carapace. Io.1911.


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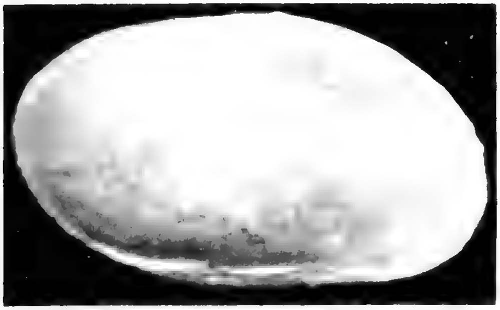
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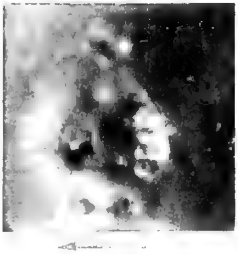
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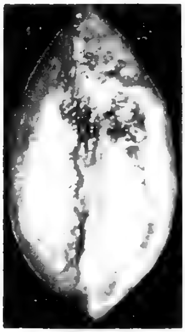
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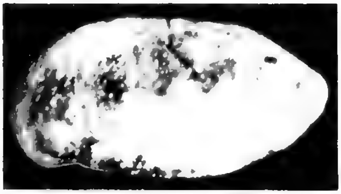
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PLATE 19

Eocytheropteron ? sp. p. 126.

Specimen from bed 11, Hawsker.

FIGS. 1–4. Right, left, dorsal and ventral views, female carapace. Io.1909.

Paracytheridea ? **caytonensis** sp. nov. p. 127.

All specimens from bed 6, Cayton Bay.

FIGS. 5–8. Dorsal, ventral, left and right views, female carapace. Holotype, Io.2137.
FIGS. 9–12. Right, left, dorsal and ventral views, female carapace. Paratype, Io.2140.
FIGS. 13–16. Right, left, dorsal and ventral views, male carapace. Paratype, Io.2138.


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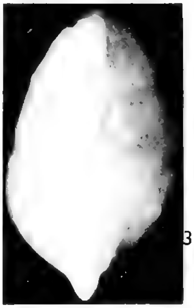
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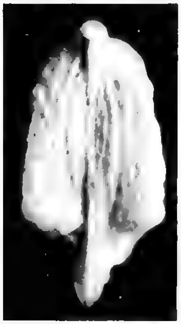
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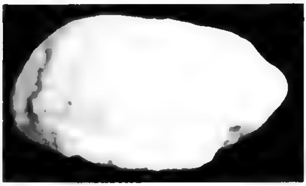
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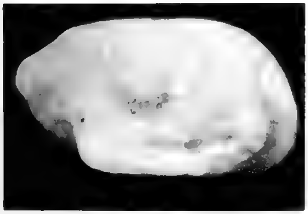
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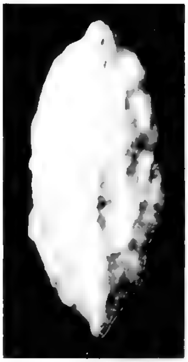
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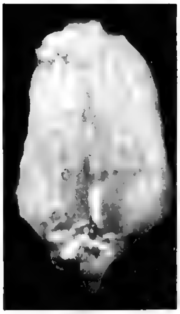
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PLATE 20

Southcavea microcellulosa sp. nov. p. 128.

FIGS. 1–8, 11–13. Bed 5, Stonecliff Wood.

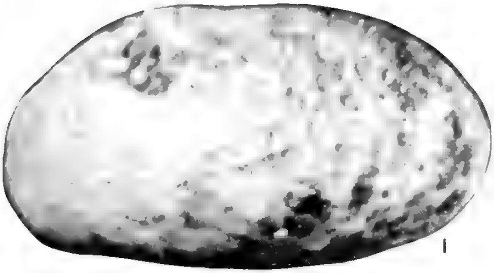
FIGS. 9, 10. Bed 3, Stonecliff Wood.

FIGS. 1–4. Left, right, dorsal and ventral views, male carapace. Holotype, Io.1882.

FIGS. 5–8. Left, right, ventral and dorsal views, female carapace. Paratype, Io.1883.

FIGS. 9, 10. Dorsal view of hinge and muscle scars (× 120), female right valve. Paratype, Io.1886.

FIGS. 11–13. Dorsal view of hinge and internal views showing hinge and radial pore canals, female right valve. Paratype, Io.1885.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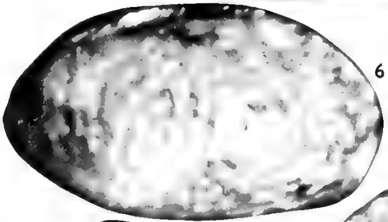
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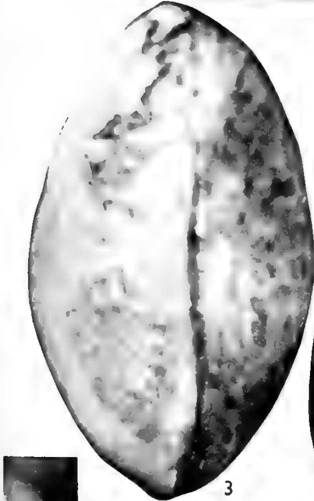
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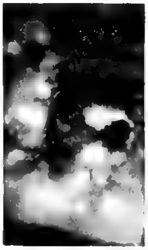
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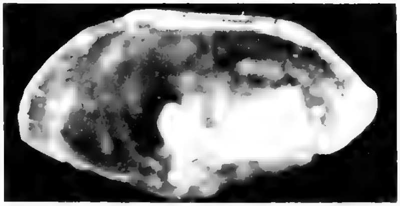
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PLATE 21

Southcavea microcellulosa sp. nov. p. 128.

Specimen from bed 8, Stonecliff Wood.

FIGS. 1–4. Right, left, dorsal and ventral views, male carapace. Paratype, Io.1888.

Systenocythere ovata sp. nov. p. 130.

FIGS. 5–8. Bed 7, Hawsker.

FIGS. 9–11. Bed 6, Cayton Bay.

FIG. 12. Bed 4, Cayton Bay.

FIGS. 5–8. Right, left, dorsal and ventral views, carapace. Holotype, Io.1900.
FIGS. 9–11. External, internal and dorsal views, right valve. Paratype, Io.1907.
FIG. 12. Muscle scars, note V-shaped antennal scar, left valve. Paratype, Io.1903, ×240.


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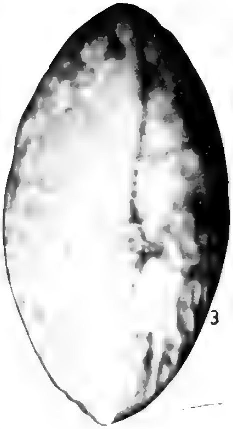
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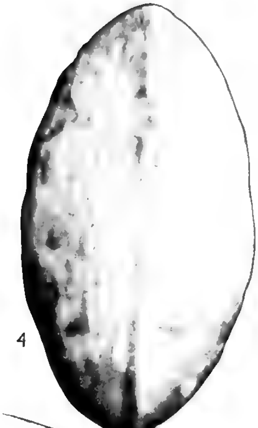
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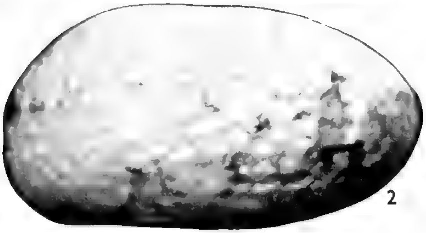
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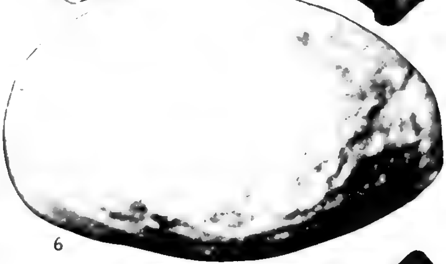
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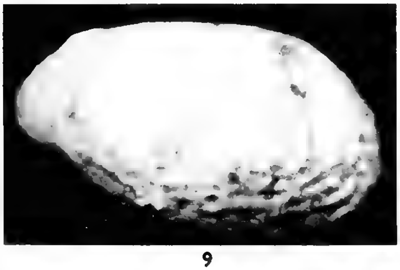
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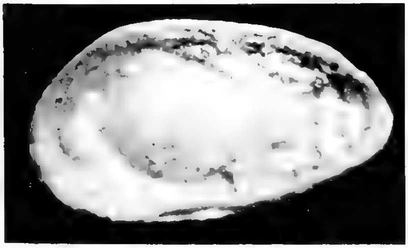
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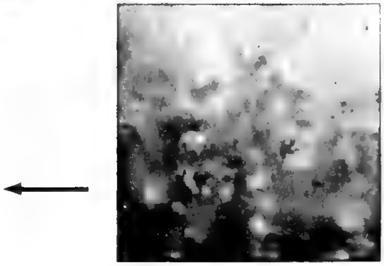
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HUMAN SKELETAL MATERIAL FROM CEYLON, WITH AN ANALYSIS OF THE ISLAND'S PREHISTORIC AND CONTEMPORARY POPULATIONS

K. A. R. KENNEDY

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 11 No. 4
LONDON : 1965

HUMAN SKELETAL MATERIAL FROM CEYLON, WITH AN ANALYSIS OF THE ISLAND'S PREHISTORIC AND CONTEMPORARY POPULATIONS

BY

KENNETH A. R. KENNEDY, Ph.D.

(Department of Anthropology, Cornell University, Ithaca, New York)

Pp. 135–213; 15 *Plates*; 9 *Text-figures*
12 *Tables*

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THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

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HUMAN SKELETAL MATERIAL FROM CEYLON, WITH AN ANALYSIS OF THE ISLAND'S PREHISTORIC AND CONTEMPORARY POPULATIONS

By K. A. R. KENNEDY

CONTENTS

SYNOPSIS

The fossilized human skeletal remains from the prehistoric site of Bellan Bandi Palassa in Sabaragamuva Province, Ceylon, are analysed anthropometrically and biochemically. Results of uranium and radiocarbon assays indicate a relatively contemporary population living at a period around 114 B.C. ± 200 years, a date that confirms the archaeological evidence which ascribed the cultural associations of the site to the Bandarawelian, a regional variant of the Indian " Mesolithic " or Late Stone Age. Comparative anthropometric studies of these Balangodese fossils with other hominid specimens, both fossil and living, reveal that their closest phenotypic affinities are with the Veddas of Ceylon. Many of the physical traits regarded by earlier investigators as distinguishing the Veddas from their Ceylonese and Indian neighbours and which have been the basis for separating the Veddas into racial sub-types are apparent in the fossil " pre-Vedda " remains from Bellan Bandi Palassa. This suggests a close genetic affinity between these Balangodese–Vedda phenotypes at the dawn of the historic period in Ceylon. The evidence from the ethnographic and prehistoric record for this region strongly supports the view of a continuous cultural tradition with local modifications extending from Late Stone Age times to the present, a situation which lends independent but supportive evidence for the postulation of Balangodese and Vedda phenotypic affinities. The association of contemporary hill tribes or relict populations with the manufacturers of prehistoric lithic industries has hitherto been unsubstantiated in the Indian Sub-Continent, and the anthropological problems inherent in this line of research are discussed.

I INTRODUCTION

The Site of Bellan Bandi Palassa

THE presence of palaeolithic artifacts in India and Pakistan testifies to the human occupation of the Sub-Continent during the Pleistocene, but the skeletal remains of the manufacturers of these stone implements have not been found. The most ancient human bones from this part of Asia have been recovered from Langhnaj in Northern Gujarat (Ehrhardt 1960, 1963, Karve & Kurulkar 1945, Khan & Karve 1946, Karve-Corvinus & Kennedy 1964, Kennedy 1964, Sankalia 1945, 1946, 1949, Sankalia & Karve 1944, 1945, 1949, Subbarao 1952, 1955 : 73–74, 1958 : 71–74, Zeuner 1950 : 44, 1951 : 7) and from the District of Mirzapur in Uttar Pradesh (Personal communication with Shri Radhakant Varma in May 1964, Deccan College, Poona) where the cultural associations are ascribed to the Indian Late Stone Age, or Mesolithic, period. For the Island of Ceylon the discovery of the makers of the lithic industries has long been awaited. The work of the Sarasins (1892–93, 1907) confirmed the claims of earlier investigators that the island possessed Stone Age tools, and from their data two problems originate : (1) To which of the prehistoric ages, as understood in terms of conventional typological classifications, can the Ceylonese stone artifacts be assigned : (2) What kinds of hominids manufactured these tools?

> " Until definite stratigraphic evidence, showing a sequence of distinct cultures with perhaps associated animal and skeletal remains, have been established at several sites, the only procedure seems to be to treat the implements as provisionally of one culture . . . Subdivisions into cultures and phases can be made when adequate evidence is discovered justifying it . . . The Sarasins believed that the people who lived in the rock shelters and made stone implements were ancestors of the Veddah, but without skeletal evidence there is nothing to support such a conclusion." (Noone & Noone 1940 : 20–21).

It is with this latter problem that the present study is concerned, for the anthropometric analysis of the human remains from Bellan Bandi Palassa, Ceylon, indicates that the manufacturers of its Bandarawelian (Late Stone Age) industries bear striking phenotypic similarities to the surviving Vedda population of the island.

The site of Bellan Bandi Palassa is situated at 6 degrees 31 minutes North longitude and 80 degrees 48½ minutes East latitude between the 400 and 300 foot contours in the Balangoda District of Sabaragamuva Province. Three and a half miles to the east of the site is the Pansadara Chena near Hath Kinda where the Valave Ganga ramifies into its seven channels. Traversing the site is an intermittent stream which joins the Pusalli Ara just before its junction with the Valave south of Pansadara (Text-fig. 1). Within the palassa, or glade, of Bellan Bandi an expanse of flat crystalline limestone extends for about a quarter of a mile from the northwest to the southeast and has a width of 70 yards. At right angles to the stream bed and extending across the limestone exposure is a ridge of earth eroded by the stream to form a gap of some 60 feet across. This erosion has exposed on the left bank a kitchen midden some 30 feet wide and averaging 3 feet in height above the limestone.

Some materials have been redeposited about 150 yards downstream from the midden. Erosion has produced along the left bank for a distance of about 100 yards a number of small rock shelters which have since collapsed leaving large limestone blocks which overlie the midden. The surface soil is primarily red sandy loam ranging in depth from 3 feet 6 inches to 4 feet 6 inches above the limestone outcrop. Within this soil cover were found human and animal bones, molluscan shells, chert and quartz implements and potsherds.

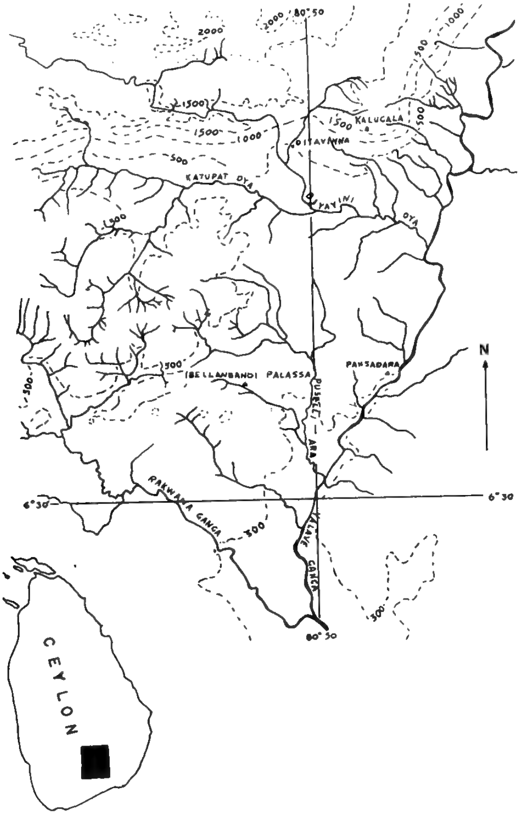

FIG. 1. The region of Bellan Bandi Palassa in the Balangoda District of Sabaragamuva Province, Ceylon. One inch to one and a half miles.

The excavation was carried out from 24th June to 6th July, 1956, then resumed on 9th September, 1956. A site survey had been conducted in March of that same year as a result of reports of fossil remains to be found in the forest near the Valave. Mr. Arthur Delgoda sent to Dr. P. E. P. Deraniyagala, Director of the National Museums, some fossilized fragments of human and animal bones, and on 12th March, 1956 led a party of archaeologists under Dr. Deraniyagala to the site. Before the commencement of the excavation the site was pegged out into forty squares each

6 feet by 6 feet. The north–south base line was represented by the plots Beta, Alpha, A, B, C, D, E, F, and the series beginning with Beta in the south end. The east–west base line was represented by the plots 1, 2, 3, 4, and 5, the series beginning with 5 in the west end and adjacent to square Beta. Such a grid was superimposed on the site so that the areas of limestone exposure and the left bank of the stream were approximately equal in extent, the edge of the stream forming a diagonal from square F5 in the northwest to square Beta 1 in the southeast. Consequently the squares which were possible to excavate were Beta 1, Alpha 1, A1, A2, B1, B2, B3, C1, C2, C3, C4, D1, D2, D3, D4, D5, E1, E2, E3, E4, and E5. Digging was continued in each square until the limestone bed rock was encountered. This base was humped with an apex at the C-line and declinations at A to the south and E to the north of the site. The loci of the specimens in this midden are represented in Text-fig. 2.

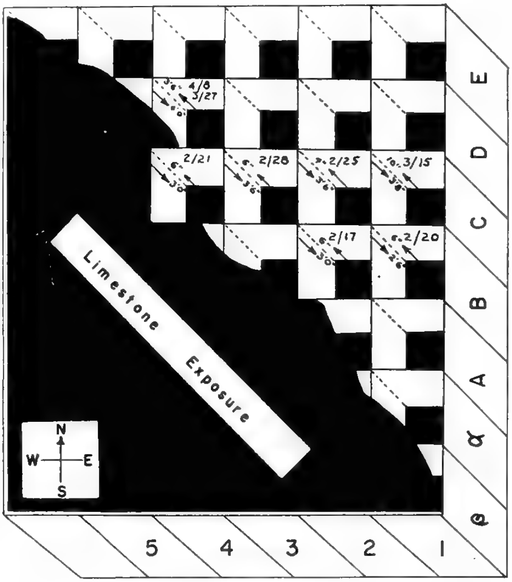

FIG. 2. The plan of excavation at Bellan Bandi Palassa showing the relative distances of the skeletal remains from the ground surface and from the limestone bedrock.

In some of the burials the corpse was flexed and lying upon its left side (specimens BP2/17, BP4/8, BP2/21) or right side (BP2/25, BP3/27–34). Other skeletons were flexed but supine (BP 3/15a, BP2/15b). Fractional burial and bag burial cannot be excluded from consideration, although difficult to establish. The particular artifacts found in direct contact with the skeletons are as follows: with BP2/17 were three unpitted hammer pebbles, of which one was discoidal, plus a bone dart. A cluster of twelve small pebbles in close proximity to one another suggest that they had once been encased in a bag and placed at the head of the corpse. In cleaning this specimen from its soil matrix, the mandible of a *Macaca sinica*, probably female, was discovered (Personal communication with Dr. W. C. Osman Hill in January 1961, London). With BP2/20 was uncovered the left molar of *Melursus valaha*. With BP2/21 were found unworked spherical pebbles some 60 mm. in diameter which perhaps were bola stones. The mandible of *Hystrix leucurus leucurus* lay across the right zygoma of the specimen. Specimen BP3/27–34 was associated with an unpitted pebble above the level of the skull and a block of quartz under the right humerus.

During the excavation of 1956 the remains of some nine individuals were uncovered. In the decade prior to this discovery, Deraniyagala had found fragmentary skeletal remains of single specimens from the middens of neighbouring sites. The significance of these sites has been discussed by Deraniyagala (1956*b*, 1956*c*, 1956*d*, 1957*a*, 1957*b* : 8, 20, 1958*a*, 1958*b* : 64–71, 1959, 1960*a*, 1960*c*, 1962, 1963*a*, 1963*b*), Clark (1961 : 189–190), Cole (1963 : 87) and Coon (1962 : 424–425). However, no thorough laboratory examination of the bones was undertaken until 1960 and 1961 when the specimens were sent on loan to the British Museum (Natural History) in London. It was advantageous to conduct the programme of research at this institution where the present investigator had available comparative osteological material from several collections of Vedda specimens and where excellent opportunities for subjecting the specimens to various biochemical tests existed.

The Nature and Condition of the Specimens

An abbreviated list of the skeletal specimens described in this report is given in Table 1. These are from the collection made during the 1956 season of excavation. There are, however, two fragments included in the collection sent to the British Museum (Natural History) which cannot be assigned to any of the numbered and catalogued specimens. These are :

1. A fragment of right ischium labelled BP2/17g found in Square B2 with specimen BP2/17.
2. A fragment of right scapula which includes the glenoid cavity and a portion of the axillary border. This fragment is unlabelled but is associated with BP3/27–34 in Square D4.

Two specimens were found at Bellan Bandi Palassa which have not been described by the writer but which are noted in Deraniyagala's report of the site. These are :

1. Specimen BP3/11 from Square C2 which lay at a depth of 2 feet 6 inches below the surface and 2 feet above the limestone. Only the maxilla and femur are described (Deraniyagala 1958*a* : 230, 233, 236–237, table 1).
2. Specimen BP3/15a was excavated from Square C1 at a depth of 3 feet 8 inches above the limestone. A second skeleton, specimen BP3/15b, was discovered beneath it and it has been described by Deraniyagala (1958*a* : 230, 233, 260, pls. 11–13, table 1, 1963*a* : 92–97). The skull of BP3/15b (Deraniyagala 1958*a* : 233, pls. 11, 12) was sent to the American Museum of Natural History in New York where its restoration is now under way. This is the specimen called T–23–B by Coon (1962 : 424–425). Through the kindness of Dr. Harry L. Shapiro the writer was permitted to examine this specimen.

TABLE 1

A TABULAR LIST OF THE SKELETAL MATERIAL DESCRIBED

				Calvaria					Face			
Specimen number	Site location	Sex	Age	Frontal	Parietal	Occipital	Temporal	Sphenoid	Maxilla	Zygoma	Nasal	Palatine
BP2/17	B2	Male	25–30	+	RL	+	RL	R	+	RL	..	..
BP2/17i	B2	Male	Adult	..	..	..	..	..	..	..	..	..
BP2/20–41	B1	Male	Adult	..	..	..	..	..	+	..	..	..
BP4/8	D4	Male	Adult	..	..	..	..	..	+	R	..	+
BP1/6	..	Female	Old Adult	..	..	..	..	..	+	..	..	..
BP2/21	C4	Female	20–22	+	RL	+	RL	R	+	RL	..	..
BP2/25	C2	Female	18–20	+	RL	+	RL	..	+	R	..	..
BP3/27–34	D4	Female	35+	+	RL	+	RL	RL	+	R	RL	+

Note: A plus (+) indicates the presence of a bone for any given specimen.
The side of the skeleton for which a bone is available is indicated by an R for right side, an L for left side.

TABLE 1 (*continued*)

A TABULAR LIST OF THE SKELETAL MATERIAL DESCRIBED

Specimen number	Mandible		Dentition	Trunk vertebral column			Upper extremity					
	Corpus	Ramus		Ver. col.	Rib	Sternum	Clavicle	Scapula	Humerus	Radius	Ulna	Hand
BP2/17	..	..	Maxilla	Lumbar 3, 4, 5	+	+	L	RL	..	..	..	..
BP2/17i	+	RL	Mandible	..	..	..	..	..	..	..	..	..
BP2/20–41	+	RL	Maxilla Mandible	..	..	..	..	..	..	..	..	..
BP4/8	..	..	Maxilla	..	..	..	..	..	RL	RL	L	..
BP1/6	..	R	Maxilla Mandible	..	..	..	..	..	..	..	..	..
BP2/21	..	..	Maxilla Mandible	..	..	..	L	..	L	..	..	Trapezius Capitate Schaphoid 5 Metacarpals 1 Carpal
BP2/25	..	..	Maxilla	Cervicle 1, 2, 3, 4	+	..	R	..	..	L	..	..
BP3/27–34	..	..	Maxilla Mandible	..	..	..	RL	R	L	L	L	..

Specimen number	Lower extremity				Pelvis			
	Femur	Tibia	Fibula	Foot	Sacrum	Ilium	Ischium	Pubis
BP2/17	RL	RL	..	Talus Cuboid Calcaneum	+	RL	RL	..
BP2/17i	..	..	..	..	..	..	..	..
BP2/20–41	..	..	..	..	..	..	..	..
BP4/8	RL	RL	L	..	..	..	..	..
BP1/6	..	..	..	..	..	..	..	..
BP2/21	..	..	..	..	..	..	..	..
BP2/25	RL	R	..	..	..	..	..	..
BP3/27–34	..	..	..	..	..	..	..	..

Of the specimens examined by the present writer, two are deserving of special comment. These are :

1. The mandible of BP2/17i which was found some 10 inches away from the calvarium of specimen BP2/17. This was regarded at the time of discovery as belonging to specimen BP2/17, but upon cleaning the calvarium from its matrix it became obvious that the wear patterns of the maxillary and mandibular dentitions were strikingly different for the two specimens.

2. Deraniyagala (1958*a* : 232) mentions the presence of another skeleton in the vicinity of the deposit where specimen BP2/21 was found. Its skull lay in Square C4 with BP2/21 and its post-cranial parts extended into Square C3. Elsewhere in his report Deraniyagala (1958*a* : 230, 233) notes the presence of a specimen uncovered in Square C3 at approximately the same level as BP2/21. This specimen in C3 is called BP2/28 and it is without a cranium. The question arises as to whether these post-cranial bones in C3 may not belong to specimen BP2/21 rather than to another individual. The bones of BP2/28, namely a left humerus, left talus, calcaneum and femur were not available for study by the present writer. Furthermore, the great difference in the appearance of the cranial fragments of specimen BP2/21 is such that they could be certified as belonging to a single individual only after they had been cleaned of their matrix and concretion and examined for the purpose of reconstruction. This question of the presence of one or two individuals in Squares C3 and C4 is further complicated by the fact that Deraniyagala (1958*a* : 232, 260, pl. 9, tables 1–2) notes the presence of certain post-cranial bones belonging to specimen BP2/21—a scapula, humerus, tibia, femur, talus, calcaneum—which again were not observed by the writer.

As the bones were encountered in progress of excavation they were coated with shellac and labelled and packed in cotton. Fragile pieces were plaster-jacketed in a position exactly as they were found *in situ*. The plaster jacket for the calvarium of BP2/17 was later removed from one side and shellac dissolved in alcohol was poured into the mass of matrix and bone. Specimens that were placed into the plaster jackets were BP2/17 (calvarium and pelvis), BP2/21 (cranium), BP2/25 (cranium), BP3/15a (skeleton). Photographs were taken of the specimens *in situ* and some measurements were made upon the bones before their complete excavation. Upon the return of the archaeologists to the laboratory at Colombo these specimens were superficially cleaned. No reconstruction was attempted, save for the mending of bones which had been broken as a result of their transport from the field. Laboratory measurements carried out at the Colombo Museum were of a limited nature since the specimens were not entirely removed from their plaster jackets.

The reconstruction and anthropometric analysis of the specimens was undertaken by the present writer at the British Museum (Natural History). All of the specimens required some restoration, but warping and erosional damage, rather than actual breakage of bone, have most severely altered their pristine condition. Because of the poor state of preservation of the series, a morphological description is of necessity more significant than the tabulation of the metrical data. Nevertheless, where a metrical analysis could be undertaken, a record was made of the quantitative values.

The anthropometry is based upon the particular reconstruction that was considered by the writer to be of greatest accuracy for each specimen. The reconstructions are intentionally impermanent in order that other scholars may realize their own interpretations of the data. The reconstructing media are acetone cement and plaster of Paris, both of which can be flaked or washed from the specimens with ease.

The osseous remains were not found in a uniform state of mineralization, but all were hard, due to the chemical nature of the soil in which they were embedded: the water acidulated by the humus had dissolved the limestone over which it flowed and formed a protecting environment for the calcium content of the bones. The bones of the lowest level were almost resting upon the limestone outcrop. The effluvia of the corpses had caused the limestone to disintegrate into yellow flakes to a depth of 5 cm., and these flakes had been subsequently impacted into a solid mass partially adhering to the bones.

In addition to the osseous remains this series contains 120 permanent teeth of which 52 belong to male specimens and 68 to female specimens.

II DESCRIPTION

The Methodology of the Metrical Analysis

The method of measurement for each of the values listed in Table 2 is to be found in Martin & Saller (1957 : 453–499, 520–595). In this compendium the standard procedures for each measurement are described and listed by number. That number relevant to each measurement in Table 2 is given in parentheses immediately after its name. Indices are based upon these measurements. Variations and additions to these procedures are the following:

1. Auricular-Vertex Height is taken according to the method devised by Ranke with the use of the Mollison craniophor, as described by Hooton (1946 : 738).

2. The Frontal Arc is the first segment of the Glabella-Opisthion Arc and differs from the Nasion-Opisthion Arc described by Martin & Saller (1957, Measurement 25) in its selection of the initial landmark. In the absence of a well defined nasion for any skull in the Bellan Bandi Palassa series, the most anterior point of the glabella in the median-sagittal plane was substituted for the conventional landmark in this arc measurement.

3. The External Palatal Arc is measured from alveolon on one side of the upper jaw to alveolon on the opposite side, the tape passing across prosthion and parallel to the anterior aspect of the dental arcade.

4. Height of the Zygomatic Bone is the distance measured with the sliding caliper from the anterior superior border of the frontal process of the malar to its anterior inferior border at the point of articulation with the maxilla.

5. Breadth of the Zygomatic Bone is the distance measured with the sliding caliper from the superior border of the maxillary process to the anterior inferior border of the frontal process.

6. Breadth of the Frontal Process of the Zygomatic Bone is taken as its greatest anterior–posterior diameter. The sliding caliper is placed at the level of the zygomatico-facial foramen when this measurement is taken.

7. The Mental Foramen Diameter is taken with the sliding caliper, the points being placed upon the medial–lateral borders and the inferior–superior borders of the foramen for the determination of its maximum size.

8. Sternal Head Diameter is the maximum anterior–posterior dimension of the medial extremity of the clavicle taken with the sliding caliper.

9. Corocoid Process Breadth is the maximum anterior–posterior diameter of the corocoid process of the scapula, taken perpendicularly to the plane that the sliding caliper assumes in the measurement of Corocoid Process Length (Martin & Saller 1957, Measurement 11).

10. Length of the Iliac Lines is measured with the sliding caliper from the anterior origin of the arcuate line on the pubic bone to its posterior termination at the sacro-iliac joint just superior to the pre-auricular sulcus. Both ilia are measured for this feature.

In the discussion of the dentitions, the following abbreviations have been used: R = right side; L = left side; M3 = third molar; M2 = second molar; M1 = first molar; PM2 = second premolar; PM1 = first premolar; C = canine; I2 = lateral incisor; I1 = central incisor; the placement of the number above or below the line indicates that reference is made to either the upper or lower dentition, *viz.* RM$\underline{3}$ = maxillary right third molar.

Sex and Age Determination

Specimen BP2/17: This is a male who died between the ages of 25 and 30 years. The calvaria is the largest and most rugged in the series. The brow ridges are prominent and posterior to them is the trace of a frontal sulcus. The mastoid process is large with a supramastoid crest that exhibits a rough inferior margin. This robusticity of the mastoid is reflected also in the area of insertion for the splenius capitis and longissimus capitis. The digastric fossa is deep. The lateral border of the superior nuchal crest forms a moderately well defined ridge, but as its median portion is not represented in the fragment, its overall dimensions cannot be observed. Temporal lines are sharp at their frontal aspect and sweep posteriorly as an arc, of medium prominence on the parietals. The supramastoid crest is large. The zygomatic processes of the temporal are rough along their inferior margins, particularly in the region of the anterior tubercle where some fibres of the masseter have their origin. The region of the attachments of zygomaticus major and minor on the malar shows prominent bossing. Medial to this is an elongated crest for the levator labii superioris and levator labii superioris alaeque nasi. The malar is short but massive. The maxilla exhibits very pronounced subnasal grooves. The alveolar arch of the palate is high. A basal view of the calvaria reveals further evidence of male robusticity: a deep mandibular fossa and a stout occipital condyle.

The right and left innominates are characterized by narrow and deep ischiatic notches, large acetabulum, prominent sacro-iliac articulation, and a high upright ilium. A pre-auricular sulcus is present, but its dimensions are small and narrow. There is pronounced ridging of the region above the posterior superior iliac spine where gluteus maximus originates. The crest of the ilium is sharp, especially along the line of origin of obliquus abdominis externus. The ilium is thick and heavy and the pelvic basin is small. Male characteristics are exemplified in the shoulder girdle with its relatively large clavicle and large scapular glenoid fossa and in the lower extremities where the linea aspera of the femur forms a pronounced pilaster.

The absence of the pubic bones precludes the possibility of aging this specimen on the basis of progressive changes of the symphysial region. The dentition of the maxilla shows that the third molars have erupted and, like the other teeth, have undergone only a slight degree of attrition. Suture closure as an age indicator is of dubious value for this specimen due to trauma it has received from erosional forces and crushing. However, a general impression of its pristine condition can be obtained in a limited number of instances. Of the coronal suture, pars bregmatica is still undergoing closure but pars pterica is advanced. Of the sagittal suture, partes verticis and lambdica are advanced. The bregmatic and obelionic parts are eroded. Pars lambdica of the occipital suture has begun closure, but pars asterica is irregular, being most patent at its inferior portion. The masto-occipital suture is half closed. The squamous portion of the temporal is patent, but the spheno-temporal is advanced. Both spheno-parietal and spheno-frontal are commencing closure. Radiography of the vault confirms visual observation that arachnoid granulations are not present. These observations suggest an age at time of death for the specimen of between 25 and 30 years.

Specimen BP2/17i: This is an adult male. Its mandible, in comparison with those associated with specimens sexed as females, is of greater size, weight and thickness. The symphysis is higher, and the rami form a less obtuse angle in relation to the corpus. The short broad rami have robust pterygoid attachments at their gonia, which are thick and strongly everted. The mylo-hyoid ridge is pronounced.

All of the teeth have erupted, and the third molars are moderately worn. The other molars reveal pronounced attrition.

Specimen BP2/20–41: This specimen may be that of an adult male, but criteria for sexing and aging are less certain than for other specimens of the series. Subnasal grooves are moderately developed. Of more masculine appearance is the mandible which is large and heavy with a pronounced mylo-hyoid ridge, very prominent pterygoid attachments, medium-sized genial tubercles and large digastric fossae.

The dentition has erupted completely, and there is a moderate degree of abrasion, except for the upper left distomolar which is unworn.

Specimen BP4/8: This is an adult male characterized by robust musculature of the face and long bones. The malars are large and heavy, as is also the zygomatic process of the temporal. Subnasal grooves are pronounced, particularly in the incisive region. The palate is of moderate height with a large lump-shaped torus. The suborbital fossa is deep. Orbital and nasal borders are dull.

The humeral supracondylar ridges are sharp, but the head of the humerus is reported by Deraniyagala as being comparatively small. The muscularity of the radius is pronounced as represented in the sharpness of the interosseous crest and the inferior border of the pronator quadratus attachment. The oblique line of the flexor digitorum sublimus muscle is well developed. Radial tuberosities are large.

The interosseous border of the ulna is less pronounced, but the groove where the extensor pollicis longus originates is marked. Likewise apparent is the insertion for brachialis on the anterior surface of the coronoid process. The supinator crest is high. The linia aspera of the femur forms a very prominent pilaster, and other well-developed areas of this bone are the crista hypotrochanterica and the trochanter minor. The femur is heavy and massive. The tibia is characterized by a moderate degree of muscularity. Its interosseous borders are sharp. Similarly the fibula has a sharp anterior margin, and the bone is deeply fluted.

The teeth of this individual have completely erupted. The third molar has undergone slight attrition, but the other teeth reveal a moderate degree of wear.

Specimen BP1/6 : This is a female whose mandible exhibits signs of senile modification. The maxilla is delicate and the sub-nasal grooves are of medium development. The mandibular corpus is fragile and constricted at the molar region, but well developed, heavy and wide at the symphysial region. The chin form is median, and projection is pronounced. The mylo-hyoid ridge is of medium muscularity. The ramus is not robust, and its gonion is thin with reduced pterygoid attachments. Eversion of the gonia is medium.

The teeth are erupted and, save for the slightly worn third molars, the remainder of the dentition shows a moderate to pronounced degree of wear.

Specimen BP2/21 : This is a female whose age at time of death was between 18 and 20 years. The supraciliary arches are reduced in development, and the superior orbital border reveals a delicate lipping. The mastoid process is medium in size, but the bossing for the sternomastoid is prominent. The mastoid shows a slight lateral projection. The occipital crests observed from their external aspects are reduced to traces. The supramastoid crest is moderately developed, but the temporal lines are traceable only on the frontal bone, where their conformation is rounded. The zygomatic processes and malars are small and gracile. For the maxilla the subnasal grooves are of medium development and the nasal sills are sharp. The palate is medium in height. Viewed basally, the calvarium presents a shallow mandibular fossa, small postglenoid process, and a minute stylo-mastoid foramen.

The mandible is of medium size. The mylo-hyoid ridge is low, and the fossa for the mandibular gland is prominent. The gonia converge, but are strikingly thick and knobby as in specimen BP2/17i, a male. The mandibular condyles are small and converging, and the coronoid process is high.

The degree of muscularity of the post-cranial bones is within the moderate category. The humerus has a well-marked bicipital groove and tuberosity. The clavicle is sharply ridged in the region of the deltoid attachment. It is the low muscularity of the calvaria, rather than the features of the mandible and post-cranial bones, that suggests that the specimen is a female.

The criteria for age determination are more satisfactory for this specimen. The third molars of the maxilla and mandible have not completed their eruption and lie partially embedded in their alveoli. Save for the lower incisors, attrition is negligible for all of the teeth. Further proof of the young adulthood of this specimen is adduced by the metacarpal bones of the right hand where the epiphyses of the heads and basal condyles have not completed ossification with the shaft. This fusion normally terminates in the twentieth year of life. Finally, sutural closure of the calvaria gives confirming data. The partes bregmatica and pterica of the coronal are commencing closure, but pars complicata remains patent. Of the sagittal suture, pars bregmatica is patent while the partes verticis, obelica and lambdica are commencing closure. The lambdoid suture is open at all regions save for pars media where closure has started. The masto-occipital suture is patent as are the spheno-parietal, spheno-frontal, and spheno-temporal sutures. The squamous portion of the temporal, however, is closed, which is an artifact of the degree of preservation of the specimen.

Specimen BP2/25: This is a sub-adult female under 18 years of age. The sex criteria are less certain for this specimen than for the others of the series, but the cranium is small and its muscularity is reduced. Unfortunately the frontal and occipital tori can not be observed. There is a moderate degree of ridging of the squamous portion of the temporal. The supramastoid crest is of moderate development, but the zygomatic process of the temporal is very thick. Nasal sills are sharp. Subnasal grooves are pronounced. The mandible is small and has a short corpus with little muscular development. The ramus is short and narrow with negative gonial eversion.

Muscularity is very much reduced on the clavicle which is smooth and gracile. The radius is moderately fluted, but the interosseous crest is high. The radial tuberosity is low. The pilaster of the femur is of medium development and is mound-shaped. The fossa hypo-trochanterica is deep. For the tibia, the anterior ridge is sharply defined but overall muscularity is reduced.

Age is established on the basis of the unerupted state of the third molars of maxilla and mandible. Due to the inferior condition of the specimen the degree of suture closure on the cranium cannot be determined. Epiphyses of the long bones are complete, and this specimen can most accurately be aged as a sub-adult.

Specimen BP3/27–34: This is a female whose age at time of death was between 30 and 35 years.

The cranium is of medium size and exhibits a low degree of muscularity. The frontal torus is hardly discernible and glabella is very low. The occipital crests are reduced to low mounds. Inion is absent. Temporal crests are sharply defined on the frontal bone, but disappear in their progress posteriorly over the parietals. The anterior and posterior portions of the supramastoid crest are smooth. The malars are small and smooth. The temporal fossa has a moderate degree of roughening, particularly on the posterior sphenoidal surface. The alveolar region is small, but subnasal grooves are pronounced and the palate is high and moderately ridged. The palatine torus is mound-shaped. Orbital and nasal borders are sharp. The suborbital fossa is deep and massive. The basal aspect reveals a deep mandibular fossa and a thick postglenoid process of a length unusual in females. The petrous portion of the temporal is small.

The mandible is medium in size and light in weight. The corpus exhibits a pronounced mental spine emerging from a sharply pointed and projecting median protuberance. Genial tubercles are well defined and of medium size, but digastric fossae are small. The mylo-hyoid ridge is low. The angle formed by the ramus is more obtuse than that for the other mandibles of the series. The ramus is moderately broad and the gonia, while thin, are markedly crested for the attachment of the pterygoid and exhibit pronounced eversion. The coronoid process is high; the condylar neck is short.

The small clavicle is thin and delicate. The scapular is small, and muscular attachments are weakly developed. The humerus is likewise reduced in robusticity, although the bicipital groove is well defined and has a sharp lateral lip. The small and sinuous radius has a large ulnar notch and an extensive but low radial tuberosity. The volar aspect of the radius inferior to the anterior oblique line shows a deep hollow for the reception of the belly of flexor pollicis longus. The styloid is of medium size. The ulna has a more prominent styloid process, and its crests are sharper.

An estimate of age based upon suture closure alone would place this specimen within the range of 30 to 40 years at time of death. Conditions described below as patent or advanced are unreliable, as criteria of age in this specimen, due to absorption of the majority of the sutural margins, the post-mortem separation of the sutures as a result of dessication and the consequences of the pressure of the over-burden upon sutural areas apparently complete in their closure. Hence partes bregmatica, complicata and pterica of the coronal are patent due to erosive factors working on the bone. For the sagittal, pars verticus appears to have been advanced in its closure but the degrees of fusion for pars lambdica, obelica and bregmatica are uncertain due to post-mortem separation of the parietals. The situation is the same for the lambdoid suture where the margins are preserved but unarticulated. Those sutures which have maintained their pristine condition are the spheno-parietal which is completely closed and the spheno-frontal which is advanced. The squamous portion of the temporal is fused to the sphenoid, but its relationship to the parietal cannot be accurately observed, save for a view of its superior portion on the right aspect of the vault where closure is well advanced.

The dentition shows pronounced attrition. The upper third molars have erupted, but the status of the lower third molars is uncertain, for these teeth are not present.

The Metrical and Morphological Analysis of the Osseous Remains

THE CRANIAL SKELETON. *The Calvarium* (Table 2). All four calvaria of the series are dolichocranic, the female specimens being the narrower. There is less agreement in the indices of the Auricular Height of the vault in relation to Cranial Length and Cranial Breadth : the male specimen is hypsicranic and acrocranic, the female specimen is chamaecranic and tapeinocranic. However, if the Basion–Bregma Height is employed as a component of these cranial indices, the values for the male specimen fall within the same categories as do those of the female. Such a discrepancy in the indices of Cranial Height is due to the imperfect preservation of the basion region of specimen BP2/17. Therefore, the indices which utilize the auricular values are those which are preferable as the more reliable.

Cranial capacity cannot be directly measured for the specimens, and four formulae have been employed for the estimation of endocranial size. The calculation of von Bonin, while originally devised for male crania of natives from New Britain, has been demonstrated as suitable for male Australian crania as well (Hambly 1947 : 35–39). Isserlis (1914) worked out a formula for estimating the capacity of crania from the Gaboon area of West Africa, and Hambly has noted its applicability to male and female crania of Vedda and Australian populations (Hambly 1947 : 57). However, when Isserlis' formula is applied to specimens BP2/17 and BP3/27–34 of the Balangoda series, the results are 1589·72 cc. and 919·66 cc. respectively. Although there are known to exist two female Vedda crania with directly measured cranial capacities of 960 cc. (Hill 1941 : 90, 93–94), the value derived from Isserlis' formula in the cases under consideration is questionable. The formula of Lee & Pearson (1901) using Auricular Height confirms a low cranial capacity for specimen BP3/27–34. Without a confirmation of values for specimens of the Balangoda series that can be derived from direct measurement of cranial capacity, one is cautious in favouring the formula best suited to the series. These estimates do serve to illustrate the degree of variation between the large-headed male BP2/17 and the small, nannocranic female BP3/27–34. Differences in the values for the Cranial Module confirm this degree of variation. Specimen BP2/25, which was not reconstructed, appears to have had a small cranial vault and a greater delicacy of cranial architecture than BP3/27–34.

The walls of the cranial vault are uniformly thick and heavy, due in part to their impregnation with mineral matter but to a greater degree this condition reflects their original nature. Porous areas are not observable. Their uniformly dense and grainy character is best observed radiographically. The frontal and anterior portions of the parietals are somewhat thinner than the bones of the posterior region of the vault. There is no sexual dichotomy in the thickness of the bones, although the parietals and occipitals of the female BP2/21 are the least massive in the series. Observed vertically, the conformation of the vault is sphenoid for BP2/17 and BP3/27–34 and rhomboid for BP2/21. In all three crania the greatest breadth is across the posterior third of the skull. The anterior portion of the vault of BP2/21 differs from the others by the reduced proportions of its glabella and superorbital torus. Brow ridges are median in both female specimens. The male specimen exhibits a very large glabella and a heavy, divided frontal torus. The frontal development of BP3/27–34 falls between these extremes. Lateral aspects show a medium height of the frontal region but sexual differentiation in the frontal slope. The frontal bone of the male specimen inclines gradually from glabella to bregma with a curvature limited to the plane of the low frontal eminences. It has a large median boss. The females have a slightly bulbous frontal bone that curves evenly and smoothly to bregma, medium to pronounced frontal eminences, and no median crests. Specimen BP2/21 exhibits a median boss of modest size. Post-orbital constriction of the frontal is prominent in BP2/17 and BP3/27–34, but reduced in BP2/21. Frontal breadth is large for the male vault, small for the female. Supra-orbital foramina are large for both sexes. The frontal sinus is spacious in BP2/17.

The parietal region bears a sagittal crest of medium height in BP2/17 and BP2/21, but this region is not elevated in BP3/27–34. All the vaults of the series exhibit small post-coronal depressions. Parietal bosses are pronounced, and these lie well back towards the wider portion of the vault. From their apices, the sides of the brain case make a steep descent to the temporal fossae. Parietal foramina are not observable. The gradual curvature of the parietal portion of the vault, viewed from the lateral aspect, takes a sudden turn in a more vertical direction at lambda.

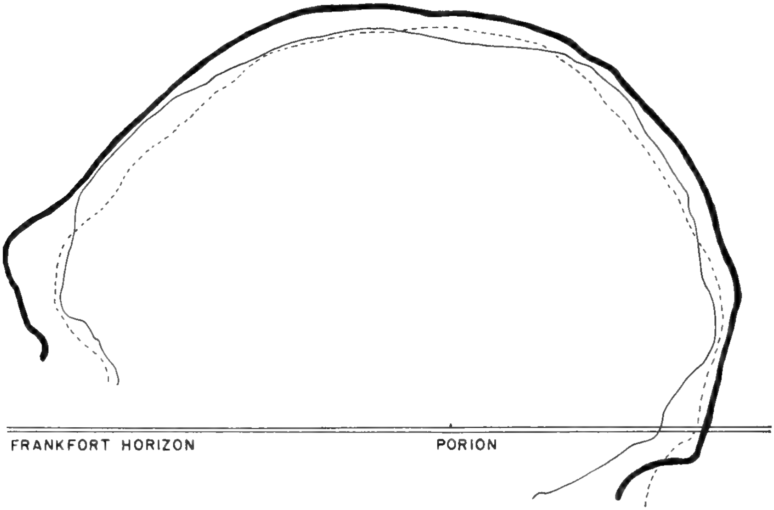

FIG. 3. Left lateral contours of three Balangodese (BP2/17 ▬▬, BP2/21– – –, BP3/27–34 ———).

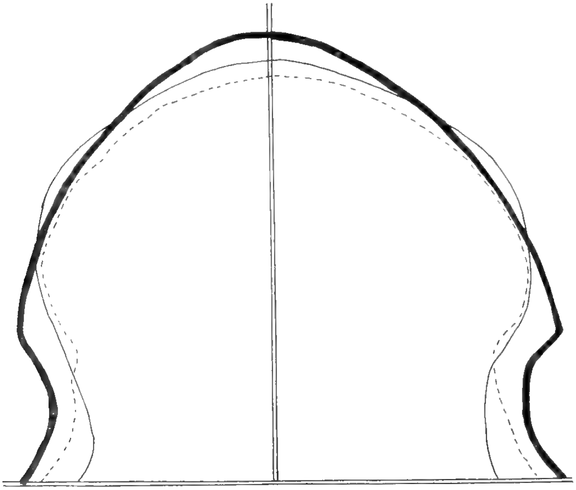

FIG 4. Frontal contours of three Balangodese (BP2/17 ▬▬, BP2/21– – –, BP3/27–34 ———).

Lambda is moderately flat in all specimens but one, BP3/27–34. The occipital curvature is pronounced for all specimens. The occipital torus of BP2/17 is remarkable for its large size and robusticity : the female crania exhibit either reduction or no development of this region (Text-figs. 3, 4).

The temporal region is full, particularly for the male specimen, and the sphenoid depression is remarkably large. The degree of cresting of the temporal lines is never pronounced along the parietals, but is marked on the frontals of the male vault. The squamous portion of the temporal is thick for BP2/17 and BP2/21, but thin for BP3/27–34. The size of the petrous portion is greater for the male. The auditory meatus is elliptical for the male, round for the females. The tympanic plate is consistently thick for both sexes. The mastoid is large for the male. Radiography reveals in the male specimen an extensive mastoid sinus. This consists of two polycameral sinuses in the superior aspect of the process along an anterior–posterior arc which traverses the width of the process. At its apex, a third polycameral sinus is visible.

Sutures of the vault are simple in conformation for all specimens. Complexity is observed only in the peripheral margins of the coronal suture at pterion and of the sagittal at lambda. Wormian bones are not observable. Metopism is absent. The form of Pterion is H.

Facial indices are ascertainable for specimen BP3/27–34. Its total facial index places it at the lower limit of the leptoprosopic class. The upper face is leptene. The nose is chamaerrhine. Whereas its orbits are chamaeconch, the orbits of BP2/17 are hypsiconch. The palates of all specimens are brachystaphyline.

The angle of the upper face of BP3/27–34 places it within the orthognathous category as estimated by both the von Camper and Martin methods. The protrusion is of the alveolar sort rather than subnasal or total maxillary. Facial bones of the other specimens exhibit pronounced alveolar prognathism, save for the males BP2/17 and BP2/20–41 where alveolar protrusion is medium and slight respectively. The very pronounced alveolar prognathism of BP2/25 is to some degree an artifact of post-mortem distortion of the facial bones. Mid-facial prognathism is medium in the two cases where it is observable—specimens BP4/8 and BP2/27–34.

The form of the orbit is rhomboid for the males and the female BP2/21, but square for the other female, BP3/27–34. Orbital inclination is 15° for BP2/17 and 16° for BP2/21, but the inclination is only 8° in the case of BP3/27–34. There is a striking sexual differentiation in the size and robusticity of the malars and zygomatic processes. Lateral malar projection is common to the females, but of the males, BP4/8 shows pronounced anterior malar projection. The total absence of nasal bones in the series precludes any comment as to the structure of this portion of the face save insofar as the maxillary walls and floor of the piriform aperture are preserved in BP4/8. From this evidence the nose appears to have been very broad with a large nasal spine and both sharp and dull sills. The nasal notch appears to have been deep for BP2/17 and BP3/27–34. Subnasal grooves of the incisive region are consistently prominent. The palate is elliptical except in specimens BP2/20-41 and BP3/27–34 where the form is hyperparabolic, an appearance ascribable in part to the absence of third molars. The height of the palate is medium, but specimens BP2/17 and BP3/27–34 have deep palates. Palatine ridges are larger in males than in females and are mound-shaped rather than ridged for both sexes. The palates are unusual in their large overall size and in their considerable breadth (Pls. 1–7, 10–14).

TABLE 2

CRANIAL MEASUREMENTS AND INDICES

	Males			Females		
Measurements	BP2/17	BP2/20–41	BP4/8	BP2/21	BP2/25	BP3/27–34
Cranial Length (1)	200	..	..	183	..	177
Cranial Breadth (8)	147	..	..	133	..	130
Basion-Bregma Height (17)	135	..	..	..	..	..
Auricular-Vertex Height (21)	132	..	..	..	..	93
Auricular-Bregma Height (20)	127	..	..	..	..	95
Minimum Frontal Diameter (9)	117	..	..	110	..	91
Bizygomatic Diameter (45)	..	..	..	121	..	110
Menton-Nasion Height (47)	..	..	..	..	..	101
Prosthion-Nasion Height (48)	..	..	..	..	60	64
Nasal Height (55)	..	..	..	..	..	44
Nasal Breadth (54)	..	23	..	..	..	23
Orbital Height-Right (52)	37	..	..	36	..	..
Orbital Height-Left (52)	37	..	..	..	..	40
Orbital Breadth-Right (51)	41	..	..	..	..	..
Orbital Breadth-Left (51)	41	..	..	..	..	30
Biorbital Breadth (44)	131	..	..	..	..	..
Zygomatic Breadth-Right	55	..	52	40	..	..
Zygomatic Height-Right	52	..	44	42	..	47
Zygomatic Frontal Process Breadth-Right	29	..	22	24	..	22
Zygomatic Frontal Process Breadth-Left	25	..	..	..	..	..
Palate-External Length (60)	61	..	..	62	..	53
Palate-External Breadth (61)	69	70	..	65	..	63
Palate-Internal Length (62)	52	..	..	50	..	45
Palate-Internal Breadth (63)	36	47	..	42	..	42
Palate Height at M^2 (64)	19	15	14	14	..	18
Arc-External Palate	185	..	152	..	..	..
Arc-Transverse (24)	355	..	..	300	..	270
Arc-Glabella-Opisthion (25)	355	..	..	320	..	285
Arc-Frontal Length (25)	132	..	..	135	..	115
Arc-Sagittal Length (27)	146	..	..	152	..	128
Arc-Occipital Length (28)	77	..	..	53	..	58
Chord-Frontal Length (29–1)	118	..	..	120	..	105
Chord-Sagittal Length (30)	130	..	..	132	..	112
Maximum Circumference (23)	..	..	..	520	..	495
Indices						
Cranial	73·50	..	..	72·68	..	73·45
Basion-Bregma Height-Length	67·50	..	..	..	..	..

TABLE 2 (*continued*)

CRANIAL MEASUREMENTS AND INDICES

	Males			Females		
Indices	BP2/17	BP2/20–41	BP4/8	BP2/21	BP2/25	BP3/27–34
Basion-Bregma Height-Breadth	91·84	..	..	..	..	..
Auricular-Vertex Height-Length	66·00	..	..	..	..	52·54
Auricular-Vertex Height-Breadth	89·69	..	..	..	..	71·54
Auricular-Bregma Height-Length	63·50	..	..	..	..	53·67
Auricular-Bregma Height-Breadth	86·53	..	..	..	..	73·08
Total Facial	..	..	..	..	..	91·82
Upper Facial	..	..	..	..	..	58·18
Nasal	..	..	..	..	..	52·27
Orbital-Right	90·24	..	..	..	..	..
Orbital-Left	90·24	..	..	..	..	75·00
External Palate	113·11	..	..	104·84	..	118·87
Internal Palate	69·23	..	..	84·00	..	93·33
Cranial Module	159·67	..	..	..	..	133·33
Cranial Capacity						
Basion-Bregma Height : von Bonin (1934 : 14)	1448·75	..	..	..	..	..
Lee & Pearson (1901 : 225–264)	1580·35	..	..	..	..	..
Auricular Height : Lee & Pearson (*Ibid.*)	1775·83	..	..	..	..	1098·87
Isserlis (1914 : 189)	1589·72	..	..	..	..	919·66

The Mandible (Table 3). In contrast to the brachystaphaline upper jaw, the lower jaw is dolichostenomandibular. The alveolar portion of the mandible conforms to the characteristic shape of the palate, but the ramus describes an obtuse angle with the corpus, and moreover, is very broad. This results in a great Condylo-Symphysial Length but a moderate Bigonial Diameter. The corpus is thick and heavy at the symphysis, but is reduced in size, particularly among the females, as it sweeps posteriorly to the gonia. The chin is prominent and median for all mandibles, save for that of BP2/21 where the chin form is bilateral. The corpora of males are thicker and higher than the corpora of females, due in part to their more developed mylo-hyoid crests. There is less sexual diversity in the development of the digastric fossae and genial tubercles. These range in size from sub-medium to large. Alveolar prognathism is small in males and medium in females. The rami are robust in the males, their pterygoid attachments are well developed and gonial eversion is pronounced. Female rami are delicate and the gonia may be strikingly everted or convergent. The mandibular notch is small to medium, save for specimen BP2/21 which has a deep notch due to the greater length of the coronoid process. In all

TABLE 3

MANDIBULAR MEASUREMENTS AND INDICES

	Males		Females		
Measurements	BP2/17i	BP2/20–41	BP1/6	BP2/21	BP3/27–34
Condylo-Symphysial Length (68)	106	79	..	99	93
Bicondylar Breadth (65)	118	115	..	105	112
Symphysial Height (69)	28	26	31	31	28
Bigonial Diameter (66)	96	110	..	99	101
Height of Ascending Ramus—Right (70)	..	57	70	54	49
Height of Ascending Ramus—Left (70)	65	..	..	48	49
Minimum Breadth of Ascending Ramus —Right (71)	..	..	30	31	31
Minimum Breadth of Ascending Ramus Left (71)	34	35	..	33	31
Maximum Breadth of Ascending Ramus—Right (71–1)	..	..	..	36	41
Maximum Breadth of Ascending Ramus—Left (71–1)	44	..	..	36	40
Bimental Diameter (67)	45	30	..	..	41
Depth at PM^2—Right (69–2)	31	27	..	..	27
Depth at PM^2—Left (69–2)	31	26	27	..	26
Depth at M^1—Right (69–2)	28	25	27	22	23
Depth at M^1—Left (69–2)	31	26	26	..	23
Depth at M^2—Right (69–2)	26	25	23	23	23
Depth at M^2—Left (69–2)	28	26	25	23	20
Depth at M^3—Right (69–2)	26	..	21	24	20
Depth at M^3—Left (69–2)	29	27	22	24	20
Thickness at M^1—Right (69–3)	16	11	14	12	10
Thickness at M^1—Left (69–3)	16	12	15	13	9
Thickness at M^2—Right (69–3)	20	12	18	15	14
Thickness at M^2—Left (69–3)	19	13	17	16	13
Thickness at M^3—Right (69–3)	18	12	17	17	11
Thickness at M^3—Left (69–3)	19	16	18	17	11
Mental Foramen Diameter—Right	..	4×3·5	15×2·5	..	..
Mental Foramen Diameter—Left	..	4×3·5	25×3	..	..
Mean Angle (79)	118	123	..	116	133
Indices					
Mandibular	89·83	68·69	..	94·28	83·03
Fronto-Gonial	..	..	..	104·76	81·25
Zygo-Gonial	..	..	..	81·82	101·81

mandibles the condylar process does not rise very high above the coronoid process and the mandibular head is small. The lingula of the mandibular fossa is uniformly small. The ramus is broad and moderately high. The Balangodese mandible is of medium size but is distinctive for its broad and elevated rami and thick corpora. Sexual differences are difficult to isolate (Pls. 8, 9).

The Post-Cranial Skeleton. *The Skeleton of the Trunk.* Vertebrae were available for two specimens: BP2/17 and BP2/25. Their fragmentary and badly warped condition renders a metrical description of dubious value, but measurements were feasible for the fourth and fifth lumbar vertebrae of BP2/17. The cervical vertebrae are small and delicate with cordiform bodies and triangular neural foramina. The transverse processes are short. The atlas has a thin posterior arch and a very reduced posterior tubercle. The facet for the odontoid process is proportionately large for the accommodation of the thick, bulbous axial dens. The thoracic vertebrae are small. Their vertebral foramina are round and their bodies contain broad costal facets. The transverse processes are bulbous. The spinous processes are not large. In contrast to the pre-lumbar vertebrae, the last five segments of the spine are robust and are equipped with prominent posterior and transverse processes. The kiolorachic lumbar vertebrae of BP2/17 exhibit thick centra and wide epiphysial rings. For the fifth lumbar vertebra the Vertical Ventral (1) and Vertical Dorsal (2) Diameters are 23 mm. and 27 mm. respectively: the Depth of the Body is 30 mm. for the anterior–posterior diameter (4) and 46 mm. for the lateral diameter (7).

Rib fragments accompany the vertebral remnants but none of the ribs is complete. The ribs of BP2/17 are very large at their sternal ends but never exceed 6·0 mm. in thickness. The costal grooves are deep with sharp borders. The ribs of the female specimen attain their greatest size at a point some distance lateral to the sternal head. The first rib shows a well-marked groove for the subclavian vessels, but the ribs just inferior to it are smooth and their thickness averages 3·0 mm. For both sexes the neck of the rib is robust and massive.

The sternum of specimen BP2/17 is lacking its manubrium, but the body measures 96 mm. in length and 32 mm. in breadth. Fusion of the sternal components is complete. Facets for six sternal articulations are well marked. Curvature is very slight. There are no sternal foramina.

The Skeleton of the Upper Extremity (Table 4). The clavicle of the male specimen is large and shows a moderate degree of curvature. The sternal head is oval in form. The acromial head is moderately flat. Muscularity is reduced. In contrast to this condition are the clavicles of the female specimens which are small, delicately built, and with a medium to pronounced degree of curvature. Muscularity is much more apparent among the female clavicles which are characterized by sharp ridges for the deltoid attachment. These also show wide grooves for the subclavian vessels. Like the male clavicles, those of the females have oval sternal heads and flat acromial heads.

The scapula is medium in size for the male, small for the female. For both sexes this portion of the upper extremity is robust. For the male specimen there is a pronounced obliquity in the direction of this spine in relation to a line tangent to the vertebral border. Since this border has undergone damage at the region inferior to the spine, the spino-vertebral angle can only be inferred and cannot be qualitatively or quantitatively ascertained. The axillary borders of both male and female scapulae are thick and tend to double their thickness in the vicinity of the glenoid fossa. The superior border is narrow and is lacking a scapular notch. The angle

TABLE 4

MEASUREMENTS AND INDICES OF THE BONES OF THE UPPER EXTREMITY

	Males		Females		
	BP2/17	BP4/8	BP2/21	BP2/25	BP3/27–34
Clavicle					
Measurement					
Maximum Length—Left (1)	. .	. .	. .	. .	123
Mid-Shaft Circumference—Right (6)	. .	. .	. .	28	32
Mid-shaft Circumference—Left (6)	39	. .	. .	. .	33
Mid-shaft Diameter—Anterior-Posterior —Right (5)	. .	. .	. .	. .	10
Mid-shaft Diameter—Anterior-Posterior —Left (5)	. .	. .	. .	. .	10
Sternal Head Diameter—Right	. .	. .	. .	18	19
Sternal Head Diameter—Left	. .	. .	22	. .	. .
Index					
Length—Thickness—Left	. .	. .	. .	. .	29·46
Scapula					
Measurement					
Morphological Length—Left (2)	87	. .	. .	. .	. .
Corocoid Process Length—Left (11)	43	. .	. .	. .	. .
Corocoid Process Breadth—Right	14	. .	. .	. .	. .
Corocoid Process Breadth—Left	14	. .	. .	. .	. .
Acromion Process Length—Right (10)	53	. .	. .	. .	. .
Acromion Process Length—Left (10)	52	. .	. .	. .	. .
Acromion Process Breadth—Right (9)	30	. .	. .	. .	22
Acromion Process Breadth—Left (9)	26	. .	. .	. .	. .
Glenoid Fossa Height—Right (12)	36	. .	. .	. .	30
Glenoid Fossa Height—Left (12)	38	. .	. .	. .	. .
Glenoid Fossa Breadth—Right (13)	. .	. .	. .	. .	20
Glenoid Fossa Breadth—Left (13)	28	. .	. .	. .	. .
Humerus					
Measurement					
Maximum Length—Left (1)	. .	. .	. .	. .	302
Bicondylar Length—Left (2)	. .	. .	. .	. .	298
Bicondylar Breadth—Right (4)	. .	53	. .	. .	. .
Bicondylar Breadth—Left (4)	. .	52	. .	. .	. .
Maximum Head Diameter—Right (9, 10)	. .	. .	. .	. .	35
Maximum Head Diameter—Left (9, 10)	. .	. .	. .	40	35
Mid-Shaft Diameter—Anterior-Posterior —Right (6c)	. .	21	. .	. .	12
Mid-Shaft Diameter—Anterior-Posterior —Left (6c)	. .	21	. .	. .	12
Mid-Shaft Diameter Lateral—Right (6b)	. .	18	. .	. .	17
Mid-Shaft Diameter Lateral—Left (6b)	. .	18	. .	. .	17
Mid-Shaft Circumference—Right (7a)	. .	59	. .	. .	. .
Mid-Shaft Circumference—Left (7a)	. .	59	. .	. .	48
Index					
Robusticity—Left	. .	. .	. .	. .	9·60

TABLE 4 (*continued*)
MEASUREMENTS AND INDICES OF THE BONES OF THE UPPER EXTREMITY

	Males		Females		
	BP2/17	BP4/8	BP2/21	BP2/25	BP3/27–34
Radius					
Measurement					
Maximum Length—Left (1)	..	248	..	..	..
Least Circumference—Left (3)	..	38	..	35	38
Maximum Head Diameter—Right (4–1, 5–1)	..	22	..	..	..
Maximum Head Diameter—Left (4–1, 5–1)	..	22	..	18	19
Mid-Shaft Diameter—Anterior-Posterior —Left (5)	..	11	..	15	9
Mid-Shaft Diameter—Lateral—Left (4)	..	16	..	19	18
Ulna					
Measurement					
Maximum Length—Left (1)	..	261	..	..	259
Least Circumference—Left (3)	..	33	..	..	25
Mid-Shaft Diameter—Anterior-Posterior —Left (11)	..	15	..	..	12
Mid-Shaft Diameter—Lateral—Left (12)	..	11	..	..	8
Capitate					
Measurement					
Length (1)	..	..	25	..	..
Breadth (2)	..	..	20	..	..
Height (3)	..	..	18	..	..
Trapezium					
Measurement					
Length (1)	..	..	23	..	..
Breadth (2)	..	..	19	..	..
Height (3)	..	..	11	..	..
Scaphoid					
Measurement					
Length (1)	..	..	23	..	..
Breadth (2)	..	..	13	..	..
Height (3)	..	..	8	..	..
Metacarpals					
Digit I Length (2)	..	..	71	..	..
,, II ,,	..	..	71	..	..
,, III ,,	..	..	68	..	..
,, IV ,,	..	..	68	..	..
,, V ,,	..	..	48	..	..
Phalanges					
Digit I ,, (3)	..	..	31	..	..
,, IV ,,	..	..	38	..	..

of the glenoid fossa to the scapular body lies in a plane slightly lateral and superior to it. In form the fossa is elliptical, the inferior half being broad and the superior half narrowly constricted. Lipping of the fossa is submedium. The acromion is long and rectangular. The clavicular facet is unlipped. The corocoid process is flat and extensive.

The humeral shaft is long and only slightly curved. A transverse section shows a prismatic pattern in the male specimen, a plano-convex pattern in the female. Muscularity is pronounced : the tuberosities are large, the bicipital groove is deep, the supracondylar ridges are sharp on medial and lateral aspects of the bone. The head is medium in size. The olecranon fossa is shallow and unperforated. Supracondylar processes are absent.

The radius is large for specimens BP4/8 and BP2/25, but small and sinuous for BP3/27. The shaft is straight in the male, but shows moderate anterior–posterior bowing in the female. The transverse section is oval in these bones for both sexes. The extremities of the radius are more massive for the male, but both sexes have shafts with well-marked muscular attachments. Tuberosities are extensive and low in females, prominent in males. The neck is longer for the male. Lipping of the capitulum occurs in the bones of both sexes. The styloid process is particularly well marked for males. Both sexes exhibit prominent muscular attachments on their radii.

The ulna is triangular in transverse section. Curvature of the shaft is slight, occurring in the male only to a limited degree in the region of the brachialis attachment just inferior to the coronoid process. Muscularity is pronounced for the male, moderate for the female. Both sexes show a prominent styloid process. The interosseous space is large as a result of radial rather than ulnar curvature.

The bones of the hand tend to be large. The crests of the carpals are weakly developed. The form of the capitate is square. The scaphoid assumes a dumbbell conformity, but the trapezium is prominently ridged and metacarpals irregular. The metacarpals are long and exhibit pronounced dorso-ventral curvature. This being the hand of a sub-adult individual, the heads of the shaft are ununited. The metacarpal formula is II > III > IV > V(?) > I(?). The fifth metacarpal is not available for examination.

The Skeleton of the Lower Extremity (Table 5). The femur of BP2/17 is stenomeric, and femora of the other male and the female of this series are eurymeric. Transverse section pattern is either round or quadrangular for the males but plano-convex for the female. The linea aspera is marked with a prominent pilaster, particularly in the case of the males. The shaft is uniformly thick and bowing is slight to medium in its degree. Tortion is slight to medium in its degree. Tortion is within the medium category (10°–20°), save for specimen BP2/17 where the tortion is more pronounced. The crista hypotrochanterica is of medium development for BP4/8, but the fossa hypotrochanterica is deep for all specimens. Trochanters major and minor are large and smooth. The neck of the femur is short and narrow and supports a small head. The intercondylar fossa is deep and broad in its transverse plane. There is a pronounced inferior orientation of the medial condyle and a slight anterior prominence of the lateral condyle. The adductor tubercle is reduced.

Table 5

Measurements and Indices of the Bones of the Lower Extremity

	Males		Females
	BP2/17	BP4/8	BP2/25
Femur			
Measurement			
Maximum Length—Right (1)	419	..	..
Bicondylar Length—Right (2)	414	..	..
Mid-Shaft Circumference—Right (8)	72	80	66
Mid-Shaft Circumference—Left (8)	..	79	71
Sub-Trochanteric Diameter—Anterior-Posterior—Right (10)	25	24	..
Sub-Trochanteric Diameter—Anterior-Posterior—Left (10)	..	26	20
Sub-Trochanteric Diameter—Lateral—Right (9)	20	27	..
Sub-Trochanteric Diameter—Lateral—Left (9)	..	26	23
Mid-Shaft Diameter—Anterior-Posterior Right (6)	24	25	24
Mid-Shaft Diameter—Anterior-Posterior—Left (6)	25	27	25
Mid-Shaft Diameter—Lateral—Right (7)	20	23	18
Mid-Shaft Diameter—Lateral—Left (7)	21	23	19
Maximum Head Diameter—Right (18, 19)	35	..	..
Indices			
Platymeria—Right	125·00	88·89	86·96
Platymeria—Left	..	100·00	..
Middle—Right	83·33	92·00	75·00
Middle—Left	84·00	85·18	76·00
Pilastric—Right	120·00	108·59	133·33
Pilastric—Left	119·05	117·39	131·59
Robusticity—Right	10·63	..	..
Tibia			
Measurement			
Mid-Shaft Diameter—Anterior-Posterior—Right (8)	26	27	23
Mid-Shaft Diameter—Anterior-Posterior—Left (8)	25	27	..
Mid-Shaft Diameter—Lateral—Right (9)	19	22	16
Mid-Shaft Diameter—Lateral—Left (9)	18	21	..
Nutrient Foramen Diameter—Anterior-Posterior—Right (8a)	..	..	27
Nutrient Foramen Diameter—Anterior-Posterior—Left (8a)	26	33	..
Nutrient Foramen Diameter—Lateral—Right (9a)	..	..	19

TABLE 5 (*continued*)

MEASUREMENTS AND INDICES OF THE BONES OF THE LOWER EXTREMITY

	Males		Females
	BP2/17	BP4/8	BP2/25
Nutrient Foramen Diameter—Lateral—Left (9a)	19	23	..
Least Circumference—Right (10b)	69	..	61
Least Circumference—Left (10b)	66	72	..
Index			
Middle—Right	73·07	81·48	69·56
Middle—Left	72·00	77·78	..
Platycnemia—Right	..	..	65·52
Platycnemia—Left	73·08	69·60	..
Fibula			
Measurement			
Mid-Shaft Diameter—Anterior-Posterior—Left (3–2)	..	15	..
Mid-Shaft Diameter—Lateral—Left (3–1)	..	9	..
Least Circumference—Left (4a)	..	33	..
Distal Breadth—Left (4–2)	..	23	..
Talus			
Measurement			
Length—Right (1)	45	..	..
Breadth—Right (2)	32	..	..
Height—Right (3)	18	..	..
Calcaneum			
Measurement			
Length—Right (1)	67	..	..
Breadth (2)	37	..	..
Cuboid			
Measurement			
Length—Left (1)	35	..	..
Breadth—Left (2)	29	..	..

The tibiae are eurycnemic for specimen BP2/17 and mesocnemic for BP4/8 and BP2/25, although these latter two stand at the upper and central loci of the mesocnemic category. Tibial lengths could not be ascertained. The posterior half of the transverse section of the shaft is oval, but in BP4/8 the conformation is closer to plano-convex. The bones are heavy and thick for the males. Bowing of the shaft is very slight. Muscularity is moderate for both sexes.

The fibula is represented by the single fragment belonging to BP4/8. It is the left fibula. The form of its transverse section is triangular. Whereas the anterior border is sharp, fluting of the shaft is sub-medium in development. The lateral malleolus is medium in size and its articular facet is extensive. The shaft is straight.

The talus possesses a large triangular articular facet for the fibular malleolus. The groove for the flexor hallicus longus is medium in development. The neck of the talus is not constricted. The calcaneum is short and deep with a round posterior curvature of the sustentaculum tali. The cuboid exhibits pronounced curvature of the cuboid-lateral cuneiform facet. The articular facet is large, round, and its borders poorly defined. There is no lipping of the facet. The cuboidal ridge is prominent.

TABLE 6

MEASUREMENTS AND INDICES OF THE BONES OF THE PELVIS

	Male BP2/17
Sacrum	
Measurement	
Anterior Length (2)	102
Sacral Breadth (5)	125
Lateral Diameter of Body 1 (19)	46
Anterior-Posterior Diameter of Body 1 (18)	29
Anterior Height of Body 1 (24)	29
Anterior Height of Body 2 (24)	28
Index	
Sacral	122·55
Innominate	
Measurement	
Innominate Length—Right (1)	207
Innominate Length—Left (1)	184
Innominate Breadth—Right (6a)	141
Innominate Breadth—Left (6a)	142
Distance from Acetabulum to Apex of Ilium—Right (9)	132
Distance from Acetabulum to Apex of Ilium—Left (9)	114
Length of Iliac Lines—Right	262
Length of Iliac Lines—Left	260
Vertical Diameter of Acetabulum—Right (22)	42
Horizontal Diameter of Acetabulum—Right (22)	37
Breadth of Sciatic Notch—Right (8)	50
Distance from Anterior Superior to Posterior Superior Iliac Spines—Right (12)	138
Sacrum and Innominates	
Measurement	
Bi-iliac Diameter (2)	218
Sagittal Diameter of the Pelvic Inlet (23)	157
Transverse Diameter of the Pelvic Inlet (24)	107
Index	
Pelvic Inlet	146·81
Innominate Breadth-Height—Right	129·58

The Skeleton of the Pelvis (Table 6). The single sacrum observable in the series is platyhieric. The sacral type is homobasal. Of the five sacral vertebrae the first, second and third articulate with the innominates. Curvature commences at the second sacral body but is not pronounced. Spina fissa is absent. The overall size of the sacrum is large. Deraniyagala considers the Stone Age population of Ceylon to have been steatopygous. He discusses this in relation to the small pelvis of the female skeleton found at the site of Alu galge (Telulla) (Deraniyagala 1955*b* : 301) and considers the fossils from Bellan Bandi Palassa to have exhibited the same trait (Deraniyagala 1958*a* : 255). The present writer is unable to find any evidence either to confirm or reject this opinion.

The innominates of this individual are thick and massive. Their size is moderate and the muscular attachments are prominently sculptured. The ilium has heavy and irregular crests along its superior rim and deep hollowing of the iliacus portion of the medial surface. The origin of gluteus maximus is well marked. There is considerable torsion between ilium and ischium. The anterior superior iliac spine is broad and blunt. The ischia are divergent in their orientation and are moderately elongated in size. The ischiatic notch presents a higher angle than is usual in male specimens. The pelvic inlet is cordiform and its index places it within the dolichopellic group, although the absence of the complete pubic area renders this statement subject to question.

An Estimation of Stature (Table 7). Limb proportions are unfortunately impossible to establish for the Balangoda population due to the paucity of long bones complete enough for their maximum lengths to be accurately measured, and to the absence of any bones of the upper and lower extremities belonging to the same individual. Those long bone lengths which could be measured are listed in the table below, where they are employed as components of the formulae devised by Trotter & Gleser (1952, 1958) for estimation of stature from long bones.

The lengths of the bones of two males, BP2/17 and BP4/8, and one female, BP3/27–34, are employed in formulae appropriate to American Whites, American Negroes, and American Mongoloids, mainly Chinese. The stature estimates for each of the three groups are given.

In an effort to ascertain which of the three formulae might be best suited to the Balangodese, the writer applied them to the long bone lengths of three Veddas whose stature in life was known and whose long bones had been measured by Hill. These individuals were two males—Burunda, specimen 1949–12–7–4, and Tissahamy, specimen 1949–12–7–6, both of British Museum of Natural History (Hill 1941 : 148–149, tables 1, 22). The former individual was from Dambane and was partly Sinhalese ; the latter from Kalakoluebe near Yakkure was non-Sinhalese in racial background. The female Vedda available for comparison was not measured in life but skeletal stature is known. This is the Vedda specimen in the osteological collection of the Bombay Natural History Society (Hill 1941 : 227–235).

Such estimations of stature as given here are only indicative of the order of stature which is to be anticipated for the three Balangodese individuals. For the Veddas, the formula for Mongoloids renders a value that most closely approximates the living stature of Burunda, but for Tissahamy, the formulae for the Negroes is a nearer approximation.

The Metrical and Morphological Analysis of the Dentition

In their dental morphology the Balangodese have teeth which are moderate to large in size by general standards for post-Pleistocene hominid populations (Table 8). The order of size of the molars within the molar rows of each specimen show considerable variation. For BP2/17, the RLM^1 and RLM^2 are progressively smaller than the RLM^3. This is also the case for the mandibular molar row of BP2/17i, but in the remaining male specimens the maxillary molar row shows the first molars of greater size. The mandible of BP2/20–41, however, shows a larger third molar for the row. For the female BP1/6, the maxilla has a second molar of greatest size followed in descending order by the first molar and the third, but the mandibular molar row has the third molar larger than the first and the first larger than the second.

TABLE 7

AN ESTIMATION OF STATURE BASED UPON
LENGTHS OF LONG BONES FOR BALANGODESE AND VEDDAS

BALANGODESE

	Males				Female	
	BP2/17		BP4/8		BP3/27–34	
	Length	Stature	Length	Stature	Length	Stature
	Right		Left		Left	
White :						
Humerus	..	..	..	..	302	1654
Radius	..	..	248	1734	..	..
Ulna	..	..	261	1713	259	1706
Femur	419	1627	..	..	..	..
Tibia	..	..	..	..	..	..
Fibula	..	..	..	..	..	..
Negro :						
Humerus	..	..	..	..	302	1624
Radius	..	..	248	1678	..	..
Ulna	..	..	261	1663	259	1656
Femur	419	1602	..	..	..	..
Tibia	..	..	..	..	..	..
Fibula	..	..	..	..	..	..
Mongoloid :						
Humerus	..	..	..	..	302	1641
Radius	..	..	248	1698	..	..
Ulna	..	..	261	1683	259	1676
Femur	419	1626	..	..	..	..
Tibia	..	..	..	..	..	..
Fibula	..	..	..	..	..	..

TABLE 7 (*continued*)

AN ESTIMATION OF STATURE BASED UPON LENGTHS OF LONG BONES FOR BALANGODESE AND VEDDAS

VEDDAS

	Males						Female Bombay Nat. Hist. Soc.			
	1949–12–7–4				1949–12–7–6					
	Length		Stature		Length	Stature	Length		Stature	
	R	L	R	L	Right		R	L	R	L
White :										
Humerus	300	301	1648	1650	. .	. .	250	262·5	1503	1540
Radius	241	239	1707	1700	. .	. .	202	202	1560	1560
Ulna	266	263	1732	1721	. .	. .	221	221	1566	1566
Femur	429	430	1650	1653	398	1579	361	362	1493	1495
Tibia	365	368	1703	1710	328	1613	311	311	1572	1572
Fibula	358	355	1686	1678	325	1600	301	300	1538	1535
	Mean = 1686					1597				
Negro :										
Humerus	300	301	1619	1622	. .	. .	250	262·5	1475	1512
Radius	241	239	1654	1648	. .	. .	202	202	1525	1525
Ulna	266	263	1679	1669	. .	. .	221	221	1535	1535
Femur	429	430	1823	1825	398	1558	361	362	1480	1482
Tibia	365	368	1653	1659	328	1572	311	311	1535	1535
Fibula	358	355	1638	1631	325	1561	301	300	1505	1503
	Mean = 1677					1564				
Mongoloid :										
Humerus	300	301	1636	1638	. .	. .	250	262·5	1502	1535
Radius	241	239	1673	1667	. .	. .	202	202	1535	1535
Ulna	266	263	1700	1690	.	. .	221	221	1543	1543
Femur	429	430	1648	1650	398	1681	361	362	1502	1504
Tibia	365	368	1687	1694	328	1598	311	311	1558	1558
Fibula	358	355	1665	1658	325	1586	301	300	1528	1526
	Mean = 1667					1622				
Known Stature :	(Living) 1629				(Living) 1493		(Skeletal) 1267			

Specimen BP2/21 offers another variant : the maxilla shows a large first molar, a medium second molar and a smaller third molar, but in the mandible the largest tooth is the second molar followed in size by the first and then the third. Specimen BP2/27–34 has a larger maxillary second molar than the first molar, but a larger mandibular first molar. These data can be summarized as follows :

Males :	BP2/17	*Maxilla.*	M3 > M2 > M1		
	BP2/17i			*Mand.*	M3 > M2 > M1
	BP2/20–41	*Maxilla.*	M1 > M2 > M3	*Mand.*	M3 > M1 > M2
	BP4/8	*Maxilla.*	M1 > M3 > M2		
Females :	BP1/6	*Maxilla.*	M2 > M1 > M3	*Mand.*	M3 > M1 > M2
	BP2/21	*Maxilla.*	M1 > M2 > M3	*Mand.*	M2 > M1 > M3
	BP3/27–34	*Maxilla.*	M1 > M2	*Mand.*	M2 > M1

The molars are round in their conformation, but rectangular molars are present in the $LM^{\underline{3}}$ of BP2/20–41 and in all molars of BP2/21 save for its $RLM^{\underline{1}}$ which is round. Premolars are rectangular in the maxillae of both sexes, but variability occurs in the mandibles. Specimen BP2/20–41 has $RLPM^{\overline{1}}$ and $RLPM^{\overline{2}}$ which are round; another male, BP2/17i, has a triangular LPM^{1} although its other mandibular premolars are round. In both these cases, the molar pattern is round, with the exception of the LM^{3} of BP2/20–41 noted above. There is no maxillary dentition available for BP2/17i. The female BP3/27–34 has a round $RLPM^{1}$ adjacent to a rectangular $RLPM^{2}$ and round molars. Canines of the maxillae and mandibles are triangular for both sexes, but rectangularity appears in the $RL\underline{\overline{C}}$ of the male BP2/20–41. Incisors are uniformly rectangular.

Cusp and groove patterns are not observable for all of the teeth of the series due to the high incidence of attrition. For the maxilla, the males show pronounced variability. Specimen BP2/17 shows 5 cusps for the $LM^{\underline{3}}$ and 3 cusps for $RLM^{\underline{2}}$. The other male, BP4/8, has 4 cusps on the $RM^{\underline{1}}$, RM^{2}, and $RM^{\underline{3}}$, the other molars not being observable. In contrast, the maxillary molars of the female specimens are of the 4-cusp pattern. The $RLM^{\underline{3}}$ of BP2/21 has 6 cusps. In the single male, specimen BP2/20–41, for which the cusps of the lower molars are observable, the LM^{3} has 5 cusps and the remaining left and right molars have 4 cusps. The three female specimens show one, BP1/6, with 5 cusps for the $RLM^{\overline{3}}$ and $RLM^{\overline{1}}$, but 4 cusps for the $RLM^{\overline{2}}$. Specimen BP2/21 has 5 cusps for all molars, save for the $LM^{\overline{3}}$ which has 6 cusps. For specimen BP3/27–34 only the $RLM^{\overline{2}}$ with 4 cusps is available. Of the four specimens for which both maxillae and mandibles are available, there is no case of correlation of cusp pattern except for specimen BP3/27–34 where the second molars are alone observable. The upper and lower premolars of females are bicuspid, the buccal cusp being the larger and higher. Male premolars are also of this pattern, save for the $RLPM^{\underline{2}}$ of BP2/20–41 where the premolars have 4 cusps due to the presence of accessory cusps on the distal inclination of the buccal cusp.

Carabelli's cusp is present in the $LRM^{\underline{1}}$ of one specimen, BP2/21. The cusp is small and the mesio-lingual groove is of moderate development.

Accessory cusps are found on the second and third maxillary molars of the male specimen BP2/17. They are small and occupy loci on the mesial half of the buccal surface.

Crenulation or excessive wrinkling of the occlusal surface of the upper third molars is shared by males—BP2/17 and BP2/20–41—and females—BP1/6 and BP2/21. It is absent in the remaining male maxillae and the third molars of the female BP3/27–34 are unavailable for examination. Its occurrence is marked by the presence of 5 cusps in the male maxillae. For the females, BP1/6 has the 4-cusp pattern and BP2/21 has 6 cusps. All cases are characterized by pronounced crenulation regardless of cusp number. The mandible of male BP2/20–41 shows a deeply crenulated $LM^{\overline{3}}$ with 5-cusp pattern—a reflection of the maxillary $LM^{\underline{3}}$ of this same specimen. The mandible of female BP1/6 shows a pronounced crenulation of the $RLM^{\overline{3}}$, but the cusps of these lower third molars constitute the 5-cusp pattern instead of the 4-cusp pattern of the upper third molars of the same specimen. In specimen BP2/21 six cusps are observed in both maxillary and right mandibular third molars but the RM$^{\overline{3}}$ has 5 cusps.

For the maxilla, cusp patterns are unusual in the dentition of female specimen BP2/21 where the RLM$^{\underline{1}}$ and RLM$^{\underline{2}}$ are of the +3 type. The groove patterns for the remaining maxillary dentitions of the males are of the +4 pattern. The mandible of BP2/21 shows a RLM$^{\overline{2}}$ of the +5 pattern and a RLM$^{\underline{1}}$ of the Y5 type. In specimen BP1/6 the RLM$^{\overline{1}}$ is also of Y5 type, but the RLM$^{\overline{2}}$ is +4 and the RLM$^{\overline{3}}$ is +5. The other female specimen, BP3/27–34, has a RLM$^{\overline{2}}$ of +4 type. The only male mandible which offers data on groove pattern is specimen BP2/20–41, whose LM$^{\overline{3}}$ is Y5 and whose RLM$^{\overline{2}}$ and RLM$^{\overline{1}}$ are +4 in form. Taking the series collectively, it would appear that the basic cusp pattern for the upper molars is of the +4 type. The lower molars are characterized by the groove patterns Y5, +5, and +4.

A correlation of cusp type and groove pattern reveals that the presence of 4 cusps is associated with the +4 pattern in the mandible as observed in specimens BP2/20–41, BP1/6, and BP3/27–34. However, the mandibular 5-cusp type may be associated with either the +5 type, as with the RLM$^{\overline{3}}$ of BP1/6 and RLM$^{\overline{2}}$ of BP2/21, or with the Y5 type as represented by the LM$^{\overline{3}}$ of BP2/20–41, RLM$^{\overline{1}}$ of BP1/6, and RLM$^{\overline{1}}$ of BP2/21. As is obvious from an examination of these cases for which a mandibular molar dentition is available, each specimen has its unique combination of cusp type and groove pattern. Nevertheless, where the M$^{\overline{1}}$ has 5 cusps, its groove pattern is a Y5. The M$_{\overline{2}}$ is consistently a + pattern and in three of the specimens a +4, namely with BP2/20, BP1/6, and BP3/27–34. In one specimen, BP2/21, this is +5. Crenulation of the M$^{\overline{3}}$ is associated with the presence of 5 cusps which are either of Y5 pattern like BP2/20 or a +5 pattern like BP1/6. The groove pattern of the M$^{\overline{3}}$ of BP2/21 is unobservable, but the cusp number is 5 for the RM$^{\overline{3}}$ and 6 for the LM$^{\overline{3}}$, both molars showing crenulation. This point cannot be confirmed for the mandibular third molars of BP3/27–34. In the maxilla, as noted above, crenulation of the third molar is associated with 4 cusps (BP1/6), 5 cusps (BP2/17, BP2/20–41) or 6 cusps (BP2/21).

Attrition of the molars of male and female dentitions show considerable variation. The maxillary molars are very slightly worn in BP2/17. All cusps of the RLM$^{\underline{1}}$ and the mesio-labial cusp of the LM$^{\underline{2}}$ exhibit abrasion of the enamel with consequent exposure of the dentin in the form of pits at the apices of the cusps. Direction of abrasion cannot be established for this specimen. In contrast to this condition are the heavily abraded molars of BP2/17i. The RLM$^{\overline{3}}$ show the least wear for the six teeth of the molar rows, but like them a rim of enamel surrounds a lake of dentin from the centre of which protrudes a reduced cusp which is still covered with enamel in the RLM$^{\overline{3}}$, LM$^{\overline{2}}$, and LM$^{\overline{1}}$. Wear is greatest on the labial aspects of each molar, but the enamel rim is everywhere intact. The dentin surfaces are deeply hollowed around the central reduced cusps, the sculpturing being most pronounced on the buccal sides. The maxilla of BP2/20–41 contains a fourth molar on the left side which, like the LM$^{\underline{3}}$ adjacent to it, shows an absence of attrition. The other maxillary molars show a moderate degree of wear, the greatest degree of abrasion occurring on the buccal portions of the occlusal surface. The enamel rim is thin and brittle on the mesial portion of these molars, but thick and robust on the other portions. A similar degree of wear characterizes the mandibular molars, the LM$^{\overline{3}}$ showing less wear than the remaining molars, the buccal sides being the most abraded and denuded of enamel. The male BP4/8 shows slight wear of the RM$^{\underline{3}}$ and medium wear of the RM$^{\underline{2}}$ and RM$^{\underline{1}}$. The exposed dentin forms kidney-shaped lakes over the occlusal surfaces, and the enamel borders are stout.

The RLM$^{\underline{3}}$ of female specimen BP1/6 shows very slight abrasion. The adjacent molars are moderately worn with small pits of exposed dentin on their cusps. The RLM$^{\underline{1}}$ present kidney-shaped lakes of exposed dentin on the mesio-buccal occlusal surfaces. The direction of the abrasive force is lingual for both molar rows. The mandible of this specimen reflects the maxilla in regard to attrition, save that the RLM$^{\overline{1}}$ exhibits pronounced abrasion. The maxillary and mandibular molars of BP2/21 show negligible wear, save for the first molars which have developed small pits of exposed dentin on the apices of their cusps. Direction of this slight abrasion appears to be buccal. As the third molars are in process of eruption, their elaborately crenulated occlusal surfaces are untouched by attrition. The dentition of BP3/27–34 is heavily abraded. The third molars have been lost ante-mortem, and the first and second molars exhibit occlusal surfaces denuded of enamel, save for an island of enamel forming a central cusp. Greatest wear occurs on the lingual surfaces. The enamel rims are narrow and brittle and enclose poorly sculptured lakes of the discoloured dentin.

As with the molars, the premolars of females are more frequently abraded than are the premolars of males. For specimen BP2/17 the premolars are very slightly worn, although attrition of the buccal cusps has resulted in exposure of dentin on the RLPM$^{\underline{1}}$ and RPM$^{\underline{2}}$. The mandibular premolars of BP2/17i are heavily abraded, the RPM^{2} exhibiting the greatest degree of attrition. The exposed dentin of these teeth lacks the central reduced cusps found on the molars. Orientation of the abrasive force is buccal. The enamel borders of these premolars are rounded in contrast to the sharpened ridges that constitute the enamel borders of the molars. Maxillary and mandibular premolars of BP2/20–41 show a moderate degree of attrition. The force of abrasion appears not to favour either side of the maxillary or mandibular premolar row, but the distal portions have maintained the greater parts of the enamel, particularly for the RLPM$\frac{1}{1}$. The maxillary premolars of BP4/8 show medium attrition, the RPM$^{\underline{2}}$ having the least amount of dentin visible. Wear is greatest for both RPM$^{\underline{2}}$ and RPM$^{\underline{2}}$ on the labial portion, although the lingual cusps are marked by several small pits and lines of exposed dentin.

All maxillary premolars of female BP1/6 show a moderate degree of wear, except for LPM$^{\underline{1}}$ which is heavily worn. Unlike the other premolars whose bays of exposed dentin are limited to buccal and lingual areas separated by mesio-distal ridges of enamel, the occlusal surface of LPM$^{\underline{1}}$ is denuded of all enamel and its rim is sharp and narrow. This tooth is separated by a gap of 10 mm. from LPM$^{\underline{2}}$ which is due in part to post-mortem distortion of the maxilla, but which perhaps reflects as well an abnormal orientation of this tooth in the molar-premolar row. Unfortunately the mandibular premolars of BP1/6 are missing. Direction of wear appears to have had no preference for either side of the premolar rows. Specimen BP2/21 exhibits very slight attrition of both maxillary and mandibular premolars, although the RLPM^{2} shows somewhat more abrasion than the others. Pits of dentin on the occlusal surface are numerous and are greatest in frequency on the labial portions of the premolars. In contrast are the maxillary and mandibular premolars of BP3/27–34, all of which are heavily worn, particularly on their labial sides where the enamel borders of the RLPM^{2} have broken down. Vestiges of the lingual cusps are visible on the RLPM$^{\overline{1}}$.

Canines show slight attrition in specimen BP2/17, the apices of the cusp being marked by very small pits of dentin. Those of BP2/20–41 are moderately worn with the greatest degree of attrition on the labial aspects. The R$\underline{C}$ of BP4/8 is characterized by a lingual and labial pit on its occlusal surface, but these are reduced in size. The maxillary L$\underline{C}$ of BP1/6 has moderate wear on its labial aspect. Those of BP2/21 are marked by numerous pits of exposed dentin but the cusps are not reduced in size. The canines of BP3/27–34 are very abraded in the maxilla and in the R$\overline{C}$ of the mandible, although the enamel borders are well preserved and rounded in form.

Incisors are moderately to heavily abraded for all specimens. The RLI$^{\underline{2}}$ of BP2/17 present a bar-like incisal margin of exposed dentin, portions of which are pitted. The more pronounced attrition of the LI$^{\underline{2}}$ of BP2/20–41 shows a triangular mass of exposed dentin on the cutting surface, the enamel rim being reduced in size and very thin along its mesial aspect. The lingual side is worn to the base of the crown. The RI$^{\underline{2}}$ and RI$^{\underline{1}}$ of BP1/6 are moderately worn, the central incisor showing slightly greater wear. The exposed dentin is rectangular in form. The maxillary and mandibular incisors of BP2/21 are heavily abraded with their rectangular cutting surfaces. Due to post-mortem damage to the mandible, the RI$^{\overline{2}}$ and LI$^{\overline{2}}$ have become dislocated so that the RI^{2} has been pushed to the left side where it is adjacent to the LI^{2}. The cutting edges are rectangular. Pronounced wear characterizes the maxillary LI$^{\underline{2}}$ which is worn to a triangular-shaped stub of exposed dentin.

Deraniyagala (1958*a* : 255, 260) remarks that the lower teeth are always more heavily abraded than the upper teeth. This is the tendency for the teeth taken as a whole, although for the few incisors available in the sample the upper teeth appear to be more heavily abraded. However, if the dentitions are examined according to specimen, only two, BP1/6 and BP2/21, illustrate Deraniyagala's claim. The other two specimens, BP2/20 and BP3/27–34, show an equal degree of wear for teeth in both jaws. There is a higher incidence of mandibular molar wear among males than females, but maxillary molar wear shows no sexual dichotomy. Females show a higher incidence of premolar attrition and maxillary canine attrition, but males have a higher incidence of wear among mandibular canines and maxillary incisors. No comparison by sex is possible for the lower incisors since these are lacking for male specimens.

Shovel shaping of the incisors is lacking in the male dentitions available for examination, but is present in the RI$^{\underline{2}}$ and RI$^{\underline{1}}$ of female BP1/6 and in the LI$^{\underline{1}}$ and LI$^{\overline{2}}$ and RLI^{2} and RI$^{\overline{1}}$ of the female BP2/21. It is expressed to a pronounced degree only in the maxillary incisors of BP2/21, the size of the shovel shaped depressions of this specimen's mandibular incisors being slightly developed. Development is medium in the BP1/6 incisors. The single case of a lingual tubercle occurs in the LI$^{\underline{2}}$ and RLI^{2} and RI$^{\overline{1}}$ of BP2/21. The tubercle is prominent in the mandible, but small in the maxilla of this female specimen although a foramen cecum incisal to the tubercle marks this feature with clarity.

Some features that frequently appear in the dentitions of other Recent hominid populations are not observable in the Balangoda series. Caries and dental abcesses are not observed. Ante-mortem tooth loss is suggested in the case of a single specimen—the RLM$^{\overline{3}}$ of female BP3/27–34. The alveoli in this case appear completely absorbed. The maxillary third molars of this specimen appear to have been lost post-mortem, the RM$^{\underline{3}}$ showing a small alveolus with unabsorbed borders. Supernumerary teeth are found in the case of the LM$^{\underline{4}}$ of the maxilla of BP2/20–41. The size of this distomolar tooth is reduced, and its form is of the compressional or rectangular type. It was never of any functional benefit. Buccomesial to the RM$^{\overline{2}}$ of specimen BP2/21 is a peg-shaped paramolar which is encased in enamel and is half as high as the adjacent teeth. Suppression is not a feature of the dentitions of the series. The upper and lower third molars of specimen BP2/21 were almost completely erupted at the time of death of this individual.

Deraniyagala (1958*a* : 255) remarks that bite is of the edge-to-edge type. This cannot be ascertained with certainty for any of the specimens, although it may have been a trait for those individuals with heavily worn teeth. Prominent overbite seems to be the case for specimen BP3/27–34 and possibly for BP2/25, although distortion of the skull precludes certainty for the latter.

As few of the teeth were isolated from their alveoli, examination of the root systems was approached through study of radiographic plates. The number of roots for the mandibular molars was two for all samples in the series. Maxillary molars, however, exhibit greater variation. The distomolar of BP2/20–41 has two roots although the other molars adjacent to it are triradical. The first maxillary molars of BP4/8 are double-rooted. Premolars are single-rooted in the mandibles of both sexes, but in the maxilla the first premolar is double for females BP1/6 and BP2/21. These double roots are small.

The direction of the molar roots within their alveoli shows considerable variation. The roots of the M$^{\underline{3}}$ of BP2/17 are fused and straight. Its neighbour, the M$^{\underline{2}}$, shows fusion of only two of its roots—the mesiobuccal and distobuccal. The M$^{\underline{1}}$ has divergent buccal roots with the radical apices oriented toward each other.

The mandibular molars of BP2/17i are divergent, those of the M$^{\overline{1}}$ curving toward each other.

Maxillary molars of BP2/20–41 show divergent roots for the distomolar, fused roots for the M$^{\underline{3}}$, and divergent roots for the remaining molars. The mandibular molars all have divergent roots. The medial roots curve distally, and the distal roots are straight.

TABLE 8—DENTAL MEASUREMENTS AND INDICES

			Maxilla		Mandible	
			Range	Mean	Range	Mean
Third Molar	R	Mesio-distal	8·5–10 (4)	9·25	11–12 (3)	11·50
		Bucco-lingual	11·5–13 (4)	11·87	10·5–11·5 (3)	11·00
		Index	115·00–151·94	128·94	91·30–100·00	95·71
	L	Mesio-distal	9–10 (4)	9·37	10·5–12 (4)	11·25
		Bucco-lingual	12–13 (4)	12·50	10·5–13 (4)	11·25
		Index	120·00–144·44	133·80	87·50–118·18	100·43
Second Molar	R	Mesio-distal	9–10·5 (6)	9·60	10·5–12 (5)	11·20
		Bucco-lingual	10·5–13 (6)	11·75	9·5–12 (5)	10·50
		Index	105·00–141·18	122·11	86·36–100·00	93·67
	L	Mesio-distal	9–10 (5)	9·50	10–12 (5)	11·00
		Bucco-lingual	10·5–12·5 (5)	11·90	10–11·5 (5)	10·60
		Index	110·53–138·89	125·44	91·30–104·54	96·38
First Molar	R	Mesio-distal	9–11 (6)	10·17	10·5–12 (5)	11·00
		Bucco-longual	11–12 (6)	11·50	10–11·5 (5)	10·80
		Index	109·10–122·22	113–31	91·67–104·76	98·33
	L	Mesio-distal	9·5–11 (5)	10·20	10–11·5 (5)	10·80
		Bucco-lingual	11–12 (5)	11·70	10·5–11·5 (5)	10·90
		Index	109·10–121·05	114·90	95·45–105·00	100·13
Second Premolar	R	Mesio-distal	6–7 (6)	6·75	7–7·5 (4)	7·12
		Bucco-lingual	9–10 (6)	9·67	8·5–9 (3)	8·83
		Index	128·57–153·85	143·50	120·00–128·57	123·33
	L	Mesio-distal	6·5–7 (5)	6·90	7–7·5 (4)	7·25
		Bucco-longual	9·5–10 (5)	9·80	8–8·5 (4)	8·12
		Index	135·71–153·85	142·20	106·67–121·43	112·26
First Premolar	R	Mesio-distal	6–7·5 (5)	6·80	7–7·5 (3)	7·17
		Bucco-lingual	9–10 (6)	9·50	8–9 (3)	8·33
		Index	128·57–158·33	140·42	114·28–120·00	116·19
	L	Mesio-distal	6·5–7·6 (5)	6·90	6·5–7·5 (4)	7·00
		Bucco-lingual	9–10 (5)	9·70	8–8·5 (4)	8·12
		Index	128·57–153·85	140·95	106·67–123·08	116·36
Canine	R	Mesio-distal	6·5–7 (6)	6·92	5·5–7 (2)	6·25
		Labio-lingual	7–10 (6)	8·33	9·5 (1)	9·50
		Index	100·00–142·86	120·42	172·73	172·73
	L	Mesio-distal	6·5–7·5 (4)	6·75	5–6·5 (3)	5·83
		Labio-lingual	8–8·5 (4)	8·37	7–9·5 (3)	8·00
		Index	113·33–130·77	124·49	115·38–190·00	140·68
Lateral Incisor	R	Mesio-distal	6·5–7 (2)	6·75	6 (1)	6·00
		Labio-lingual	6·5–7 (2)	6·75	6 (1)	6·00
		Index	92·86–107·69	100·27	100·00	100·00
	L	Mesio-distal	6–7 (4)	6·62	5·5 (1)	5·50
		Labio-lingual	6·5–7·5 (4)	7·00	6 (1)	6·00
		Index	100·00–108·33	105·79	109·09	109·09
Central Incisor	R	Mesio-distal	8·5 (1)	8·50	..	..
		Labio-lingual	7 (1)	7·00	..	..
		Index	82·35	82·35	..	..
	L	Mesio-distal	9 (1)	9·00	7 (1)	7·00
		Labio-lingual	7 (1)	7·00	6.5 (1)	6·50
		Index	77·78	77·78	92·86	92·86

N.B. The small size of the dental series has led the writer to include the data of male and female specimens together in the tabulations of Ranges and Means. The numbers in parentheses refer to the frequency of observations.

The double roots of the $M^{\underline{3}}$ of BP4/8 converge, but are distally oriented. The remaining molars of the maxilla diverge and are also distally oriented.

Among the females, BP1/6 shows three converging roots for the $M^{\underline{3}}$ and M^{2}, but divergent roots for the $M_{\overline{2}}$. The mandibular molars also have divergent roots. The $M^{\overline{2}}$ has a medial root that is distally oriented. The $M^{\overline{1}}$ shows distal curvature for both its roots.

For specimen BP2/21 the radical apices of the maxillary second molar are oriented distally, but this trait is less prominent in the other maxillary molars. Mandibular roots are divergent and are distally overted. The tips of the roots of the $M^{\overline{3}}$ which has not completely erupted, are still not fully developed.

BP2/25 has fused roots for the $M^{\underline{2}}$ and divergent roots for the $M^{\overline{1}}$, the apices of which are curved toward each other. The mesial root shows the greatest curvature.

The mandibular molar roots of BP3/27–34 are short and distally oriented. The $LM^{\overline{2}}$ has a functional neck that includes the upper third of its roots. The other molars have their roots buried in their alveoli.

The direction of the premolars is most usually straight. The mandibular premolars of BP2/21 and BP3/27–34 are curved distally, particularly at the radical apex.

The pulp cavities vary in size for the molars, but in the maxilla they are universally within the cynodont class. Taurodontism is present in the mandible as seen in the third molars of BP2/20–41 which is mesotaurodont and in BP2/21 which are hypotaurodont. The second mandibular molar is mesotaurodont in BP2/21 and hypotaurodont in BP2/25. The $M^{\overline{1}}$ is mesotaurodont for BP2/21, thus giving to all the lower molars of this specimen the taurodont condition.

Pulp cavities for the other teeth are variable. They are large for canines and incisors, but for premolars greater differences are observable. The maxillary premolars of BP2/17 have sinuous pulp chambers. Those of BP2/20–41 are broad. These canals are straight. BP4/8 has narrow chambers. Those of BP2/21 are short for the maxillary premolars but long and broad for the mandibular premolars. The largest pulp cavities for premolars are found in the mandible of BP2/25. The premolars of the remaining specimens are of moderate size (Pls. 7, 9, 14–15).

The Biochemical Analysis

(*Table* 9)

Fifteen samples of ground bone from the Balangoda skeletal series were selected as suitable for an analysis of their biochemical properties. Of these, two were analysed for amino acids by chromatography, three for antigen content by two paleoserological techniques, four for nitrogen content, five for the presence of fluorine, iron, calcium carbonate and the phosphate P_2O_5, and six were subjected to radioactive methods of dating. Criteria for the selection of these five samples were : (1) the observation of osseous tissue in the ground bone sample when subjected to low power microscopic examination ; (2) the separation of osseous tissue from the gross inorganic content of the sample (concretion, sand, dirt, etc.) after rapid and prolonged centrifugation in a saline suspension.

TABLE 9

BONE SAMPLES SELECTED FOR BIOCHEMICAL ANALYSIS

Skeletal Specimen Number	BP3/27–34			BP2/17g			BP2/17		
	Sample number	Portion of skeleton	Depth below surface	Sample number	Portion of skeleton	Depth below surface	Sample number	Portion of skeleton	Depth below surface
Chemical Assay F, P_2O_5, Fe, $CaCO_3$	AS.99	Rib	4′	AS.100	Ischium	3′	AS.101	Head of Humerus	3′
Amino Acid Chromotography	32	Head of Humerus and glenoid fossae of scapulae	..	..	..	..	II–III	Head of Femur and 4th–5th lumbar vertebral bodies	..
Nitrogen	32	,, ,,	..	IV	Ischium	..	II–III	,, ,,	..
Paleoserology	X	,, ,,	..	Y	,,	..	Z	,, ,,	..
Radioactivity	AS.99	Rib	..	AS.100	,,	..	AS.101	Rib	..

TABLE 9 (*continued*)

BONE SAMPLES SELECTED FOR BIOCHEMICAL ANALYSIS

Skeletal Specimen Number	BP2/21			BP2/25		
	Sample number	Portion of skeleton	Depth below surface	Sample number	Portion of skeleton	Depth below surface
Chemical Assay : F, P_2O, Fe_5, $CaCO_3$	AS.102	Cranium	3′	AS.103	Cranium	3′ 6″
Amino Acid Chromography	..	..	..	..	..	..
Nitrogen	AS.5	Tibia	..	..	..	..
Paleoserology	..	..	..	..	..	..
Radioactivity	AS.5	Tibia	..	AS.103	Femur	..
	AS.102	Cranium	..			

Chemical Assay (Table 10). In order to reduce the effects of contaminates in the ultimate samples of ground bone, the skeletal fragments were cleaned of surface dirt by means of a coarse-burred dental drill (Flat Fiss No. 9) and a wire brush. Those which were to be subjected to nitrogen (and paleoserological) analysis were washed in a solution of 2% absolute ethyl alcohol (denatured) and 98% distilled water, then air-dried for 30 minutes and oven-dried for 1 hour. The diploë was extracted from each bone fragment with the use of the coarse-burred drill after an orifice for penetration had been cleaned with a finer drilling piece (Flat Fiss No. 6). For cranial fragments, a portion of the left parietal $1\frac{1}{2}'' \times 1\frac{1}{2}''$ was removed from the brain case with a high-speed circular saw (HSS. 18). The sides of the section were cleaned with the fine-burred drill before the diploic tissue was extracted. Large bits of bone in each sample were separated from the powdery bone and inorganic residue by sifting. The ground bone samples were placed in a mortar where they underwent further pulverization. These samples were then deposited in labelled and sterilized bottles which were tightly sealed. Securing the sample from the diploic tissue has the virtue of reducing the risk of contamination as well as preserving the external morphology of the skeletal specimen for further anthropometric study. The cranial sections can be reset into the parietals from which they were taken without visible evidence of the marks of the saw. The diploë may be substituted with plaster-of-Paris in order to prevent the walls of the section from being crushed. It was at this level of preparation that the five specimens were selected from the series of nine for biochemical analysis.

The chemical assay of the Balangoda skeletal series was conducted by Mr. G. F. Phillips of the Laboratory of the Government Chemist, London. Nitrogen analysis was reported by Mr. G. C. Ross of the Central Laboratory, Department of Zoology, British Museum (Natural History). The nitrogen content and radioactivity of specimen BP2/21 had earlier been reported by Dr. Kenneth P. Oakley (Deraniyagala 1960*a* : 97). It should be noted that the results obtained from specimen BP2/25 were variable as the sample contained a high proportion of sand.

Amino Acid Chromatography. This analysis of two bone samples from the Balangoda skeletal series—BP2/17 and BP3/27–34—is taken from the report of Mr. Ross.

> " The samples were treated with 6N HCL (5 ml. to approx. 0·1–0·3 gms.) and hydrolysed at boiling pt. under reflux condensation for 16 hours. After successive evaporations to dryness in vacuo over conc. H_2SO_4 and caustic soda, and resolution in distilled water (to remove excess NCl) the filtered hydrolysates were subjected to electrolytic desalting to remove excessive inorganic ions present. To facilitate the desalting the solutions were diluted to about 1 in 10. After final evaporation to dryness the residue was dissolved in 0·5 ml. water prior to chromatography."

Mr. Ross has noted that the quantities of amino acids present in these two samples are extremely small. The limited quantities of material available for examination and the short time available for analysis have contributed to the fact that positive chromatograms could not be completed. Such duplicated chromatograms would have contained all suspected known substances run in conjunction and parallel with the mixtures of unknown composition. Furthermore, because of the trace quantities of nitrogenous material the problem of the elimination of contaminants was not investigated as thoroughly as it would have been had more time been available.

" One way chromatograms were prepared on Whatman No. 1 sheets measuring 22½″ × 18″ to give ' runs ' of approx. 18 inches. Each sheet contained base line spots of 0·2 ml. of each extract interspersed with 25 spots of known amino-acids each spot containing proline for reference Rp values.

" The runs were made as follows :

Sheet A. Solvent : Tertiary Butanol : Methyl Ethyl Detone : water : diethylamine :: 80 : 80 ; 40 : 8. Ascending 22 hours.
Sheet B. Solvent : Ethanol : water : Ammonia :: 180 : 10 : 10. Descending. Overnight.
Sheet C. Solvent : n-Butanol : acetic-acid : water :: 120 : 30 : 50.
Sheet D. Solvent : 80% Phenol : Ethanol : Ammonia :: 150 : 40 : 10. Ascending. Overnight.
Sheet E. Solvent : Methanol : water : Pyridine :: 160 : 40 : 8. Ascending. Overnight.

" Sheets were dried in a cold air stream.

" Spots were located by dipping through 0·2% Ninhydrin in acetone containing 2% Pyridine and developing in a warm air stream for ½ hour then leaving for 24 hrs. at room temperature. After marking the spots the colours were made permanent with alcoholic copper nitrate reagent.

" Distances of centres of spots were measured from the base-line and (Proline) values obtained for all substances except on sheet C where the proline was not added (to detect if any in the tests) and sheet B where the proline and substances of higher Rf values overran the paper.

" *Results*. The listed amino-acids are those probably present as determined by single substance spots shown on one or more chromatograms and/or by process of elimination from the combinations or substances in ' multiple spots '."

These results are the following :

Specimen BP2/17 :	(Granular)	(Pulverized)
	Palantine	Palantine/Tyrisine*
	Glutamic acid	Glumatic acid
	Glycine	Glycine
	Leucine/Iso Leucine	Leucine/Iso Leucine
	Methionine	Methionine
	Serine	Serine
	Glutamine	
	Lysine	Crystine/Cysteine
		Taurine

Specimen BP3/27–34 :	Palinine	Palinine
	Crystine/Cysteine	Crystine/Cysteine
	Glutamic acid	Glutamic acid
	Glycine	Glycine
	Leucine/Iso Leucine	Leucine/Iso Leucine
	Methionine	Methionine
	Ornithine	
	Serine/Asparagine	Serine
	Taurine	Taurine
		Arginine/Asparagine*
		Thrionine?
		Aspartic acid?

The asterisk (*) following the notation of certain of the above mentioned substances indicates that either one or both are present.

PALAEOSEROLOGY (Table 10). Bone fragments used as samples for palaeoserological procedures were washed and dried by the methods already described. After pulverization of the diploë for each of the three specimens, the samples were weighed out into 0·2 gm. amounts and placed in sterilized 75 × 10 mm. tubes which were then tightly stoppered. These were reserved for the Standard Absorption Technique. Bone samples for the Alcohol Extraction Test were prepared by the same methods, but the amount of bone in this second procedure was 1·0 gm. for two specimens. These amounts were placed in two 25 ml. Earlemeyer flasks bearing the appropriate label for each of the samples.

Standard Absorption Technique. This procedure is one based upon the presumption that a group specific antigen is present in the given sample if antiserum of proper concentration is inhibited in its activity with red cells of the appropriate group following its prolonged contact with the test sample. It is a technique developed originally for dried saliva and muscle tissue samples (Boyd & Boyd 1933, 1934), and later modified for bone samples (Candela 1936). It is a variation of the Standard Inhibition Test for blood group-containing substances.

Four naturally occurring human Anti-A and four Anti-B sera from individuals of known serological constitution were selected for use with each of the three bone samples. These anti-sera were recognized as yielding reliable results from previous testings with controls of known blood groups. In setting up a titration series, buffered saline, to which had been added 1% sodium azide as a preservative, was used as a dilutant. The determination of the titre for the anti-sera was established as the third or fourth dilution from the end-point for any one serum as judged from microscopic examination of a smear on a glass slide. A panel of anti-sera was regarded as preferable to pooled anti-sera by this investigator. The volumetric unit was used for all titrations in this analysis since it allows for greater accuracy than the more commonly used drop technique. To the 0·2 gm. of ground bone deposited in each of the labelled tubes was added 0·5 cc. of neat serum of the appropriate type. After these contents were mixed, the tubes were placed in the refrigerator for an incubation period of 24 hours. At the termination of this period of time, the tubes were centrifuged for 4 minutes at moderate speed. The supernatant was then drawn from each tube by means of a Pasteur pipette with its tip encased in sterilized cotton wool. The titration for the sample series and a control series was then conducted. Both series contained equal volumes of saline. In the sample series titration was carried out with the supernatant, in the control series with the neat sera. To each were added equal volumetric units of 1% suspension in saline of red cells of the appropriate type. The sample and control series were then incubated for 2 hours at room temperature. At the termination of this period smears from each of the tubes were placed on glass slides and interpreted under microscopic examination. Three tests were conducted over three 24-hour intervals.

Results are based upon the presence of agglutination in one or both of the anti-sera or the absence of agglutination in both anti-sera for any given sample. If agglutination occurs in both the Anti-A and Anti-B sera, as a result of the introduction of red cells of appropriate type, the blood group is assumed to be O. Likewise if agglutination is absent from both anti-sera, AB type blood is suggested. Type A blood is marked by the presence of agglutination in the Anti-B sera but absence of agglutination in Anti-A sera. Type B blood is marked by a reversal of this situation.

Alcohol Extraction Test. This technique is devised to reduce the problem of non-specific absorption and thus allow for the correct identification of blood type AB (Gray 1953, 1958). It was applied to the bone samples X and Z noted in Table 10. Five different anti-sera were selected for the test.

In each of two 25 ml. Earlemeyer flasks, which were labelled x and z for the two samples being tested, was deposited 1·0 gm. of ground bone of the appropriate specimen. Both flasks were then filled with 25 ml. of absolute ethyl alcohol (denatured). Each preparation was heated for a period of 2 hours at 78 degrees C. The alcohol extracts, which contained the group substance, were filtered off and placed in sterilized beakers. To the bone residues were next added 15 ml. of absolute ethyl alcohol and each preparation was heated as above. After filtering this second quantity of alcohol extract, it was added to that extract initially collected in the beakers. The two extracts were placed over a steam bath until the lipid material began to come out of solution. The extracts were removed from the heat to redissolve the precipitate. The contents of the beakers were then deposited in sterilized bottles which were tightly stoppered. These extracts are the stock antigens. The antigen suspensions were prepared by first placing 1·0 ml. of each stock antigen into test tubes containing 5·0 ml. of buffered saline. Milky-appearing emulsions resulted. These were used for the determination of the presence of blood group antigens by first adding 0·5 ml. of each antigen suspension to 0·5 ml. of Anti-A and Anti-B sera whose titres had already been established. These were mixed in 10 × 75 mm. tubes and incubated at room temperature for 2 hours. At the end of the incubation period, the tubes were centrifuged for 4 minutes at high speed. Then 0·5 ml. of supernatant was removed from each tube and placed in a sterilized tube by the same technique described for specimens in the Standard Absorption Technique. A titration for both samples and controls was arranged. To equal volumes of saline, placed in all but the first tubes of the panel, were titrated the neat sera with the controls and the supernatant with the sample series. Each tube received equal volumes of a 1% suspension in saline of red cells of appropriate type. Samples and controls were then incubated for two hours at room temperature.

After incubation the contents of each tube were read under the microscope and the results were recorded. This technique was limited to a single test.

Interpretation of these results is based upon the following conditions :

1. The known type A extract suspension should lower the titre of Anti-A by 3 or more tubes.
2. The known type B extract suspension should lower the titre of Anti-B by 3 or more tubes.
3. The known type O extract suspension should not lower the titre of either Anti-A or Anti-B by more than 1 tube.
4. If the test extract suspension lowers the titre of Anti-A by 3 tubes or more then the sample is type A.
5. If the test extract suspension lowers the titre of Anti-B by 3 tubes or more then the sample is type B.
6. If the test extract suspension lowers the titre of both Anti-A and Anti-B by 3 tubes or more then the sample is type AB.
7. If the test extract suspension lowers neither the titre of Anti-A nor Anti-B by more than 1 tube then the sample is type O or else the antigens in the sample have deteriorated to the point where conclusive typing is impossible.

RADIOACTIVITY METHODS OF DATING. Radiocarbon analyses of human bone and charcoal from Bellan Bandi Palassa have yielded results that confirm Deraniyagala's (1943*a* : 112 : 1945) contention that the Balangoda Culture persisted until comparatively recent times and existed for some time side by side with ferrolithic cultures.

Two samples of charcoal were tested by Isotopes Incorporated in 1956. Sample 394K was taken from 2′ 8″ below the surface and 1′ above the limestone bed rock in Square C1. This was the locus of skeletal specimen BP3/15a. The charcoal lay 3′ north of the skull of this specimen. Its dating is 508 ± 150 years B.P. or 1448 A.D. ± 150 years. Sample 394L was taken from 2′ 6″ to 3′ below the surface and almost resting upon the bed rock in Square B1. This was within the vicinity of skeletal specimen BP2/20. Its dating is 2070 ± 200 years B.P. or 114 B.C. ± 200 years (Deraniyagala 1958*a* : 259).

The radioactivity of the bone sample was assessed in the laboratory of the Anthropology Sub-Department, British Museum (Natural History), in 1959. This was a sample of tibia from specimen BP2/21. This skeleton was found in Square C4 some 3′ below the surface and 6″ above the limestone. Oakley's report to Deraniyagala stated :

> " In answer to your previous letter, I can tell you that the radioactivity of the human leg bone from the Ballanbandi Palassa site indicated 0. 6 p.p.m., *e*U308. This is consistent with the specimen being ancient—say, having an antiquity

> measured in millenia rather than in centuries. Chemical analysis shows 1·3% nitrogen which suggests in the circumstances of its occurrence, that the bone is Post-Pleistocene " (Deraniyagala 1960*a* : 97).

In 1962 osseous specimens from the Balangoda series were assayed by Mrs. Elizabeth Gardiner in the same Department. In a personal communication concerning the results of the assay, Oakley reports :

> " A sample of the ribs of skeleton BP3/27–34 (D) was assayed completely (For three hours), and gave the result (calculated as *e*U308 p.p.m.) : 10 ± 2. The remaining Balangoda samples were assayed for half an hour each and gave readings which when averaged amounted to approximately the same figure. As the order of magnitude is low I do not think that anything would be gained by assaying all the samples completely."

Oakley notes that all of the samples proved to have a uranium content that was fairly uniform.

TABLE 10

RESULTS OF THE BIOCHEMICAL ANALYSIS

Chemical Assay :

Skeletal specimen Number	%F	%P_2O_5	Ratio × 100 F : P_2O_5	%Fe	%$CaCO_3$	%N
BP2/21	..	..	..	..	..	1·3
BP3/27–34	0·60	23·1	2·6	2·5	17·1	0·05
BP2/17g	0·38	12·5	3·0	2·8	21·6	0·078
BP2/17	0·32	18·0	1·8	5·0	23·7	0·016
BP2/21	0·58	21·7	2·7	1·5	19·5	..
BP2/25	0·15	7·0	2·0	3·0	10·5	..

Palaeoserology :

Standard Absorption Technique

Test No.	1				2				3			
Anti-Sera Sample	81–02	90–11	B–25	R–58	81–02	90–11	R–25	R–58	81–02	90–11	R–25	R–58
X	O	O	A	O	O	O	O	O	O	O	O	O
Y	O	O	A	O	O	O	A	O	O	O	O	O
Z	A	A	A	?	A	A	A	A	A	A	A	A

Alcohol Extraction Test

Anti-Sera Sample	Gr–02	42–46	51–59
X	A	A	AB
Z	AB	A	AB

Of these five techniques of analysis of the biochemical nature of the osseous material from Bellan Bandi Palassa, four are related to the problems of chemical dating :

the palaeoserological analysis stands apart from these considerations save in so far as the identification of antigens can verify the presence of organic elements in the bone samples. Since the accumulation or depletion of substances in ancient bone is ultimately dependent upon the characteristics of the environment in which it has been deposited, and since these environments may alter due to redisposition of the bone and/or disturbances of the deposit, it is not surprising that the results of the biochemical analysis of these Balangodese specimens exhibit some variations. Not all of the skeletal remains from Bellan Bandi Palassa occurred at the same level. Thus specimen BP3/27–34 rested only 3″ above the limestone bed rock and its contact with the hard crystalline limestone caused the bones to become coated with a yellowish concretion, a very different micro-environment from that of specimen BP3/15a, from which level one of the charcoal specimens was taken for radiocarbon dating.

The presence of nitrogen in bone indicates protein and protein derivatives. Nitrogen quantities of the order of hundredths of 1% have no significance since the method of analysis becomes progressively less reliable when working with lower quantities (Barber 1939, Cook 1960 : 229, Pin 1950). Therefore the value obtained from the sample for specimen BP2/21 is more significant than the values obtained for the other specimens whose nitrogen content was examined. This discrepancy may be due to the fact that cancellous osseous tissue was used in these tests instead of the compact bone which offers more reliable analytic results. Oakley (1949, 1953, 1955) finds that the nitrogen values are reliable as a cross-check to fluorine analysis, particularly since the results from both kinds of tests may show radical differences for a single specimen. But calcite has a sealing effect on bone, and at Bellan Bandi Palassa, where the skeletal specimens lie at different levels above the limestone bed, this phenomenon cannot be excluded from a consideration of the results of tests. Temperature and moisture are other factors influencing the chemical nature of bone, and the evidence for believing that climatic changes have affected particular biotic modifications in the region around Bellan Bandi Palassa is considerable. Because of these factors of alteration and contamination, Oakley (1953 : 52) has the phosphate content of each sample checked and he regards the percentage fluorine/phosphate ratio as the best standard of comparison in fluorine dating. He has found that the average fluorine content of Lower Pleistocene bones is circa 2·0% ; of Mid-Pleistocene bones, circa 1·5% ; and of Upper Pleistocene bones, circa 0·5%. The percentages for the Bellan Bandi Palassa specimens fall within this latter category, a situation confirmed by the radiocarbon data for the site which marks the age of the site as post-Pleistocene.

The development of chromatographic techniques has expanded the data of protein analysis to include not only nitrogenous components but also the amino acids (Abelson 1954, 1955, Ezra & Cook 1957). Bones of a woolly rhinoceros from an Upper Pleistocene deposit of the Lloyds site, London, contained traces of glutamic acid, B-alanine, proline, OH-proline, leucine, valine, glycine, aspartic acid and arginine. (The writer is indebted to Dr. K. P. Oakley and Mr. A. E. Rixon of the British Museum (Natural History) for the notes of this research carried out in 1956. For illustration of the

Lloyds bone chromatogram see Oakley 1963). Those amino acids present in the Balangoda series but absent in this Pleistocene sample are taurine, serine, methionine, ornithine, cystine, glutamine, theonine (?) and tyrosine (?). The presence of different percentages by weight of amino acids for blood group substances may be explained by variations in the preparation of the serological sample and hence bear no relation to immunological specificity (Kabat 1956 : 149–151). However, should certain blood group substances be demonstrated as having characteristic components of amino acids, the findings of palaeoserology would become pertinent to problems of chemical dating. The nature and quantity of protein decomposition products in ancient bone might well be utilized as a method or technique of chemical dating which Cook (1960 : 232) suggests would be superior to the analyses of total organic matter or nitrogen content.

The problem of contaminants cannot be minimized for any of these biochemical tests but their effect, if present, is most serious in the establishment of the nature of the antigen content. It is impossible at present to detect the presence of foreign substances in the sample which would bias the results of analysis, but by running the sample through several tests and subjecting it to different techniques of analysis the researcher is encouraged in verifying a certain percentage of his results. Thus, the behaviour of sample Y in the Standard Absorption Technique cautions reservation of opinion since it may have undergone a non-specific absorption with the Anti-A sera. The Z sample is more reliable, its consistent type A reaction being hindered only at one place in the test due to lysis of the Anti-B serum. Of the four Anti-A sera used, the B sample is somewhat erratic in its behaviour and its unsuitability for testing with these bone samples is suggested. The results of the Alcohol Extraction Test cannot be accepted as being as reliable as the data derived from the initial test for antigen identification. Reactions are all very weak. The presence of type A antigen for sample Z is confirmed by both tests and the Alcohol Extraction Test suggests that this may be linked with the B antigen, thus indicating for specimen Z an AB blood type. The occurrence of the A gene in the Balangodese series is of particular interest since this gene has a very low frequency among the Veddas and its presence in this population in the past has been doubted by some investigators (Wickremasinghe, Ikin & Mourant 1963).

The presence of pottery at the upper portions of the Bellan Bandi Palassa midden and its absence in the lower portions has led Deraniyagala (1958*a* : 258) to conclude that the site had been occupied either continuously or periodically over a period of sufficient duration to allow the inhabitants to pass through both phases of his Balangoda culture. Furthermore he had suggested a correlation of cultural stratigraphy with the physical type of the skeletal specimens found in the site : the robust male specimen BP2/17 appears to him as " Australoid " while the specimens from the upper pottery-bearing levels reveal " Negroid " phenotypic traits. Regardless of what racial features one may perceive in the series, the radiocarbon methods of dating affirm that these specimens were relatively contemporary in time. In the opinion of the present writer it seems improbable that the specimens from Bellan Bandi Palassa constitute a stratigraphical progression of phenotypes representative of earlier and later phases of a pre-metal using culture, nor do the artifacts found in association with the burials suggest a cultural succession : the phenotypic variation which the series displays is what can be expected from normal sexual dimorphism and morphological variation across sexual lines, and the question of cultural sequences at the site cannot be answered without confirming evidence from further archaeological investigation of other Ceylonese sites. If the osseous specimens were not all members of the same community, the dating of the bones by radiocarbon methods indicates that they were not separated by many generations.

III COMPARATIVE ANALYSIS

The Nature of the Comparative Data Used in the Determination of the Biological Affinities of the Balangodese with Other Populations

In compiling the comparative data of Tables 11 and 12 the writer has selected several contemporary and prehistoric populations and individual specimens from the Indian–Southeast Asiatic–Oceanic area. The arrangement of the prehistoric series in the Tables corresponds to their chronological relationship to the modern populations listed. Of these, the writer has examined at first hand the Vedda series and the specimens from Brahmagiri, Adichanallur, Mohenjo-daro, Nal, Langhnaj, Bayana, Sialkot and Niah, and casts of Talgai, Keilor and Wadjak. Comparisons have also been made with the original specimens from such Indian prehistoric sites as Nevasa, Chandoli, Maski, Piklihal, Harappa, Lothal, Ruangarh and Raigir, whose metrical values are not included in Tables 11 and 12. On the basis of this extensive comparative analysis it is the thesis of the writer that of the living populations of southern Asia the Veddas of Ceylon most closely resemble the Balangodese in their physical morphology. It must be emphasized that the fragmentary nature of the Balangodese skeletal remains limits their significance in a purely metrical comparative analysis with larger and more complete osteological specimens. Hence the data of the tables are less helpful than a morphological comparison in affording the reader a clear idea of the phenotypic similarities of the prehistoric inhabitants of Ceylon. The Crown Indices of Table 12 have been calculated with the formula

$$\frac{\text{Bucco-Lingual Diameter}}{\text{Mesio-Distal Diameter}} \times 100.$$

It should also be noted that the series of five specimens from Brahmagiri are regarded as males although another investigator has regarded specimen IE as female (Sarkar 1960).

The Vedda osteological specimens employed in this analysis were examined by the writer from collections from the following institutions : Sub-Department of Anthropology, British Museum (Natural History), London ; Royal College of Surgeons, London ; Anatomical Museum, University College, London ; Museum of Comparative Anatomy, University of Oxford ; Museum of Human Anatomy, University of Cambridge. The comparative study was supplemented by the comprehensive work on the physical anthropology of the Veddas by Hill (1941). In his study of this population Hill makes a distinction between specimens that he regards as " pure Veddahs " and those of " half-breed Veddah, portraying ... certain distinctive Veddah features upon a basically different structure." (Hill 1941 : 107, 124–125). This dichotomy is a subject of discussion elsewhere in this paper, but the terminology that Hill employs is repeated here when comparing Balangodese specimens with the Veddas of his " Average " series and " Selected Average " series. Reference was made as well to Stoudt's (1961) anthropometric survey of living ethnic groups in Ceylon, a study based in part on data collected by the late J. R. de la Haule Marett.

A Comparison with the Veddas

The Calvarium. The Veddas and Balangodese are dolichocranic. Mean indices are 71·24 for Vedda males and 72·72 for Vedda females, with a " Selected Average " of 71·57 for specimens of known Vedda ancestry. The Vedda female has a Cranial Length–Breadth Index slightly greater than that of the male. Hill notes that the discarding of the indices of Vedda specimens of doubtful purity makes little difference in this Index, the average for all Vedda crania being 71·60. The Length–Height Index based on Basion–Bregma Height averages 74·64 for both male and female Veddas, thus placing them at the upper limit of the orthocranic class. However a number of Vedda crania which Hill regards as belonging to pure-blooded individuals have Basion–Bregma Height–Length Indices that place them in the hypsicranic group. When the Vedda series is examined with respect to the Auricular Height–Length Index, the male mean of 61·00 falls within the orthocranic category, but the females are hypsicranic with a mean index of 63·50. Here is a situation that is not paralleled in the Balangoda series where the male is hypsicranic and the female chamaecranic. There is closer agreement between the two populations in terms of the relation of cranial height to cranial breadth since the acrocranic condition which is common to Veddas of both sexes, is also apparent in the Balangodese male. The low Cranial Height–Breadth Index of the Balangodese female stands outside the mean values of 105·5 for Vedda males and 103·9 for Vedda females.

The " Selected Average " of cranial capacities for male and female Veddas are 1250 cc. and 1166 cc. respectively. Although the addition of values for crania of dubious ancestry does not raise these mean values to a marked degree, the values for unmixed Tamils and Sinhalese are significantly higher than those for unmixed Veddas. These low values include within their range the estimated cranial capacity for the Balangoda female BP3/27–34, but the large-headed male, BP2/17, falls well outside the range. A further comparison of cranial size is offered by the measurement of the Maximum Circumference of the vault where the values for the Veddas are close to those of the Balangoda females, but from which again the male BP2/17 stands apart.

Vedda cranial bones, which are uniformly thick and heavy, particularly in their posterior regions, are regarded by Hill as belonging to individuals of doubtful purity and it is these which most closely approximate a condition evident in the Balangodese crania. The latter series lacks the pathological thinning peculiar to the parietals of

Vedda crania of the classic type. Both series exhibit little or no sexual differentiation in cranial thickness.

The Vedda crania observed by the present writer were rhomboid although the crania of males with well developed supraorbital ridges approached a sphenoid cranial conformation. Supraorbital ridges are well developed in both Veddas and Balangodese, and the very pronounced ridges of BP2/17 are occasionally found among the Veddas as well. Confluence of ridges at glabella is present in half of the Vedda series and in both sexes, but among the Balangodese females the brow ridge form is median. A low vertical forehead with flattened parietals and a posteriorly compressed occiput is the most typical Vedda cranial contour, and it is this form which also is characteristic of the Balangodese females. The medium receding forehead of BP2/17 has been observed among Veddas where it is accompanied by some lateral compression of the frontal. The presence of a median boss and frontal eminences are frequent in the crania of both series. The Balangodese females approach that degree of frontal constriction common to Vedda crania, but the frontal of BP2/17 is considerably broader than that of most Vedda males. Supraorbital foramina are prominent in both series.

Slight keeling of the parietal region is both a Vedda and Balangodese trait. Posterior to vertex the vaults of crania from both series undergo a gradual slope to lambda, at which point a sudden change of direction brings the curve vertically downward to the basi-occiput region. The flattening of regions anterior–superior and posterior–inferior to the parietal eminences contributes to the prominence of the bosses in the vaults of both series. Differences appear in the occipital portion of

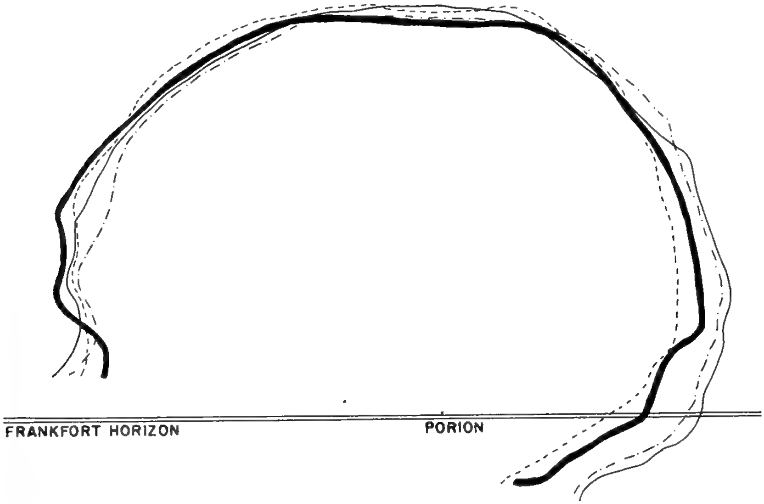

FIG. 5. Left lateral contours of one Balangodese (BP3/27–34 ——), one Vedda (1949.12.7.2 – – –), a compound tracing of eighty-two male Australians (Wagner 1937 ———), a compound tracing of one hundred and twenty-four male New Guineans (Hambly, 1940 – · – · –).

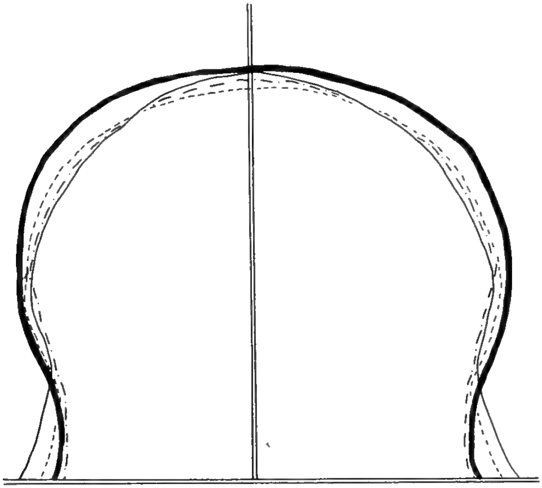

Fig. 6. Frontal contours of one Balangodese (BP3/27–34 ▬▬▬), one Vedda (1949. 12.7.2 – - –), a compound tracing of eighty-two male Australians (Wagner 1937 ————), a compound tracing of one hundred and twenty-four male New Guineans (Hambly, 1940 –·–·–).

the cranial profile. The musculature of the nuchal crests is weakly developed among the Veddas, a condition reflected in the Balangodese females but not in the robust male BP2/17 (Text-figs. 5–6).

The temporal muscles occupy extensive areas of the crania in both populations. The temporal lines rise high along the vault of the Vedda skulls. They are less prominent on the parietals of the Balangodese. The mastoid process is generally small among the Veddas, but several skulls of Hill's series possess large processes like that of BP2/17, and these generally belong to males of dubious ancestry. The tympanic plate is thick in Veddas and Balangodese. The oval form of the Vedda auditory meatus contrasts with the elliptical and round conformations of this structure in the fossil population.

Like the Balangodese, the Vedda cranial vault is characterized by suture patterns of simple design with some slight complexity apparent at peripheral margins. Metopism, which is uncommon in Veddas, is absent in the Balangodese specimens. However the former series exhibits a high frequency of Wormian bones, especially at lambda and pterion. Sutural patterns are complex in this area in Balangodese skulls but Wormian ramifications are absent (Text-fig. 7).

Hill regards the typical Vedda face as euryprosopic for males and hypereuryprosopic for females, the mean index of his " Selected Series " being 84·14. The males average 85·44, the females 79·73. However, for the living individuals that Hill examined, the average Total Facial Index is within the leptoprosopic category, the class to which the Balangoda female BP3/27–34 is also assignable. Concerning this problem he writes : " This feature is evidently very variable among the existing Veddah population. Combining this with the fact that previous writers have

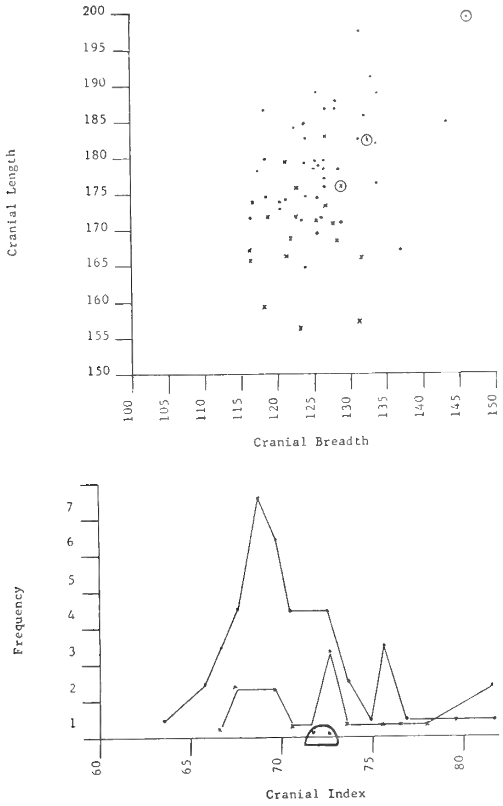

FIG. 7. Scatter diagram and frequency polygon of cranial measurements and indices of three Balangodese (BP2/17, BP2/21, BP3/27–34) and sixty-two Veddas (Hill 1941). Males are represented by a dot (.); females by a cross (×).

placed the Veddahs in the chamaeprosopic class, and also that the index based on osteometry is well within the euryprosopic category . . . it can only be inferred that the results . . . are the effect of recent miscegenation with the leptoprosopic neighboring peoples" (Hill 1941 : 74). The leptene upper face of the same Balangodese female stands in contrast to the euryene value of 49·00 for typical Vedda specimens. Closer agreement of Vedda and Balangodese indices is apparent in the chamaerrine nasal forms of both groups. The average for Veddas of the "Selected Series" is 55·80 and the male and female mean values are 54·24 and 57·30, respectively. The Orbital Index is 74·00 for Vedda males and 73·70 for Vedda females, hence both come within the chamaeconch class, a condition found in the female Balangodese BP3/27–34, but not in the male BP2/17 whose orbits are hypsiconch. The External Palatal Indices are brachystaphaline, but the indices for the Balangodese are considerably higher than the mean index of 96·50 of the Veddas of the

" Selected Series ". The Vedda males have an average External Palatal Index of 97·06, the females are even lower—94·30.

Like the Balangodese, the Vedda face owes its prognathism to the projection of the total maxillary or subnasal region, although prognathism of the latter sort is characteristic of a number of Vedda specimens. Hill finds that alveolar prognathism is more common among the Vedda crania of earlier collections : subnasal prognathism is more often found among recent specimens. The average Vedda Gnathic Index is 96·70 which places it within the orthognathic category, and in the "Selected Series" this index drops to 94·50. Males have a mean index of 95·04, females of 93·37. Facial angles of Vedda crania show that almost all values fall within the prognathous category if von Camper's method is used, but when using Martin's method almost all the faces are orthognathous.

Both Balangodese and Veddas have square or quadrilateral orbits. Further comparisons of the orbit are prohibited by the imperfect condition or the absence of the orbital walls in the fossil specimens. Malars are larger in the latter series, and the temporal process of the zygomatic and the zygomatic arch is less attenuated in Balangodese. The anatomical aberrations that Hill notes as common to the region for Vedda crania—a prominent marginal process, a maxillary-zygomatic notch—are not present in the fossil series. Malar projection is variable for both populations. The nasal aperture is wide, short, and piriform for the two series. The inferior nasal margins are variable in form, the oxycraspedote and orygmocraspedote conditions being represented in equal frequency for both series. The absence of nasal bones in the Balangoda series precludes further comparison of this region. The forms of the glabella of BP2/17 and BP3/27–34 infer a deep nasal notch for these specimens such as is found among the Vedda. The anterior nasal spine is large

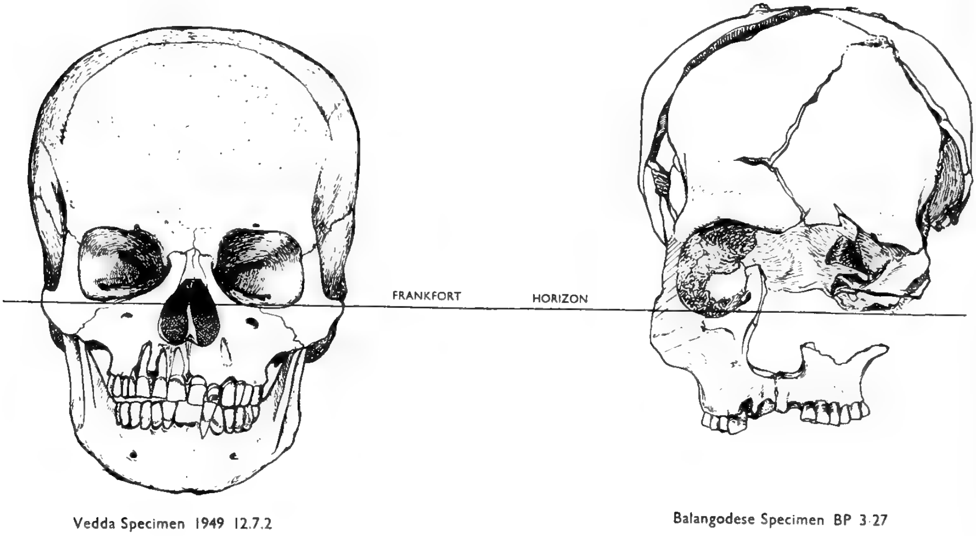

FIG. 8. Dioptrographic drawings. Frontal aspects.

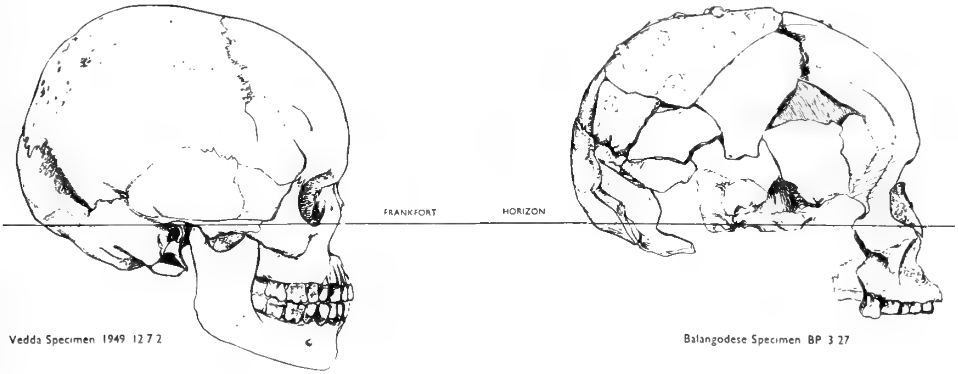

Fig. 9. Dioptrographic drawings. Right lateral aspects.

among the Balangodese, but its size is variable in Vedda crania. It is lacking in those specimens that have orygmocraspedoty. The alveolar borders of the palates of the Balangoda series are more greatly divergent than those of the Vedda series although both series may be described as having the parabolic and elliptical palatal conformation. In size and depth the palates of the fossil series attain the higher values (Text-figs. 8, 9).

The Mandible. The Mandibular Index of the lower jaws of Veddas falls within the dolichostenomandibular category with an average Index of 80·11. This is within the range represented by the fossil series. The mean Fronto-Gonial Index of the Vedda series is 97·11, and the two indices available for the Balangodese fall on either side of this value. The average Zygo-Gonial Index for the Veddas—135·79—is considerably higher than that obtained for the Balangodese, and this reflects the greater bizygomatic diameter of the latter population.

A comparison of the gross sizes of the mandibles in the two series shows close similarity, but those of the Balangodese are marked with greater muscularity and an increase in the thickness of the corpus, particularly in the symphysial region. The chin is prominent among the latter : Veddas have moderately developed mental protuberances. In both series the chins are most commonly of the median type. Genial tubercles are feebly developed in the Vedda mandibles, and not all Balangodese mandibles have prominent genial tubercles, *viz.* BP2/17i and BP3/27–34. The digastric fossae, which are prominent in some Vedda specimens, are variable in development in the fossil series. In both series the corpus tapers posteriorly from the symphysis, thus giving a gracile appearance to this portion of the jaw. The exception to this is the Balangodese male, BP2/17i whose corpus is massive throughout its length. Mental foramina are large for most Vedda specimens, but their size can be matched in only half of the individuals in the Balangoda series. The position of these foramina is the same in both series.

The rami form a wide angle with the corpora in the mandibles of both series. It is broad and short in the Vedda series, and broad and somewhat more elevated in the Balangoda series. In the fossils the gonia are frequently everted, but this is rare among Vedda specimens where the muscular development of the pterygoid attachments are reduced. The sigmoid notch is broader and shallower among Veddas. The condylar neck is reduced in both series, and a mandibular head of small dimensions is the most common condition. As with the Veddas, the linguia of the Balangodese mandibles is reduced in size, although strongly marked in the male BP2/20–41. Alveolar prognathism is most pronounced in the fossil series.

The morphological features that characterize the mandible of the Balangoda series, namely the depth of the corpus, the greater height of the ramus, and the presence of mandibular alveolar prognathism, are traits that Hill finds most frequently represented among Veddas of doubtful purity, i.e., individuals with longer and narrower faces than those of the classic Veddas with their broad chamaeprosopic faces accompanied by short, narrow mandibles. This situation parallels the conditions noted above for the cranium where the Balangodese reflect some morphological features not present in Veddas that Hill regards of pure type.

The Skeleton of the Trunk. Comparisons of the vertebral columns of Veddas and Balangodese reveal striking similarities. The cervical vertebrae are very small in the absolute sense and considering the evidence for regarding the stature of the Balangodese as taller than that of the Veddas, the sizes of their vertebral elements seem disproportionately small. Neural foramina are triangular, and transverse processes are short within both groups. However, the bodies are round rather than cordiform among the Veddas. The atlases in both series are delicate with sinuous posterior arches. The thoracic vertebrae described for the Balangodese fall within the range of normal features common to the Veddas. The lumbar vertebrae of the fossil series are uniquely robust and have a greater mass than the lumbar segments of the recent series. The Balangoda specimen BP2/17 has a Lumbar Index that falls within the koilorachic group. While this index is matched by several Vedda specimens, the average index of the latter is orthorachic. Broad truncated spines are characteristic of the lumbar vertebrae of both series. The instability of the lumbar and sacral regions and of the thoraco-lumbar and lumbo-sacral junctions, which is a characteristic of the Vedda spine cannot be ascertained for the Balangodese due to the paucity of bones from this region.

The ribs of the Balangodese and Vedda specimens have a thickness ranging from 3 mm. to 6 mm. with maximum expansion at the sternal end for males of both series. The first rib has a small head and a tapered neck. Its grooves for the subclavian vessels are apparent. Lower ribs have more massive heads. The degree of individual variation among the Veddas for this part of the thorax cannot be established for the Balangodese, since their ribs and vertebrae are fragmentary and present for only two specimens.

The sternal corpus of BP2/17 approaches the Vedda form in terms of its slight curvature, short and broad dimensions, and its number of segments for sternal rib articulations.

The Skeleton of the Upper Extremity. Except for its large size, the clavicle of BP2/17 closely resembles the clavicles of Vedda specimens, as does also the smaller clavicle of BP3/27–34. Similarities are found in the oval form of the sternal head, the moderate to slight degree of flattening of the acromial head, and a general gracility of the form of the shaft. The clavicle of the female Balangodese specimen differs from the Vedda only with regard to its greater muscularity, and the presence of pronounced grooves for the subclavian vessels. Clavicular curvature is poorly developed in the females of both series.

There is some difference in the scapulae of the two series, that of the male BP2/17 being larger and more robust than the scapulae of the Balangoda female and the majority of other scapulae of the Vedda series. Other differences are noted in the longer and more rectangular form of the acromion process of BP2/17, its shorter and narrower fossa supraspinata, and the greater curvature and length of its corocoid process. In the Vedda series, the acromion is usually triangular in form, the fossa supraspinata tends to be broad, and the corocoid process is short, massive, and flattened from its anterior to posterior aspects. The scapula of the female BP3/27–34 more closely approximates the Vedda norm, as does that of BP2/17, in all other respects than those noted above. There is a pronounced obliquity of the spino-vertebral angle. The superior border lies in the horizontal plane and the supra-scapular notch is absent. This notch is absent in half of the scapulae of the Vedda series. The axillary borders of scapulae in both series show an increased thickening in the direction of the glenoid fossae. The latter structure is broadest at its inferior portion, and its angle to the body of the scapula is slightly elevated and lateral.

The Balangodese and Vedda humeri are alike in their relatively long diaphysial lengths and small extremities. Their shafts are straight, but the sigmoid curvature that Hill notes for his Vedda series is not apparent among the Balangodese. Due to the poor condition of the humeri of the latter group their angle of torsion could not be estimated. Like the humerus of the Veddas, that of the Balangodese shows a prominent bicipital groove. The high incidence of the perforation of the olecranon fossa has been found to occur in only 25·60 per cent of the series examined by Hill and this feature is absent in the Balangodese.

The trait that most strikingly sets apart the Balangodese radius from that of the Vedda is its greater muscular development. The Vedda radius is characterized by an extensive tuberosity, rounded borders, and slender form. Both series, however, present a pronounced hollowing of the volar aspect of the shaft for the reception of the flexor pollicis longus. The styloid process is prominent in both groups, save in the case of BP3/27–34 where its size is reduced. A lateral curvature of the shaft is more common in the Vedda radius; the shafts are straight or, as in the case of the female specimens, curvature is in an anterior–posterior direction. In both series the head is small, and the neck is narrow and elongated. The ulnar notch is well marked and extensive.

The curvature of the ulna is considerably less prominent among Balangodese than among Veddas, and the muscular attachments are more obvious among the former. Where the interosseous space is large for the Balangoda series, it is a result of radial rather than ulnar curvature.

The bones of the hand of the immature specimen BP2/21 show certain features that resemble the Vedda hand. In gross size the carpals and metacarpals lie at the upper limit of the range for the Veddas. The total digital formula for the Vedda hand is III > II > IV > V > I; the metacarpal formula for the Balangodese is II > III > IV > V(?) > I. The metacarpals of both series show curvature in the dorso-ventral plane, but Hill does not regard this as a feature unique among the Veddas, since it is found as well among other Ceylonese groups. The shapes of the carpal bones which are peculiar to the Veddas are also approximated in the hand of the Balangodese, *viz.* the dumbbell conformation of the scaphoid as a result of central narrowness, the cuboidal form of the capitate, and the well-defined ridging of the trapezium.

The Skeleton of the Lower Extremity. While the Vedda femora are platymeric with an average index of 78·50 for males and 80·40 for females, the Balangodese male BP2/17 is stenomeric and the other specimens of the fossil series, both male and female, are eurymeric for this index. With regard to the Pilastric Index, the male BP4/8 comes nearest the Vedda means of 108·80 for males and 106·90 for females. There is a discrepancy in the size of the femora of BP4/8, however. The other Balangodese have a Pilastric Index which is outside the upper range observable for the Veddas. There is close agreement, however, between the two series as regards the Index of Robusticity, that of Vedda males averaging 11·69, and the females averaging 10·80. Osteological features of greatest similarity for the femora of the two series occur more frequently at the extremities of the bone rather than at the mid-shaft region. To the differences of the shaft noted above should be added the greater torsion of the femur among Veddas. Both groups have very thick shafts and a pronounced development of the pilaster with the lips of the linea aspera separated to a marked degree. A short neck, compressed antero-posteriorly, and supporting a spherical head, is common to the proximal ends of the femora of both series. The greater trochanter is prominent and the trochanteric fossa is deep. The lesser trochanter is large and smooth. A third trochanter is absent. The crista hypotrochanterica is of variable development in the femora of both series. The distal end is marked with a broad intercondylar fossa for both Veddas and Balangodese, and a further example of similarity is afforded by the weak development of the adductor tubercle. Hill notes the great backward extent of the medial condyle and the anterior development of the lateral condyle of the Vedda femur. This trait is reminiscent of the orientation of the condyles of the Balangodese femur.

The tibia is mesocnemic for the majority of Vedda and Balangodese specimens, the index for the former series averaging 65·95 for males and 68·70 for females. None of the Balangodese tibias are pathologically affected as are many of the Vedda specimens with consequent distortion of their conformation. Only BP2/17 exhibits anterior–posterior bowing of the shaft to the extent found among the greater number of Vedda tibiae. The lateral prism formed by the transverse section of the Vedda tibia is not observable in the fossil series. Muscularity is moderate for bones of both series. The Balangodese tibia is somewhat more thick and massive. Torsion of the shaft is most prominent among the Veddas.

The fibular fragment of BP4/8 resembles the Vedda form in its straightness and triangular transverse section. However its articular extremities are more prominently developed. In muscularity it is more strongly marked, although the Vedda fibula also exhibits some hollowing for the peroneal and tibialis posticus muscles.

The tali of the two series are very similar in size and muscular development. The area for the fibular malleolus is extensive. However, the neck of the talus is broader among the Balangodese and the forward extension of the superior articular facet that Hill notes as a common feature of the Vedda talus is not apparent among the fossil specimens. The calcaneus is longer and narrower for the Veddas, but the pronounced curvature of the sustentaculum tali brings it nearer to the form found in the older group. The latter have a cuboid bone that approximates that of the Vedda cuboid in its squat form. The articular facets are prominent, but the Vedda cuboid shows greater convexity of the plantar surface.

The Skeleton of the Pelvis. Apart from the greater size of the Balangodese sacrum this bone falls well within the range of variation for other features observable in Vedda sacra. The platyhieric sacrum of BP2/17 can be matched with several Vedda specimens although the average for the series lie between the dolichohieric and sub-platyhieric categories. Closer similarity is seen in the uniform curvature and hyperbasal form of this bone. Four out of the eleven Vedda sacra examined by Hill showed an articulation of three sacral vertebrae with the ilium. The other Vedda sacra have only one or two segments connecting with their ilia. The various sacral aberrations that Hill finds in his Vedda specimens are not present in BP2/17, i.e., incomplete union of sacral vertebrae, failure of closure of the neural arches, and spina fissa of the terminal segments.

The pelvic bones of BP2/17 exhibit a combination of infantile and " paedomorphic " traits which are common for Vedda pelves plus " gerontomorphic " features that are characteristic of specimens of Australian aboriginal populations. Of the traits of the latter sort, BP2/17 shows prominent muscular attachments, a thick and massive ilium, and a size that is at the upper limit of the range of variation for the Vedda pelvic dimensions. Like the more gracile innominates of the Veddas, however, the male BP2/17 shows a sciatic notch with a fairly high angle, pronounced torsion between ilium and ischium and a deep hollowing of the gluteal fossa. The ischium of BP2/17 is narrow and long, but the Vedda form is broader and shorter. The Height–Breadth Index for the Veddas measured by Hill is 80·50 for males and 76·60 for females, indices considerably lower than that obtained by the present writer for the Balangodese. The mesopellic category of the Veddas—95·60 for males and 95·20 for females of Osman Hill's series—also contrasts with the higher index for the Balangoda pelvis. The neural foramina in both groups are cordiform.

THE DENTITION. The mean values for the sizes of molar and premolar teeth of Balangodese and Veddas show that the higher values occur in the former series. Where the Balangodese means are lower—as with the bucco-lingual diameter of the RM$^{\underline{3}}$ and mesio-distal diameters of the RM$^{\underline{2}}$, LPM$^{\underline{1}}$ and RLM$^{\overline{1}}$—the differences are very slight. Only in the latter case are the grinding teeth of both sides of the mouth smaller in size. The Balangodese molars and premolars are larger bucco-lingually than those of the Vedda series, hence their greater Length–Breadth Index. The anterior teeth in the two series show a significant difference from this molar-premolar size relationship. The upper canines of the Balangodese are smaller than those of the Vedda, but the labio-lingual diameter retains its relatively greater size over the mesio-distal length, and the indices are not as low as they are in the Vedda ratios. The mandibular canines reflect this situation. The mesio-distal length is greater for the maxillary and mandibular lateral incisors of the Vedda series, but the labio-lingual diameter shows no difference, save for the $\mathrm{RI}^{\underline{2}}$ which has a higher mean value among the Balangodese. The Length–Breadth Index remains higher for the fossil series, however. Their mean index for the upper central incisors is less than that for the Veddas, due to their smaller labio-lingual diameter. The mesio-distal diameter is larger for the RI^{1} but the same for the $\mathrm{LI}^{\underline{1}}$. The mandibular central incisors cannot be compared due to the inadequate size of the sample. The Balangodese $\mathrm{LI}^{\overline{1}}$ shows the higher mean labio-lingual and mesio-distal values, but the index is below that of the Vedda series.

None of the specimens of the Vedda series exhibits on the occlusal surface of the lower molars the rectangular form, such as that found in BP2/21. However, the maxillary teeth in both series show a low incidence of occlusal rectangularity—a deviation from the common rounded molar form. The triangular premolar form is absent in the maxilla of the fossil series but present among the Veddas. The mandibles of both series have triangular premolars, but the rectangular form predominated in the Balangoda series, the round form in the Vedda. Canines are only triangular in the maxillae of the Veddas but BP2/20–41 has a $\mathrm{RL\underline{C}}$ which is rectangular. This same specimen has a $\mathrm{RL\bar{C}}$ of like pattern. This form is not absent in the Vedda mandibular canines although the common pattern is triangular. Some Vedda males have triangular upper incisors, but the only form found in the fossil series is rectangular. This is the case for upper and lower dentitions.

The Balangodese exhibit a greater variation in cusp pattern than do the Veddas, who offer no examples of molars with 5 or 6 cusps in the maxillary dentition. Cases of tricuspid molars are absent in the mandibles of both series, and 6 cusps are found in this region only among the Balangodese—the $\mathrm{LM}^{\overline{3}}$ of BP3/27–34. This variation in the molar cusp patterns, particularly in the maxilla, is a peculiar feature of the Balangodese dentition. It is further exemplified in the 4-cusp pattern of the $\mathrm{RLPM}^{\underline{2}}$ of BP2/20–41. The buccal cusp(s) of the premolars is consistently the higher in both series. The Veddas offer no cases of Carabelli's cusp nor the presence of other accessory cusps, but both are to be found in the Balangoda series. Crenulation of the third molar appears to be a common feature of both series, although it is found exclusively in the females of the Vedda group. The strict correlation of cusp number and groove pattern which is universal in the latter series does not hold true with the Balangodese. Furthermore, there are no cases of Y4 or +5 groove patterns in the Vedda series, the 4 cusp and 5 cusp patterns relating to the +4 and Y5 groove patterns, respectively. In both series the maxillary cusp pattern for molars is +4.

The greater degree of attrition of the molars and premolars of male specimens, as is the situation in the Vedda series, is not encountered in the fossil series where the degree of wear is more pronounced among females. More of the posterior teeth of the Balangodese exhibit pronounced abrasion than do the corresponding teeth of

TABLE II

COMPARATIVE ANTHROPOMETRIC DATA: THE CRANIAL VAULT

Specimen or group	Frequency by sex	Source of data	Cranial length	Cranial breadth	Cranial index	Basion-Bregmatic height	Basion-bregmatic height-length index	Basion-bregmatic height-breadth index	Auricular-vertex height	Auricular-bregmatic height	Auricular-vertex height-length index	Auricular-vertex height-breadth index	Auricular-bregmatic height-length index	Auricular-bregmatic height-breadth index
Balangodese	BP2/17	..	200 M	147 M	73·5 M	135 M	67·5 M	91·8 M	132 M	127 M	66·0 M	89·6 M	63·5 M	86·5 M
	BP2/21	..	183 F	133 F	72·6 F	..	..	..	..	..	..	..	..	..
	BP3/27–34	..	177 F	130 F	73·4 F	..	..	..	..	..	..	..	..	..
Veddas	44 M	Hill 1941	178 M	126 M	71·2 M	132 M	74·6 M	105·5 F	..	110 M	61·0 M	..	..	..
	18 F		169 F	123 F	72·7 F	128 F	74·6 F	103·9 F	..	108 F	63·5 F	..	..	..
Sinhalese	9 M	Sarasins 1892	183 M	132 M	72·5 M	135 M	73·9 M	..	..	..	..	..	..	..
	4 F		169 F	126 F	74·5 F	127 F	75·1 F	..	..	..	..	..	..	..
Ceylon Tamils	13 M	Sarasins 1892	185 M	131 M	70·8 M	136 M	73·6 M	..	..	..	..	..	..	..
	7 F		179 F	125 F	70·2 F	129 F	72·1 F	..	..	..	..	..	..	..
Mundas	5 M	Basu 1932–1933	178 M	128 M	72·0 M	130 M	72·9 M	101·3 M	..	..	..	..	..	..
	2 F		167 F	117 F	70·3 F	129 F	77·2 F	110·0 F	..	..	..	..	..	..
Oreans	4 F	Basu 1933–1934	182 M	130 M	71·4 M	130 M	71·0 M	99·8 M	..	..	..	..	..	..
Male	1 M	Sarkar 1954	167 M	121 M	72·4 M	..	..	..	..	107 M	..	..	..	..
	1 F		157 F	125 F	79·6 F	118 F	75·1 F	94·4 F	..	105 F	..	..	..	..
Andamanese	23 M	Sullivan 1921	164 M	136 M	83·4 M	130 M	..	95·7 M	..	..	..	..	..	..
	18 F		160 F	131 F	81·0 F	124 F	..	94·2 F	..	..	..	..	..	..
Papuans	124 M	Hambly 1940	177 M	131 M	74·0 M	131 M	74·3 M	99·6 M	..	..	..	..	..	..
	70 F		170 F	126 F	74·3 F	128 F	75·4 F	98·8 F	..	..	..	..	..	..
Australians	162 M	Morant 1927	187 M	132 M	70·8 M	133 M	71·8 M	..	115 M	113 M	..	..	..	..
	75 F		175 F	127 F	72·2 F	125 F	71·6 F	..	110 F	108 F	..	..	..	..
Tasmanians	60 M	Morant 1927	182 M	136 M	74·2 M	130 M	71·3 M	..	109 M	108 M	..	..	..	..
	36 F		174 F	132 F	75·1 F	125 F	71·6 F	..	..	..	..	..	..	..
Tirukketiswaram	1 F	Chanmugam and Jayawaradena 1954	184 F	136 F	74·0 F	131 F	71·4 F	96·4 F	124 F	..	..	..	..	..
Brahmagiri	5 M	Sarkar 1960	187 M	144 M	77·1 M	138 M	74·8 M	94·5 M	..	112 M	..	..	59·9 M	78·0 M
Adichanallur 1	1 M	Zuckerman 1930	183 M	124 M	67·8 M	..	69·4 M	103·2 M	..	..	61·2 M	98·2 M	..	..
Prehistoric	64 M	Black 1928	180 M	138 M	76·0 M	137 M	75·9 M	99·2 M	116 M	..	64·1 M	..	..	..
Chinese	20 F		175 F	134 F	77·8 F	130 F	76·3 F	98·1 F	111 F	..	65·6 F	..	..	..
Mohenjo-daro	3 M	Sewell & Guha 1931*a*	197 M	130 M	66·0 M	139 M	70·6 M	107·2 M	112 M	..	..	..	62·0 M	..
Nal	1 M	Sewell & Guha 1929	188 M	132 M	70·0 M	146 M	77·4 M	110·6 M	120 M	..	63·6 M	90·9 M	..	..
Makran B	1 M	Sewell & Guha 1931*b*	..	..	..	119 M	..	..	..	..	..	..	..	..
Sampung	1 M(?)	Mijsberg 1932	170 M	133 M	78·2 M	..	..	..	117 M	..	..	..	68·8 M	81·5 M
Langhnaj	3 M	Karve & Kurulkar 1945	197 M	136 M	69·3 M	..	..	..	119 M	..	60·4 M	87·5 M	..	..
Bayana	1 M	Keith 1919	178 M	127 M	71·3 M	131 M	73·6 M	103·1 M	108 M	..	60·6 M	85·0 M	..	..
Sialkot	1 M	Keith 1919	180 M	128 M	71·1 M	140 M	77·7 M	109·3	119 M	..	66·1 M	92·9 M	..	..
Talgai	1 M	Smith 1918	192 M	141 M	73·4 M	..	..	..	105 M	..	54·7 M	..	..	..
Keilor	1 M	Wunderly 1943	197 M	143 M	72·6 M	143 M	72·6 M	100·0 M	120 M	..	60·9 M	83·9 M	..	..
Niah	1 M	Brothwell 1960	180 M	140 M	77·8 M	128 M	..	112·0 M	..	..	..	..	..	..
Wadjak	1 M	Dubois 1922	200 M	145 M	72·5 M	140 M	70·1 M	96·5 M	..	..	59·0 M	..	..	..

TABLE II (*continued*)

COMPARATIVE ANTHROPOMETRIC DATA: THE PALATE AND MANDIBLE

		External palate length	External palate breadth	Palate index	Condylo-Symphysial length	Bicondylar breadth	Symphysial diameter	Bigonial diameter	Maximum breadth of the ascending Ramus	Minimum breadth of the ascending Ramus	Mean angle of the Ramus-Corpus
Balangodese	BP2/17	61 M	69 M	113·1 M	..	..	..	..	..	..	..
	BP2/17i	..	..	..	106 M	118 M	28 M	96 M	..	..	118 M
	BP2/20	70 F	..	..	79 M	115 M	26 M	110 M	..	..	123 M
	BP1/6	..	..	..	..	..	31 F	..	..	30 F	..
	BP2/21	62 F	65 F	104·8 F	99 F	105 F	31 F	99 F	36 F	31 F	116 F
	BP3/27–34	53 F	63 F	118·8 F	93 F	112 F	28 F	101 F	41 F	31 F	133 F
Veddas	..	50 M	44 M	97·0 M	104 M	111 M	27 M	89 M	33 M	30 M	119 M
		46 F	42 F	94·3 F	98 F	99 F	26 F	83 F	33 F	26 F	118 F
Sinhalese	..	56 M	61 M	108·2 M	..	116 M	..	97 M	..	..	..
Ceylon Tamils	..	62 M	55 M	88·7 M	..	..	..	..	..	..	..
Mundas	..	49 M	41 M	83·6 M	..	112 M	31 M	89 M	42 M	32 M	120 M
		49 F	37 F	75·5 F		112 F	31 F				
Oreans	..	55 M	40 M	67·1 M	..	114 M	29 M	94 M	42 M	29 M	113 M
Male	..	..	35 F	..	..	116 F	27 F	92 F	..	27 F	132 F
Andamanese	..	..	..	..	..	..	26 M	91 M	..	..	..
							26 F	83 F			

TABLE II (*continued*)

COMPARATIVE ANTHROPOMETRIC DATA: THE FACE

	Minimum frontal diameter	Bizygomatic diameter	Upper facial height	Upper facial index	Total facial height	Total facial index	Nasal height	Nasal breadth	Nasal index	Orbital height	Orbital breadth	Orbital Index
Balangodese												
BP2/17	117 M	..	..	..	..	..	..	..	..	37 M	41 M	90·2 M
BP4/8	..	..	..	..	..	..	..	23 M	..	..	..	..
BP2/21	110 F	121 F	..	..	..	..	..	..	..	36 F	..	..
BP2/25	..	..	60 F	..	..	..	..	..	..	..	..	..
BP3/27–34	91 F	110 F	64 F	58·1 F	101 F	91·8 F	44 F	23 F	52·2 F	40 F	30 F	75·0 F
Veddas	91 M	121 M	60 M	49·0 M	105 M	85·4 M	44 M	24 M	54·2 M	32 M	38 M	74·0 M
	88 F	116 F	56 F	49·1 F	90 F	79·7 F	41 F	22 F	57·3 F	31 F	36 F	73·7 F
Sinhalese	94 M	126 M	67 M	53·2 M	114 M	89·7 M	49 M	24 M	50·6 M	31 M	37 M	83·6 M
		114 F	60 F							32 F	36 F	89·1 F
Ceylon Tamils	93 M	125 M	65 M	52·2 M	111 M	88·2 M	47 M	25 M	53·7 M	32 M	38 M	86·7 M
		118 F	65 F	54·0 F						32 F	36 F	86·7 F
Mundas	90 M	125 M	61 M	48·9 M	108 M	85·7 M	47 M	24 M	52·3 M	31 M	38 M	82·0 M
	88 F	116 F	56 F	48·2 F	99 F	85·3 F	42 F	25 F	59·5 F	30 F	35 F	85·7 F
Oreans	91 M	126 M	61 M	48·6 M	119 M	92·9 M	46 M	25 M	54·7 M	31 M	37 M	85·1 M
Male	91 M	..	..	..	..	..	..	..	..	..	..	..
	91 F	..	..	52·0 F	..	..	41 F	25 F	60·9 F	31 F	34 F	97·1 F
Andamanese	92 M	124 M	61 M	..	99 M	..	45 M	23 M	51·0 M	32 M	36 M	89·0 M
	89 F	117 F	56 F	..	92 F	..	43 F	22 F	52·0 F	31 F	35 F	89·1 F
Papuans	95 M	128 M	66 M	69·1 M	..	..	49 M	25 M	51·7 M	33 M	39 M	86·3 M
	90 F	119 F	63 F	69·3 F	..	..	46 F	24 F	52·6 F	33 F	38 F	84·9 F
Australians	96 M	133 M	66 M	50·2 M	..	..	49 M	26 M	54·6 M	33 M	40 M	78·9 M
	91 F	122 F	62 F	51·1 F	..	..	45 F	25 F	55·7 F	32 F	38 F	78·9 F
Tasmanians	94 M	131 M	62 M	49·6 M	..	..	47 M	27 M	29·1 M	31 M	38 M	..
	90 F	122 F	59 F	49·6 F	..	..	44 F	26 F	59·0 F	..	..	81·5 F
Tirukketiswaram	95 F	122 F	..	..	114 M	93·4 F	48 F	24 F	50·0 F	33 F	40 F	82·7 F
Brahmagiri	94 M	89 M	59 M	57·3 M	..	..	48 M	25 M	58·8 M	33 M	42 M	73·3 M

TABLE II (*continued*)

COMPARATIVE ANTHROPOMETRIC DATA: THE FACE

	Minimum frontal diameter	Bizygomatic diameter	Upper facial height	Upper facial index	Total facial height	Total facial index	Nasal height	Nasal breadth	Nasal index	Orbital height	Orbital breadth	Orbital index
Adichanallur 1	90 M	128 M	70 M	54·6 M	..	..	50 M	27 M	54·0 M	35 M	40 M	87·5 M
Prehistoric	91 M	132 M	75 M	56·0 M	120 M	90·6 M	54 M	25 M	47·6 M	33 M	44 M	76·1 M
Chinese	87 F	125 F	70 F	56·0 F	114 F	92·1 F	51 F	25 F	46·4 F	33 F	43 F	82·0 F
Mohenjo-daro	95 M	127 M	..	53·9 M	..	88·9 M	46 M	22 M	51·0 M	31 M	37 M	84·4 M
Nal	93 M	120 M	72 M	60·0 M	..	..	49 M	23 M	49·9 M	33 M	40 M	82·5 M
Makran B	..	116 M	81 M	70·3 M	130 M	97·4 M	54 M	23 M	43·5 M	..	..	..
Sampung	91 M	134 M	45 M	61·0 M	..	..	45 M	25 M	56·7 M	31 M	43 M	72·1 M
Langhnaj	105 M	118 M	..	..	..	..	..	..	..	..	..	..
Bayana	90 M	136 M	..	..	..	..	..	..	..	..	..	..
Sialkot	98 M	..	..	..	..	..	..	..	..	..	..	..
Talgai	99 M	128 M	65 M	..	..	..	..	25 M	61·6 M	32 M	40 M	81·2 M
Keilor	101 M	136 M	74 M	54·4 M	..	..	52 M	27 M	51·9 M	30 M	39·5 M	76·0 M
Niah	98 M	..	55 M	..	..	..	42 M	28 M	66·3 M	..	..	..
Wadjak	99 M	140 M	73 M	52·1 M	..	..	50 M	30 M	60·0 M	33 M	42 M	78·6 M

TABLE II (*continued*)

COMPARATIVE ANTHROPOMETRIC DATA: THE PALATE AND MANDIBLE

	External palate length	External palate breadth	Palate index	Condylo-symphysial length	Bicondylar breadth	Symphysial height	Bigonial diameter	Maximum breadth of the ascending Ramut	Minimum breadth of the ascending Ramus	Mean angle of the Ramus Corpus
Papuans	53 M	40 M	75·2 M	. .	. .	. .	. .	. .	. .	. .
Australians	50 M	41 M	81·8 M	. .	. .	. .	. .	. .	. .	. .
	50 F	39 F	77·9 F	. .	. .	. .	. .	. .	. .	. .
Brahmagiri	. .	44 M	. .	. .	. .	. .	. .	. .	. .	. .
Tirukketiswaram	. .	. .	. .	. .	110 F	23 F	86 F	. .	28 F	. .
Adichanallur I	53 M	65 M	122·6 M	. .	. .	. .	. .	. .	. .	. .
Prehistoric Chinese	46 M	50 M	95·2 M	. .	. .	. .	. .	. .	. .	. .
	45 F	49 F	92·0 F							
Mohenjo-daro	53 M	46 M	89·3 M	. .	121 M	. .	. .	. .	. .	. .
					115 F					
Nal	. .	. .	79·2 M	. .	. .	. .	. .	. .	. .	. .
Makran B	50 M	42 M	84·0 M	. .	108 M	. .	95·5 M	. .	. .	. .
Talgai	62 M	42 M	67·7 M	. .	. .	. .	. .	. .	. .	. .
Keilor	56 M	47 M	83·6 M	. .	. .	. .	. .	. .	. .	. .
Niah	47 M	37 M	78·9 M	. .	. .	. .	. .	. .	. .	. .

the Vedda series. The condition of the canines is similar in both groups, the lower canines being the more heavily worn. There are no incisor teeth in the Balangoda series whose abrasion might be described as "slight" or "sub-medium" as is the case for the Veddas. The condition of moderate to pronounced wear is the norm for this fossil series. Only among Vedda females do the lower molars appear more heavily worn: among the Balangodese the more severe forms of mandibular molar abrasion are represented by the males. The Vedda male specimens show greater maxillary molar abrasion, but for the Balangodese this sort of sexual differentiation does not exist. Both groups, however, show greater wear of the upper incisors among the males. The assymetrical wear pattern observable in the right and left sides of the dentitions of certain Vedda specimens is not apparent in the fossil series.

The occurrence of shovel-shaped incisors, while present only in the dentitions of the females of the Balangoda series, is found in both sexes of the Veddas. Furthermore the development of this feature is considerably more prominent among the Veddas. This trait appears in the lower dentition of a single Balangodese female—BP2/21. Lingual tubercles are absent from the anterior teeth of males of both series. Among females their presence may or may not be coincident with shovel-shaping.

With respect to dental anomalies the Balangodese and Veddas exhibit some striking differences. Caries and evidence of abscess are absent in the former but not infrequent in the latter population. The frequency of ante-mortem tooth loss is high for Veddas, negligible in the fossil series. Both populations show cases of supernumerary teeth. Among the Balangodese these are found in the molar portions of both jaws and for the Veddas there is a single case of a supernumerary tooth in

TABLE 12

COMPARATIVE ANTHROPOMETRIC DATA: THE MAXILLARY MOLAR DENTITION

			M^1			M^2			M^3		
			MD	BL	I	MD	BL	I	MD	BL	I
Balangodese	BP2/17	..	10	12	114·2	10·5	12	114·2	10	11·5	115·0
	BP2/20	..	10	11	110·0	8·5	12	141·1	..	..	..
	BP4/8	..	10	11	110·0	9	11	122·2	9	11·5	127·7
	BP1/6	..	10·5	12	114·2	10	12	120·0	9·5	11·5	121·0
	BP2/21	..	11	12	109·1	10	13	130·0	8·5	13	151·9
	BP3/27	..	9	11	122·2	10	10·5	105·0	..	..	..
Veddas	..	..	8·5	12	150·0	10	10·6	107·4	10	10·9	109·4
Mundas	..	..	9·6	10·2	106·2	8·5	10·2	120·5	..	..	..
Oreans	..	..	9·2	10·7	116·2	8·7	10·7	122·8	..	..	..
Male	..	..	10	10	100·0	8	10	125·0	..	..	..
Australians	..	..	11·4	12·8	105·2	10·9	13·1	120·1	10	12·3	123·0
Sampung	..	..	11·2	12·8	114·2	10·9	12·8	117·4	10	12·4	124·0
Gua Cha	..	Brothwell 1960	10·3	12·1	117·4	10·2	12·2	109·6	9·3	12·0	119·0
Talgai	..	Campbell 1925	12·6	13·1	103·9	11·3	13·3	117·6	..	..	..
Keilor	..	Adam 1943	11	13·2	120·0	9·9	13	131·3	9·7	12	123·7
Niah	..	..	10·2	12·3	120·5	10·7	13	121·4	11·5	12·4	107·8

the mandibular incisive region. Suppression of teeth is not a feature in either series. Crowding is found only in the third mandibular molars in the prehistoric group. Crowding is not observable among the Veddas who show, however, a high incidence of maladjustment for other parts of the dentition.

The first molar is more commonly the larger in the posterior dental rows of both series, but the presence of the third molar as the one of greater size is found more frequently in the earlier series, particularly in the mandibles. There are no cases of the first molar being the larger in the lower jaws of the Balangoda series, although the Vedda series affords several such cases. Where the third molars are absent, the second molar is larger than the first.

The overbite type of occlusion, which is common for jaws of the Vedda series, appears to have been present also among the Balangodese, although only BP2/25 and BP3/27–34 afford evidence of this.

IV DISCUSSION

From the anthropometric and comparative analyses of the human remains from Bellan Bandi Palassa originate certain problems of interpretation which require comment. Regarding the question of the phenotypic affinities of the Balangodese, Deraniyagala has entertained several views. His earliest opinion, conceived at a time when the only prehistoric Ceylonese hominid specimen was the one from the site of Batadomba lena, was that the Veddas were a composite race of several different population elements from India which had introduced the Neolithic culture to the Island. " The tendency of the Veddas to throw back to two physical types differing from other races in Ceylon ... " suggested this hypothesis (Anonymous 1941 : 354). Later he remarked that " ... the supposedly autochthonous Vaddha of Ceylon possibly carries some proportion of the blood of Balangoda man ... " (Deraniyagala 1943*a* : 112), but following the discovery of the specimens from the sites of Ravan alla and Telulla he wrote,

> " This race may be termed ' Proto-Vaddoid '. The so-called Vaddahs who do not differ in culture, religion, and language from the forest villagers can only be regarded as hybrids between this extinct autochthonous Stone Age race and the more modern metal using ones of Ceylon. Supporting this view is the fact that the so-called Vaddahs display a variety of physical types that have puzzled the anthropologists who attempted to study them under the impression that they were a distinct race " (Deraniyagala 1955*a* : 40).

As to the Sinhalese he conjectures,

> " The blood of *Homo sapiens balangodensis* however exists in almost equal intensity in the colonies of the so-called Vaddahs of today, and among the Sinhalese so that in most cases it would be impossible to distinguish a so-called Vaddah from a Sinhalese if both were clothed alike and placed in the same village ... the only recognizable autochthonous race in Ceylon is the extinct one in a lithic culture phase ... " (Deraniyagala 1955*b* : 301–302).

Since the appearance of the fossils from Bellan Bandi Palassa, he has insisted that the Balangodese show a combination of Neanderthaloid and Australoid traits that he calls " Proto-Australoid ", plus a Negroid element added at a later time (Deraniyagala 1957*a* : 3, 4). He suggests that the Balangodese replaced the people of the " Ratnapura " culture who were the true autochthones of Ceylon and that the Balangodese continued to practice their distinctive culture until the fifth century A.D. The Veddas are, he concludes, " a degenerate mixed population " of Balangodese and Sinhalese racial elements (Deraniyagala 1958*a* : 258, 1960*a* : 96, 108).

The only other published discussion of the racial affinities of the Balangodese known to the present writer is Coon's (1962 : 424–425). This author agrees with Deraniyagala that there is a Negroid element in the series, but believes that the dominant strain is " Caucasoid " rather than " Australoid " ; although he hastens to add that the presence of some " Australoid " features should not be surprising considering the location of the Island of Ceylon just south of a " Caucasoid–Australoid zone of contact ". He appears to base this opinion upon the presence of reduced frontal brow ridges, a sharply pointed chin, the lack of a prominent nuchal crest and what he regards as a narrow and prominent nasal structure which are represented in the single specimen now on loan at the American Museum of Natural History in New York (Specimen T–24–B or BP3/15b). Although Dr. Coon saw six of the Balangodese specimens in Ceylon in 1957, these had not yet been cleaned, repaired or described. While the present writer, basing his analysis upon the restored specimens, agrees that Balangoda Man did not differ subspecifically from the living Veddas, as Coon states, the complete series supports an interpretation that must take into consideration the non-Caucasoid phenotypic traits of the Balangodese. Since Coon regards the living Veddas as " Caucasoids " along with their Sinhalese neighbours, it is not surprising that he has emphasized the racial criteria of this phenotype in his interpretation of the Balangodese population.

Emerging from this very general comparative analysis of the Balangoda phenotype with the phenotypes of other populations and individual specimens, both prehistoric and contemporary, are two major considerations : (1) the high frequency of similar morphological traits shared by the Balangodese and the Veddas which suggests a positive genetic affinity between them ; (2) the number of unique morphological traits that characterize the Balangodese which are among those traits recognized by various students of the Veddas as the phenotypic hallmarks of half-breeds or " Vedda sub-types ". Hill (1941 : 134) lists the main effects of miscegenation in the Vedda population as the tendency to increase of the cranial capacity above 1,300 cc., an increase in the relative height and/or breadth of the cranial vault with a consequent lessening of the steepness of the lateral walls and the formation of reduced temporal fossae, an elongation of the face, especially in the increased depth of the mandible, an absence of prognathism, a constriction of the orbits and rounding off of the outlet of the orbital fossae, a narrowing of the spheno-maxillary fissure, a reduction in the extent of the frontal bone on the inner wall of the orbit, and the presence of leptorrhiny which is accompanied by longer nasal bones, an elevated nasion and an oxycraspedote apertura pyriformis. In the majority of cases Hill can confirm the mixed ancestry of certain Vedda crania by facts relating to their history. Indeed the proportion of these atypical crania is greatest for those collected since 1886. However, Hill is cautious in assigning to these crania on the basis of his observations alone any traits that would identify the non-Vedda phenotype per se, i.e., absolute traits indicative of admixture from Sinhalese, Tamils, Malays, etc. Nor does he regard *all* crania well outside the modal values for the Vedda phenotype as specimens which are non-Vedda in pedigree. Rather, he notes the presence of a third type of cranium which is less typical than his " classic Vedda " type but which he cannot place with the " half-breed Veddas ". He suggests that these individuals may either be the result of remote miscegenation followed by a later addition of Vedda genes from unadulterated gene pools, or else representatives from within the range of variation of pure Veddas. The skulls of the second type, he notes, exhibit a number of traits described as " primitive, even simian " (Hill 1941 : 124, 125, 134).

This is the most recent of several schemes to account for physical subtypes among the Veddas. That of von Eickstedt (1927*a*) allows for five types : (1) the " Veddoid " which corresponds to the conventional " pure Vedda " type living the old way of life ; (2) the " Singhalesoid " or acculturated Vedda living in villages ; (3) the " Mongoloid " type which shows admixture with Malays ; (4) the " pseudo-Australoid " whose criterion is a heavier facial beard than that of the Veddoid type ; (5) the Coast Vedda who has become mixed with Tamils. Two or three subtypes were mentioned by Topinard (1885) after an examination of twelve Vedda crania at the Royal College of Surgeons. Hocart (1931 : 5) suggests that there is an element in Ceylon's population that has not as yet been identified, and Raghaven (1953 : 51), seeing Mediterranean and Australoid elements at opposite ends of the range of variation of Vedda morphology, finds a third type. This he claims is shorter in stature than the Australoid and Mediterranean and has been called Negritoid.

This observation that certain physical features found in the Balangodese are among those features that anthropologists have held to be the criteria of Vedda crosses or sub-types does not weaken the claim that considerable miscegenation of the Veddas with the Sinhalese, Tamil and other ethnic groups of Ceylon has transpired : rather, it attempts to explain how those physical features which cannot be attributed to the modern non-Vedda populations happen to be manifested in certain proportions among the Veddas of the present day. That the presence of relatively compressed temporal fossae and the absence of total facial prognathism in Vedda populations are related to their recent genetic crossings cannot be doubted. But other features—leptoprosopy, hypsicrany, greater thickness of the cranial bones, prominent mastoid development, the peculiar morphology of the mandible—are examples of physical features shared by both the Balangodese and the Veddas. On the basis of the Balangoda specimen T–24–B the presence of leptorrhiny in the Balangodese gene pool cannot be excluded, although specimen BP4/8 indicates that platyrrhiny was also a feature of the group. In addition to these traits which have been selected as evidence of Vedda miscegenation or penetrance of archaic sub-types are a number of others which the Veddas share with the Balangodese but which have a very low frequency among any of the Ceylonese populations today. The most striking of these are the similarities in cranial conformation, prominence of supra-orbital tori, the depth of the nasal notch, platyrrhiny, chaemaeconchy and certain similarities of the post-cranial skeleton. Of those physical traits that distinguish Balangodese from Veddas as well as from other Ceylonese, the majority appear in the post-cranial skeleton. Apart from their greater lengths, the long bones are more robust and lack the bowing and torsion that characterizes those of the Veddas. Some cranial distinctions are reflected in their greater palate dimensions, pronounced mandibular muscularity and a dentition in which the molars are larger in size and exhibit cusp patterns of a more complex development. These would appear to be physical characteristics that were never manifested in the Vedda phenotype. But while the Balangodese may share a similar genetic background with the Veddas, they are " pre-Vedda " primarily in the chronological sense of that term. Genetically both Balangodese and Veddas appear to have been recipients of a common gene pool in the past. Affinities with other phenotypic groups, living and prehistoric, cannot be questioned, as the comparative Tables are able to illustrate to a certain degree. But of all the populations with which the Balangodese were compared by the present describer, none approached them in number and significance of morphological similarities to the degree represented by the Veddas of the historic period of Ceylon.

Historically the Veddas have been treated as though they were a homogeneous racial or sub-racial entity which the physical anthropologist could clearly distinguish from other ethnic groups living in Ceylon. However a little investigation into the problem of how the Veddas have been biologically and culturally defined indicates that this subject has been the focus of considerable debate, as attested by the fact that certain writers have declared the Veddas to be extinct while their contemporaries have estimated that they number in the thousands. It is suggested here that the matter of how the concept of the Veddas as a distinctive phenotypic pattern within Ceylon came to be is deserving of some careful research in the light of the new osteological evidence from Bellan Bandi Palassa. Conceivably such a programme of research could be approached along three avenues of investigation : (1) the problem of how the term " Veddas " has been employed and the determination of what this means when applied to the population as a whole as well as to individuals within the population so defined, (2) the problem of how the Veddas have been described in scientific and popular literature and in oral traditions, (3) the analysis of the various interpretations that have been made by those writers concerned with the Veddas when applying their data to the wider fields of human evolution and cultural behaviour.

Regarding the first problem, it must be understood that the concept of the Veddas as a relict population with ancient indigenous roots in Ceylon has been a basic assumption behind all definitions of their culture and phenotype. For the Sinhalese, Tamils, Malays, Chinese, Moormen, Europeans and other ethnic groups of the Island there are historical accounts of their colonization, but for the Veddas (and Balangodese) there is no historical documentation of their longer habitation here. Their past must be reconstructed from prehistoric archaeology, native Sinhalese and Tamil chronicles, and anthropometric data. The problem is further complicated by the fact that the term Vedda has become defined not only as a distinct physical type but on the basis of sociological criteria as well. By the close of the 19th Century three concepts regarding the physical morphology of the Veddas had been put forward (1) the Veddas constituted a single homogeneous racial population morphologically distinct from the macro-population of Ceylon ; (2) the Veddas were racially heterogeneous save for " true ", i e., " pure Veddas ", who followed a primitive hunting-gathering economy ; (3) the " true Veddas ", whatever their economic status, were definable in terms of one or more osteological specimens proclaimed as typical of the Vedda phenotype. An additional concept has been offered by Hill (1945 : 202–203) who considers the geographical area rather than the degree of acculturation to be the vital factor in the recognition of a physical type definable as Vedda.

In scientific and popular descriptions of the Vedda phenotype, selection has been the major stumbling block of physical anthropologists. The number of osteological specimens collected from Ceylon since 1827 and bearing the name " Vedda " on their labels is impressive and exceeds in size the series accessible for many other Asiatic tribal groups of higher population frequency, and the amount of anthropometric data pertaining to both osseous and living Vedda specimens is not inconsiderable. Nevertheless this abundance of data has not deceived the more perceptive students of the Veddas who have troubled themselves to investigate the histories of particular so-called Vedda specimens and Vedda communities. The history of the scientific investigation of Ceylon's aboriginal population has yet to be written, but a cursory glance at the published data indicates that evidence gleaned from small samples often has been considered applicable to the Vedda population as a whole. In most cases the fact that the specimens were from Vedda populations at all is questionable, for the majority of collectors obtained them through Sinhalese and Tamil contacts by offering to pay the latter for every skull they could procure, leaving it up to the contacts to decide what was or was not a Vedda. The care taken by the Sarasins and Hill to get their osseous specimens from Vedda cave sites and cemeteries, personally excavated, is a commendable but infrequent condition in the history of Vedda osteological collections. Furthermore, even those specimens which most experts would recognize as Veddas were taken from a fairly circumscribed sector of the eastern portion of the Island, although historical accounts make it clear that in the past the Veddas were more widespread if not ubiquitous.

Scientific research on the Veddas, which may be said to have commenced in the early decades of the last century, has never been completely independent of the notions contained in fantastic traveller's accounts or of the oral and written traditions concerning this population. Even in the rigour of the determination to select those Vedda specimens, osseous or living, which are " typical ", scientific workers have repeatedly emphasized the importance of certain phenotypic traits and thus introduced additional selective factors into the interpretation of What is a Vedda? Of these notions of the Vedda phenotype, the most common is that it is infantile and/or anthropoidal and hence representative of a very primitive and even atavistic kind of humanity. Some writers have barely accorded the Veddas human status. The selection of certain Vedda crania as prototypes, even though it was an attempt to define with clarity the concept of the Vedda phenotype, has tended to obscure the factor of normal variability of this population. The ghost of this tradition lingers in the works of those researchers who, even in the manipulation of large series of Vedda specimens, have not been emancipated from the employment of such terms as " typical Veddas ", " pure Veddas " or " classic Veddas " in their writings. Such expressions may be useful when denoting specimens for which no admixture with non-Vedda phenotypes is suspected, but they are misleading when the total Vedda phenotype is the subject of consideration. Such terms are meaningless when the physical anthropologist attempts to understand the phylogeny of the Veddas since the gene pool of any population is never static. In Ceylon population shifts have been especially encouraged through the operation of frequent genetic intercourse between groups as well as by the dynamics of genetic drift and natural selection in local areas of the Island.

An examination of the archaeological complex at Bellan Bandi Palassa forces the anthropologist to ask these questions : (1) How are the cultural artifacts found in association with the Balangoda skeletal series related to the prehistoric picture of Ceylon and the Indian mainland and to southern Asia as a whole? (2) What affinities, if any, can be demonstrated between the cultures of the Balangodese and the historic Veddas? These problems of the archaeological significance of the cultural assemblage at Bellan Bandi Palassa are complementary to the problems of the physical anthropology of the human remains. In comparing certain elements of the Balangoda culture with that of the Veddas, attention is directed to a paper by Allchin (1959). In summarizing the evidence of the prehistoric cultures of Ceylon, Allchin has pointed out striking similarities between certain of its elements and particular cultural traits of the Veddas. The present writer, although restricting himself to the cultural evidence from the single site of Bellan Bandi Palassa, finds grounds for justifying a similar comparison. To the early prehistorians who pioneered research into Ceylon's prehistory the suggestion that the ancestors of the Veddas were the manufacturers of the ubiquitous stone tools seemed obvious. Those who questioned this apparent relationship between the prehistoric or contemporary cultures did so because they thought the Veddas incapable of producing a lithic industry, and not because they questioned the validity of the archaeological evidence in the Vedda caves. Now that the physical remains of the artisans of these lithic industries have been recovered, the contentions of the Sarasins and the Seligmanns must be re-evaluated along with the concepts of their opponents about the role that the ancestors of the Veddas played in Ceylon's prehistory.

As a final point in this discussion it must be mentioned that what is now required of the prehistorians of Ceylonese studies is a compilation of data concerning the Veddas from ancient native chronicles and later travellers' accounts. Whatever the affinities of the Veddas to the prehistoric and historic populations of Ceylon might be, the invasion of the Sinhalese in the Fifth Century B.C. caused a concentration of the indigenes in the eastern wilderness of the Island—the Veddarata—where they are still to be found in isolated chena villages. That they once occupied the entire Island, as has been suggested by the Sarasins (Sarasin & Sarasin 1907 : 189, F. Sarasin 1926 : 83) cannot be proved as yet, but references to their presence in other portions of Ceylon can be inferred from a cursory glance at the native Sinhalese and later European records as well as from a mapping of the Vedda place names across Ceylon. These data establish that the territory of the Veddas extended far beyond the present limits of this relict group within the recent historic period. What their area of occupation may have been during the period that Ceylon was known only along its coastline and before its interior had been penetrated by Sinhalese and Tamil colonization awaits further research. The migration of Vedda communities over the Island during the past three millenia and earlier is relevant to the problems of their physical morphology today. One wonders what selective factors, be these biological or cultural, influenced the preservation of certain Vedda populations in the relict areas of the Island while other Vedda groups became incorporated in communities of invading peoples or failed to pass on their genes at all. Useful as Hill's concept of Vedda geographical–biological areas may be to the physical anthropologist desirous of obtaining " typical Vedda " specimens, it must be borne in mind that these individuals are a segment of a much larger Vedda gene pool which existed in the past and the factors conducive to their survival are unknown. Furthermore we are ignorant of the genetic shifts that have taken place within these population segments since the commencement of their isolation. Such considerations are relevant to the problem of identifying the Balangodese when one considers that this stone-using prehistoric population was in existence at the dawn of the period of Sinhalese settlement and that the genetic complex that makes it distinctive as a phenotypic entity at this period must have had considerable influence upon the genetic composition of the present-day peoples of Ceylon.

V CONCLUSIONS

The Balangoda skeletal series from Bellan Bandi Palassa constitutes a unique phenotypic pattern present in Ceylon at the dawn of the historic period, a time within the second and third millenia B.P. While possessing certain biological features that distinguish them from other fossil hominids found thus far, the Balangodese fall within the range of polytypic variation representative of post-Pleistocene *Homo sapiens* of the Indian–southeast Asian–Australian gene pool. The phenotypic pattern most closely resembling that of the Balangodese is that of the Veddas of Ceylon. Similarities are not only quantitatively provocative but striking as well in terms of particular isolated physical traits that distinguish both Veddas and Balangodese from other southern Asiatic populations. Indeed, certain of the morphological and anthropometric characteristics of the fossil series have been cited by physical anthropologists studying the Veddas as indicative of Vedda sub-types or as the evidence of their miscegenation with other living racial groups. It would seem therefore that both the Balangodese and the Veddas are biologically united through their possession in the past of a common gene pool, although it must be stressed that the former are " pre-Veddas " in a chronological rather than in any direct phylogenetic kind of relationship. Both populations appear to have been subject to separate evolutionary pressures for a long period of time, but for reasons which are yet unknown the Balangodese phenotypic pattern did not persist into the historic period. It is the variety and nature of physical differences between these two populations that suggests their bifurcation from a common stem at a time several millenia prior to the occupation of Bellan Bandi Palassa. At the dawn of the historic period in Ceylon, the Veddas were in all probability distributed throughout the Island, save perhaps along the northern coastline, and as a dispersed population their phenotype reflected local variations as a consequence of isolation between the segments of their population. That the Veddas are simply the hybrid descendants of a crossing of Balangodese with Sinhalese or Tamils cannot be supported on the basis of the anthropometric and historic data, although the presence of a yet unidentified phenotypic element in Ceylon in the prehistoric period must not be entirely excluded from considerations of the Balangodese–Vedda phylogeny.

The cultural affinities of the Balangodese from Bellan Bandi Palassa are with the manufacturers of the lithic industries which have been assigned to the Indian Late Stone Age or its Ceylonese manifestation, the Bandarawelian. The number and kinds of similarities that exist between the prehistoric and Vedda cultures forcefully suggests the existence of a cultural continuum in Ceylon that extends into the historic period. Such traits as the use of iron and Sinhalese weapons by the Veddas of recent centuries find their parallels in the acquisition of painted pottery, ground stone tools, and perhaps other traits by the hunting-gathering and microlith-using Balangodese who may well have been introduced to these by trading peoples from coastal Ceylon and the Indian mainland. Further speculations of the biological and cultural affinities of this prehistoric population await additional research along these lines : (1) a resolution of the problem of what constitutes the Vedda phenotype apart from the traditional methods of defining this population, (2) an orientation of archaeological investigation in Ceylon that can demonstrate the role that the Vedda's have played in the manufacturing of the Island's prehistoric industries, (3) the mapping of Vedda occupation sites throughout the Island with the view of establishing the migration patterns and degree of mobility of the Veddas within the period of recorded history, (4) the recovery of additional osteological material from Ceylonese sites for the purpose of broadening our knowledge of the physical anthropology of the region. This present analysis of the Balangodese is an initial attempt to extend our understanding of the evolution of human populations during that interim which is marked by the close of the Pleistocene and the dawn of the historic period in southern Asia.

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PLATE 1

Specimen BP2/17. Unreconstructed calvarium cleared from its matrix. Left lateral aspect.

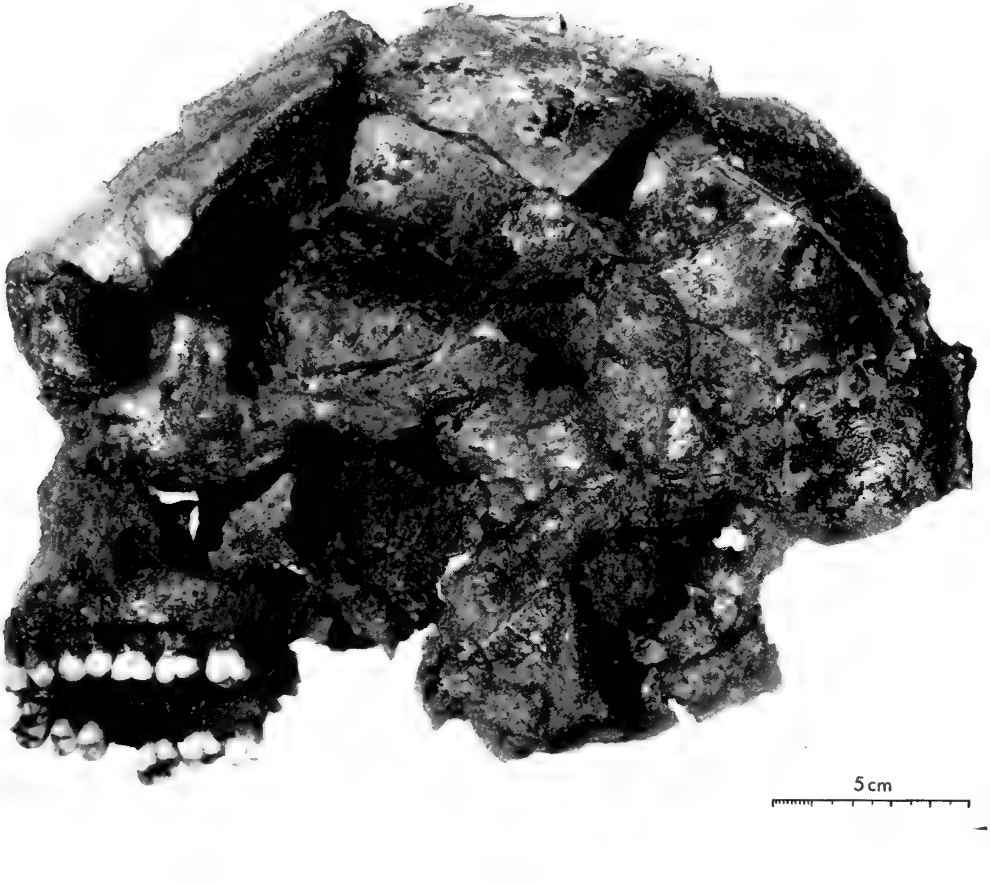
5 cm

PLATE 2

Specimen BP2/17. Unreconstructed calvarium cleared from its matrix. Left lateral aspect.

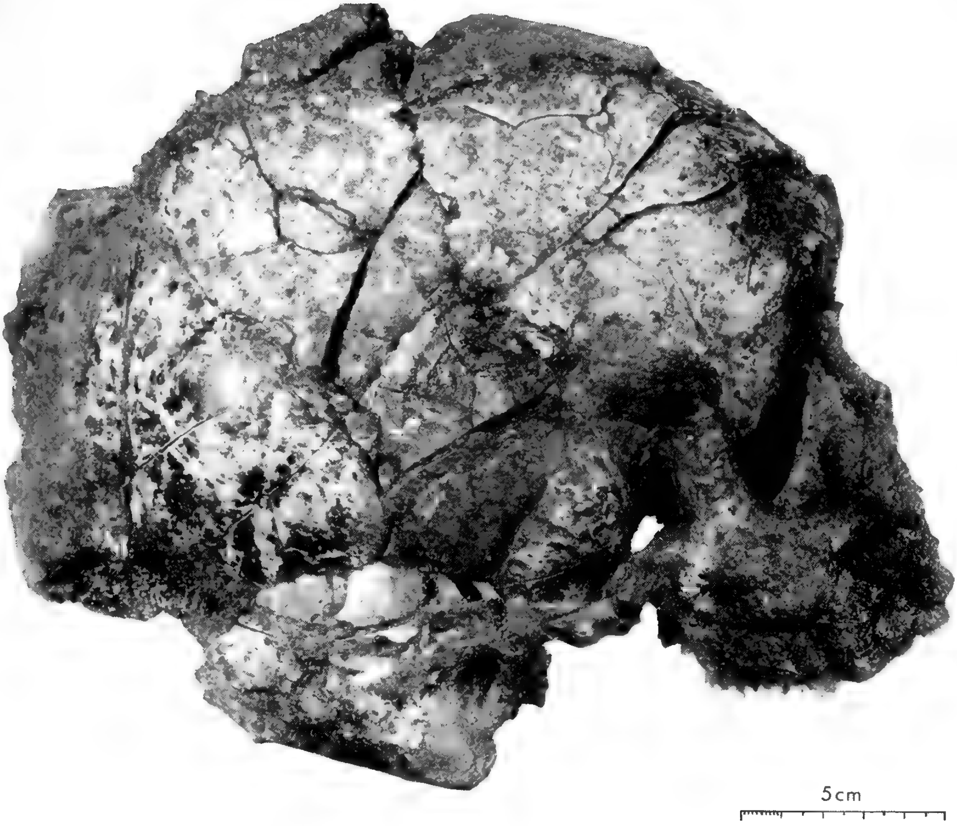
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PLATE 3

Specimen BP2/17. Partial reconstruction of calvarium.
Frontal aspect.

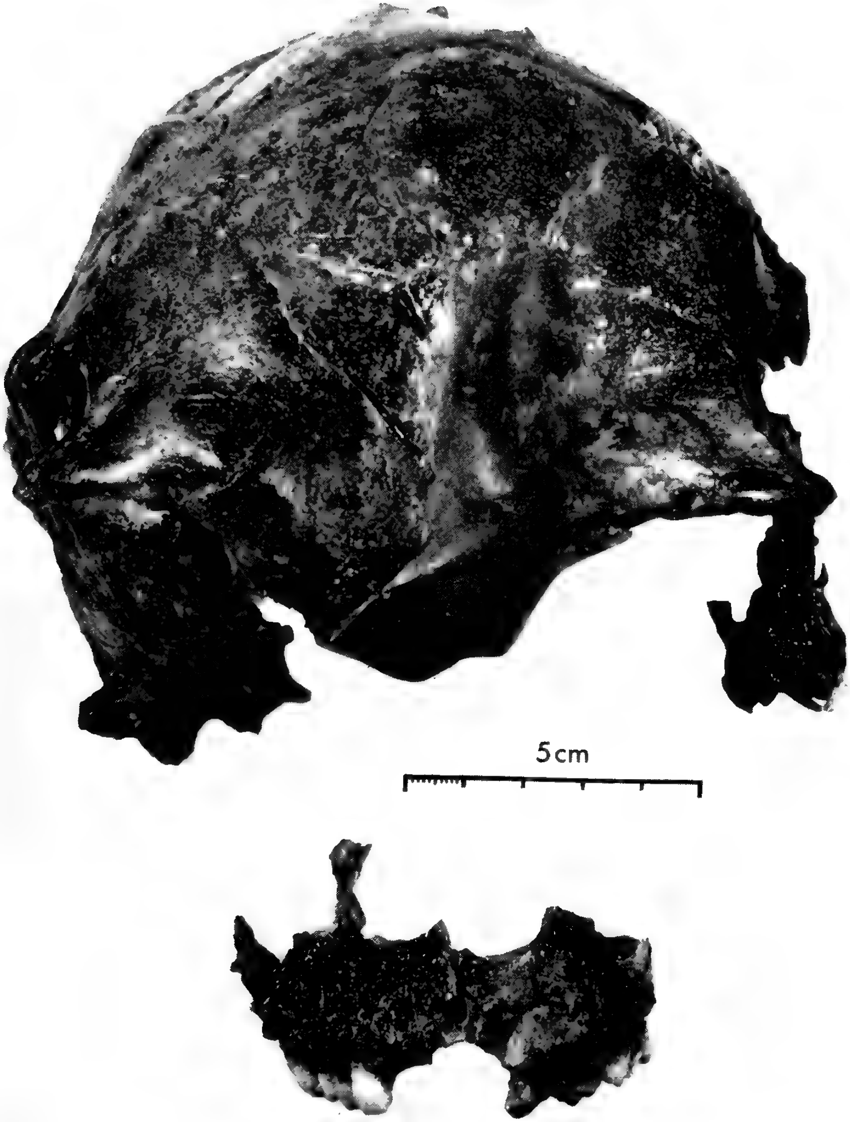

5cm

PLATE 4

Specimen BP2/17. Partial reconstruction of calvarium.
Left lateral aspect.

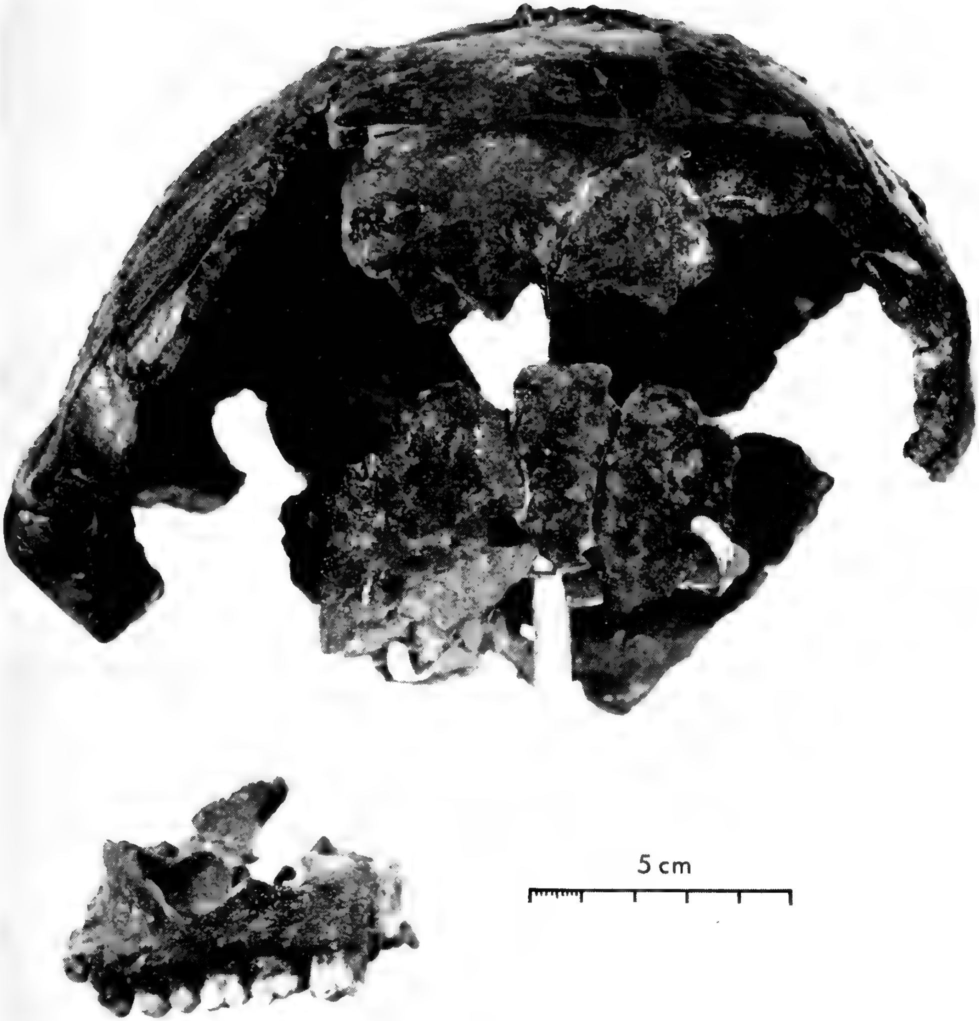

5 cm

PLATE 5

Specimen BP2/17. Partial reconstruction of calvarium.
Right lateral aspect.


5 cm

PLATE 6

Specimen BP2/17. Partial reconstruction of calvarium.
Superior aspect.


5cm

PLATE 7

Specimen BP2/17. Unreconstructed maxilla. Palatal aspect.

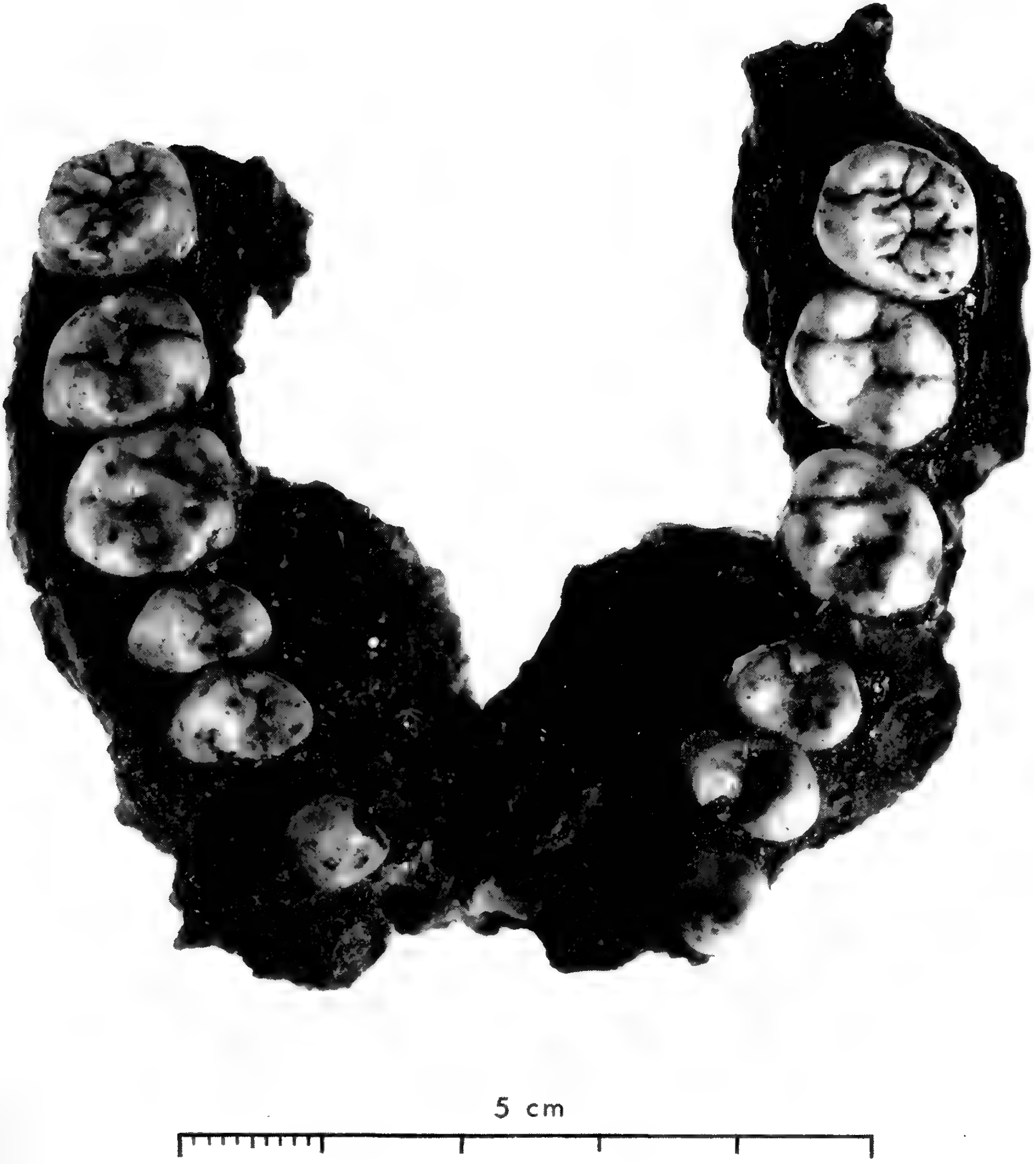

5 cm

PLATE 8

Specimen BP2/171. Mandible. Left lateral aspect.


5 cm

PLATE 9

Specimen BP2/17i. Mandible. Superior aspect.


5cm

PLATE 10

Specimen BP3/27–34. Partial reconstruction of calvarium.
Left lateral aspect.

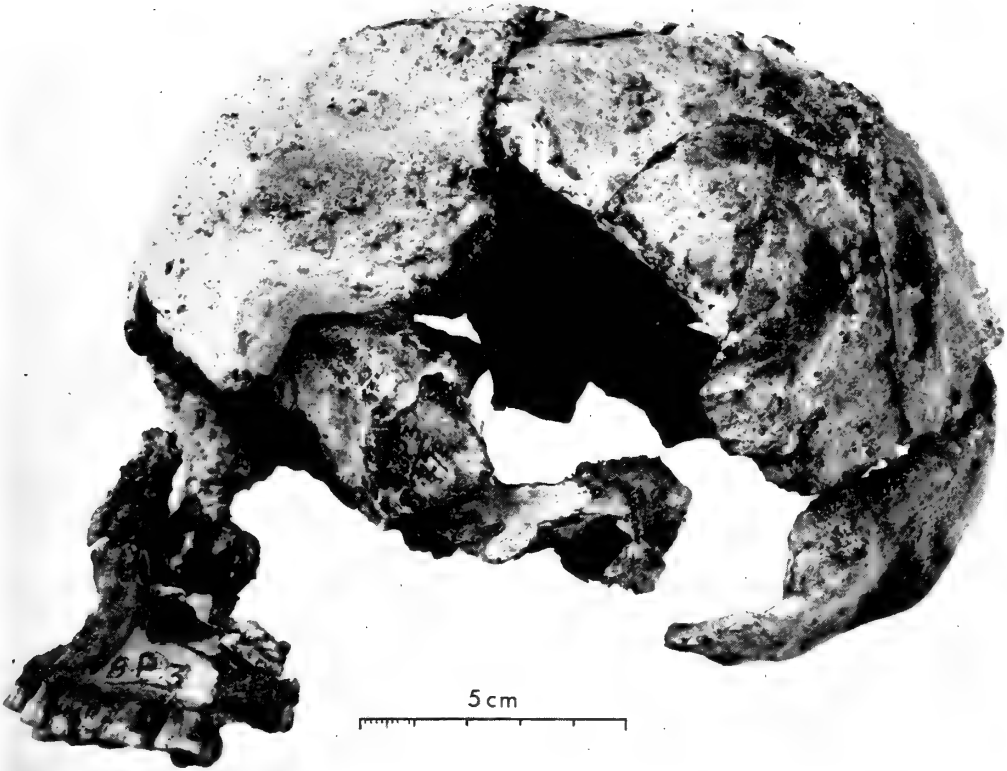

BP 3
5 cm

PLATE 11

Specimen BP3/27–34. Partial reconstruction of calvarium.
Right lateral aspect.

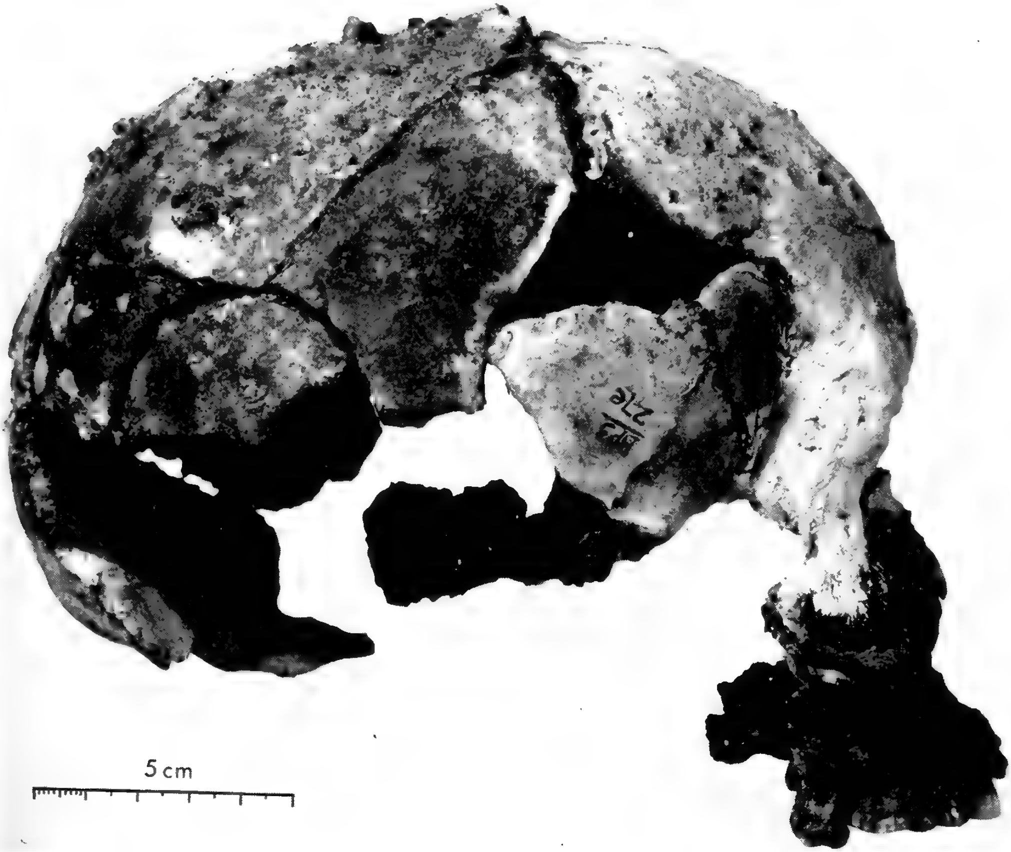

5 cm

PLATE 12

Specimen BP3/27–34. Partial reconstruction of calvarium.
Occipital aspect.


5cm

PLATE 13

Specimen BP3/27–34. Partial reconstruction of calvarium.
Superior aspect.

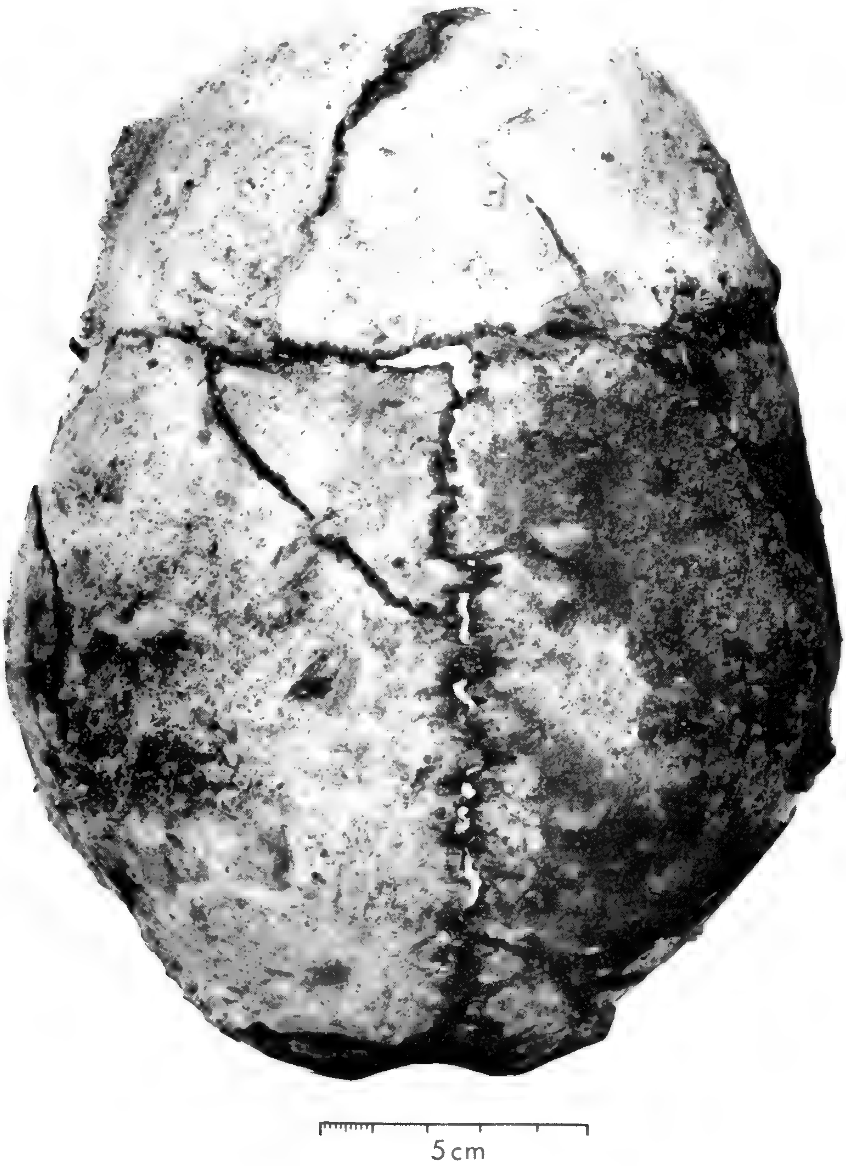

5 cm

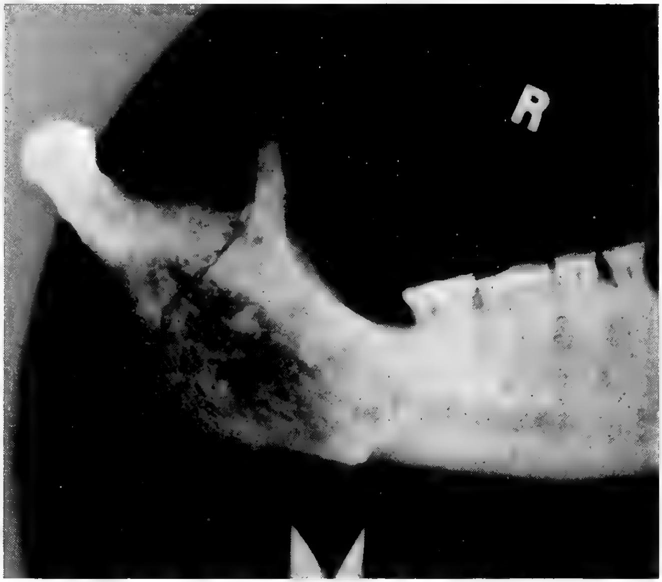
PLATE 14

Specimen BP3/27–34. Mandible. Superior aspect.


5cm

PLATE 15

Specimen BP3/27–34. Radiograph of mandible and the premolar and molar teeth. Right lateral aspect.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SOME NEW BRITISH ALBIAN OSTRACODA

P. KAYE

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 11 No. 5
LONDON: 1965

SOME NEW BRITISH ALBIAN OSTRACODA

BY

PETER KAYE, Ph.D.

Burmah Oil Exploration Co. Ltd., 20 Esplanade, Scarborough

Pp. 215–253 ; 11 *Plates* ; 5 *Text-figures*

BULLETIN OF
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THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

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This paper is Vol. 11, *No.* 5 *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued December, 1965 *Price* £2 10s.

SOME NEW BRITISH ALBIAN OSTRACODA

By P. KAYE

CONTENTS

SYNOPSIS

Twenty new species and subspecies of Ostracoda are described from the Gault Clay (Middle and Upper Albian) of England. Additiona information is given on nine already described species and four ostracod synonyms (*Clithrocytheridea ventricola* Damotte & Grosdidier, *Cytheropteron punctata* Kaye, *Cythereis angulata* Kaye and *Cythereis lamplughi* Kaye) are corrected. Four forms are left under open nomenclature.

I INTRODUCTION AND ACKNOWLEDGEMENTS

A quantitative study of the distribution of Ostracoda in the English Gault (Middle and Upper Albian) has been carried out by the collection of accurately localized samples at small vertical intervals in as many Gault exposures as are currently available. Over three hundred and fifty samples have been collected, a large proportion of which have already been analysed working on a 1,500 gram basic starting weight of sediment. The project as a whole is only partially complete but a certain number of undescribed species have already been found. The description of these new species together with other relevant taxonomic information is the subject of the present paper. Twenty species and subspecies belonging to fifteen genera are described for the first time. Additional information is given on nine already known species and four Cretaceous ostracod synonyms are corrected. Four forms are left under open nomenclature. The known range of each described species is given and its value as an index fossil is noted where possible. A complete list of the Gault exposures sampled during the course of the overall project is given. A palaeontological zonation of the Middle and Upper Albian based on ammonites is given as Text-fig. 1. All specimens described and illustrated in this paper are deposited in the collections of the British Museum of Natural History (B.M.N.H.) but considerable numbers of comparative forms are retained in the author's private collections.

This study has been carried out during the tenure of a D.S.I.R. Research Fellowship at the Sedimentology Research Laboratory, Dept. of Geology, Reading University, and I am extremely grateful to Professor P. Allen for all his help and encouragement. I would also like to thank many of my colleagues at Reading, particularly Dr. A. W. Medd, Mr. G. H. Scott and Mr. D. B. Williams for help in field work and Mr. J. L. Watkins for the photography. I would also like to express my gratitude to Mr. H. G. Owen and Mr. R. A. Milbourne whose help concerning Gault stratigraphical problems has been of immense value.

II LOCATION OF SAMPLES

A list of the localities from which Gault Ostracoda have been obtained is as follows :

(i) Lower and Upper Gault at the British Portland Cement Co's pit, Small Dole near Henfield, Sussex. Grid. Ref. TQ. 218131

(ii) Lower Gault at the Honey Lane Brickworks, Selbourne, Hampshire. Grid. Ref. SU. 768342

(iii) Lower Gault at the Greatness Lane Brick pit, Sevenoaks, Kent. Grid. Ref. TQ. 536578.

(iv) Lower and Upper Gault at Ford Place pit, Wrotham, Kent. Grid. Ref. TQ. 636591

(v) Upper Gault at the Rugby Portland Cement Co's pit, Paddlesworth, near Maidstone, Kent. Grid. Ref. TQ. 695623

(vi) Upper Gault at Sandown Bay and also Blackgang, Isle of Wight

(vii) Upper Gault at Pinhay Point, Devon. Grid. Ref. SV. 342928

(viii) Lower Gault at Devizes, Wiltshire. Grid. Ref. ST. 986612

(ix) Lower Gault at Culham, near Abingdon, Oxfordshire. Grid. Ref. SV. 510949

(x) Lower and Upper Gault at Mundays Hill pit, Leighton Buzzard, Bedfordshire. Grid. Ref. TL. 915978

(xi) Upper Gault at the London Brick Co's pit, Arlesey, Bedfordshire. Grid. Ref. TL. 185352

(xii) Upper Gault at Fisons Brickpit, Burwell, Cambridgeshire. Grid. Ref. TL. 516691

(xiii) Upper Gault at Eastwoods Cement pit, Barrington, Cambridgeshire. Grid. Ref. TL. 394507

ALBIAN ZONES and SUB ZONES

UPPER ALBIAN	*Stoliczkaia dispar*	*Mortoniceras perinflatum*
		Arraphoceras substuderi
	Mortoniceras inflatum	*Mortoniceras inflatum* var. *aequatorialis*
		Callihoplites auritus
		Hysteroceras varicosum
		Hysteroceras orbignyi
MIDDLE ALBIAN	*Euhoplites lautus*	*Dipoloceras cristatum*
		Anahoplites daviesi
		Euhoplites nitidus
		Euhoplites meandrinus
		Dipoloceras subdelaruei
		Dimorphoplites doris
	Hoplites dentatus	*Dimorphoplites niobe*
		Anahoplites intermedius
		Hoplites spathi
		Hoplites benettianus
		Hoplites eodentatus
LOWER ALBIAN	*Douvilleiceras mammillatum*	*Protohoplites puzosianus*
		Otohoplites raulinianus
		Cleoniceras floridum
		Sonneratia kitchini
	Leymeriella tardefurcata	*Leymeriella regularis*
		Hypacanthoplites milletioides
		Farnhamia farnhamensis

(xiv) Lower Gault at Castles Farm pit, near Ely, Cambridgeshire. Grid. Ref. TL. 600775

(xv) Lower Gault at Speeton, E. Yorkshire. Grid. Ref. TA. 150758

(xvi) Lower Gault at West Heslerton, E. Yorkshire. Grid. Ref. TA. 913759

(xvii) Lower and Upper Gault at Folkestone, Kent. Grid. Ref. TR. 242365

(xviii) Upper Gault at Ashford, Kent. Grid. Ref. TR. 058435

(xix) Gault at Swanage, Lulworth, Osmington and Black Ven near Lyme Regis, Dorset.

Many other pits, particularly in the Lower Gault of the Wealden area have been found to be barren of Ostracoda. These include :

(i) Lower Gault at Hassocks, Sussex. Grid. Ref. TQ. 310155

(ii) Lower Gault at the Marley Tile pit, Storrington, Sussex. Grid. Ref. TQ. 094138

(iii) Lower Gault at Nyewood Brick pit, Nyewood, near Petersfield, Hampshire. Grid. Ref. SU. 800218

(iv) Lower Gault at Wrecclesham, near Farnham, Hampshire. Grid. Ref. SU. 826448

(v) Lower Gault at Arnold's sand pit, Buckland, Kent. Grid. Ref. TQ. 231512

(vi) Lower Gault at Squerry's pit, Westerham, Kent. Grid. Ref. TQ. 442538

(vii) Lower Gault at Uffingham, Oxfordshire. Grid. Ref. SU. 315905

(viii) Lower Gault at Badbury Wick, near Swindon, Wiltshire. Grid. Ref. SU. 192818

(ix) Lower Gault at Thame, Oxfordshire. Grid. Ref. SP. 691055

(x) Lower Gault at Coney Hill Sandpit, Oxted, Surrey. Grid. Ref. TQ. 375526

III SYSTEMATIC DESCRIPTIONS

Suborder CLADOCOPINA

Family **POLYCOPIDAE**

Genus ***POLYCOPE*** Sars 1866

Polycope nuda sp. nov.

(Pl. 4, figs. 1–3)

Derivation of name. nuda—referring to the lack of surface ornament.

Diagnosis. Large moderately inflated *Polycope* with subcircular outline and smooth valve surface.

Holotype : A single left valve, B.M.N.H. Io. 2847, from the Lower Gault *niobe* Subzone ; Wrotham, Kent.

Paratypes : B.M.N.H. Io. 2848–2850. Three carapaces from the same subzone and locality.

MEASUREMENTS.

	Length (mm.)	Height (mm.)	Width (mm.)
Left valve (B.M.N.H. Io. 2847, holotype) .	0·55	0·50	0·16
Carapace (B.M.N.H. Io. 2848) . . .	0·58	0·50	0·32

DESCRIPTION. Valves large, moderately inflated, subcircular in outline. There is a slight flattening dorsally along the hinge line forming two weak cardinal angles. The anterior margin is more bluntly rounded than the posterior margin. Lateral surface mainly smooth but with some weak irregular reticulation particularly antero-ventrally in certain specimens. Overlap strong particularly posteriorly and ventrally. Hinge simple with a groove in the margin of the right valve to accommodate the sharp edge of the left valve. Duplicature not seen. Muscle scars, a triangular patch composed of three scars, the apex pointing dorsally. The two ventral scars are roughly triangular in shape, the dorsal scar is diamond shaped, fitting between the points of the other two scars.

FIG. 2. Muscle scars of *Polycope nuda* sp. nov. ×2500.

REMARKS. Only one other species of the genus *Polycope* has been previously recorded from the Cretaceous. This species, *P. bonnemai* Herrig 1964, is known from the Maastrichtian of the Isle of Rugen and a similar form *Polycope* sp. was described by Bonnema (1940) from the Maastrichtian of the Netherlands. *P. nuda* is therefore the first pre-chalk Cretaceous reference to the genus and is closely related and presumably ancestral to *P. bonnemai*. It is closely similar in size and ornamentation to the latter but differs in details of the shape and overlap, lacking the anterior and postero-dorsal marginal thickening of *P. bonnemai*. In shape the anterior and posterior margins are more evenly rounded in *P. nuda*. *P. oweni* described below, also from the British Albian, is much smaller and strongly ornamented. The genus is fairly common in the Jurassic where several species are known, particularly from the Liassic and Oxfordian. In general these forms are smaller, much more flattened and usually strongly ornamented. *P. nuda* is found consistently throughout the Gault first making its appearance in the *niobe* Subzone. It is never very common though its relative abundance in the *niobe* Subzone is a useful indicator of that horizon.

Polycope oweni sp. nov.

(Pl. 4, figs. 11–15)

DERIVATION OF NAME. After H. G. Owen whose work on Gault stratigraphy has been invaluable to me in my studies of the distribution of the Ostracoda in the Gault.

HOLOTYPE. A left valve, B.M.N.H. Io. 2859, from the *H. orbignyi* Subzone (Upper Gault); Wrotham, Kent.

PARATYPES. B.M.N.H. Io. 2858, 2860–63. Four valves and two carapaces from the same horizon and locality.

DIAGNOSIS. Small subcircular *Polycope* with valve reticulately ornamented. Along and at the junction of the reticulation are numerous small spines.

MEASUREMENTS.

	Length (mm.)	Height (mm.)	Width (mm.)
Left valve (B.M.N.H. Io. 2859, holotype) .	0·42	0·37	0·11
Carapace (B.M.N.H. Io. 2858) . . .	0·42	0·37	0·22

DESCRIPTION. Valves small, weakly inflated, subcircular in outline. The valves have a slightly greater length than height but there is only very slight flattening along the hinge line. The valves are slightly asymmetrical anteriorly but the anterior and posterior margins are without cardinal angles. Marginal protuberances are absent but the whole of the margin is thickened. The lateral surfaces are strongly but variably ornamented ranging from reticulation to spination. The basic ornament is the reticulation covering the whole of the surface on a somewhat concentric pattern. Small spines are developed along the ridges of the reticulations giving rise to a completely spined appearance in many of the specimens. Overlap is marked all round the margin except dorsally.

The hinge is simple ; the margins in both valves being flattened to form sharp marginal bars which overlap each other. Dorsally in the right valves there is a weak groove above the bar. Muscle scars, three equal-sized oval scars arranged in a triangle. One apex of the triangle points dorsally.

REMARKS. *P. oweni* is not abundant in the Gault and is found rarely in clays of post *A. intermedius* Subzone age. It differs from *P. nuda* in the details of the shape, hinge, muscle scars and ornamentation and is smaller.

Suborder PODOCOPINA

Family **BAIRDIIDAE**

Genus ***BAIRDIA*** McCoy 1844

Bairdia pseudoseptentrionalis (Mertens)

(Pl. 2, figs. 1, 3–6)

? 1840 *Cytherina subdeltoidea* Munster ; Roemer : 105, pl. 15, fig. 22.
? 1845 *Cytherina subdeltoidea* Munster ; Reuss : 16, pl. 5, fig. 38.
1849 *Bairdia subdeltoidea* (Munster) ; Jones : 23, pl. 5, figs. 15*a–f*.
? 1874 *Bairdia subdeltoidea* (Munster) ; Reuss : 140, pl. 26, figs. 5*a–c*.
1890 *Bairdia subdeltoidea* (Munster) ; Jones & Hinde : 5, pl. 2, figs. 31–34.
? 1927 *Bairdia subdeltoidea* (Munster) ; Alexander, pl. 6, figs. 2, 4.
? 1929 *Bairdia subdeltoidea* (Munster) ; Alexander : 61, pl. 3, fig. 5.
1956 *Bairdoppilata pseudoseptentrionalis* Mertens : 182, pl. 8, figs. 7–10, pl. 13, figs. 89–90.
? 1956 *Bairdoppilata roemeri* Deroo : 1509, pl. 1, figs. 9–12.
1958 *Bairdoppilata pseudoseptentrionalis* Mertens ; Howe & Laurencich : 82.
? 1958 *Bairdoppilata ? roemeri* Deroo ; Howe & Laurencich : 82.

Material. B.M.N.H. Io. 2828–2832, 4 valves and 1 carapace from the Gault just below the Cambridge Greensand at Arlesey, Beds.

Measurements.

	Length (mm.)	Height (mm.)
Left valve (B.M.N.H. Io. 2828)	1·32	0·87
Right valve (B.M.N.H. Io. 2829)	1·34	0·75

Remarks. For a long time all Cretaceous species of *Bairdia* were placed in *B. subdeltoidea* (Munster) a Tertiary form. In 1956 Deroo re-named the Cretaceous references to *B. subdeltoidea* as *Bairdoppilata roemeri*. Earlier in the same year Mertens had, however, erected a new species *Bairdoppilata pseudoseptentrionalis* which seems to be identical with Deroo's form. Both authors had referred their species to the genus *Bairdoppilata* which is said to differ from true *Bairdia* in having two rows of denticles at either end of the hinge line in the right valves. However, as van Morkhoven (1963) has pointed out, the presence or absence of such denticles is a characteristic of most of the genera within the Bairdiidae each genus containing species both with and without them. It therefore seems unwise to perpetuate the genus *Bairdoppilata*.

Bairdia pseudoseptentrionalis occurs rarely in the Lower Gault but is more abundant in the Upper Gault.

Genus ***PONTOCYPRELLA*** Mandelstam 1956

Pontocyprella semiquadrata sp. nov.

(Pl. 3, figs. 1–8)

Derivation of name. Semiquadrate–alluding to the shape.

Diagnosis. *Pontocyprella* with semiquadrate shell. Anterior margin semicircular, posterior margin bluntly rounded.

Holotype. A left valve, B.M.N.H. Io. 2834, from the *H. orbignyi* Subzone, Upper Gault ; Wrotham, Kent.

Paratypes. B.M.N.H. Io. 2835–2837. Three valves from the same horizon and locality.

Measurements.

	Length (mm.)	Height (mm.)
Left valve (B.M.N.H. Io. 2834, holotype) . .	0·70	0·40
Right valve (B.M.N.H. Io. 2836)	0·73	0·40

Description. Valves elongate, compressed, semiquadrate in shape. Dorsal margin weakly convex, without cardinal angles ; ventral margin weakly concave. Anterior margin semicircular, posterior margin bluntly rounded forming a weak bulge at $\frac{2}{3}$ height. Greatest height and width at mid-length. Lateral surface smooth. Inner lamella broad with large anterior and posterior vestibules. Dupli-

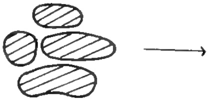

FIG. 3. Muscle scars of *Pontocyprella semiquadrata* sp. nov. ×2500.

cature narrow, crossed by numerous short straight fine radial pore canals. Normal pore canals few, small and irregularly scattered. Muscle scars a central rosette of 4 scars. Hinge simple. In the left valve there is a marginal bar with a long narrow shelf-like furrow below it. In the right valve there is a narrow marginal shelf with a high bar below it.

REMARKS. *Pontocyprella semiquadrata* occurs rarely in the upper part of the Lower Gault and more commonly in the Upper Gault. Its overall shape and particularly the shape of the anterior and posterior margins distinguish it from other Cretaceous species of the genus *P. superba* Neale 1962 and *P. rara* Kaye 1965 have an acute posterior end whilst *P. harrisiana* Jones is larger, more elongate and has the anterior margin bulged dorsally and the posterior margin bulged ventrally. *P. semiquadrata* is closest to *P. mandelstami* Kaye 1965 differing in that the latter is kidney shaped rather than semiquadrate. *P. maynci* Oertli 1958 has the dorsal margin strongly arched.

Family **CYPRIDIDAE**

Genus ***ARGILLOECIA*** Sars 1866

Argilloecia valvula sp. nov.

(Pl. 7, figs. 20–25)

DERIVATION OF NAME. valvulus L. = husk.

DIAGNOSIS. *Argilloecia* with arched dorsal margin and acute posterior margin.

HOLOTYPE. A right valve, B.M.N.H. Io. 2914, from the *H. orbignyi* Subzone, Upper Gault ; Wrotham, Kent.

PARATYPES. B.M.N.H. Io. 2915–2920. Four valves and two carapaces from the same horizon and locality.

MEASUREMENTS.

	Length (mm.)	Height (mm.)
Right valve (B.M.N.H. Io. 2914, holotype) . .	0·52	0·20
Left valve (B.M.N.H. Io. 2915)	0·48	0·16

DESCRIPTION. Valves, thin, small, elongate, laterally compressed. Dorsal margin strongly arched, without cardinal angles ; ventral margin long and straight. Anterior margin forming a blunt point antero-ventrally ; posterior margin meeting ventral margin at an angle of 90° ventrally. Greatest height just in front of mid-length ; greatest width just behind mid-length. Right valve larger than left, overlapping around the entire margin but particularly strongly antero-dorsally and postero-dorsally. Lateral surface smooth. Duplicature narrow, crossed by few short, straight radial pore canals. Inner margin and line of concrescence separate, forming large vestibules anteriorly and posteriorly. Normal pore canals few, irregularly scattered. Hinge simple consisting of a groove in the dorsal margin of the right valves to accommodate the dorsal edge of the smaller left valves.

Muscle scars a central rosette of five scars.

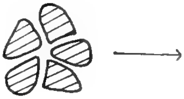

FIG. 4. Muscle scars of *Argilloecia valvula* sp. nov. ×2500.

REMARKS. *Argilloecia valvula* occurs rarely in the Upper Gault and the upper part of the Lower Gault. It is the first record of the genus in the Lower Cretaceous. The larger right valve separating the genus from most Cyprids, a feature only otherwise occurring in *Macrocypris* and *Pontocypris*. *Argilloecia* differs from these latter two genera in size, hinge and marginal features. The large size of the known Albian species of *Macrocypris* easily differentiates them from *A. valvula*. *M. parva* Kaye 1965 from the Hauterivian and Barremian of Northern England is similar in size but differs appreciably in shape.

Genus ***PARACYPRIS*** Sars 1866

Paracypris wrothamensis sp. nov.

(Pl. 9 figs. 9–14)

DERIVATION OF NAME. After the village of Wrotham, Kent the type locality for the species.

DIAGNOSIS. Large *Paracypris* with strongly drawn out acute posterior end and high strongly angular anterior cardinal angle.

HOLOTYPE. A left valve B.M.N.H. Io. 2959 from the *H. orbignyi* Subzone (Upper Albian) ; Wrotham Kent.

PARATYPES. B.M.N.H. Io. 2955–58, 2960, 2961. Three left valves, three right valves and two carapaces from the same horizon and locality.

MEASUREMENTS.

	Length (mm.)	Height (mm.)
Left valve (B.M.N.H. Io. 2959, holotype) . .	0·92	0·35
Right valve (B.M.N.H. Io. 2958)	0·90	0·35
Carapace (B.M.N.H. Io. 2957)	0·90	0·35

Description. Valves large, compressed, very elongate. Greatest height at $\frac{1}{4}$ length, greatest width at $\frac{1}{3}$ length. In lateral view elongate subtriangular with the dorsal margin straight and the ventral margin weakly concave. Anterior margin broadly rounded forming a marked cardinal angle with the strongly sloping dorsal margin. Posterior drawn out forming a strongly acute point postero-ventrally. A well marked postero-dorsal cardinal angle occurs. Lateral surface smooth. Left valve larger than right overlapping particularly dorsally and ventrally.

Large crescentic anterior and large triangular posterior vestibules occur. Zone of fusion very narrow anteriorly and posteriorly, doubling in width ventrally. Crossed by few thick short radial pore canals branching distally (8–10 anteriorly). Normal pore canals small, few, irregularly scattered. Hinge simple, the dorsal edge of the right valve fitting into a narrow shelf-like groove along the dorsal margin of the left valve. An anterior prolongation of the dorsal marginal bar of the left valve forms a tooth-like extension corresponding with a slight incurving of the margin in front of the anterior cardinal angle in the right valve. Muscle scars a central rosette of five or six oval scars.

Remarks. *P. wrothamensis* occurs throughout the Gault in England. It first appears in the *intermedius* Subzone but is rare in the Lower Gault. It becomes abundant in the Upper Gault and its abundance is a useful indicator of Upper Gault age. It is strongly related to the Lower Cretaceous species *P. acuta* (Cornuel) 1848. This latter species is poorly described and rather confused but is smaller and not so acute posteriorly as *P. wrothamensis*. *P. sinuata* Neale 1963 from the Hauterivian and Barremian is probably, at least in part, synonymous with *P. acuta*. *P. sinuata* differs from *P. wrothamensis* in being lower, having a less well marked anterior cardinal angle and being much less acute. Of other Cretaceous species *P. depressa* Bonnema 1940 and *P. jonesi* Bonnema 1940 have the cardinal angles rounded and the greatest height further forward ; *P. gracilis* (Bosquet) and *P. siliqua* Jones & Hinde 1890 differ markedly in outline.

Genus ***KRAUSELLA*** Ulrich 1894

Krausella sp.

(Pl. 3, figs. 15, 16)

Material. Two right valves B.M.N.H. Io. 2845–2846, from the upper part of the Lower Gault at Castles Farm, Ely.

Measurements.

	Length (mm.)	Height (mm.)
Right valve (B.M.N.H. Io. 2845)	0·55	0·27

Remarks. Only one other species of this genus (*K. minuta* Triebel) is known from the Cretaceous. It is smaller and is not so pointed posteriorly. The strong inequality of the valves distinguishes the genus.

Family **CYTHERIDEIDAE**

Genus ***CLITHROCYTHERIDEA*** Stephenson 1936

Clithrocytheridea heslertonensis Kaye

(Pl. 1, figs. 8–12)

1963*a* *Clithrocytheridea heslertonensis* Kaye : 30, pl. 1, figs. 10–13.
1963 *Clithrocytheridea ? ventricola* Damotte & Grosdidier : 53, pl. 1, figs. 1*a–f*.

MATERIAL. B.M.N.H. Io. 2825–2827, Female left and right valves, and carapace from Bed N. 5, Middle Albian *spathi* Subzone, West Heslerton, East Yorks.

REMARKS. Specimens of *Clithrocytheridea ? ventricola* kindly sent to me by Dr. E. Grosdidier show that this form is synonymous with *C. heslertonensis* Kaye. *Clithrocytheridea heslertonensis* is found abundantly in the *H. spathi* Subzone of the Lower Gault and appears to be confined to that subzone. It is a valuable zonal index and has been recorded from West Heslerton, Speeton, Devizes, Culham and Henfield in clays of that age.

Genus ***SCHULERIDEA*** Swartz & Swain 1946

Schuleridea dimorphica sp. nov.

(Pl. 5, figs. 1–6)

DERIVATION OF NAME. Alluding to the strongly dimorphic nature of the species.

DIAGNOSIS. Small strongly dimorphic *Schuleridea* with weak ocular sulcus and without cardinal angles.

HOLOTYPE. A male left valve, B.M.N.H. Io. 2864, from the *H. orbignyi* Subzone, Upper Gault ; Wrotham, Kent.

PARATYPES. B.M.N.H. Io. 2865–2870. Twelve valves and two carapaces from the same horizon and locality.

MEASUREMENTS.

	Length (mm.)	Height (mm.)
Male left valve (B.M.N.H. Io. 2864, holotype) .	0·64	0·41
Female left valve (B.M.N.H. Io. 2867) . . .	0·52	0·40
Male right valve (B.M.N.H. Io. 2866) . . .	0·63	0·35
Female right valve (B.M.N.H. Io. 2868) . .	0·50	0·34

DESCRIPTION. Valves relatively small, ovate, laterally compressed. Dorsal margin strongly arched in left valves, weakly arched in right valves. Cardinal angles absent from both valves. Ventral margin convex in the left valves, straight in the right. Anterior margin broadly rounded ; posterior bluntly pointed just below mid-height. Greatest height just in front of mid-length, greatest width at mid-length. Eye spot very weak with a short, shallow, oblique sulcus posterior to it. Lateral surface smooth. There is a slight ventral tumidity particularly in the right valves. Duplicature broad, crossed by numerous fine radial and pseudoradial pore canals. These canals are bent upwards anterodorsally. No marginal denticulation in either valve. Inner margin and line of concrescence coincide throughout Normal pore canals abundant and irregularly scattered over the lateral surface. Hinge strongly developed, having in the left valves two terminal divided sockets, open ventrally, separated by a shelf-like furrow. Dorsal of the median furrow is a high, smooth bar and a narrow, shallow accommodation groove. In the right valves there are two bar-like denticulate terminal teeth (5 denticles in each) separated by a low, median bar. Above the hinge is a prominent median shelf.

Sexual dimorphism is particularly strong.

REMARKS. *Schuleridea dimorphica* occurs abundantly in the Upper Gault and is a valuable index form for that age. Its small size and ovoid shape distinguish it from most other species of the genus. It is closest to *S. sulcata* Kaye 1965*a* from the Aptian of the Isle of Wight, differing in the poorer development of the eye tubercle and ocular sulcus and in the shape of the dorsal and posterior margins. Smaller and differing in hingement from the only other known Albian species *S. jonesiana* (Bosquet) 1852, it is also flatter and lacks the cardinal angles and prominent eye tubercle of *S. virginis* Grosdidier 1964 and the truncate posterior end of *S. bernouilensis* Grosdidier 1964. In shape and dimorphic features it differs also from *S. derooi* Damotte & Grosdidier 1963*a*.

Genus ***HABROCYTHERE*** Triebel 1940

Habrocythere fragilis Triebel

(Pl. 6, figs. 7–13)

1940 *Habrocythere fragilis* Triebel : 166, pl. 1, figs. 10–13, pl. 9, fig. 101.
1956 *Habrocythere fragilis* Triebel ; Mertens : 198, pl. 10, figs. 51–52.
1963 *Habrocythere fragilis* Triebel ; Kaye : 33, pl. 3, figs. 8–9.

MATERIAL. Four normal specimens B.M.N.H. Io. 2882, 2884, 2887, 2888, from the *D. cristatum* Subzone (Middle Albian) ; Wrotham, Kent.

Three anomalous specimens, B.M.N.H. Io. 2883, 2885, 2886, from the same subzone and locality.

REMARKS. *Habrocythere fragilis* is common throughout the English Albian. Certain specimens have, however, been found that may throw light upon the origin of this monotypic genus. Amongst the normal assemblages of this species certain specimens occur which are identical to the species in its general accepted sense but have a large eye spot mounted on a large tubercle set antero-dorsally. They also have the ventro-lateral portion of the valves drawn out into a weak alate expansion. These specimens have to be included in *H. fragilis* on the basis of their other features and their close association with normal specimens of the species but are closely similar to species of the genus *Euryitycythere*. It is therefore, very likely that *Euryitycythere* known from Valanginian to Aptian strata has evolved into the genus *Habrocythere* with certain specimens of the latter genus showing recapitulation. The major diagnostic features of *Euryitycythere* are the eye tubercle, the inflated alate ventro-lateral area, the wide flattened marginal area and the hinge. The wide flattened marginal area and associated radial canals are found in all specimens of *Habrocythere* whilst the eye tubercle and inflation are shown in the " recapitulation " specimens.

The variability of the hinge in Ostracoda and its modification during phylogeny is well known in Ostracoda and modification during the Hauterivian-Albian time interval is quite feasible. The Aptian occurrence of the genus (Kaye 1965*a*) is of a single closed carapace and the hinge features are not known. Slight simplification of the hinge structure during the phylogeny can perhaps be related to the small size and light build of *Habrocythere* and can be used as evidence against making *Euryitycythere* Oertli 1958 a synonym of *Habrocythere* Triebel 1940.

Specimens of *H. fragilis* showing affinities with *Euryitycythere* have been found from several localities. They occur mainly in the *daviesi* and *cristatum* Subzones at Wrotham and in the *subdelaruei* Subzone at Sevenoaks. They are useful indicators for recognizing the upper part of the Lower Gault and it is possible that ecological conditions in the Weald at this time stimulated this diversification.

Genus ***DOLOCYTHERIDEA*** Triebel 1938

Dolocytheridea typica sp. nov.

(Pl. 3, figs. 9–14)

Derivation of name. Typicus L. = typical.

Diagnosis. Small *Dolocytheridea*, inflated posteriorly, with dorsal margin strongly arched postero-dorsally. Posterior end rather truncated.

Holotype. A left valve, B.M.N.H. Io. 2839, from the basal Upper Gault (Upper Albian); Pinhay, Devon.

Paratypes. B.M.N.H. Io. 2838, 2840–44. Eight valves and two carapaces, from the same horizon and locality.

Measurements	Length (mm.)	Height (mm.)
Left valve (B.M.N.H. Io. 2839 holotype) . .	0·59	0·33
Right valve (B.M.N.H. Io. 2838)	0·57	0·28

Description. Valves small, elongate, laterally inflated particularly posteriorly. Dorsal margin strongly arched, without cardinal angles; ventral margin straight. Anterior margin broadly rounded, posterior margin bluntly rounded rather truncate. Greatest height and width at $\frac{2}{3}$ length. Lateral surface smooth, eye spots absent. Duplicature broad, crossed by a very large number of thin, rather sinuous, simple radial pore canals. Inner margin and line of concrescence coincide throughout. Normal pore canals fairly abundant, irregularly scattered. Muscle scars, not usually seen, appear to consist of a vertical row of four oval scars with a V-shaped scar anterior to them. Other smaller scars probably occur above and below the main group. The hinge is simple consisting in the left valves of a curved smooth groove deepened at its ends accommodating the dorsal edge of the smaller right valve. The dorsal margin of the right valve is enlarged to form weak smooth terminal teeth.

Remarks. This species is much smaller than most other species of the genus. It differs significantly from the even smaller *D. minuta* Kaye in shape and greater inflation.

From the *D. hilseana—D. intermedia—D. bosquetiana* lineage it differs in the greater inflation posteriorly and the truncation of the posterior end as well as in size.

D. typica has so far only been found from the basal Upper Gault at Pinhay in Devon.

Family **CYTHERURIDAE**

Genus ***EUCYTHERURA*** Muller 1894

Eucytherura aff. ***nuda*** Kaye

(Pl. 7, figs. 17, 18)

MATERIAL. B.M.N.H. Io.2912–13. Two specimens from the *H. orbignyi* Subzone, Upper Gault ; Wrotham, Kent.

REMARKS. Specimens similar to the Barremian form *E. nuda* Kaye 1964 occur rarely in the Upper Gault. They are comparable with true *E. nuda* but have the postero-ventral lobe more strongly inflated and a stronger surface reticulation. It is almost certain that extra material will show that the Gault specimens belong to a separate species or subspecies. A single valve of a related but distinct form has been found from the uppermost Lower Gault at Castles Farm, Ely. This specimen is similar in shape and size to *E. nuda* but has two rows of low surface nodes, one row dorsally and a more prominent one ventrally.

Genus ***HEMICYTHERURA*** Elofson 1941

Hemicytherura euglyphea sp. nov.

(Pl. 8, figs. 1–4)

DERIVATION OF NAME. euglypheus L. = distinctly marked.

DIAGNOSIS. Sexually dimorphic *Hemicytherura* with strong surface ornament of longitudinal ridges.

HOLOTYPE. A male left valve, B.M.N.H. Io. 2921, from the *H. orbignyi* Subzone, Upper Gault ; Wrotham, Kent.

PARATYPES. B.M.N.H. Io. 2922–2925. Five valves and one carapace from the same horizon and locality.

MEASUREMENTS.

	Length (mm.)	Height (mm.)
Male left valve (B.M.N.H. Io.2921, holotype) .	0·40	0·19
Female left valve (B.M.N.H. Io. 2924) . . .	0·33	0·16
Male right valve (B.M.N.H. Io. 2923) . . .	0·40	0·20
Female right valve (B.M.N.H. Io. 2922) . .	0·33	0·17

DESCRIPTION. Valves small, elongate, laterally compressed. Dorsal margin well arched in the right valves, weakly arched in the left valves ; without cardinal angles.

Ventral margin straight. Anterior margin broadly rounded; posterior drawn out into a short acute caudal process just above mid-height. Greatest height and width at mid-length. Lateral surface strongly ornamented, tumid ventrally. Eye spot distinct, low and glassy. Ornament consists of a series of longitudinal ridges joined by weaker vertical cross ridges. The pattern of longitudinal ridges is not regular in the centro-lateral area where a flattened irregularly ridged patch occurs. The strong ornament covers the whole of the valve exterior, even anteriorly where several longitudinal ridges run strongly across the marginal area.

Duplicature moderately broad, crossed by few straight, simple radial pore canals. There is a well developed ocular pit antero-dorsally in the interior of the valves. Hinge rather complex. In the right valve there are two faintly denticulate terminal bar-like teeth. Above each tooth is a shelf-like furrow accommodating the dorsal edge of the left valve. Between and in line with the teeth and furrows the valve remains open but above the general line of the hinge there is a median dorsal marginal bar. In the left valve the dorsal margin is enlarged to form a curved marginal bar, more prominent at the ends where it fits above the terminal teeth of the right valve. Below this marginal bar both anteriorly and posteriorly there are shelf-like terminal grooves to accommodate the terminal teeth of the right valve. Sexual dimorphism well marked.

REMARKS. *H. euglyphea* occurs rarely in the upper part of the Lower Gault and more commonly in the Upper Gault, being distinguished from most other species of related genera on account of shape, hinge and ornament. It is closest to *Cytherura reticulosa* (Chapman) which itself is probably a *Hemicytherura*, differing in being less arched dorsally, in lacking the alate spine postero-ventrally and in details of the surface ornamentation. *H. euglyphea* differs from other Cretaceous species such as *H. unisulcata* Veen, *H. bisulcata* Veen and *H. asiculcata* Veen in lacking vertical sulcation and in surface ornamentation.

Genus ***CYTHEROPTERON*** Sars 1866

Cytheropteron (C.) arguta sp. nov.

(Pl. 8, figs. 12–17)

DERIVATION OF NAME. arguta L. = distinct.

DIAGNOSIS. *Cytheropteron* with strongly reticulate lateral surface and ridged posteriorly pointing alate expansion.

HOLOTYPE. A left valve, B.M.N.H. Io. 2936, from the *H. orbignyi* Subzone, Upper Gault; Wrotham, Kent.

PARATYPES. B.M.N.H. Io. 2933–2935, 2937–2939. Six valves and one carapace from the same horizon and locality.

MEASUREMENTS.

	Length (mm.)	Height (mm.)
Left valve (B.M.N.H. Io. 2936 holotype) . .	0·42	0·26
Right valve (B.M.N.H. Io. 2933)	0·42	0·24

Description. Valves small, ovate, strongly ornamented. Dorsal margin strongly arched, without cardinal angles ; ventral margin weakly convex. Anterior margin bluntly rounded, posterior drawn out into a caudal extension at mid-height. Greatest height and width at mid-length. A rounded ventro-lateral alate expansion occurs. Along its crest there is a prominent ridge starting anteriorly at the margin at $\frac{1}{4}$ height and terminating posteriorly in a small posteriorly directed spine. The anterior end of the ridge forms a spine on the margin. The lateral surface is strongly reticulate. The ventral undersurface is weakly striated. Duplicature moderately broad, crossed by few straight, thick radial pore canals. Normal pore canals and muscle scars not seen. Hinge very strongly developed with two long, almost interdentate, terminal sockets separated by a short straight coarsely crenulate bar in the left valve. Above the hinge is a wide marginal shelf. In the right valve there are two terminal rows of denticles (6 or 7 in each) decreasing in height towards the median element and separated by a short interdentate furrow. Above the hinge is a narrow marginal shelf.

Remarks. *Cytheropteron* (*C.*) *arguta* appears to be confined to the Upper Gault. It is extremely abundant in the *H. orbignyi* Subzone and can be used as an index species. It has been found so far at Wrotham, Henfield and Pinhay.

The strength of the ornamentation and hinge make *C.* (*C.*) *arguta* distinct from other known species as does the shape of the alae. It is closest to *C.* (*C.*) *punctata* Kaye from the Barremian of Northern England which has a similar ridged alae. The latter, however, has the ridge separated from the anterior margin and lacks the strong ornamentation.

Cytheropteron (C.) milbournei sp. nov.

(Pl. 7, figs. 4, 6–9)

Derivation of name. After R. H. Milbourne whose stratigraphical work on the Gault has been an invaluable assistance to my study of the distribution of Ostracoda in the Gault.

Diagnosis. *Cytheropteron* with drawn out postero-ventrally directed alate expansion and punctate ornament over whole lateral surface.

Holotype. A left valve, B.M.N.H. Io. 2898, from the *subdelaruei* Subzone, Lower Gault ; Wrotham, Kent.

Paratypes. B.M.N.H. Io. 2899, a left valve from the same horizon and locality as the holotype ; B.M.N.H. Io. 2900–02. Two valves and one carapace from the *niobe* Subzone at Sevenoaks.

Measurements.

	Length (mm.)	Height (mm.)
Left valve (B.M.N.H. Io. 2898, holotype) . .	0·37	0·22
Right valve (B.M.N.H. Io. 2900)	0·35	0·22

Description. Valves small, elongate, laterally compressed and with a prominent ventro-lateral alate expansion. Dorsal margin weakly arched ; ventral margin straight. Anterior margin semicircular, posterior end drawn out into a blunt caudal extension at $\frac{2}{3}$ height. Greatest height in front of mid-length ; greatest width at $\frac{2}{3}$ length. Dorsal margin without cardinal angles. Alae directed postero-ventrally and bearing a weak vertical sulcus on its crest. Whole of lateral surface covered with a series of pits. The ventral underside of the alae bears a few short longitudinal riblets. Duplicature moderately broad, crossed by few thick, straight radial pore canals (5 anteriorly). Hinge merodont consisting of a long straight denticulate median bar and two small divided terminal sockets in the left valve. Above the median element is a wide marginal shelf.

Remarks. *Cytheropteron* (*C.*) *milbournei* is known from the top part of the Lower Gault at Sevenoaks and Wrotham and it is never very abundant. It differs from *C.* (*C.*) *nanissimum* principally in the shape of the alae and in its ornamentation.

Cytheropteron (C.) nanissimum nanissimum Damotte & Grosdidier

(Pl. 7, figs. 13, 15)

1963 *Cytheropteron* (*C.*) *nanissumum* Damotte & Grosdidier : 56, pl. 1, figs. 2*a–f*.

Material. B.M.N.H. Io. 2907–08, two left valves from the *H. orbignyi* Subzone, Upper Gault ; Wrotham, Kent.

Remarks. This subspecies occurs throughout the Gault, appearing first in the *niobe* Subzone but not becoming abundant until the Upper Gault.

Cytheropteron (C.) nanissimum fenestrata subsp. nov.

(Pl. 7, figs. 14, 16. 19)

Derivation of name. fenestrata L. = window.

Diagnosis. Subspecies of *Cytheropteron* (*C.*) *nanissimum* with fenestrate ornamentation on ventral alae.

Holotype. A left valve, B.M.N.H. 2910, from the *H. spathi* Subzone, Lower Gault ; Henfield, Sussex.

Paratypes. B.M.N.H. Io. 2909, 2911. Two left valves from the same horizon and locality.

Measurements.

	Length (mm.)	Height (mm.)
Left valve (B.M.N.H. Io. 2910, holotype) . .	0·33	0·20

Description. Valves small, elongate with a ventro-lateral alate expansion. Dorsal and ventral margins convex, greatest height at mid-length. Anterior margin semicircular, posterior margin bluntly pointed forming a weak cardinal angle dorsally. Alae directed, posteriorly, with a small spine at its end and a weak vertical sulcus on its upper surface. Above the alae near the dorsal margin is a low node. From this node a rib runs downwards to the crest of the alae, whilst a short longitudinal rib runs across the ala at mid-height of the valves. The two ribs cross on the alae and form a " window like " pattern of ornament. The rest of the lateral surface is smooth.

Internal features identical with *C. nanissumum* s.s.

REMARKS. This subspecies is closely similar to *C.* (*C.*) *nanissimum* s.s. differing only in the nature of the ornamentation on the alae. In *C. nanissumum* s.s. the dorsal node and vertical rib are much stronger than in *C.* (*C.*) *nanissumum fenestrata* whilst the cross rib is absent.

The limited occurrence of *C.* (*C.*) *nanissumum fenestrata* in the *H. spathi* Subzone points to an ancestral relationship to *C. nanissumum* s.s. which does not appear until the *A. niobe* Subzone. *C.* (*C.*) *reightonensis* Kaye 1964 from the Barremian of Northern England is also very closely related being ornamented with rows of pits along the alae.

Cytheropteron (Cytheropteron) lamplughi nom. nov.

1964 *Cytheropteron* (*C.*) *punctata* Kaye : 103, pl. 5, figs. 7–8.

REMARKS. Professor W. A. Van den Bold of Louisana State University has kindly pointed out that the form I erected from the Lower Barremian at Speeton is in synonomy with *Cytheropteron punctatum* Brady (1868 : 449). I have therefore renamed my form *Cytheropteron* (*C.*) *lamplughi* in honour of G. W. Lamplugh and his basic research on the British Lower Cretaceous.

Subgenus ***EOCYTHEROPTERON*** Alexander 1933

Cytheropteron (Eocytheropteron) protonsa sp. nov.

(Pl. 6, figs. 1–6)

DERIVATION OF NAME. Protonsa L. = stretched out.

DIAGNOSIS. Large *Cytheropteron* with bilobed wing-like alate expansion and prominent upturned posterior caudal process.

HOLOTYPE. A left valve, B.M.N.H. Io. 2879, from the *D. cristatum* Subzone, Lower Gault ; Wrotham, Kent.

PARATYPES. B.M.N.H. Io. 2880–81. Two valves from the same horizon and locality.

MEASUREMENTS.

	Length (mm.)	Height (mm.)
Left valve (B.M.N.H. Io. 2879 holotype) . .	0·70	0·42
Right valve (B.M.N.H. Io. 2880)	0·67	0·42

DESCRIPTION. Valves large, elongate, laterally compressed. Dorsal margin strongly arched ; without cardinal angles in the left valves but with weak cardinal angles in the right valves. Ventral margin straight totally obscured by the prominent ventral alate expansion. Anterior margin broadly rounded ; posterior elongated into a prominent upturned caudal process at $\frac{2}{3}$ height. A large wing-like bilobed alate expansion occurs ventro-laterally; the posterior lobe being more extended. The lateral surface is covered with irregular vertical riblets which are only poorly developed anteriorly but are stronger posteriorly. The ventral undersurface bears a series of longitudinal ridges. A weak eye node occurs antero-dorsally. Duplicature rather narrow, crossed by few, straight, simple radial pore canals. Inner margin and line of concrescence coincide. Normal pore canals few. Hinge strongly developed. In the left valve there is a long interdentate furrow widest and deepest at the ends. In the right valve there is a long curved row of denticles, highest at the anterior and posterior ends.

REMARKS. *C.* (*E.*) *protonsa* occurs rarely in the upper part of the Lower Gault and in the Upper Gault. The wing-like bilobed alae, strong upturned caudal process, hinge and ornament make it quite unlike any other described species of *Cytheropteron* s.l.

Subgenus ***INFRACYTHEROPTERON*** Kaye 1964

Cytheropteron ? (Infracytheropteron) obscura sp. nov.

(Pl. 7, figs. 10–12)

DERIVATION OF NAME. obscura L. = obscure.

DIAGNOSIS. Ovate *Cytheropteron* s.l. with smooth lateral surface and rounded ventro-lateral tumidity. Hinge simple.

HOLOTYPE. A left valve, B.M.N.H. Io. 2903, from the *H. orbignyi* Subzone, Upper Gault, Wrotham, Kent.

PARATYPES. B.M.N.H. Io. 2904–06. Three valves and two carapaces from the same locality and horizon.

MEASUREMENTS.

	Length (mm.)	Height (mm.)
Left valve (B.M.N.H. Io. 2903 holotype) . .	0·42	0·25
Right valve (B.M.N.H. Io. 2905)	0·40	0·25

DESCRIPTION. Valves small, smooth, ovate with a marked ventro-lateral tumidity. Dorsal margin strongly arched, without cardinal angles. Ventral margin short and straight. Anterior margin broadly rounded, posterior drawn out into a blunt caudal process at just over mid-height. Greatest height at $\frac{1}{3}$ length, greatest width at mid-length. Lateral surface strongly and evenly inflated but with a flat marginal shelf anteriorly, posteriorly and postero-ventrally. A low, smooth eye tubercle occurs antero-dorsally. Duplicature moderately broad, particularly anteriorly and postero-ventrally, crossed by few straight, thick radial pore canals (7–8 anteriorly). Inner margin and line of concrescence coincide. Normal pore canals small and few. Hinge simple consisting of a smooth marginal bar in the left valve which fits on a marginal shelf in the right valve. Below the marginal shelf is a narrow median bar being discontinuous anteriorly and posteriorly.

REMARKS. *C.* (*I.*) *obscura* occurs throughout the bulk of the Gault. It first appears in the *niobe* Subzone but only becomes common in the Upper Gault. The relationship of the species is rather problematical, and it has been placed in the genus *Cytheropteron* s.l. on account of its shape and size. The lack of a marked alate expansion makes it akin to the subgenus *Eocytheropteron* but the hinge places it in the subgenus *Infracytheropteron.* The species shows strong similarities to the Tertiary genera *Bythocythere* and *Loxoconcha.* It differs primarily in the hingement and lack of vestibules though it does have a wide marginal shelf anteriorly and postero-ventrally. It is closest to *Loxoconcha minuta* Jennings 1936 from the Maastrichtian of New Jersey which is similar in shape and size but has ornamented valves. This latter form is doubtfully referred to the genus *Loxoconcha.*

Genus ***ORTHONOTACYTHERE*** Alexander 1934

Orthonotacythere fordensis sp. nov.

(Pl. 5, figs. 7–13)

DERIVATION OF NAME. After Ford Place near Wrotham, Kent, the location of the holotype.

DIAGNOSIS. *Orthonotacythere* with weak but distinct ribbing, low tubercles and wide deep median sulcus. The postero-lateral area is reticulate and strongly inflated.

HOLOTYPE. A male left valve, B.M.N.H. Io. 2871, from the *intermedius* Subzone, Lower Gault, Wrotham, Kent.

PARATYPES. B.M.N.H. Io. 2872–78. Six valves and two carapaces from the same horizon and locality.

MEASUREMENTS.

	Length (mm.)	Height (mm.)
Male left valve (B.M.N.H. Io. 2871, holotype) .	0·57	0·30
Male right valve (B.M.N.H. Io. 2872) . . .	0·55	0·28
Female left valve (B.M.N.H. Io. 2873) . . .	0·50	0·30

DESCRIPTION. Valves elongate, compressed, divided by a wide deep vertical median sulcus. Dorsal margin straight, ventral margin convex. Anterior broadly rounded, posterior forming a blunt postero-dorsal process. The median sulcus is limited ventrally by an irregular longitudinal ridge, below which, on the ventral undersurface, lies a further straight longitidunal ridge. Faint cross riblets join the two ribs. Antero-dorsally there is a prominent glassy eye tubercle jointed by a short rib to a reticulate tubercle immediately below it. Two ridges run from this lower tubercle, one anteriorly to meet the anterior margin, the other posteriorly towards the sulcus to meet a small tubercle where it turns abruptly through 90° to run vertically to connect with an irregular tubercle at the anterior end of the upper ventral longitudinal ridge. The area between the ridges is reticulate and irregularly ribbed. The lower ventral ridge runs anteriorly to reach the margin at $\frac{1}{4}$ height and posteriorly to fade out on the postero-ventral surface. The upper ventral ridge bears two weak tubercles ventrolaterally, the posterior one being more prominent. Faint irregular ridges run vertically from these tubercles merging with the general reticulation of the postero-lateral surface. This reticulation is made up of a series of weak longitudinal ridges joined by cross members. Antero-dorsally on the postero-lateral surface lies a low ridged tubercle. Internal features and hinge typical of the genus.

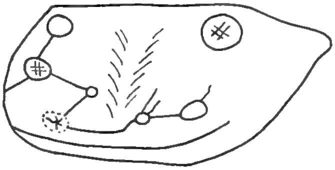

FIG. 5. Diagrammatic representation of the distribution of the ornamentation of *Orthonotacythere fordensis* sp. nov. ×75

REMARKS. *O. fordensis* occurs fairly commonly in the *A. intermedius* Subzone of the Lower Gault. It seems to be restricted to that subzone and is a valuable index form. *O. fordensis* is closely related to *O. inversa* (Cornuel) and related species forming an evolutionary sequence in the British Lower Cretaceous. It has all the major features of the group differing in minor details of the ornamentation and particularly in the subdued nature of the costation and tuberculation. Though almost certainly derived from these Lower Cretaceous forms it does not, however, show continuation of the trends seen there. The tendency towards increased tuberculation and simplification of costation is not followed and the species must therefore not be on the main "Boreal" stock. The related species of *Orthonotacythere* found in the "Tethyan" province do not follow the same trends during evolution, and ornamental patterns anomalous to that seen at Speeton have already been found (Kaye 1965*a*) in the Aptian of the Isle of Wight. It is to these species that close ancestry of *O. fordensis* must be attributed. The ornamentation of these Aptian species such as *O. catalaunica* Damotte & Grosdidier and *O. atypica* Kaye is closely similar to *O. fordensis* having the costation fairly complex with particularly the irregular nature of the upper ventral longitudinal ridge and the nature of the antero-dorsal costation in good agreement. The absence of *O. fordensis* s.s. from the Lower Gault at Speeton and its replacement by fragmentary specimens of a form intermediate between *O. fordensis* and *O. inversa tuberculata* seem to bear this out particularly on consideration of the joining of the " Boreal " and " Tethyan " seas in this area in Apto-Albian times.

Only a single specimen belonging to this group of the genus *Orthonotacythere* has so far been found from post *H. spathi* age Gault deposits. This specimen from the *nitidus* Subzone (Bed 31) at Henfield shows increased tuberculation, poor costation, poor development of the ventral longitudinal ridge and no surface reticulation. These features seem consistent with the overall trends seen at Speeton and the specimen perhaps shows a further stage of this major evolutionary pattern.

Orthonotacythere minutissima sp. nov.

(Pl. 8, figs. 5–11)

DERIVATION OF NAME. minutissimum L. = very small.

DIAGNOSIS. Very small *Orthonotacythere* with ventral alate longitudinal rib and prominent eye tubercle.

HOLOTYPE. A left valve, B.M.N.H. Io. 2926, from the *H. varicosum* Subzone, Upper Gault, Wrotham, Kent.

PARATYPES. B.M.N.H. Io. 2927–32. Five valves and one carapace from the same horizon and locality.

MEASUREMENTS.

	Length (mm.)	Height (mm.)
Left valve (B.M.N.H. Io. 2926, holotype) . .	0·28	0·16
Right valve (B.M.N.H. Io. 2927)	0·28	0·15

DESCRIPTION. Valves very small, elongate, compressed. Dorsal margin long and straight; ventral margin straight, shorter and parallel to it. Anterior margin bluntly rounded; posterior with a weak caudal process at the postero-dorsal cardinal angle. Eye tubercle exceedingly prominent, protruding well above the dorsal margin. Greatest height at $\frac{1}{5}$ length at the anterior cardinal angle; greatest width just behind mid-length. Lateral surface divided by a vertical median sulcus which is limited ventrally by a prominent alate longitudinal ridge. This ridge increases in height posteriorly, being drawn out into a blunt laterally directed spine. The base of the sulcus does, however, notch this rib slightly, weakly dividing it into two sections. A large tubercle occurs dorsally on the postero-lateral area. Lateral surface smooth or pitted. Anterior margin denticulate (5 denticles). Duplicature moderately broad, crossed by few, straight radial pore canals. Inner margin and line of concrescence coincide. Interior eye pit prominent. Hinge simple consisting of a long, straight denticulate bar in the left valve. In the right valve there is a long, straight interdentate furrow with a high smooth bar above it.

REMARKS. *O. minutissima* occurs rarely in the Upper Gault but has not yet been found in the Lower Gault. Its exceptionally small size makes it distinct from other species of the genus. The pattern of the main ornamentation shows no affinities to any other described form but I have found identical or closely comparable forms from the Hauterivian/Barremian of Lincolnshire. The hinge of this species is not strictly typical of the genus *Orthonotacythere*, lacking well defined terminal elements, but the shape, sulcus and ornamentation are all closely comparable to that genus. It may, however, be possible to include this species in a redefined subgenus such as *Stillina* Laurencich.

Orthonotacythere spinifera sp. nov.

(Pl. 7, figs. 1–3, 5)

DERIVATION OF NAME. Spinifera L. = spined.

DIAGNOSIS. Small *Orthonotacythere* with weak median sulcus, pronounced reticulation over whole of valves, and a series of large spines arranged over lateral surface.

HOLOTYPE. A left valve, B.M.N.H. Io. 2895, from the *A. intermedius* Subzone (Bed 13), Lower Gault, Wrotham, Kent.

PARATYPES. B.M.N.H. Io. 2894, a right valve from the *H. orbignyi* subzone (Bed 13), Upper Gault, Wrotham. B.M.N.H. Io. 2896–97, two valves from the *A. intermedius* Subzone, Lower Gault, Henfield, Sussex.

MEASUREMENTS.

	Length (mm.)	Height (mm.)
Left valve (B.M.N.H. Io. 2895, holotype) . .	0·42	0·22
Right valve (B.M.N.H. Io. 2894)	0·42	0·22

DESCRIPTION. Valves small, elongate, strongly laterally compressed. Dorsal margin long and straight; ventral margin short, straight and parallel to it. Anterior margin bluntly rounded forming a well marked antero-dorsal cardinal angle; posterior drawn out to form an acute postero-dorsal caudal process. Anterior and posterior margins strongly spined. Vertical median sulcus very weak or absent. Eye tubercle rounded and glassy, set at dorsal end of a short high, blade-like vertically elongated spine. A similar bladed spine lies at $\frac{2}{3}$ length on the dorsal margin with a further smaller spine at $\frac{1}{3}$ length just below the dorsal margin. An arcuate row of four extremely prominent spines runs parallel to the ventral margin. Below this row is a series of smaller semi-fused spines culminating posteriorly in a larger bilobed spine. A pair of smaller spines occur posteriorly, one on the dorsal margin, the other being vertically below it at $\frac{3}{4}$ height. The whole of the lateral surface is strongly reticulate.

Duplicature narrow, crossed by few straight radial pore canals. Normal pore canals and muscle scars not seen. Hinge strongly developed consisting in the left valve of two short, subdivided sockets separated by a long, straight, lobed bar. Above the median bar is a narrow marginal shelf. In the right valve there are two bar-like denticulate terminal teeth (5 denticles in each) separated by a wide, strongly divided, median groove.

REMARKS. *Orthonotacythere spinifera* is rare in most of the Gault, a few specimens having been found at a variety of levels and localities. It is more abundant in the Gault at Pinhay in Devon and is perhaps a littoral species. *O. spinifera* is quite unlike other described species of the genus having such characteristic features as the weak median sulcus entirely covered by the surface reticulations and the series of marginal and lateral spines. It is smaller than most other species of the genus but does show some affinities with the *O. inversa* group in the arrangement of the spines.

Family **BRACHYCYTHERIDAE**

Genus ***ALATACYTHERE*** Murray & Hussy 1942

Alatacythere robusta robusta (Jones & Hinde)

(Pl. 10, figs. 9, 10)

1964*b* *Alatacythere robusta* (Jones & Hinde); Kaye: 51, pl. 2, fig. 18.

MATERIAL. B.M.N.H. Io. 2964, 2965, two valves from the uppermost Gault immediately below the Cambridge Greensand, Arlesey Beds.

MEASUREMENTS.

	Length (mm.)	Height (mm.)
Left valve (B.M.N.H. Io. 2965)	1·05	0·51

Alatacythere robusta langi subsp. nov.

(Pl. 10, figs. 1–4)

DERIVATION OF NAME. After W. D. Lang in appreciation of his stratigraphical and palaeontological work on the Cretaceous in Devon and Dorset.

DIAGNOSIS. Subspecies of *Alatacythere robusta* (Jones & Hinde) 1890 having ventro-lateral alae less drawn out and dorsal longitudinal ridge more pronounced.

HOLOTYPE. A male left valve, B.M.N.H. Io. 2940, from the basal Upper Gault; Pinhay, Devon.

PARATYPES. B.M.N.H. Io. 2941–44. Six valves from the same horizon and locality.

MEASUREMENTS.

	Length (mm.)	Height (mm.)
Male left valve (B.M.N.H. Io. 2940, holotype) . .	1·02	0·54
Male right valve (B.M.N.H. Io. 2943) . . .	0·98	0·53
Female Right valve (B.M.N.H. Io. 2942) . . .	0·92	0·50
Female left valve (B.M.N.H. Io. 2941) . . .	0·95	0·50

DESCRIPTION. Valves large, elongate, laterally compressed. Dorsal and ventral margins straight, converging slightly posteriorly. There are well marked antero-dorsal and postero-dorsal cardinal angles. Anterior margin broadly rounded; posterior margin weakly pointed at mid-height, both strongly denticulate. Each marginal tubercle corresponds to the extremity of a radial pore canal. Greatest height at $\frac{1}{4}$ length; greatest width at $\frac{3}{4}$ length. Eye tubercle large and glassy, joined to a prominent anterior marginal ridge which follows the entire anterior margin to be continued along the crest of the high extended ventral alate expansion. This alate expansion obscures the whole of the ventral margin and strongly increases in height posteriorly where it terminates in a short ventro-laterally directed spine. The ventral undersurface lacks marked costation. A short, high longitudinal ridge occurs obscuring the posterior and central part of the dorsal margin. It is not continued to join the eye tubercle. The lateral surface is smooth. Duplicature moderately broad, crossed by numerous straight radial and pseudoradial pore canals. Inner margin and line of concrescence coincide throughout. Normal pore canals scarce over the bulk of the lateral surface but abundant along the ridged crest of the alae. Hinge strong, amphidont, consisting in the left valve of two terminal sockets, open ventrally and separated by a long, straight, denticulate bar. Below the anterior end of the median bar there is a high, smooth, circular tooth, whilst above the whole of it there is a narrow marginal shelf but no accommodation groove. In the right valve there is a high " boss-like " anterior terminal tooth and a triangular, elongate, divided posterior tooth separated by a long straight locellate furrow. Anteriorly the median groove opens into a deep smooth circular socket. Above and below the median groove are narrow bars.

Remarks. *A robusta langi* has so far been found from the basal Upper Gault, *H. orbignyi* Subzone at Pinhay, Devon, at Swanage, Dorset and in the Isle of Wight. It occurs earlier than *A. robusta* s.s. which is found in the topmost Gault of the Wealden Area and East Anglia. *A. robusta* s.s. is distinguished from *A. robusta langi* by the greater lateral elongation of the alae and the weak development of the dorsal ridge which does not obscure the margin. The greater elongation of the alae makes the valves higher. *A. robusta langi* is the earliest occurrence of the genus in the Cretaceous and specimens of *Cythereis reticulata* s.l. Jones & Hinde from the top Lower Gault have been found at Henfield showing weak ventral alation and typical *Alatacythere* shape though retaining the reticulation. Such forms are possibly intermediates between the two genera and indicate the origin of the genus *Alatacythere*.

Family **BYTHOCYTHERIDAE**

Genus ***MONOCERATINA*** Roth 1928

Monoceratina longispina (Bosquet)

(Pl. 1, figs. 3–7)

1854 *Cythere longispina* Bosquet: 86. pl. 6. figs 7*a* *d*
1941 *Monoceratina longispina* (Bosquet); Bonnima: 40, pl. 6 fihs 67-76
1964*b* *Monoceratina longispina* (Bosquet); Kaye: 53, pl. 3 fig 1
1964 *Monoceratina longispina* (Bosquet); Szczechura: 388, pl, 3, fig 5 pl. 11, fig. 1:

Material. B.M.N.H. Io. 2820–23 from the *H. orbignyi* Subzone, Upper Gault ; Wrotham, Kent. B.M.N.H. Io. 2824 from the *E. doris* Subzone, Lower Gault ; Wrotham, Kent.

Measurements.

	Length (mm.)	Height (mm.)
Adult left valve (B.M.N.H. Io. 2820) . . .	0·82	0·42
Adult right valve (B.M.N.H. Io. 2821) . . .	0·80	0·38
Juvenile carapace (B.M.N.H. Io. 2822) . . .	0·65	0·35
Juvenile left valve (B.M.N.H. Io. 2823) . . .	0·56	0·32

Description. The finding of additional material allows a fuller description of this species than that given by Kaye (1964*b*).

Valves elongate, inflated laterally. Dorsal and ventral margins straight and parallel. Cardinal angles well developed. Anterior margin broadly rounded ; posterior triangular, angled postero-dorsally. Lateral surface inflated with a prominent vertical median sulcus. Below the sulcus is a broad based conical, laterally directed spine. This spine and associated swelling limit the sulcus strongly. Apart from a few rows of faint concentric reticulation along the crest of the alae the lateral surface is smooth. Some faint reticulation does, however, occur on the swollen antero-lateral part of the valves in certain specimens. The greatest width is just posterior to the mid-point of the valves. The marginal parts of the valves are rather flattened particularly anteriorly and ventrally.

The hinge consists of a long narrow groove in the right valve which accommodates the long, straight, smooth marginal bar of the left valve. Weak false sockets are sometimes developed, particularly anteriorly in the left valve. The porcellaneous preservation of the specimens obtained make the radial pore canals and muscle scars invisible, normal pore canals are, however, rather small and irregularly scattered over the lateral surface.

Juveniles are rather dissimilar to the adults. In general they have a rounded alate expansion and no spine. This difference is, however, seen in the adults of certain species of *Monoceratina* (particularly from the British Oxfordian) and is possibly a dimorphic feature. By no means all the juveniles of *M. longispina* are just alate and a few specimens with spines have been found. The occurrence of specimens without spines is not common to all species of *Monoceratina* and no specimens without spines belonging to *M. umbonata* Williamson have been found in the Gault even though the species is much more abundant than *M. longispina*. The juveniles of *M. longispina* are themselves variable in ornamentation and two instars are illustrated. Penultimate instars have a wide marginal flattened area. The inflated alate expansion is strongly reticulate and a large node covered with reticulation occurs anterior to the sulcus. A narrow ridge crosses the sulcus and runs on to the postero-lateral area. Smaller instars are much less inflated and lack the flattened marginal area. They are completely smooth and have the sulcus wider and more open. Besides being strongly limited ventrally the sulcus is weakly limited dorsally giving the form of a wide median depression.

Remarks. This species is not common but occurs consistently throughout the Gault. The original description was from the Senonian and I have recorded it from the Cambridge Greensand at Barrington. It has so far been found in the Gault of the Wealden area at Folkestone, Wrotham, Sevenoaks and Henfield where specimens occur in clays ranging in age from *A. intermedius* Subzone to *H. varicosum* Subzone. It has not been found in the *spathi* Subzone assemblages but probably occurs in the higher subzones of the Upper Gault which have not yet been studied. The closest species of *M. longispina* seems to be *M. parallela* Alexander 1934 from the Santonian of Texas which is a little smaller and more strongly inflated. Good details of *M. parallela* are lacking and it is possible that the two forms are synonymous. *M. longispina* differs from *M. acanthoptera* (Marsson) 1880 in that the latter is much smaller and has the spine set much further back on the carapace. The form recorded as *M. acanthoptera* (Marsson) by Alexander (1934) probably belongs to *M. parallela*. As shown earlier *M. umbonata acanthoptera* (Jones & Hinde) is a separate species viz. *M. umbonatoides* Kaye 1964*b*.

Monoceratina sp.

(Pl. 11, figs. 9–10)

Material. A right valve, B.M.N.H. Io. 2945, from the *H. spathi* Subzone, Middle Albian ; Devizes, Wiltshire.

Measurements.

	Length (mm.)	Height (mm.)
Right valve (B.M.N.H. Io. 2945)	0·55	0·25

Description. Valves elongate, with straight parallel dorsal and ventral margins. Lateral surface inflated with a vertical median sulcus, limited ventrally by an alate expansion. The crest of the ala bears a short broad based conical spine. This spine is set just behind the ventral end of the sulcus and is laterally directed. A large smooth semicircular swelling occurs dorsally on the antero-lateral surface whilst a short slightly curved ridge runs near to the dorsal margin on the postero-lateral surface. A weak anterior marginal rib occurs which is not joined to the ala ventrally. The ventral and posterior marginal areas are flattened. The lateral surface is smooth.

Remarks. Only a single specimen of this species has so far been found, which seems to bear no relationship to other species of the genus found in the Albian and occurs earlier than them (in the *H. spathi* Subzone). Its closest relative is *M. bonnemai* Kaye 1964*b* from which it differs in size and ornamentation and in having only one laterally directed spine.

Family **PROGONOCYTHERIDAE**

Genus ***ACROCYTHERE*** Neale 1960

Acrocythere striata sp. nov.

(Pl. 4, figs. 4–10)

Derivation of name. Striatus L. = striate.

Diagnosis. *Acrocythere* with ornamentation of numerous longitudinal striate ridges.

Holotype. A left valve, B.M.N.H. Io. 2853, from the basal Upper Gault (Upper Albian) ; Pinhay, Devon.

Paratypes. B.M.N.H. Io. 2851–52, 2854–57. Eight valves and two carapaces from the same horizon and locality.

Measurements.

	Length (mm.)	Height (mm.)
Left valve (B.M.N.H. Io. 2853, holotype) . .	0·58	0·28
Right valve (B.M.N.H. Io. 2852)	0·58	0·23

Description. Valves small, elongate, strongly compressed laterally. Dorsal and ventral margins long and straight ; tapering slightly posteriorly in the left valves but parallel in the right valves. Dorsal margin without marked cardinal angles. Anterior margin broadly rounded ; posterior margin pointed at mid-height. Greatest height at $\frac{1}{4}$ length ; greatest width at mid-length. Lateral surface ornamented by numerous longitudinal striate ridges. The ridges continue over the whole of the lateral surface being usually ten in number. Anteriorly they tend to swing slightly ventrally and certain of them coalesce. Vertical cross ribbing is absent, the area between the ridges being finely pitted. Eye spots are absent.

Duplicature fairly broad crossed by few, very fine, simple radial pore canals (8–10 anteriorly). Normal pore canals rather few, confined to the crests of the ridges. Inner margin and line of concrescence coincide throughout. Muscle scars not seen. Hinge strong merodont consisting in the left valves of two deep strongly divided terminal sockets separated by a long, straight, coarsely denticulate bar. In the right valve there are two triangular terminal teeth, highest away from the centre of the valve and each divided into four large denticles. Between the terminal teeth there is a long, straight coarsely crenulate (almost interdentate) furrow.

Remarks. *A. striata* differs considerably from the other members of the genus in ornamentation and lack of even a rudimentary median sulcus and eye spots. Its dissimilarities are such that it could possibly belong to a new genus. The hinge and basic longitudinal striate ornamentation are strongly reminiscent of *Pleurocythere* and *Lophocythere*.

Genus **NEOCYTHERE** Mertens 1956

Subgenus ***PHYSOCYTHERE*** Kaye 1963

Neocythere (Physocythere) tenuis sp. nov.

(Pl. 6, figs. 14–17)

Derivation of name. Tenuis L. = thin.

Diagnosis. Small *Neocythere* with thin shell and weakly developed hinge. Lateral surface devoid of ornamentation.

Holotype. A left valve, B.M.N.H. Io. 2889, from Bed 1, *A. intermedius* Subzone, Lower Gault ; Small Dole, Henfield, Sussex.

Paratypes. B.M.N.H. Io. 2890–93 from the same horizon and locality.

Measurements.

	Length (mm.)	Height (mm.)
Left valve (B.M.N.H. Io. 2889 holotype) . . .	0·50	0·30
Right valve (B.M.N.H. Io. 2890)	0·50	0·28

Description. Valves small, ovate, thin shelled. Dorsal margin straight ; ventral margin weakly convex and subparallel to it. Anterior and posterior margins broadly rounded. Lateral surface smooth, inflated. Greatest height at $\frac{1}{3}$ length ;

greatest width at mid-length. In dorsal view valves convex with acute anterior and posterior ends. A slight ventro-lateral tumidity occurs. Duplicature rather narrow, crossed by few (7–8 anteriorly) thick, straight radial pore canals. Inner margin and line of concrescence coincide throughout. Normal pore canals rather large, irregularly scattered over most of the lateral surface, but forming two concentric rows along the crest of the ventro-lateral expansion. Hinge weak having, in the left valves, two faintly divided sockets separated by a weakly denticulate bar. Above the median bar is a prominent marginal shelf but no accommodation groove. The terminal teeth in the right valve are low, triangular in shape and weakly divided. Muscle scars a slightly postero-dorsally inclined row of four oval scars with a U-shaped scar antero-dorsally and a small oval scar antero-ventrally of them.

REMARKS. This species has been recorded from the Lower Gault *A. intermedius* Subzone at Henfield but is known to occur abundantly in the Upper Gault in East Anglia. It differs from other species of *Neocythere* s.l. in its shape, thinness of shell, weak hinge and lack of ornamentation. In shape and size it is nearest to *N.* (*P.*) *pustulosa* Kaye 1965*a* from the Upper Aptian of the Isle of Wight but lacks the strong ornamentation. Certain related undescribed specimens occur in the Aptian but they are larger and of unequal inflation.

Family **PROTOCYTHERIDAE**

Genus ***VEENIA*** Butler & Jones 1957

Veenia compressa Kaye

(Pl. 11, figs. 13–15)

1965*a* *Veenia compressa* Kaye : 44, pl. 7, figs. 6, 7.

MATERIAL. Two valves and one carapace, B.M.N.H. Io. 2868–70, from the basal Upper Gault ; Pinhay, Devon.

REMARKS. This species previously recorded from the Upper Aptian of the Isle of Wight has now been found rather more abundantly and somewhat better preserved in the basal Upper Aptian at Pinhay in Devon. These latter specimens are identical although somewhat smaller (0·58 mm.).

Veenia florentinensis Damotte

(Pl. 11, figs. 1–8)

1961 *Veenia* (*Protoveenia*) *florentinensis* Damotte : 102, pl. 1, figs. 1–3, pl. 2, figs. 1–6.

MATERIAL. B.M.N.H. Io. 2974–75, two valves from the *H. spathi* Subzone Lower Gault ; Henfield. B.M.N.H. Io. 2971–73, 2976–79, ten valves and two carapaces from the *H. orbignyi* Subzone Upper Gault ; Pinhay, Devon.

MEASUREMENTS.

	Length (mm.)	Height (mm.)
Left valve (B.M.N.H. Io. 2975)	0·50	0·28
Right valve (B.M.N.H. Io. 2974)	0·49	0·25
Left valve (B.M.N.H. Io. 2978)	0·70	0·36
Left valve (B.M.N.H. Io. 2971)	0·65	0·35
Right valve (B.M.N.H. Io. 2976)	0·58	0·28
Right valve (B.M.N.H. Io. 2977)	0·54	0·28
Left valve (B.M.N.H. Io. 2972)	0·50	0·30
Left valve (B.M.N.H. Io. 2979)	0·48	0·27
Right valve (B.M.N.H. Io. 2973)	0·48	0·25

REMARKS. Damotte erected this species in 1961 placing it within a new subgenus *Protoveenia*. This subgenus was differentiated primarily on a basis of having very few radial pore canals. Damotte's specimens came from the Lower Gault and comparable specimens occur in the *H. spathi* and *A. intermedius* Subzones in Britain. Other specimens of this species occur at higher horizons particularly in Devon, Dorset and the Isle of Wight in clays from the *H. orbignyi* Subzone, Upper Gault and these specimens have a much larger size range than those from the Lower Gault. The Lower Gault forms have a length in the range of 0·40–0·50 mm., whilst specimens from the Upper Gault reach as much as 0·70 mm. in length. The largest specimens differ slightly from the smaller ones but specimens of typical Lower Gault size and features and all intermediates occur together with them in the same sample. The larger specimens are more inflated, have the longitudinal ribs less keel-like than the small ones and have the dorsal ridge and antero-dorsal hinge ear less well separated. They also have more radial pore canals and therefore make the subgenus *Protoveenia* unusable and its postulated ancestry to *Veenia* improbable. The smaller specimens in the Upper Gault are identical with Damotte's Lower Gault forms and it appears that the species is therefore not only of variable size but that the number of radial pore canals is a direct function of the size. Sexual dimorphism is not known from the Lower Gault specimens but is well marked in the Upper Gault forms.

Family **TRACHYLEBERIDIDAE**

Genus **CYTHEREIS** Jones 1849

Cythereis angulatoides nom. nov.

1964*a* *Cythereis angulata* Kaye : 327, pl. 54, fig. 11.

REMARKS. Professor W. A. Van den Bold of Louisiana State University has kindly pointed out that the form erected as *C. angulata* from the Upper Aptian of Surrey has the name preocupied by Sars (1866 : 40). I have therefore renamed my form *C. angulatoides*.

Cythereis gatyensis Damotte & Grosdidier

(pl. 11, figs. 11, 12)

1963 *Cythereis ? gatyensis* Damotte & Grosdidier : 58, pl. 3, figs. 8*a–g*.
1963*b* *Cythereis lamplughi* Kaye : 236, pl. 19, figs. 14–16.
1965*a* *Cythereis lamplughi* Kaye; Kaye: 46, pl. 7, figs. 14, 15.

MATERIAL. B.M.N.H. Io. 2966–67. Two specimens from the *H. spathi* Subzone, Lower Gault ; Culham, Oxfordshire.

REMARKS. Specimens kindly sent to me by Dr. E. Grosdidier show that *Cythereis lamplughi* Kaye 1963*b* is synonymous with *Cythereis gatyensis* Damotte & Grosdidier 1963, the latter having two months' priority. *C. gatyensis* is abundant but restricted to the *H. spathi* Subzone in the Gault. It is also known from the Upper Aptian of the Isle of Wight. It is a valuable index fossil for the *H. spathi* Subzone having been found in clays of that age at Speeton, West Heslerton, Culham and Henfield.

Cythereis glabrella Triebel

(Pl. 10, figs. 5–8)

1940 *Cythereis glabrella* Triebel : 196, pl. 6, figs. 60–62.

MATERIAL. B.M.N.H. Io. 2962–63. Two valves from the basal Upper Gault at Pinhay, Devon.

MEASUREMENTS.

	Length (mm.)	Height (mm.)
Left valve (B.M.N.H. Io. 2962)	0·90	0·55
Right valve (B.M.N.H. Io. 2963)	0·90	0·50

REMARKS. This smooth, inflated species is not common in the British Gault having been found so far only at Pinhay and in the top Red Chalk at Speeton, Yorks. It differs from the much more abundant *C. folkstonensis* Kaye 1964*b* in its less angular appearance, smaller size and in having a smooth rather than spined median rib. It is similar to *C. nuda* Jones & Hinde 1890 differing in being larger, more inflated and in having the median rib well developed.

Cythereis pinhayensis sp. nov.

(Pl. 9, figs. 1–8)

DERIVATION OF NAME. After Pinhay Point, Devon, the only known occurrence of the species.

DIAGNOSIS. Small, reticulate but not spined *Cythereis* with prominent muscle node and weakly convergent long margins.

HOLOTYPE. A male left valve, B.M.N.H. Io. 2946, from the basal Upper Gault ; Pinhay Point, Devon.

PARATYPES. B.M.N.H. Io. 2947–54. Ten valves and two carapaces from the same horizon and locality.

MEASUREMENTS.

	Length (mm.)	Height (mm.)
Male left valve (B.M.N.H. Io. 2946 holotype) . .	0·95	0·50
Male right valve (B.M.N.H. Io. 2947) . . .	0·95	0·48
Female left valve (B.M.N.H. Io. 2948) . . .	0·85	0·50

DESCRIPTION. Valves elongate, laterally compressed. Dorsal and ventral margins straight, converging slightly posteriorly. Antero-dorsal and postero-dorsal cardinal angles well marked. Anterior margin broadly rounded, posterior triangular, angled just below mid-height. Anterior and posterior margins strongly denticulate, each tubercle marking the distal end of a radial pore canal. Greatest height at $\frac{1}{5}$ length; greatest width at $\frac{2}{5}$ length. Eye tubercle glassy, distinct, joined to a prominent anterior marginal ridge. This ridge bears a row of tubercles on its upper surface each marking the extremities of a pseudoradial pore canal. A large, high, smooth subcentral muscle node occurs, separated from the anterior end of a short median longitudinal ridge but it is joined by a weak vertical ridge to the eye tubercle. A short straight low ridge follows the dorsal margin, being connected by a vertical cross ridge posteriorly to the posterior end of the median ridge. A shallow depression separates the anterior end of the dorsal rib and the muscle node. A prominent ridge, increasing in height posteriorly follows the ventral margin. Anteriorly it is continuous with the anterior marginal ridge. A small tubercle, the porenkagel, occurs at mid-length between the median and ventral longitudinal ribs. Ventral undersurface covered with faint longitudinal riblets. Lateral surface strongly reticulate.

Duplicature fairly broad, crossed by numerous thin, straight radial and pseudoradial pore canals. Hinge strong amphidont, consisting in the left valve of two terminal divided sockets, open ventrally, separated by a long, straight, smooth bar. Below the anterior end of the median bar is a high, smooth, circular tooth whilst above the median element is a narrow marginal shelf. In the right valve there are two high boss-like terminal teeth, each with weak lobation on the summit, separated by a long, straight, shelf-like median furrow. Anteriorly the furrow opens into a deep circular socket. Above the median furrow is a high narrow smooth marginal bar.

REMARKS. *C. pinhayensis* is only known from the basal Upper Gault at Pinhay Point in Devon where it is one of the most abundant members of the fauna. It differs from the *C. reticulata* (Jones & Hinde) 1890, *C. hirsuta* Damotte & Grosdidier 1963 group in being smaller, less inflated and lacking the spination of the longitudinal ribs. *C. lurmannae* Triebel 1940*a* and *C. corrigenda* Kaye 1964*b* differ in being more strongly compressed laterally, more strongly convergent posteriorly and lacking the pronounced reticulation. *C. glabrella* Triebel 1940*a* is more inflated and smooth whilst *C. folkstonensis* Kaye 1964*b* has all the characteristics of *C. reticulata* in addition to being smooth. *C. matronae* Damotte & Grosdidier 1963 is smaller, smooth and has rows of spines rather than well marked longitudinal ridges whilst *Cythereis thorenensis* 1940*a* Triebel lacks the muscle node and median longitudinal ridge. The closest form is *C. geometrica fittoni* Kaye 1965*a* from the Upper Aptian of the Isle of Wight which differs in being more angular in outline, particularly posteriorly and in having the long margins more strongly convergent. True *C. geometrica* Damotte & Grosdidier 1963*a* is smooth whilst *C. sutterbyensis* Kaye 1965*b* and *C. bekumensis* Triebel 1940*a* have less marked reticulation and a short spined median longitudinal rib. *C. acuticostata* Triebel 1940*a* has the median rib and muscle node joined. *C. blanda* Kaye 1963*b* is similar and lacks surface reticulation. *C. angulata* Kaye 1964*a* differs in the distribution of the ribs and lacks a muscle node whilst *C. cristata* Kaye 1964*a* is much more strongly compressed, pitted and has weak ribbing.

Suborder MYODOCOPINA

Family **CONCHOECIIDAE**

Genus ***CONCHOECIA*** Dana 1849

Conchoecia sp. A

(Pl. 2, figs. 2, 7)

MATERIAL. A single carapace, B.M.N.H. Io. 2833, from the Upper Albian, *H. orbignyi* Subzone ; Wrotham, Kent.

MEASUREMENTS.

	Length (mm.)	Height (mm.)
Carapace (B.M.N.H. Io. 2833)	0·58	0·35

REMARKS. Only one previous fossil occurrence of the genus *Conchoecia* is known. This species, *C. cretacea* Pokorny 1964, is known as two pyrite infilled carapaces from the Upper Cretaceous of Bohemia. The present record extends the range of the genus into the Lower Cretaceous. The valves are extremely thin and very fragile, the single specimen being a pyrite filled carapace. It is similar to Pokorny's form in shape and ornamentation but is approximately half the size. This may indicate that it is an instar of *C. cretacea.* The anterior rostrum is particularly well developed but the posterior prolongation of Pokorny's form is absent. It also differs in ornamentation being less strongly ribbed and having the cross ribs more prominent.

Conchoecia sp. A. differs markedly from the form described as ? *Conchoecia* sp. B. in shape, ornament and in the weak or absent rostrum in the latter.

? ***Conchoecia*** sp. B

(Pl. 1, figs. 1–2)

MATERIAL. A carapace, B.M.N.H. Io. 2819, from the basal Upper Albian, *H. orbignyi* Subzone ; Wrotham, Kent.

MEASUREMENTS.

	Length (mm.)	Height (mm.)
Carapace (B.M.N.H. Io. 2819)	0·87	0·62

Description. One large pyrite filled carapace of this species has been found together with four smaller similarly preserved specimens. The shell is extremely thin and is broken in places. In shape the specimens are suboval and inflated ; the greatest height and width being at $\frac{2}{3}$ length. The dorsal margin is strongly arched ; the ventral margin is weakly convex or straight. The anterior and posterior ends are bluntly rounded, without prominent extensions or a marked rostrum. The valves are ornamented with a series of shallow longitudinal grooves. They are scattered irregularly over the surface, being more concentrated posteriorly. They measure 0·10–0·12 mm. in length.

Remarks. The inflation, shape and ornamentation of the specimen differs somewhat from Pokorny's form and it is undoubtedly a distinct species. The lack of a pronounced rostrum could place it in a different genus, its similarities in shape and ornamentation layout to the Palaeozoic Entomozoidae perhaps indicating a relationship.

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PLATE 1

All figures ×60

? ***Conchoecia*** sp. B p. 250

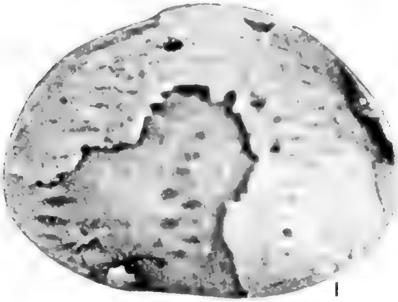
FIG. 1. Carapace, from left. Io. 2819, Wrotham
FIG. 2. Carapace, from right. Io. 2819, Wrotham

Monoceratina longispina (Bosquet) p. 242

FIG. 3. Adult left valve, lateral view. Io. 2820, Wrotham
FIG. 4. Adult right valve, lateral view Io. 2821, Wrotham
FIG. 5. Juvenile carapace, lateral view Io. 2822, Wrotham
FIG. 6. Juvenile carapace, dorsal view. Io. 2822, Wrotham
FIG. 7. Juvenile left valve, lateral view. Io.2823, Wrotham

Clithrocytheridea heslertonensis Kaye p. 228

FIG. 8. Female left valve, lateral view. Io. 2825, W. Heslerton
FIG. 9. Female right valve, lateral view. Io. 2826, W. Heslerton
FIG. 10. Female right valve, internal view. Io. 2826. W. Heslerton
FIG. 11. Female carapace, dorsal view. Io. 2827, W. Heslerton
FIG. 12. Female left valve, internal view. Io. 2825, W. Heslerton



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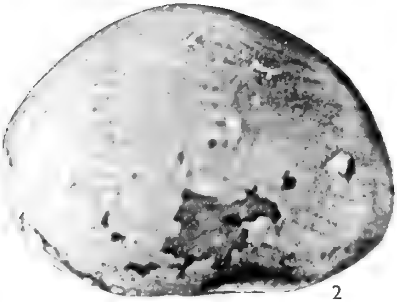

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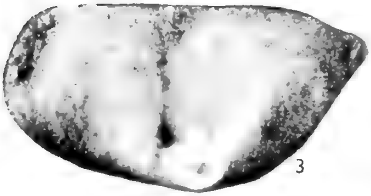

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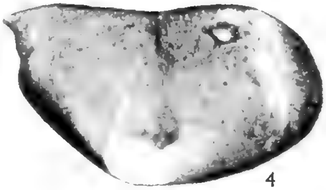

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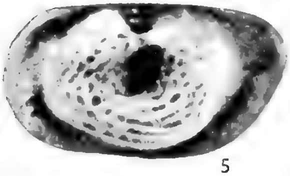

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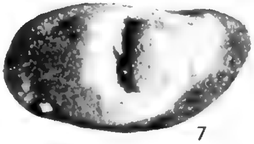

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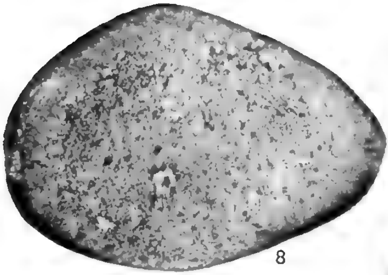

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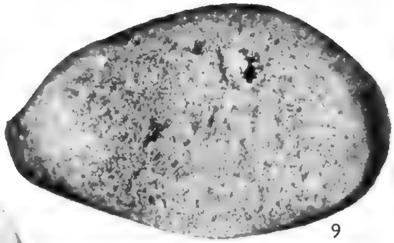

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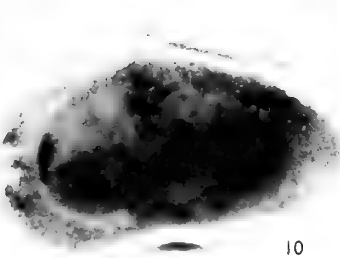

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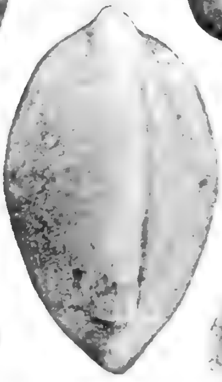

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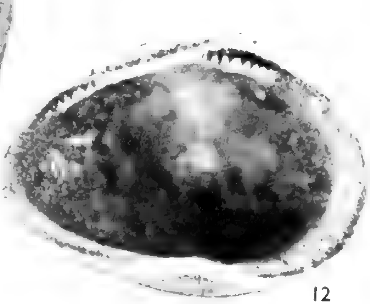

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PLATE 2

All figures ×60

Bairdia pseudoseptentrionalis (Mertens) p. 223

Fig. 1. Left valve, lateral view. Io. 2828, Arlesey
Fig. 3. Right valve, lateral view. Io. 2929, Arlesey
Fig. 4. Right valve, internal view. Io. 2830, Arlesey
Fig. 5. Left valve, internal view, Io. 2831, Arlesey
Fig. 6. Carapace, from right. Io. 2832, Arlesey

Conchoecia sp. A p. 250

Fig. 2. Carapace, from left. Io. 2833, Wrotham
Fig. 7. Carapace, from right. Io. 2833 Wrotham


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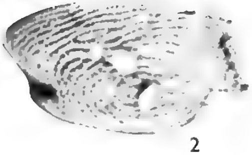
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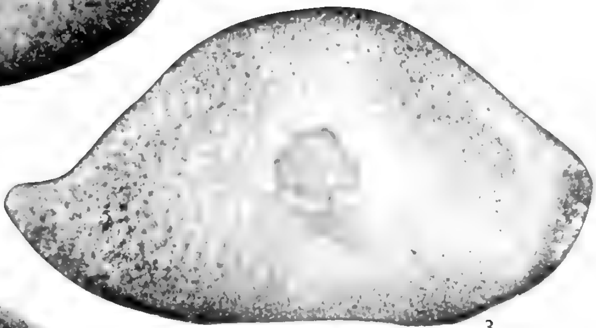
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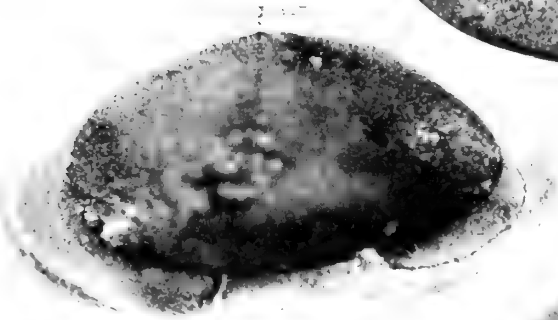
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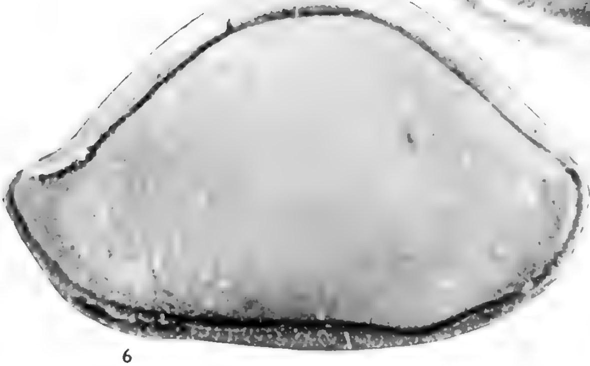
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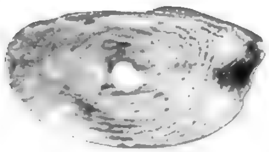
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PLATE 3

All figures ×80

Pontocyprella semiquadrata sp. nov. p. 224

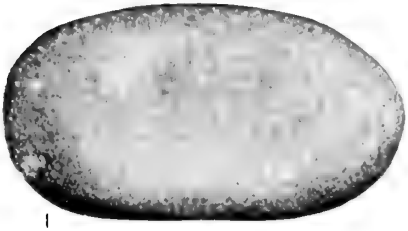
FIG. 1. Left valve holotype lateral view. Io. 2834. Wrotham
FIG. 2. Right valve, dorsal view. Io. 2836, Wrotham
FIG. 3. Left valve, lateral view. Io. 2835, Wrotham
FIG. 4. Right valve, lateral view. Io. 2836, Wrotham
FIG. 5. Right valve, lateral view. Io. 2837, Wrotham
FIG. 6. Left valve, internal view. Io. 2835, Wrotham
FIG. 7. Left valve, holotype, dorsal view. Io. 2834, Wrotham
FIG. 8. Right valve, internal view. Io. 2837, Wrotham

Dolocytheridea typica sp. nov. p. 230

FIG. 9. Right valve, lateral view. Io. 2838, Pinhay
FIG. 10. Left valve, holotype, lateral view. Io. 2839, Pinhay
FIG. 11. Left valve, lateral view. Io. 2840, Pinhay
FIG. 12. Carapace, dorsal view. Io. 2841, Pinhay
FIG. 13. Right valve, lateral view. Io. 2842, Pinhay
FIG. 14. Left valve, internal view. Io. 2843, Pinhay

Krausella sp. p. 227

FIG. 15. Right valve, lateral view. Io. 2845, Ely
FIG. 16. Right valve, internal view. Io. 2845, Ely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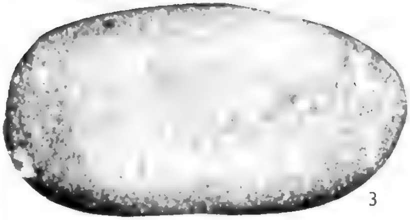
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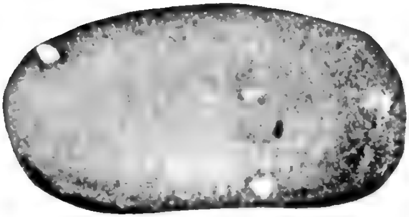
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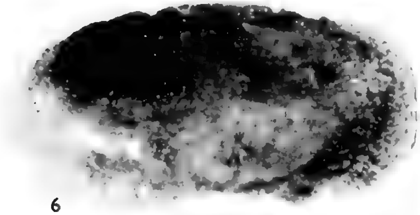
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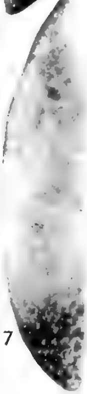
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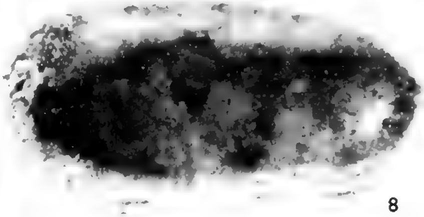
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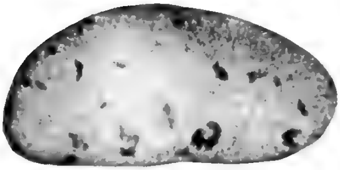
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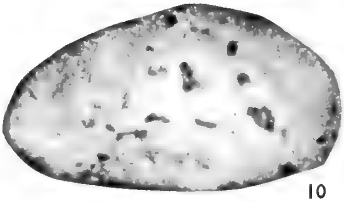
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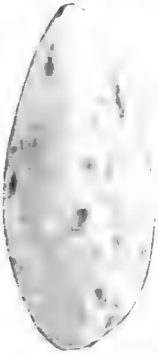
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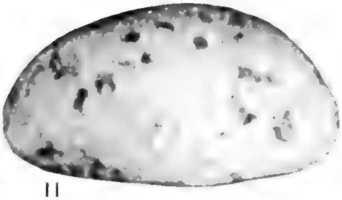
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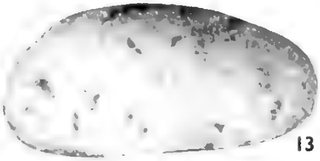
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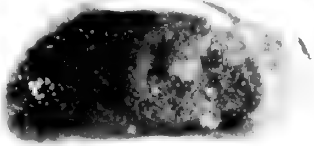
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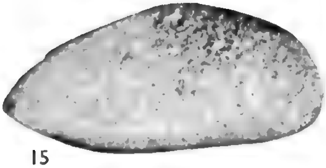
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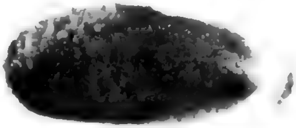
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PLATE 4

All figures ×80

Polycope nuda sp. nov. p. 221

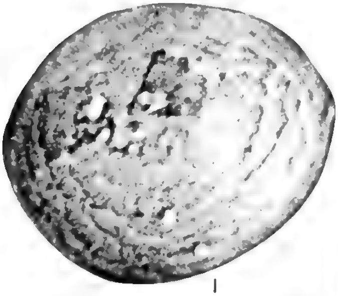
FIG. 1. Left valve, holotype, lateral view. Io. 2847, **Wrotham**
FIG. 2. Carapace, from left. Io. 2848, Wrotham
FIG. 3. Carapace, from left. Io. 2849, Wrotha

Acrocythere striata sp. nov. p. 244

FIG. 4. Left valve, lateral view. Io. 2851, Pinhay
FIG. 5. Right valve, lateral view. Io. 2852, Pinhay
FIG. 6. Left valve, holotype, lateral view. Io. 2853, Pinhay
FIG. 7. Carapace, dorsal view. Io. 2854, Pinhay
FIG. 8. Right valve, lateral view. Io. 2855, Pinhay
FIG. 9. Right valve, lateral view. Io. 2856, Pinhay
FIG. 10. Right valve, internal view. Io. 2856, Pinhay

Polycope oweni sp. nov. p. 222

FIG. 11. Carapace, from left. Io. 2858, Wrotham.
FIG. 12. Left valve, holotype, lateral view. Io. 2859, Wrotham.
FIG. 13. Left valve, lateral view. Io. 2860, Wrotham.
FIG. 14. Carapace, from left. Io. 2861, Wrotham
FIG. 15. Left valve, internal view. Io. 2862, Wrotham



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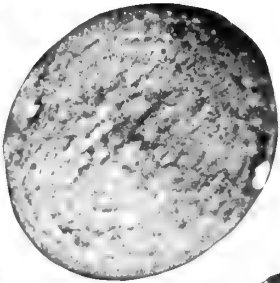

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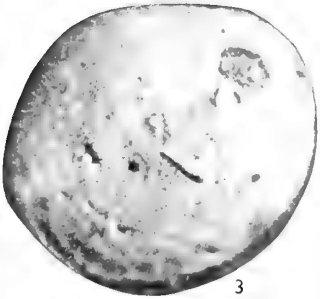

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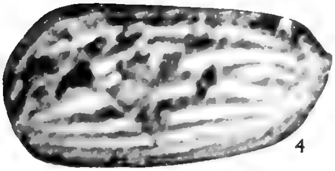

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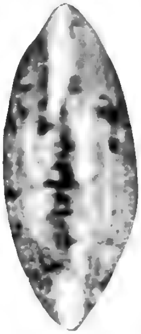

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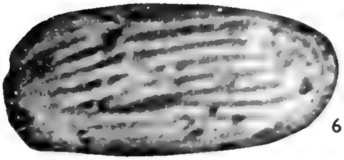

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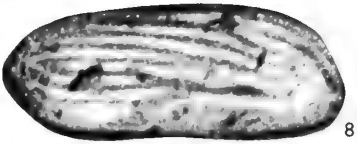

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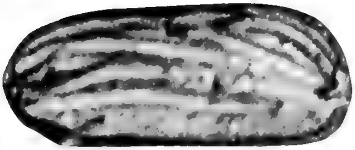

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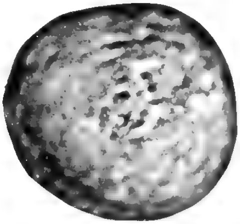

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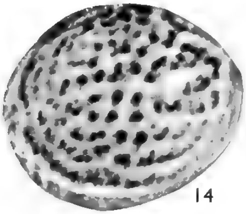

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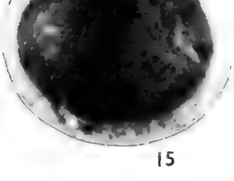

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PLATE 5

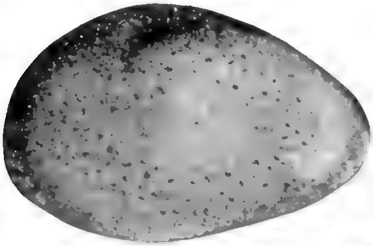
All figures × 80

Schuleridea dimorphica sp. nov. p. 228

Fig. 1. Male left valve, holotype, lateral view. Io. 2864, Wrotham
Fig. 2. Male left valve, internal view. Io. 2865, Wrotham
Fig. 3. Male right valve, lateral view. Io. 2866, Wrotham
Fig. 4. Female left valve, lateral view. Io. 2867, Wrotham
Fig. 5. Female right valve, lateral view. Io. 2868, Wrotham
Fig. 6. Male right valve, internal view. Io. 2869, Wrotham

Orthonotacythere fordensis sp. nov. p. 237

Fig. 7. Male left valve, holotype, lateral view. Io. 2871, Wrotham
Fig. 8. Male right valve, lateral view. Io. 2872, Wrotham
Fig. 9. Female left valve, lateral view. Io. 2873, Wrotham
Fig. 10. Male carapace, dorsal view. Io. 2874, Wrotham
Fig. 11. Female right valve, lateral view. Io. 2875, Wrotham
Fig. 12. Male left valve, internal view. Io. 2876, Wrotham
Fig. 13. Female right valve, internal view. Io. 2877, Wrotham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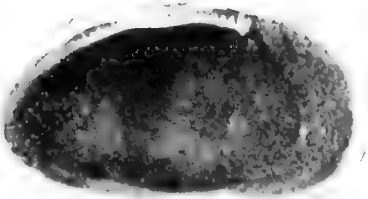
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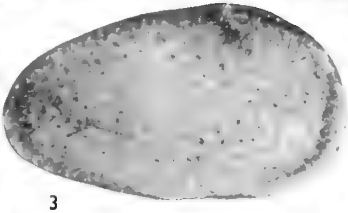
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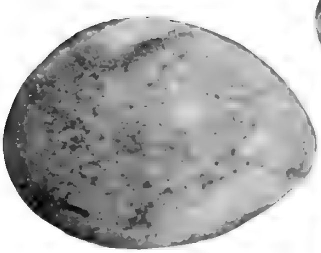
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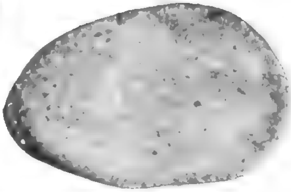
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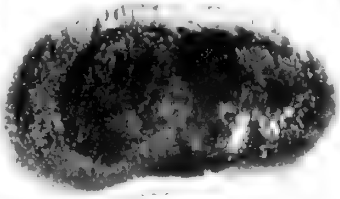
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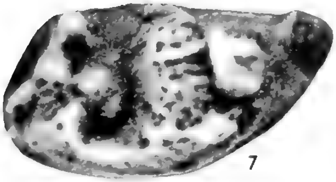
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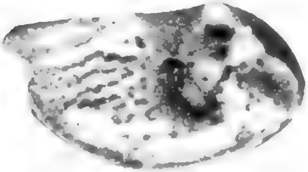
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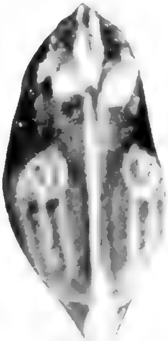
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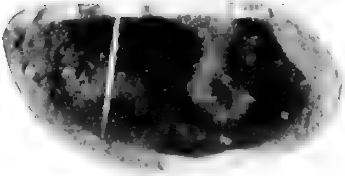
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13

PLATE 6

All figures ×80

Cytheropteron (Eocytheropteron), protonsa sp. nov. p. 235

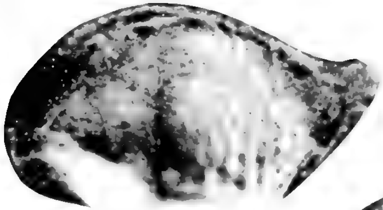
Fig. 1. Left valve, holotype, lateral view. Io. 2879, Wrotham
Fig. 2. Right valve, lateral-view. Io. 2880, Wrotham
Fig. 3. Left valve, dorsal view. Io. 2881, Wrotham
Fig. 4. Left valve, lateral view. Io. 2881, Wrotham
Fig. 5. Right valve, dorsal view. Io. 2880, Wrotham
Fig. 6. Left valve, holotype, internal view. Io. 2879, Wrotham

Habrocythere fragilis Triebel p. 229

Fig. 7. Male left valve, normal type, lateral view. Io. 2882, Wrotham
Fig. 8. Male left valve anomalous type, lateral view. Io. 2883, Wrotham
Fig. 9. Female left valve, normal type, lateral view. Io. 2884, Wrotham
Fig. 10. Male left valve, anomalous type, lateral view. Io. 2885, Wrotham
Fig. 11. Female right valve, anomalous type, lateral view. Io. 2886, Wrotham
Fig. 12. Male right valve, normal type, lateral view. Io. 2887, Wrotham
Fig. 13. Female right valve, normal type, lateral view. Io. 2888, Wrotham

Neocythere (Physocythere) tenuis sp. nov. p. 245

Fig. 14. Left valve, holotype, lateral view. Io. 2889, Henfield
Fig. 15. Right valve, lateral view. Io. 2890, Henfield
Fig. 16. Left valve, lateral view, Io. 2891, Henfield
Fig. 17. Right valve, lateral view. Io. 2892, Henfield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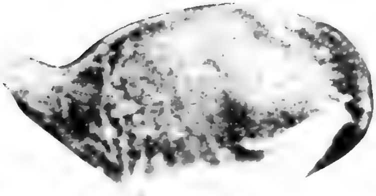
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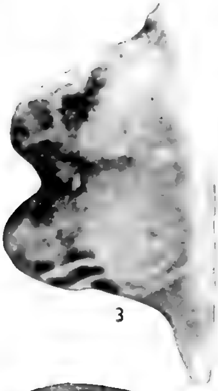
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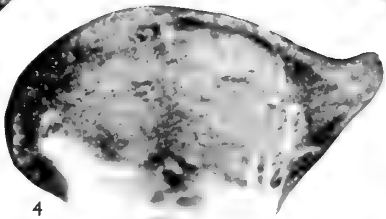
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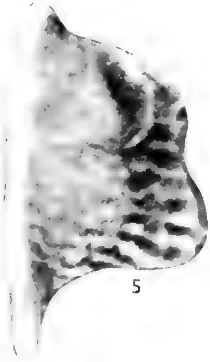
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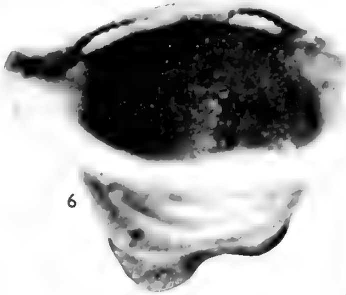
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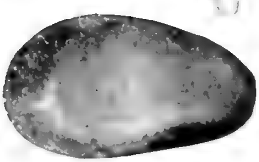
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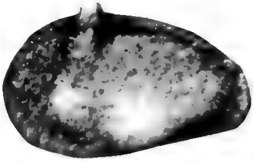
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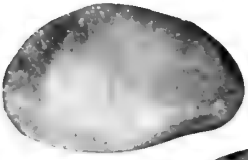
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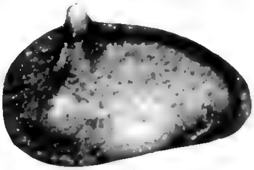
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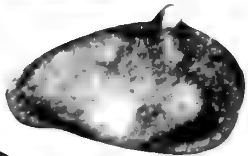
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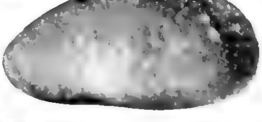
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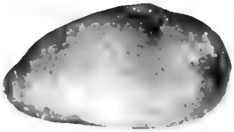
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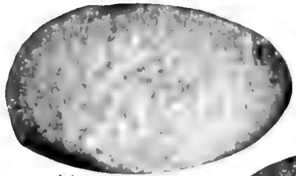
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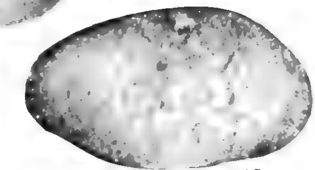
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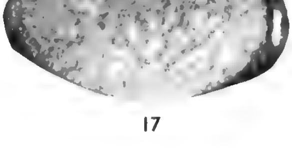
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PLATE 7

All figures ×80

Orthonotacythere spinifera sp. nov. p. 239

FIG. 1. Right valve, lateral view. Io. 2894, Wrotham
FIG. 2. Right valve, lateral view. Io. 2896, Henfield
FIG. 3. Left valve, holotype, lateral view. Io. 2895, Wrotham
FIG. 5. Left valve, lateral view. Io. 2897, Henfield

Cytheropteron (C.) milbournei sp. nov. p. 233

FIG. 4. Left valve, holotype, lateral view. Io. 2898, Wrotham
FIG. 6. Left valve, lateral view. Io. 2899, Wrotham
FIG. 7. Right valve, lateral view. Io. 2900, Sevenoaks.
FIG. 8. Carapace, dorsal view. Io. 2901, Sevenoaks.
FIG. 9. Left valve, internal view. Io. 2902, Sevenoaks

Cytheropteron (Intracytheropteron) obscura sp. nov. p. 236

FIG. 10. Left valve, holotype, lateral view. Io. 2903, Wrotham
FIG. 11. Right valve, lateral view, Io.2904, Wrotham
FIG. 12. Right valve, lateral view. Io. 2905, Wrotham

Cytheropteron (C.) nanissimum nanissimum Damotte & Grosdidier p. 234

FIG. 13. Left valve, lateral view. Io. 2907, Wrotham
FIG. 15. Left valve, lateral view. Io. 2908, Wrotham.

Cytheropteron (C.) nanissimum fenestrata ssp. nov. p. 234

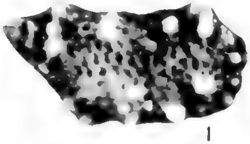
FIG. 14. Left valve, lateral view. Io. 2909, Henfield
FIG. 16. Left valve, holotype, lateral view. Io. 2910, Henfield
FIG. 19. Left valve, lateral view. Io. 2911, Henfield

Eucytherura aff. nuda Kaye p. 231

FIG. 17. Left valve, lateral view. Io. 2912, Wrotham
FIG. 18. Right valve, dorsal view. Io. 2913, Wrotham

Argilloecia valvula sp. nov. p. 225

FIG. 20. Right valve, holotype, lateral view. Io. 2914, Wrotham
FIG. 21. Left valve, lateral view. Io. 2915, Wrotham
FIG. 22. Carapace, from left. Io. 2916, Wrotham
FIG. 23. Right valve, lateral view., Io. 2917, Wrotham
FIG. 24. Left valve, lateral view. Io. 2918, Wrotham
FIG. 25. Right valve, internal view. Io. 2919, Wrotham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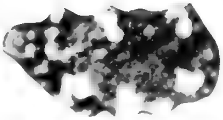
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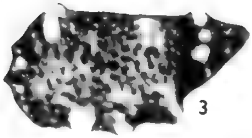
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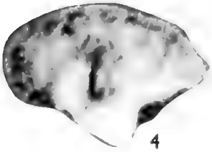
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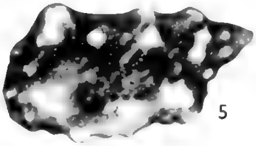
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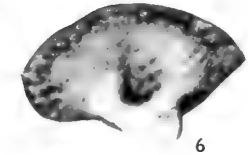
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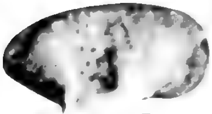
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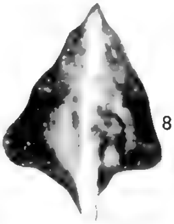
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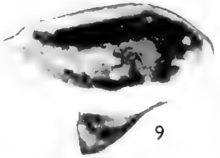
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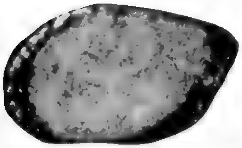
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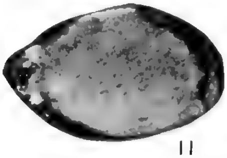
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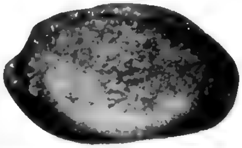
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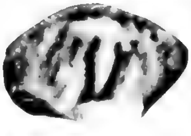
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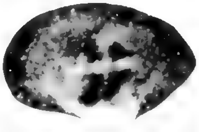
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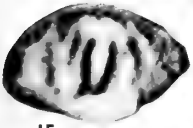
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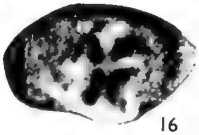
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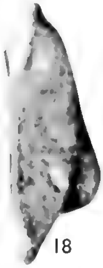
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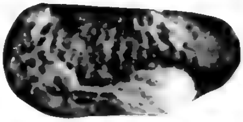
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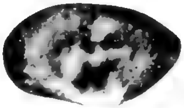
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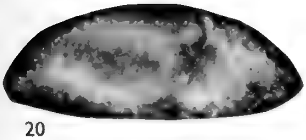
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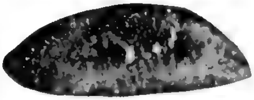
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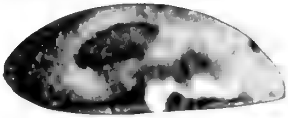
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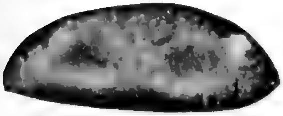
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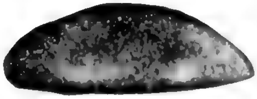
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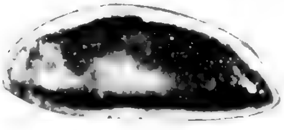
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PLATE 8

All figures × 120

Hemicytherura euglyphea sp. nov. p. 231

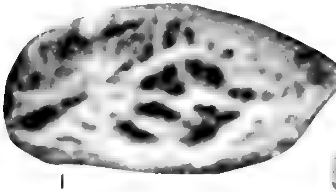
Fig. 1. Male left valve, holotype, lateral view. Io. 2921, Wrotham
Fig. 2. Female right valve, lateral view. Io. 2922, Wrotham
Fig. 3. Male right valve, lateral view. Io. 2923, Wrotham
Fig. 4. Female left valve, lateral view. Io. 2924, Wrotham

Orthonotacythere minutissima sp. nov. p. 239

Fig. 5. Left valve, holotype, lateral view. Io. 2926, Wrotham
Fig. 6. Right valve, lateral view. Io. 2927, Wrotham
Fig. 7. Carapace, dorsal view. Io. 2928, Wrotham
Fig. 8. Left valve, internal view. Io. 2929, Wrotham
Fig. 9. Right valve, lateral view. Io. 2930, Wrotham
Fig. 10. Left valve, lateral view. Io. 2931, Wrotham
Fig. 11. Left valve, lateral view. Io. 2932, Wrotham

Cytheropteron (C.) arguta sp. nov. p. 232

Fig. 12. Right valve, lateral view. Io. 2933, Wrotham
Fig. 13. Carapace, dorsal view. Io. 2934, Wrotham
Fig. 14. Right valve, lateral view. Io. 2935, Wrotham
Fig. 15. Left valve, holotype, lateral view. Io. 2936, Wrotham
Fig. 16. Left valve, lateral view. Io. 2937, Wrotham
Fig. 17. Left valve, internal view. Io. 2938, Wrotham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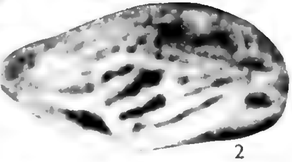
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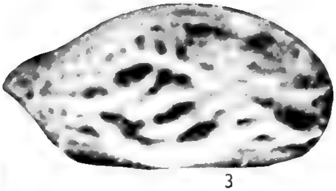
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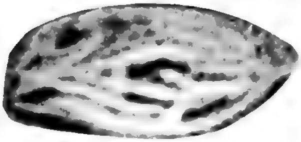
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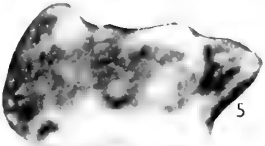
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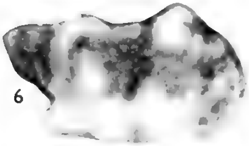
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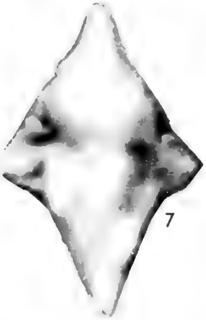
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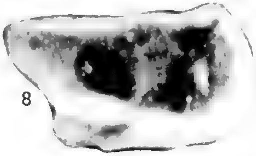
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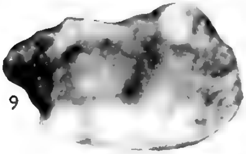
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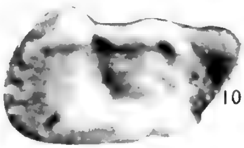
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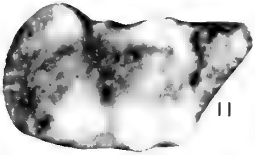
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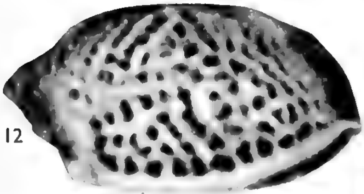
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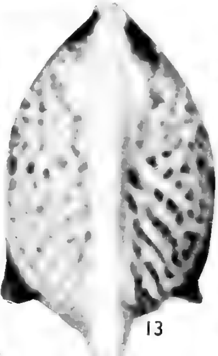
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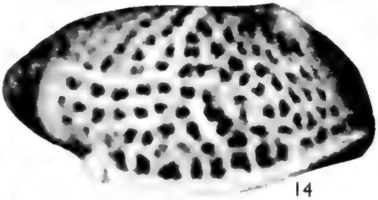
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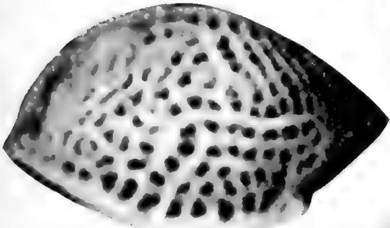
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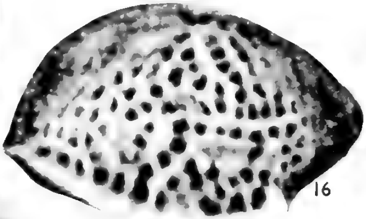
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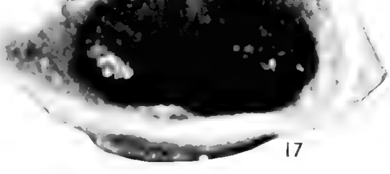
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PLATE 9

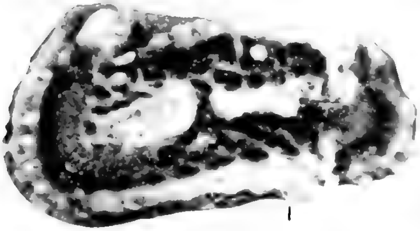
All figures ×60

Cythereis pinhayensis sp. nov. p. 248

FIG. 1. Male left valve, holotype, lateral view. Io. 2946, Pinhay
FIG. 2. Male right valve, lateral view. Io. 2947, Pinhay
FIG. 3. Female left valve, lateral view. Io. 2948, Pinhay
FIG. 4. Female right valve, lateral view. Io. 2949, Pinhay
FIG. 5. Male left valve, lateral view. Io. 2950, Pinhay
FIG. 6. Female carapace, dorsal view. Io. 2951, Pinhay
FIG. 7. Female right valve, internal view. Io. 2952, Pinhay
FIG. 8. Male left valve, internal view. Io. 2953, Pinhay

Paracypris wrothamensis sp. nov. p. 226

FIG. 9. Left valve, internal view. Io. 2955, Wrotham
FIG. 10. Left valve, lateral view. Io. 2956, Wrotham
FIG. 11. Carapace, dorsal view. Io. 2957, Wrotham
FIG. 12. Right valve, lateral view. Io. 2958, Wrotham
FIG. 13. Left valve, holotype, lateral view. Io. 2959, Wrotham
FIG. 14. Right valve, lateral view. Io. 2960, Wrotham



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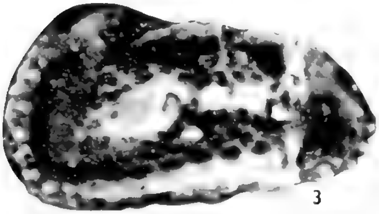

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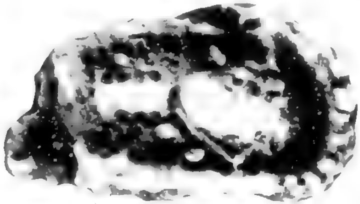

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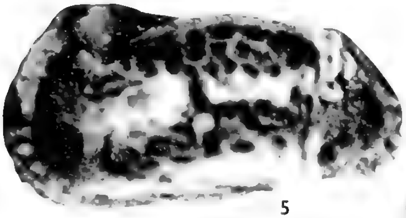

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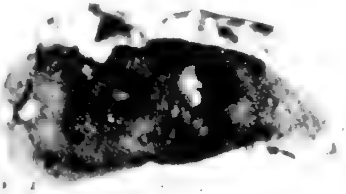

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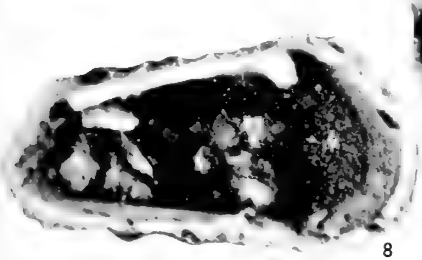

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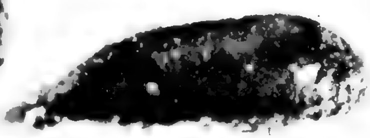

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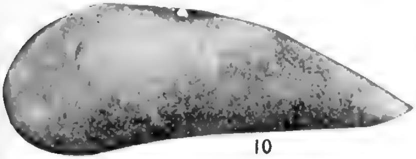

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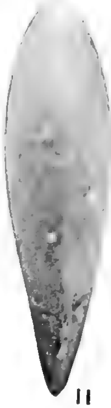

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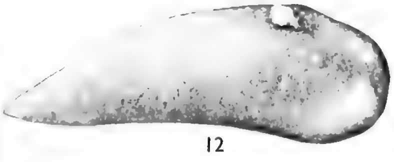

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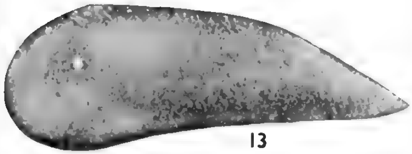

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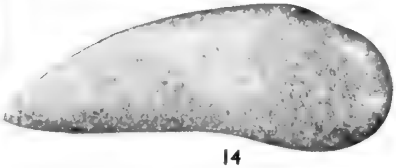

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PLATE 10

All figures ×60

Alatacythere robusta langi ssp. nov. p. 241

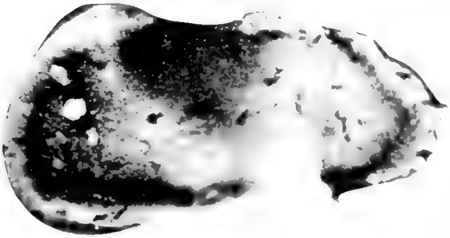
FIG. 1. Male left valve, holotype, lateral view. Io. 2940, Pinhay
FIG. 2. Female left valve, lateral view. Io. 2941, Pinhay
FIG. 3. Female right valve, lateral view. Io. 2942, Pinhay
FIG. 4. Male right valve, lateral view. Io. 2943, Pinhay

Cythereis glabrella Triebel p. 248

Fig. 5. Left valve, lateral view. Io. 2962, Pinhay
FIG. 6. Left valve, dorsal view. Io. 2962, Pinhay
FIG. 7. Right valve, dorsal view. Io. 2963, Pinhay
FIG. 8. Right valve, lateral view. Io. 2963, Pinhay

Alatacythere robusta robusta (Jones & Hinde) p. 240

FIG. 9. Right valve, lateral view. Io. 2964, Arlesey
FIG. 10. Left valve, lateral view. Io. 2965, Arlesey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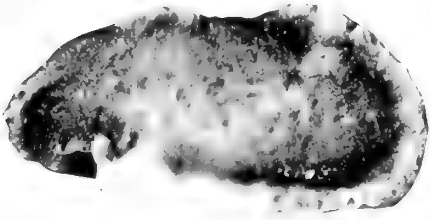
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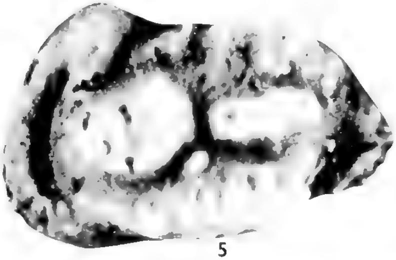
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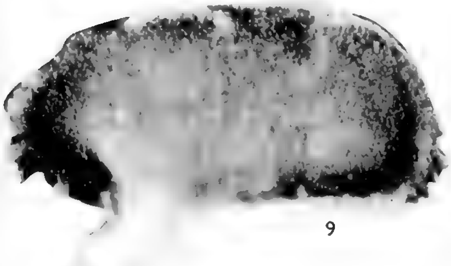
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PLATE 11

All figures ×80

Veenia florentinensis Damotte p. 246

Fig, 1. Left valve, lateral view. Io. 2971, Pinhay
Fig. 2. Left valve lateral view Io. 2971, Pinhay
Fig. 3. Right valve lateral view, Io: 2973 Pinhay
Fig. 4. Right valve, lateral view. Io. 2974, Henfield
Fig. 5. Left valve, lateral view. Io. 2975, Henfield
Fig. 6. Right valve, lateral view. Io. 2976, Pinhay
Fig. 7. Right valve, lateral view. Io. 2977, Pinhay
Fig. 8. Left valve, lateral view. Io. 2978, Pinhay

Monoceratina sp. p. 244

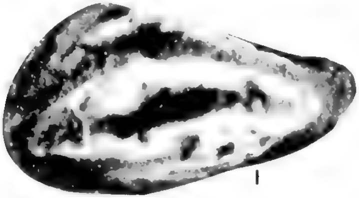
Fig. 9. Right valve dorsal view. Io. 2945, Devizes
Fig. 10. Right valve, lateral view. Io. 2945, Devizes

Cythereis gatyensis Damotte & Grosdidier p. 248

Fig. 11. Right valve, lateral view. Io. 2966, Culham
Fig. 12. Left valve, lateral view. Io. 2967, Culham

Veenia compressa Kaye p. 246

Fig. 13. Right valve, lateral view. Io. 2968, Pinhay
Fig. 14. Carapace, dorsal view. Io. 2969, Pinhay
Fig. 15. Left valve, lateral view. Io. 2970, Pinhay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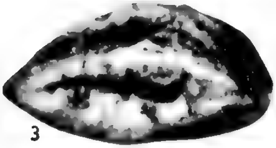
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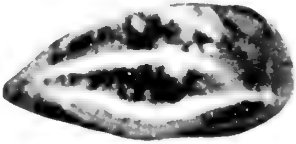
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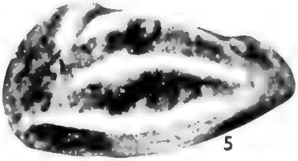
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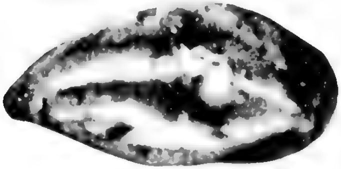
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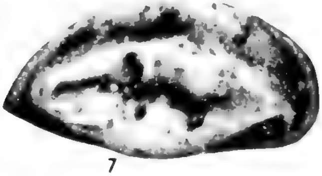
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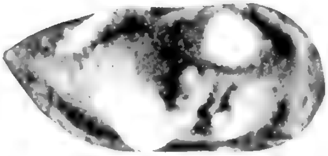
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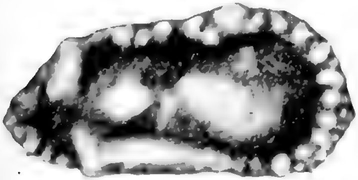
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TERTIARY RED ALGAE FROM BORNEO

J. HARLAN JOHNSON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 11 No. 6
LONDON: 1966

TERTIARY RED ALGAE FROM BORNEO

BY

J. HARLAN JOHNSON

(Professor, Department of Geology, Colorado School of Mines)

Pp. 255–280; 6 *Plates*; 1 *Text-figure*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 11 No. 6
LONDON: 1966

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TERTIARY RED ALGAE FROM BORNEO

By J. HARLAN JOHNSON

CONTENTS

SYNOPSIS

Forty-one species belonging to fifteen genera are described. Of these two species and one variety are considered to be new. The material comes from the Melinau Gorge and from the Upper Baram and Belukan Rivers, Northeast Sarawak, Borneo, Malaysia.

I. ACKNOWLEDGMENTS

I AM deeply indebted to Dr. C. G. Adams for his kindness in arranging for me to borrow this collection from the British Museum (Natural History) for study and for his assistance in supplying necessary data. Thanks are due the Colorado School of Mines who supplied the working space and laboratory facilities, and the Colorado School of Mines Foundation, Inc., for financing the project. Our secretary Mrs. Ruth Loomis typed the manuscript and read the proof.

II. INTRODUCTION

The coralline algae of the Paleocene are only slightly known. As of October 1963 only a single short paper had been published on them. In 1961 the author started a series of studies of the red calcareous algae from the Paleocene based on a series of collections obtained from oil companies, geological surveys, and museums. This paper, in so far as it deals with Paleocene algae from the Upper Baram area of Sarawak, represents the third of these studies. It does, however, also deal with

Miocene algae from the Upper Baram and with Upper Eocene (Tb), Oligocene (Tcd), and Lower Miocene (Lower and Upper Te) algae from the Melinau limestone in north-east Sarawak. This study is based on a collection of petrographic slides belonging to the British Museum (Natural History). They were made from a series of limestone samples collected by the Geological Survey of Sarawak, Sarawak Shell Oilfields Ltd., and by Dr. C. G. Adams who has also studied the foraminifera of these limestones and has supplied the data for determining the age of the samples.

III. LOCALITY AND AGE DATA

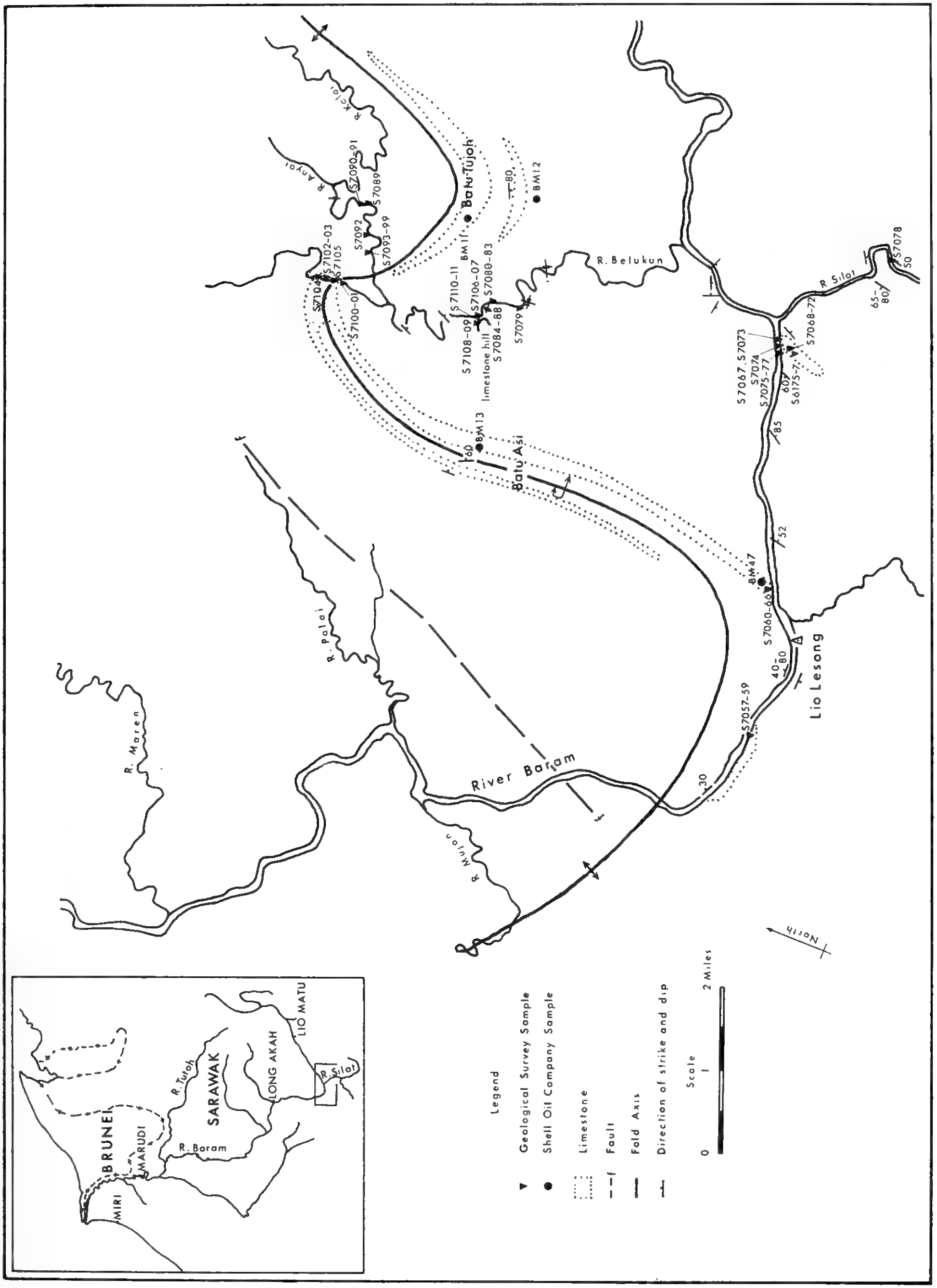
Limestones from the Upper Baram and Belukan Rivers

The locations of the samples from this area are shown on Text-fig. 1. The precise stratigraphical relationships of most samples are uncertain since the geological structure of the district is only known in outline. This is particularly true of the outcrops along the Belukan River where the tectonic picture appears to be fairly complex. The geological setting of the major limestones in the area has been briefly described by Liechti *et al.* (1960). All the Paleocene limestones in the area were assigned to the Kelalan Formation by Haile (1962). The same author considered that the associated Miocene limestones should be assigned to the Melinau Limestone Formation.

It should be noted that some of the samples dated as Paleocene are from conglomeratic limestones, and the possibility that the fossil content of these samples is reworked cannot be entirely ignored. All such samples are asterisked in the list below.

LIMESTONES FROM THE UPPER BARAM AND BELUKAN RIVERS

Sample number	*Age*	
S-7058 (1 slide)	Palaeocene	Baram River
S-7059 (2 slides)	Palaeocene	Baram River
S-7063 (7 slides)	Palaeocene	Baram River
S-7067 (1 slide)	Palaeocene	Baram River
*S-7068 (2 slides)	Palaeocene	Baram River
S-7070 (1 slide)	Palaeocene	Baram River
S-7072 (1 slide)	Palaeocene	Baram River
*S-7073 (2 slides)	Palaeocene	Baram River
S-7075 (4 slides)	Palaeocene	Baram River
S-7076 (1 slide)	Palaeocene	Baram River
*S-7077 (5 slides)	Palaeocene	Baram River
S-7080 (3 slides)	Miocene (Te1-4)	Belukan River
S-7081 (2 slides)	Miocene (Te1-4)	Belukan River
S-7082 (3 slides)	Miocene (Te1-4)	Belukan River
S-7085 (1 slide)	Miocene (Te1-4)	Belukan River
S-7087 (1 slide)	Palaeocene	Belukan River
S-7095 (1 slide)	Palaeocene	Kalai River
S-7111 (2 slides)	Miocene (Te)	Belukan River


R. Kelai
R. Anyoi
S7090-91
S7089
Batu Tujoh
BM11
BM12
80
S7092
S7093-99
S7102-03
S7105
S7104
S7100-01
S7110-11
S7106-07
S7080-83
S7108-09
limestone hill
S7084-88
S7079
R. Belukun
S7078
50
R. Silat
65-80
S7068-72
S7067, S7073
S7074
S7075-77
60
S6175-7
85
BM13
60
Batu Asi
52
BM47
S7060-66
Lio Lesong
40-80
S7057-59
30
River Baram
R. Palai
R. Maren
R. Mulon
North
Legend
▼ Geological Survey Sample
● Shell Oil Company Sample
Limestone
Fault
Fold Axis
Direction of strike and dip
Scale
0
1
2 Miles
BRUNEI
MIRI
MARUDI
R. Tutoh
SARAWAK
R. Baram
LONG AKAH
LIO MATU
R. Silat

LIMESTONES FROM THE UPPER BARAM AND BELUKAN RIVERS *(contd.)*

Sample number	*Age*	
S–7109 (3 slides)	Miocene (Te)	Belukan River
*S–6175 (1 slide)	Palaeocene	Baram River
*S–6176 (1 slide)	Palaeocene	Baram River
*S–6177 (1 slide)	Palaeocene	Baram River
BM 47 (1 slide)	Palaeocene	Baram River
BM 13 (1 slide)	Palaeocene	Batu Asi ridge

The Melinau limestone

The slides studied are listed below with their age as determined from the foraminifera. Full information regarding the provenance of the samples from the Melinau limestone has been given by Adams (1965). It is sufficient to state here that this limestone has a maximum thickness of almost 7,000 feet, that its base is in the Upper Eocene (Tb), and that it includes a great thickness of Oligocene (Tc and Td) and Lower Miocene (Te 1–5) beds. Most of the Melinau samples referred to in this account come from the north face of the Melinau Gorge where a large number of samples (S–10000–S–10194) were collected in stratigraphical order from the base upwards. The remainder come from different parts of the outcrop. Examination of the foraminifera has shown that the main stratigraphical boundaries occur at about the following levels in the Melinau Gorge :

Tb/Tc . between S–10085 and S–10094 ; i.e., at least 1,850 feet above the base.
Tc/Td . between S–10152 and S–10153 ; i.e., about 3,290 feet above the base.
Td/Te . between S–10165 and S–10166 ; i.e., about 3,400 feet above the base.
The junction between Lower Te (Te 1–4) and Upper Te (Te 5) is not reached in the gorge.

MELINAU LIMESTONE

Sample number	*Age*
S–6610 (2 slides)	Oligocene (Tc)
S–6613 (3 slides)	Miocene (Te 1–4)
S–6614 (3 slides)	Miocene (Te 5)
S–6624 (2 slides)	Miocene (Te 5)
S–6921 (3 slides)	Oligocene (Tc)
S–6952 (3 slides)	Oligocene (Tc)
S–6970 (1 slide)	Miocene (Te 5)
S–6971 (1 slide)	Miocene (Te 5)
S–6972 (1 slide)	Miocene (Te 5)
S–6976 (1 slide)	Miocene (Te 5)
S–6977 (2 slides)	Miocene (Te 5)
S–6979 (1 slide)	Miocene (Te 5)
S–6620 (1 slide)	Oligocene (Te 1–4)
S–6623 (2 slides)	Oligocene (Te 1–4)

BRITISH MUSEUM SLIDES
GEOLOGICAL SURVEY—SARAWAK

Samples from the Melinau Gorge

Sample number	*Age*	*Sample number*	*Age*
S–10006a (1 slide)	Eocene (Tb)	S–10145b (1 slide)	Oligocene (Tc)
S–10015b (1 slide)	Eocene (Tb)	S–10148b (1 slide)	Oligocene (Tc)
S–10021a (1 slide)	Eocene (Tb)	S–10149a (1 slide)	Oligocene (Tc)
S–10025a (1 slide)	Eocene (Tb)	S–10153c (6 slides)	Oligocene (Td)
S–10030a (1 slide)	Eocene (Tb)	S–10154f (2 slides)	Oligocene (Td)
S–10032a (1 slide)	Eocene (Tb)	S–10155b (1 slide)	Oligocene (Td)
S–10040a (1 slide)	Eocene (Tb)	S–10160b (3 slides)	Oligocene (Td)
S–10055a (2 slides)	Eocene (Tb)	S–10162a (1 slide)	Oligocene (Td)
S–10060b (1 slide)	Eocene (Tb)	S 10176b (1 slide)	Miocene (Te 1–4)
S–10061a (2 slides)	Eocene (Tb)	S–10177b (1 slide)	Miocene (Te 1–4)
S–10087b (1 slide)	? Eocene (?Tb)	S–10179a (1 slide)	Miocene (Te 1–4)
S–10096a (1 slide)	Oligocene (Tc)	S–10184a (1 slide)	Miocene (Te 1–4)
S–10100a (1 slide)	Oligocene (Tc)	S–10189a (1 slide)	Miocene (Te 1–4)
S–10101a (1 slide)	Oligocene (Tc)	S–10194b (1 slide)	Miocene (Te 1–4)
S–10109a (1 slide)	Oligocene (Tc)	S–10207b (1 slide)	Eocene (Tb) South face of gorge

IV. SYSTEMATIC DESCRIPTIONS

Phylum RHODOPHYCOPHYTA Papenfuss 1946

Class *RHODOPHYCEAE* Ruprecht 1851

Order CRYPTONEMIALES Schmitz *in* Engler 1892

Family **CORALLINACEAE** (Lamouroux) Harvey 1849

Subfamily **MELOBESIEAE**

Genus ***ARCHAEOLITHOTHAMNIUM*** Rothpletz 1891

Archaeolithothamnium aschersoni (Schwager)

(Pl. 1, figs. 3, 4)

1883 *Lithothamnium aschersoni* Schwager : 147, pl. 29, fig. 25.
1891 *Lithothamnium aschersoni* (Schwager) Rothpletz : 316.
1961 *Archaeolithothamnium aschersoni* (Schwager) Segonzac : 437.

DESCRIPTION. A crustose form, commonly with small mammillated protuberances. Hypothallus poorly developed or absent. Hypothallic cells measure $12–20\ \mu \times 8–12\ \mu$. The perithallus forms most of the crust. Tissue quite regular. Cell threads fairly prominent, cross partitions thinner, cells $9–19\ \mu \times 8–15\ \mu$. Sporangia ovoid, arranged in regular rows (layers), height $73–86\ \mu$, diameter $40–52\ \mu$.

REMARKS. This widespread species is one of the most abundantly represented in the Borneo collection.

SAMPLE NUMBER AND LOCALITY. S–7068, Upper Baram River.

AGE. Paleocene (the figured specimens occur in a conglomeratic limestone).

Archaeolithothamnium cf. ***cyrenaicum*** Raineri

(Pl. 1, fig. 5)

1923 *Archaeolithothamnium cyrenaicum* Raineri : 30, text-fig. 2.

Description. Thallus crustose with protuberances or short stubby branches. Perithallic tissue fairly regular with well defined cell " layers ". At irregular intervals " layers " of very short cells are interlayered with the normal perithallic cells. Normal cells measure 14–30 μ × 8–13 μ. Sporangia in layers or lenses. They measure 38–45 μ × 70–74 μ. This is very close to, if not identical with, Raineri's species from the Miocene of Cyrenaica.

Remarks. Represented in the Borneo collection by a single, oblique section.

Sample number and locality. S–10153, Melinau Gorge, north-east Sarawak.

Age. Middle Oligocene (Td).

Archaeolithothamnium intermedium Raineri

(Pl. 1, fig. 6)

1923 *Archaeolithothamnium intermedium* Raineri : 29, text-fig. 1.

Description. Crustose with rounded protuberances. The tissue of the protuberances is quite regular with " layers " of cells. The cells measure 12–19 μ × 8–15 μ. Sporangia moderately to closely packed in regular layers. They measure 36–42 μ in diameter and 79–111 μ high.

Remarks. This closely approximates Raineri's species. Represented in the Borneo collection by a single good specimen and a couple of fragments.

Sample number and locality. S–7111, Belukan River.

Age. Lower Miocene (Lower Te).

Archaeolithothamnium lauensum Johnson & Ferris

(Pl. 1, fig. 1)

1950 *Archeolithothamnium lauensum* Johnson & Ferris : 11, pl. 1, figs. A, D.

Description. Thallus forms a fairly regular crust up to 9 mm. thick. Hypothallus of curved cell threads. Cells square or rectangular in section, measuring 8–17 μ × 8–12 μ. Perithallus compact, quite regular, with cells measuring 8–15 μ × 8–11 μ. Conceptacles large, commonly much higher than wide, ovoid, 95–108 μ in diameter and 120–205 μ high.

Remarks. Represented by only a few specimens, mostly small fragments. They fit the description of *A. lauensum* in all respects.

Sample number and locality. S–7111, Belukan River.

Age. Lower Miocene (Lower Te).

Archaeolithothamnium liberum Lemoine

1939 *Archaeolithothamnium liberum* Lemoine : 61, pl. 1, fig. 14, text-fig. 26.

DESCRIPTION. Thallus develops as thin crust from which protuberances may arise. Hypothallus consists of curved threads of cells. Cell size 7–28 μ × 7–18 μ. Perithallus fairly regular, cell size 8–17 μ × 6–18 μ.

REMARKS. Represented in the Borneo collection by several young infertile crusts.

SAMPLE NUMBER AND LOCALITY. S–7076, Upper Baram River.

AGE. Paleocene.

Archaeolithothamnium lugeoni Pfender

(Pl. 1, fig. 2)

1926 *Archaeolithothamnium lugeoni* Pfender : 324, pls. 8, 9.
1935 *Archaeolithothamnium lugeoni* Pfender ; Miranda : 280.
1936 *Archaeolithothamnium lugeoni* Pfender ; Rama Rao & Pia : 35, pl. 4.
1939 *Archaeolithothamnium lugeoni* Pfender ; Lemoine : 52–53.

DESCRIPTION. Thin crusts growing superimposed to form a thick mass. Hypothallus very thin or absent, difficult to distinguish and measure. Perithallic tissue fairly regular with suggestions of layers of cells, but the horizontal partitions not all continuous. Perithallic cells 11–16 μ × 8–13 μ. Sporangia long ovoid to nearly subspherical, dimensions 80–104 μ high and 57–58 μ in diameter.

REMARKS. Represented by only a few fragments in the collection studied.

SAMPLE NUMBER AND LOCALITY. S–7077, Upper Baram River, Sarawak.

AGE. Paleocene.

Archaeolithothamnium macrosporangium n. sp.

(Pl. 3, fig. 4)

DIAGNOSIS. Crustose, hypothallus thin, cells 16–36 μ × 7–14 μ ; perithallus regular, cells 9–29 μ × 7–13 μ. Sporangia abundant and unusually long (135–200 μ).

HOLOTYPE. Slide V–51765.

SAMPLE NUMBER AND LOCALITY. S–6921, mouth of Tukuruk River, Melinau, north-east Sarawak.

AGE. Lower Oligocene (Tc).

DESCRIPTION. Thallus develops as a crust probably with protuberances or small mammelons on the upper surface. Several may grow superimposed. Hypothallus slightly to moderately developed consisting of curved cell threads. Cells measure 16–36 μ × 7–14 μ. Perithallus regular with the appearance of cell " layers " as well as cell threads. Both the horizontal and vertical partitions between the cells are moderately thick. Cells measure 9–29 μ × 7–13 μ. Sporangia numerous and unusually large. Commonly they occur in layers or lenses, appearing as rows in vertical sections. Sporangia measure 117–124 μ in diameter and 144–200 μ high. Where closely packed they are long ovoid in shape. If loosely packed, they tend to be round ovoid to nearly spherical.

REMARKS. This species is characterized by the cell size, regular perithallic tissue, and unusually large, especially unusually long, sporangia. It belongs in the same general group as *A. nummuliticum* (Gümbel) Rothpletz, *A. saipanense* Johnson, and *A. lauensum* Johnson & Ferris. It differs from *A. nummuliticum* in having larger, especially longer, cells, better developed hypothallus, more regular perithallic tissue, and much larger sporangia. *A. saipanense* has smaller cells which are nearly cubic in the perithallic tissue, and smaller sporangia (50–100 μ × 70–140 μ against 117–124 μ × 144–200 μ). *A. lauensum* from the late Lower Miocene of Fiji is probably the nearest described species, but it has smaller, especially shorter cells, and narrower sporangia.

Archaeolithothamnium sarawakense n. sp.

(Pl. 2, fig. 5)

DIAGNOSIS. Thallus crustose, well developed hypothallus and perithallus. Cells of hypothallus 16–23 μ × 9–14 μ. Cells of perithallus 7–14 μ × 5–11 μ, tissue fairly regular. Sporangia regularly arranged, diameter 31–48 μ, height 38–54 μ.

HOLOTYPE. Slide V.51762.

SAMPLE NUMBER AND LOCALITY. S–7063, south-west end of Batu Asi limestone, Upper Baram River, Sarawak, Borneo.

AGE. Paleocene.

DESCRIPTION. Crustose. Hypothallus well developed, composed of curved threads of cells. Cells measure 16–23 μ long by 9–14 μ wide. Perithallic tissue fairly regular. Cells 7–14 μ × 5–11 μ. Sporangia subspherical, in regular rows, lenses, or short layers (appearing as short rows in vertical sections). Size 38–54 μ high, diameter 31–48 μ.

REMARKS. The dimensions of the cells and the size and shape of the sporangia are the same as those of *A. oulianovi* Pfender. However, the present species has a fairly regular perithallic tissue, a well developed hypothallus and the sporangia regularly arranged in layers or lenses; while *A. oulianovi* is characterized by having a very irregular perithallic tissue, sporangia irregularly scattered throughout the tissue, and a poorly developed hypothallus. It resembles the late Cretaceous *A. brevium* Lemoine but has somewhat smaller cells and a more strongly developed hypothallus.

Archaeolithothamnium saipanense Johnson

(Pl. 2, fig. 1)

1957 *Archaeolithothamnium saipanense* Johnson : 220, pl. 38, figs. 1–4, 6.

DESCRIPTION. Thallus develops a thick crust with protuberances. Hypothallus thin, commonly consisting of only a few curved threads of cells. Cells measure 8–17 $\mu \times$ 7–14 μ. Perithallic tissue regular, with regularly spaced horizontal and vertical cell walls. Cells 8–13 $\mu \times$ 6–13 μ. Sporangia long elliptical, commonly closely packed in regular rows, and a single thallus may bear a number of successive layers. Sporangia measure 75–120 μ high and 38–55 μ wide.

REMARKS. Essentially the same as material described by the author from the Upper Eocene of Saipan. This species is very similar to *Archaeolithothamnium sociabile* Lemoine. The cells are essentially the same size. The main differences are in growth habit and sporangia. *A. sociabile* develops thin crusts. Normally a fertile crust bears only a single layer of sporangia and these are rather widely spaced. *A. saipanense* develops thick crusts with rounded protuberances. Fertile crusts may bear numerous successive layers of tightly packed sporangia. The sporangia are usually longer and narrower than those of *A. sociabile.*

SAMPLE NUMBER AND LOCALITY. S–10021, S–10149, S–10153 ; all from the north face of the Melinau Gorge, Sarawak.

AGE. Upper Eocene (Tb) to Middle Oligocene (Td). S–10021 (Tb), S–10149 (Tc), S–10153 (Td).

Archaeolithothamnium sociabile Lemoine

(Pl. 2, fig. 3)

1939 *Archaeolithothamnium sociabile* Lemoine : 53–54, text-figs. 16–17.
1961 *Archaeolithothamnium* cf. *A. sociabile* Lemoine ; Johnson : 919, pl. 267, figs. 3, 4.

DESCRIPTION. Crusts, commonly thin, may be superimposed. Hypothallus thin and may be difficult to recognize as commonly composed of only two or three horizontal or very slightly curved cell threads. Cells measure 8–24 $\mu \times$ 7–14 μ, commonly 8–16 $\mu \times$ 7–11 μ. Perithallic tissue regular with horizontal partitions more conspicuous than the vertical. Cells 7–22 $\mu \times$ 7–12 μ, commonly 11–17 $\mu \times$ 7–12 μ. Sporangia in regular rows (as seen in vertical section), commonly only a single row to a thallus. Sporangia 80–100 μ high and 35–65 μ wide.

REMARKS. Numerous specimens observed at one locality which very closely fit Lemoine's descriptions of the type material from the Upper Eocene and Oligocene of Algeria.

SAMPLE NUMBER AND LOCALITY. S–10153, north face of Melinau Gorge, north-east Sarawak.

AGE. Oligocene (Td).

Lithothamnium aggregatum Lemoine

1939 *Lithothamnium aggregatum* Lemoine : 66–67, pl. 1, fig. 12 ; pl. 3, figs. 3, 4, text-fig. 27.

Description. Thin crusts, commonly less than 600 μ thick, which may grow superimposed or interstratified with other species or other organisms. Hypothallus slightly developed, commonly around 100–125 μ thick, of curved cell threads. Cells measure 15–22 μ long and 9–13 μ wide. Perithallic tissue fairly regular, 300–600 μ thick, with cells 14–27 μ × 8–13 μ. No conceptacles observed.

Remarks. Several infertile specimens observed in the Borneo collection which fit Lemoine's description of the species from the Oligocene of Algeria.

Sample number and locality. S–10160, Melinau Gorge, north-east Sarawak.

Age. Oligocene (Td).

Lithothamnium cantabricum Lemoine

(Pl. 2, fig. 2)

1934 *Lithothamnium cantabricum* Lemoine *in* Lemoine & Mengaud : 175, text-fig. 1.
1961 *Lithothamnium cantabricum* Lemoine ; Segonzac : 442.

Description. Thallus develops as an undulating crust 0·25 to 0·4 mm. thick. The hypothallus is well developed (0·14 to 0·17 mm. thick), with cells 13–24 μ long and 9–11 μ thick. Perithallus 0·11 to 0·17 mm. thick with cells 7–11 μ × 8–11 μ.

Remarks. Represented by a single specimen in the Borneo collection. It differs from the holotype only in having a better developed hypothallus.

Sample number and locality. S–7063, south-west end of Batu Asi limestone, Upper Baram River, Sarawak.

Age. Paleocene.

Lithothamnium cf. ***caucasicum*** Maslov

(Pl. 2, fig. 4)

1956 *Lithothamnium caucasicum* Maslov : 116–117, pl. 33, fig. 2, text-fig. 46.

Description. Thallus develops short stubby branches. The branches consist mainly of a medullary area of arched " layers " of cells and a narrow marginal area. The central portion is composed of threads of cells 29–56 μ × 12–17 μ. In the lower part of the branch, this central tissue is irregular with the cell threads branching frequently and the cross partitions between the cells irregularly spaced. Higher up the tissue becomes regular with cross partitions strong and regularly spaced, giving the suggestion of " layers " of cells. There are also suggestions of growth zones.

The marginal tissue is thin and fairly regular. Cells 14–17 μ × 11–14 μ. No conceptacles present.

REMARKS. The cell dimensions and frequent branching of the cell threads in the lower central area agree with Maslov's species from the Danian of the Caucasus region. The upper portion (not described or illustrated by Maslov) may be more regular.

SAMPLE NUMBER AND LOCALITY. S–6177, Upper Baram River, Sarawak.

AGE. Paleocene.

Mesophyllum curtum Lemoine

(Pl. 3, fig. 3)

1939 *Mesophyllum curtum* Lemoine : 92, text-fig. 61.

DESCRIPTION. Long slender branches. Tissue somewhat irregular, the vertical cell threads commonly as pronounced as the curved horizontal " layers ". Numerous growth zones but their boundaries not pronounced. Cells unusually small, 7–9 μ × 8–10 μ. Conceptacles 325–343 μ in diameter, 140–149 μ high.

REMARKS. This form has unusually small cells. In character of tissue and size of cells and conceptacles, it fits almost exactly Lemoine's type material. It differs only in having longer and more narrow branches.

SAMPLE NUMBER AND LOCALITY. S–10177, Melinau Gorge, Sarawak.

AGE. Lower Miocene (Lower Te).

Mesophyllum cf. ***pfenderae*** (Lemoine)

(Pl. 3, figs. 1, 2)

1928 *Lithophyllum pfenderae* Lemoine : 100, text-fig. 14.
1939 *Mesophyllum pfenderae* (Lemoine) Lemoine : 87.
1961 *Mesophyllum pfenderae* (Lemoine) ; Segonzac : 438–439, text-fig. 4.

DESCRIPTION. The plants develop short sinuous branches 1·0 to 1·3 mm. thick. Medullary hypothallus forms most of the branch. It is composed of arched layers of cells arranged in pronounced growth zones, 5 to 9 cell layers to a zone. Cells rectangular, 28–40 μ × 9–15 μ. Marginal perithallus commonly formed of 3 to 6 layers of cells which measure 13–40 μ × 9–14 μ. Conceptacle 352 μ × 125 μ.

REMARKS. The Borneo material closely resembles the descriptions given by Lemoine and by Segonzac. It differs in having somewhat longer hypothallic cells. The branches may be more sinuous. Unfortunately, neither Lemoine nor Segonzac illustrates the branches or gives any descriptions of them, beyond diameter and length measurements.

SAMPLE NUMBER AND LOCALITY. S–6175, Upper Baram River, Sarawak.

AGE. Paleocene.

Mesophyllum vaughanii (Howe) Lemoine

(Pl. 4, fig. 3; Pl. 5, fig. 5)

1918 *Lithothamnium vaughanii* Howe : 6–7, pls. 7, 8.
1939 *Mesophyllum vaughanii* (Howe) Lemoine : 89, pl. 1, figs. 2, 8, 11, 15.
1962 *Mesophyllum vaughanii* (Howe) ; Johnson : 157, pl. 3, figs. 1, 2.

DESCRIPTION. The plant starts as a basal crust from which develop irregular protuberances or long slender branches. Basal hypothallus of curved rows of cells. The branches are formed of numerous, irregularly disposed growth zones. These consist of " layers of cells ", commonly quite regularly arranged. Cells of central part of growth zones of branches slightly longer than those of basal hypothallus. Conceptacles large, numerous, and multiple apertured.

TABLE I.—Dimensional data of *Mesophyllum vaughanii* (in mu)

Slide	*Hypothallic Cells*	*Perithallic Cells*	*Conceptacles*
S–10109a		11–21 × 10–15?	475–528 × 220
S–10148b	13–22 × 8–13	13–20 × 8–13	364–510 × 144–176
S–10032a		14–21 × 6–11	
S–10100a	27–32 × 8–19	7–12 × 9–12	
S–10032a		19–26 × 8–14	
S–10087b		12–19 × 8–13	448–589 × 167–220
Range	13–32 × 8–19	11–21(26) × (6)8–15	364–589 × 167–220

REMARKS. This is a widely distributed Upper Eocene–Lower Oligocene species. It is represented abundantly in the Borneo collection.

SAMPLE NUMBER AND LOCALITY. S–10032 (Tb), S–10087 (Tb or Tc), S–10100 (Tc), S–10109 (Tc), S–10100 (Tc), S–10148 (Tc), S–10153 (Td). Melinau Gorge, north-east Sarawak.

AGE. Upper Eocene (Tb) to Middle Oligocene (Td).

Mesophyllum vaughanii (Howe) var. ***sarawakense*** nov.

(Pl. 4, figs. 1, 6)

DIAGNOSIS. Strongly branching with thick medullary hypothallus and thin marginal perithallus. Medullary tissue regular with cells 15–40 $\mu \times$ 7–26 μ. Perithallic cells 9–18 $\mu \times$ 7–12 μ. Suggestions of marginal conceptacles.

HOLOTYPE. Slide V.51772.

SAMPLE NUMBER AND LOCALITY. S–10153 and 10154, north face of Melinau Gorge, north-east Sarawak.

AGE. Middle Oligocene (Td).

DESCRIPTION. Thallus starts as a rather thin crust from which develop long medium to thick branches. Branches consist of a strongly developed medullary hypothallus surrounded by a thin marginal perithallus. Growth zones strongly developed in some specimens, not so prominent in others. Branches 1·6–3·8 mm.

thick and more than 6·0 mm. long. Growth zones 8–12 layers thick. Medullary cells 15–40 μ × 7–26 μ, commonly 20–28 μ × 10–17 μ. Cells in regular " layers " with thick horizontal partitions and thin vertical partitions. Marginal perithallus thin, cells commonly 9–18 μ × 7–12 μ. Several specimens show suggestions of marginal conceptacles with diameters up to about 600 μ. However, they are badly overgrown and precise measurements cannot be made.

Remarks. This species closely resembles the typical *Mesophyllum vaughanii* (Howe) Lemoine in general appearance and growth habits. It differs slightly but consistently in several respects: the medullary cells are longer but narrower, the medullary tissue is more regular without the frequent development of secondary hypothallia so characteristic of *M. vaughanii*, and while there are suggestions of alternating layers of longer and shorter cells in some areas or all of the medullary tissue, this is not so common as in *M. vaughanii* and there is less difference in the actual size of the cells in alternate layers.

This form occurs abundantly in samples S–10153 and 10154.

Lithophyllum besalotos Johnson

1962 *Lithophyllum besalotos* Johnson : 159, pl. 4, figs. 4, 5.

Description. Plant forms thin irregular crusts which may grow superimposed. Hypothallus thin but easily recognizable, of irregularly curved cell threads. Cells measure 14–25 μ × 7–11 μ. Perithallic cells wider than high with thick horizontal cell walls. Cells arranged in layers like bricks. Cells measure 9–14 μ × 12–22 μ. No conceptacles observed.

Remarks. Represented by only a few poorly preserved specimens.

Sample number and locality. S–10162, Melinau Gorge, Sarawak.

Age. Middle Oligocene (Td).

Lithophyllum capederi Lemoine

(Pl. 5, fig. 6)

1900 *Lithothamnium tenue* Capeder : 180, pl. 6, fig. 15.
1900 *Lithothamnium dentatum* Capeder : 178, pl. 6, fig. 7.
1926 *Lithophyllum capederi* Lemoine : 11, text-fig. 11.

Description. Thallus forms a thin crust. Hypothallus coaxial with exceptionally thick concentric partitions. Hypothallic cells 13–19 μ × 8–11 μ. Perithallic tissue regular, composed of small, square or rectangular cells 6–10 μ × 4–9 μ.

Remarks. This species is characterized by a coaxial hypothallus with unusually thick cell walls and very small perithallic cells. In cell measurements it closely resembles *Lithophyllum johnsoni* Ishijima.

Sample number and locality. S–7080, Belukan River, Sarawak.

Age. Lower Miocene (Te).

Lithophyllum densum Lemoine

(Pl. 5, fig. 8)

1934 *Lithophyllum densum* Lemoine : 282, text-fig. 14.
1956 *Lithophyllum* aff. *L. densum* Lemoine ; Maslov : 117, pl. 34, figs. 1–4.

Description. Long straight cylindrical branches with diameters ranging from 0·9 to 1·1 mm. A medullary hypothallus with gently arched layers of cells attains a diameter of 0·7 to 0·8 mm., with cells 25–40 μ long and 8–15 μ wide. The marginal perithallus is 88–180 μ thick, with cells 13–16 μ long and 7–12 μ wide.

Remarks. This species is characterized by the long straight branches, thick medullary hypothallus with gently arched layers, and the long narrow hypothallic cells. The cells of the Borneo specimens are appreciably longer than those in the holotype of Mid-Eocene age, and slightly longer than Maslov's early Paleocene material. The other dimensions are the same.

Sample number and locality. S–6177, Upper Baram River, Sarawak.

Age. Paleocene.

Lithophyllum dubium Lemoine

1934 *Lithophyllum dubium* Lemoine : 282, text-fig. 13.
1961 *Lithophyllum dubium* Lemoine ; Segonzac : 443, text-fig. 9.

Description. Thallus thin, crustose. Several may grow superimposed. Hypothallus about 200 μ thick with cells 17–25 $\mu \times$ 7–12 μ. Perithallus regular, up to 300 μ thick, with cells 15–17 $\mu \times$ 11–15 μ.

Remarks. Represented by several infertile specimens.

Sample number and locality. S–7073, Upper Baram River, Sarawak.

Age. Paleocene.

Lithophyllum* cf. *obliquum Lemoine

(Pl. 4, fig. 5)

1930 *Lithophyllum obliquum* Lemoine : 266, text-figs. 1, 2.
1939 *Lithophyllum* cf. *L. obliquum* Lemoine ; Lemoine : 97, 98, text-fig. 64.

Description. Crustose, 0·4–0·55 mm. thick. Hypothallus 130–155 μ thick, poorly coaxial, " layers " only slightly curved, almost oblique with thick walls. Cells 20–25 $\mu \times$ 6–14 μ. Perithallus 350–450 μ thick with well defined " layers " of cells. Cells measure 8–12 $\mu \times$ 8–14 μ.

Remarks. The general structure suggests *L. obliquum* Lemoine and the cells are about the same size. The main difference is a greater development of perithallic tissue. It is similar to *Lithophyllum* cf. *obliquum* Lemoine from Algeria.

Sample number and locality. S–7081, Belukan River, Sarawak.

Age. Lower Miocene (Te).

***Lithophyllum* cf. *ovatum* (Capeder)**

1900 *Lithothamnium ovatum* Capeder : 177, pl. 6, figs. 5*a*, *b*.
1926 *Lithophyllum ovatum* (Capeder) Lemoine : 245–246, text-fig. 3.
1932 *Lithophyllum ovatum* (Capeder) ; Airoldi : 70, pl. 10.
1957 *Lithophyllum ovatum* (Capeder) ; Johnson : 228, pl. 45, figs. 4, 8.

DESCRIPTION. Thallus crustose with a well developed hypothallus and perithallus. Hypothallus 90–250 μ thick, poorly coaxial. Cells 11–22 μ × 12–16 μ. Perithallus 100–250 μ thick with cells in slightly irregular " layers ". Cells measure 7–17 μ × 7–11 μ. No conceptacles observed.

REMARKS. This form strongly suggests *L. ovatum* but the material available for study is too limited to be certain.

SAMPLE NUMBER AND LOCALITY. S–10100, Melinau Gorge, north-east Sarawak.

AGE. Lower Oligocene (Tc).

***Lithophyllum quadrangulum* Lemoine**

(Pl. 4, fig. 4)

1934 *Lithophyllum quadrangulum* Lemoine : 279, text-fig. 10.
1934 *Lithophyllum quadrangulum* Lemoine ; Lemoine & Mengaud : 178, text-fig. 4.

DESCRIPTION. Plant forms a very thin crust (175–220 μ thick), composed entirely of hypothallic tissue. Hypothallus coaxial but the curved layers of cells form only gentle arcs and they are almost vertical. Cells large, measuring 28–34 μ × 13–17 μ.

REMARKS. This species has very characteristic features : (1) a thin crust consisting entirely or almost entirely of hypothallus ; (2) the unusual structure of the hypothallus ; and (3) the large cells. It has a long time range (Mid-Eocene to Mid-Miocene), and apparently became widely distributed geographically.

SAMPLE NUMBER AND LOCALITY. S–10160, Melinau Gorge, north-east Sarawak.

AGE. Middle Oligocene (Td).

***Lithoporella melobesioides* (Foslie)**

(Pl. 2, fig. 6)

1904 *Mastophora* (*Lithoporella*) *melobesioides* Foslie ; Weber van Bosse & Foslie : 73–77, text-figs. 30–32.
1939 *Melobesia* (*Lithoporella*) *melobesioides* Foslie ; Lemoine : 108–110, text-figs. 78, 79.
1943 *Lithoporella melobesioides* (Foslie) ; Lignac-Grutterink : 292–293, pl. 2, fig. 8.
1949 *Lithoporella* (*Melobesia*) *melobesioides* (Foslie) Johnson & Ferris : 196–197, pl. 37, figs. 4, 5 ; pl. 39, fig. 2.
1950 *Lithoporella melobesioides* (Foslie) ; Johnson & Ferris : 18, pl. 8, fig. A.
1957 *Lithoporella melobesioides* (Foslie) ; Johnson : 234, pl. 37, fig. 5 ; pl. 43, figs. 1, 2 ; pl. 49, fig. 4 ; pl. 56, fig. 6.

DESCRIPTION. Thallus consists of a single layer of large cells except around the conceptacles. Cells elongated vertically and commonly slightly obliquely. Cells range greatly in size even in a single slice across a thallus. Range of cell size of 17 specimens measured was 26–82 μ high and 12–35 μ wide.

REMARKS. This is probably the most common species of coralline algae observed in the Borneo collections. Fragments occur on many slides. The cell dimensions all fit within those of the highly variable, widespread, long ranged *L. melobesioides*.

SAMPLE NUMBER AND LOCALITY. S–7063, south-west end of Batu Asi limestone, Upper Baram River, Sarawak.

AGE. Paleocene.

TABLE 2.—*Lithoporella melobesioides* (Foslie)
Cell Size of Typical Specimens (in mu)

Slide	*Cell dimensions*	*Age*
S–7063e	48–75 × 21–26	Paleocene
S–7063g	49–70 × 29–35	Paleocene
S–6175a	45–82 × 24–33	Paleocene
S–7063h	66–70 × 16–19	Paleocene
S–7063m	56–73 × 30–48	Paleocene
S–7077e	26–39 × 14–18	Paleocene
S–6175a	41–53 × 17–24	Paleocene
BM. 13	30–48 × 14–22	Paleocene
S–10153c	30–51 × 14–29	Middle Oligocene
S–10176b	28–43 × 22–30	Lower Miocene
S–7111i	27–40 × 17–21	Lower Miocene

Lithoporella antiquitas Johnson

(Pl. 6, fig. 3)

1961 *Lithoporella antiquitas* Johnson : 937, pl. 276, figs. 1, 2.

DESCRIPTION. Thallus very small, encrusting, consisting of a single layer of vertically elongated cells, 44–53 μ long and 14–17 μ wide. Conceptacle small, 341 μ in diameter and 128 μ high.

REMARKS. Closely resembles the holotype from the Miocene of Eniwetok, Marshall Islands, except for a slightly larger conceptacle.

SAMPLE NUMBER AND LOCALITY. S–7081, Belukan River, Sarawak.

AGE. Lower Miocene (Te).

Lithoporella cf. ***minus*** Johnson

(Pl. 3, fig. 5)

1964 *Lithoporella minus* Johnson : C10, pl. 2, fig. 6.

DESCRIPTION. Thallus tiny, irregular crustose, consisting of a single layer of cells except around the conceptacle. Cells 8–20 μ high, and 11–18 μ wide. Conceptacle 373 μ × 200 μ, with a single large pore.

REMARKS. Only one specimen observed in the Paleocene collection. It closely resembles the holotype from the Eocene of Ishigaki Ryukyu Islands, except for slightly shorter cells.

SAMPLE NUMBER AND LOCALITY. S–7077, Upper Baram River, Sarawak.

AGE. Paleocene.

Melobesia cf. ***cuboides*** Johnson

1957 *Melobesia ? cuboides* Johnson : 234, pl. 43, figs. 6, 7.
1962 *Melobesia cuboides* Johnson ; Johnson : 164, pl. 5, fig. 6.

DESCRIPTION. Thallus monostromatic. Cells cubic or horizontally elongated with thick walls. Cell size 15–34 μ × 12–21 μ.

REMARKS. Similar to material previously described by Johnson (1962) from Batu Gading, Sarawak.

SAMPLE NUMBER AND LOCALITY. S–6623, south-west end of Melinau limestone, S–10176, Melinau Gorge, north-east Sarawak.

AGE. Lower Miocene (Lower Te).

Dermatolithon saipanense Johnson

(Pl. 6, fig. 4)

1957 *Dermatolithon saipanense* Johnson : 235, pl. 57, figs. 4, 6.

DESCRIPTION. Thallus forms a thin crust. Hypothallus of one or two layers of elongated cells 32–46 μ high and 14–21 μ wide. Perithallus of square or vertically elongated cells, 30–33 μ long and 24–32 μ wide.

REMARKS. The one Borneo specimen observed has cells within the size range of this species, although the average cell size is a little smaller than that of the Saipan material.

SAMPLE NUMBER AND LOCALITY. S–7111, Belukan River, Sarawak.

AGE. Lower Miocene (Lower Te).

THAUMATOPORELLA Pia 1927

Thaumatoporella parvovesiculifera (Raineri)

(Pl. 6, fig. 6)

1922 *Gyroporella parvovesiculifera* Raineri : 83, pl. 13, figs. 17, 18.
1927 *Thaumatoporella parvovesiculifera* (Raineri) Pia : 69.
1938 *Thaumatoporella parvovesiculifera* (Raineri) ; Pia : 491, pl. 1, figs. 1–5 ; pl. 2, figs. 6–14.
1956 *Lithoporella melobesioides* (Foslie) ; Elliott : 327, pl. 2, figs. 8, 9.
1957 *Polygonella incrustata* Elliott : 230, pl. 1, figs. 11, 12.
1957 *Lithoporella elliotti* Emberger : 625, pl. 32, figs. 1–4.
1959 *Thaumatoporella* cf. *parvovesiculifera* (Raineri) ; Gasche, pl. 1, fig. 3.
1959 *Thaumatoporella parvovesiculifera* (Raineri) ; Sartoni & Crescenti : 129, pl. 2, figs. 1–5.
1960 *Thaumatoporella parvovesiculifera* (Raineri) ; Radoicic : 133, pls. 1, 2.

DESCRIPTION. Thallus consists of a single layer of long cells, polygonal in cross-section. Cells 34–91 μ long, and 16–22 μ wide.

REMARKS. Grows encrusting a shell or other hard object. Closely resembles Elliott's (1957) late Jurassic–early Cretaceous material except in having slightly smaller cells (34–91 μ × 16–22 μ instead of 65–104 μ × 26–33 μ) and more undulating growth habit. Only a single specimen observed.

Sample number and locality. S–7063, south-west end of Batu Asi limestone, Upper Baram River, Sarawak.

Age. Paleocene.

Subfamily **CORALLINOIDEAE** (Articulated Corallines)

Genus *CORALLINA* Linnaeus 1758

Corallina sp. *A*.

Description. Segments small, 0·8–1·3 mm. long and 0·16–0·25 mm. wide, 14 to 18 tiers of cells to a segment. Cells at centre of tiers 47–64 μ long and 6–12 μ wide. Marginal cells 22–35 μ long and 6–14 μ wide.

Remarks. Only a few worn segments of *Corallina* were observed in the Paleocene collection. Data from the two best specimens are given above. They closely resemble *Corallina* sp. *l*. (Segonzac 1961 : 444).

Sample number and locality. S–7063, south-west end of Batu Asi limestone, Upper Baram River, Sarawak.

Age. Paleocene.

Corallina cf. ***abundans*** Lemoine

(Pl. 3, figs. 6, 7)

1934 *Corallina abundans* Lemoine : 284–285, text-fig. 16.

Description. Segments 0·14–0·22 mm. wide. Cells of medullary hypothallus at middle, 52–64 μ long and 7–12 μ wide. Marginal cells 13–14 μ × 8–11 μ wide.

A fragment of *Corallina* with a conceptacle chamber occurs on the same slide and probably represents the same species. The conceptacle space is rounded conical, 218 μ wide near base and 356 μ high.

Remarks. Represented by only a few frayed fragments from a single locality. Their cells, both medullary and marginal, agree in length with Lemoine's species but are much narrower (hypothallus 7–12 μ versus 8–20 μ, perithallus 8–11 μ versus 15–25 μ).

Sample number and locality. S–6610, south-west end of Melinau limestone, Sarawak.

Age. Lower Oligocene (Tc).

Corallina neuschelorum Johnson

(Pl. 5, fig. 4)

1957 *Corallina neuschelorum* Johnson : 239, pl. 37, fig. 3 ; pl. 50, figs. 1–4.

Description. Segments flattened, mainly hypothallic tissue, with cells in centre of layers 48–76 μ long and 9–15 μ wide. Marginal cells 19–27 μ × 8–16 μ.

Remarks. The cell dimensions closely fit those of the Saipan species, although the marginal cells are somewhat longer (19–27 μ versus 15–21 μ).

Sample number and locality. S–7111, Belukan River, Sarawak.

Age. Lower Miocene (Lower Te).

***Corallina* cf. *prisca* Johnson**

1957 *Corallina prisca* Johnson : 239, pl. 37, fig. 4 ; pl. 44, figs. 1, 2, 7–11.

DESCRIPTION. Pieces of segments about 0·35 mm. wide. Cells at centre of medullary tissue 63–88 μ long and 7–8 μ wide. Node between two segments 201 μ long.

REMARKS. The dimensional data for these fragments is within the range of *Corallina prisca* from the Upper Eocene of Saipan.

SAMPLE NUMBER AND LOCALITY. S–10025 (Tb) and S–10153 (Td), both from north face of Melinau Gorge, Sarawak.

AGE. Upper Eocene (Tb) and Middle Oligocene (Td).

***Jania miocenica* Johnson**

(Pl. 5, fig. 3)

1961 *Jania miocenica* Johnson : 938–939, pl. 278, figs. 6–8.

DESCRIPTION. Slender segments with dimensional data tabulated below.

TABLE 3.—*Jania miocenica* (Dimensions in mu)

Slide	*Number*	*Hypothallic Cells*		*Perithallic Cells*		*Age*
number	*cells in row*	*Length*	*Width*	*Length*	*Width*	
S–6921d	19	33–39	13–17	15–26	14–24	Lower Oligocene
S–6921d	17–19	35–46	12–18	14–30	9–21	Lower Oligocene
S–6921d	27–32	36–50	14–20	13–28	16–21	Lower Oligocene
S–7111d	22	33–40	14–22	11–21	11–18	Lower Miocene

REMARKS. In general appearance and dimensional data, the Borneo specimens agree exactly with those described by Johnson (1961) from the Lower Miocene of Eniwetok.

SAMPLE NUMBER AND LOCALITY. S–6921 (Tc), mouth of Tukuruk River, Melinau, Sarawak. S–7111 (Te), Belukan River, Sarawak.

AGE. Lower Oligocene (Tc) and Lower Miocene (Lower Te).

***Jania* cf. *nummulitica* Lemoine**

(Pl. 6, fig. 5)

1934 *Jania nummulitica* Lemoine : 285.

DESCRIPTION. Piece of a segment 2·12 mm. long and 0·33 mm. wide. It contains 35 layers of cells, with approximately 18 cells in a row as cut by the section studied. The cells at the centre of the rows measure 63–76 μ high and 11–18 μ wide. The marginal cells are 25–30 μ high and 16–21 μ wide.

REMARKS. Represented by a couple of fragments. The largest is described above. The cell dimensions are close to those of *J. nummulitica* Lemoine from the Upper Eocene of Hungary. However, the cells of the Borneo specimens are slightly shorter and wider than the holotype.

Sample number and locality. S–6921, mouth of Tukuruk River, Melinau, Sarawak.

Age. Lower Oligocene (Tc).

Jania vetus Johnson

(Pl. 4, fig. 2)

1957 *Jania vetus* Johnson : 237, pl. 52, fig. 2.
1961 *Jania vetus* Johnson ; Johnson : 939.

Description. Long, sometimes branching segments 0·26 to 0·48 mm. wide. Medullary cells from near centre measure 50–77 μ long and 15–26 μ wide. Marginal cells 13–16 μ × 26–46 μ.

Remarks. The cell sizes are within the ranges of the species described from the Miocene of Saipan.

Sample number and locality. S–7111, Belukan River, Sarawak.

Age. Lower Miocene (Lower Te).

Amphiroa cf. ***fortis*** Johnson

(Pl. 6, fig. 7)

1961 *Amphiroa fortis* Johnson : 939, pl. 277, figs. 8, 9.

Description. Segments probably long, with diameters ranging from 0·7 to 0·9 mm., commonly 0·8 to 0·87 mm. Medullary hypothallus of layers of cells. The cells at the centre measure 42–79 μ long and 9–30 μ wide. There is a suggestion of alternating layers of long and short cells, but the difference in length is slight, 62–79 μ versus 49–64 μ. Marginal perithallic cells 15–29 μ × 12–26 μ.

Remarks. This form is very close to *Amphiroa fortis* Johnson from the late Eocene of Eniwetok. The Borneo specimens have cells about the same length but wider, 9–30 μ versus 6–11 μ in the hypothallus, and 12–22 μ versus 7–11 μ in the perithallus.

Sample number and locality. S–7073, Upper Baram River, Sarawak.

Age. Paleocene.

Amphiroa sp.

Description. Segments around 0·3 mm. wide. Medullary tissue shows an alternation of layers of long and short cells, formula 1-long, 1-short. Cells at centre of medullary area measure: long 42–56 μ × 7–8 μ, short 34–40 μ × 7–8 μ.

Remarks. Represented by a few fragments.

Sample number and locality. S–10055, Melinau Gorge, Sarawak.

Age. Upper Eocene (Tb).

Subterraniphyllum thomasi Elliott

(Pl. 6, figs. 1, 2)

1957b *Subterraniphyllum thomasi* Elliott : 73–74, pl. 13, figs. 1–9.

DESCRIPTION. Segments composed of wide medullary hypothallus and very narrow marginal perithallus. Hypothallus composed of slightly curved layers of large irregular cells. Cell layers shaped much the same as in *Amphiroa* with flattened top and sharply inclined margins. Cells irregular to almost regular in vertical section ; very irregular, rounded to polygonal in horizontal section. Cells 85–118 μ long and 58–99 μ wide. Marginal perithallus thin, cells rectangular, 15–26 $\mu \times$ 7–21 μ.

REMARKS. In sections the medullary hypothallus appears light while the perithallic tissue is unusually dark, practically black. The Borneo material consists of fragments of segments. They fit Elliott's description of the type material from Iraq except that the perithallic cells are slightly larger.

SAMPLE NUMBER AND LOCALITY. S–6921, mouth of Tukuruk River, Melinau, Sarawak.

AGE. Lower Oligocene (Tc).

Genus *DISTICHOPLAX* Pia 1934

Distichoplax biserialis (Dietrich)

(Pl. 5, fig. 7)

1918 *Lithothamnium ? sp.*, Trauth : 220, pl. 11, figs. 2, 3.
1918 *Lithothamnium nummuliticum* Trauth : 219, pl. 11, fig. 1.
1927 *Lithothamnium biseriale* Dietrich : 461, pl. 11, fig. 1.
1930 *Lithoporella* Pia : 133.
1934 *Distichoplax biserialis* (Dietrich) Pia : 15, text-figs. 5–8.
1956b *Distichoplax biserialis* (Dietrich) ; Elliott : 332, pl. 11, fig. 1.
1958 *Distichoplax biserialis* (Dietrich) ; Lemoine : 2145.
1960 *Distichoplax biserialis* (Dietrich) ; Elliott : 226, pl. 8, figs. 2, 3.
1961 *Distichoplax biserialis* (Dietrich) ; Segonzac : 446, pl. 13, figs. 3, 4.
1963 *Distichoplax biserialis* (Dietrich) ; Keij : 153–160, pl. 1.

DESCRIPTION. The thallus develops as small undulating plaque or sheet. They may occur singly or a number may grow in close association. Commonly each one will be oriented somewhat differently. Sections cutting the thallus at different angles look very differently. The most characteristic is a transverse section cut parallel to the length of the cells. This gives the " fishbone fossil " with two rows of obliquely elongated cells coming together at a wide angle (Pl. 5, fig. 7). In the specimen illustrated, the cells have lengths of 76–81 μ and widths of 30–41 μ.

REMARKS. This is a very widespread Paleocene and early Eocene fossil, with its greater development in the Paleocene.

SAMPLE NUMBER AND LOCALITY. BM13, Batu Asi limestone, Upper Baram area, Sarawak.

AGE. Paleocene.

Family **SOLENOPORACEAE**

Genus ***SOLENOMERIS*** Douvillé

" *Solenomeris* " sp.

(Pl. 5, fig. 1)

Description. Thallus forms rounded masses from which branches or irregular protuberances may develop. The fragments observed in the Borneo collection consisted of perithallic tissue. This is composed of threads of coarse semirectangular cells, regularly arranged. The walls of the cell threads are quite thick. The cross partitions between the cells are thinner. They develop at approximately the same levels in adjoining threads, giving the tissue an articulated or layered appearance in vertical sections. Cells measure 21–33 μ high and 41–65 μ wide.

Remarks. This is one of the characteristic Paleocene fossils. It occurs in beds of about Danian age from Morocco to the East Indies and in Guatemala and Cuba. [Since this paper was submitted, Professor Johnson has pointed out that *Solenomeris* may be a hydrozoan, in which case he thinks that the present species should be referred to *Parachaetetes*. *Ed.*]

Sample number and locality. B.M. 47, south-west end of Batu Asi limestone, Upper Baram River, Sarawak.

Age. Paleocene.

Family **SIPHONOCLADACEAE** Schmitz 1879

Genus *PYCNOPORIDIUM* Yabe & Toyama 1928

Pycnoporidium sinuosum Johnson & Konishi

(Pl. 5, fig. 2)

1960 *Pycnoporidium sinuosum* Johnson & Konishi : 1100–1101, pl. 134, figs. 1–4.

Description. Thallus consists of an irregular mass of loosely interwoven, coarse, sinuous, filaments. These filaments are 41–58 μ in diameter. They are partitioned by cross walls (septa) at irregular intervals (47 μ to 72 μ). Second branching occurs sparsely at irregular intervals. The filaments have thick walls with occasional uncalcified chambers occupying the spaces within the tubes between the septa.

Remarks. This species was originally described from the late Cretaceous of Guatemala. It differs from the only previously described Paleocene species from Iraq, *P. levantian* Johnson, in having slightly smaller tubes and more closely spaced septa. Represented by only a few specimens in the Borneo collection.

Sample number and locality. S–7077, Upper Baram River, Sarawak.

Age. Paleocene.

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PLATE 1

(All ×50)

Fig. 1. ***Archaeolithothamnium lauensum*** Johnson & Ferris. Vertical section of a fertile fragment. Lower Miocene. V.51758.

Fig. 2. ***Archaeolithothamnium lugeoni*** Pfender. A somewhat oblique section. Paleocene. V.51760.

Figs. 3, 4. ***Archaeolithothamnium aschersoni*** (Schwager). 3, Vertical section of a thin crust. V.51762. 4, Oblique section of a small rounded knob. Paleocene. V.51761.

Fig. 5. ***Archaeolithothamnium*** cf. ***cyrenaicum*** Raineri. A slightly oblique section. Middle Oligocene. V.51759.

Fig. 6. ***Archaeolithothamnium intermedium*** Raineri. A nearly vertical section. Lower Miocene. V.51758.

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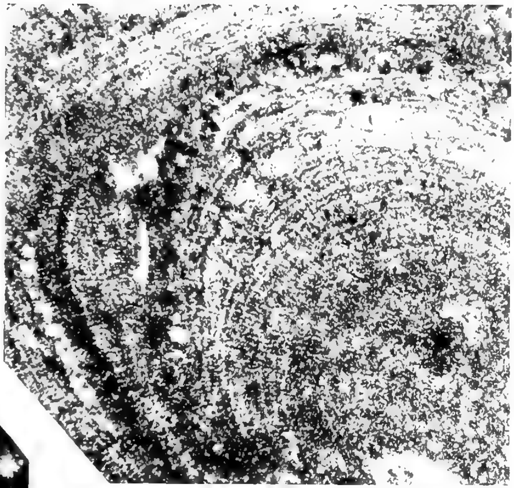

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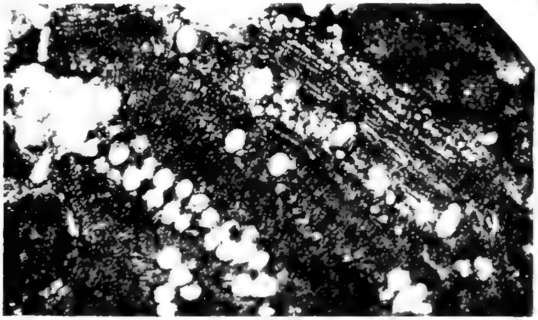

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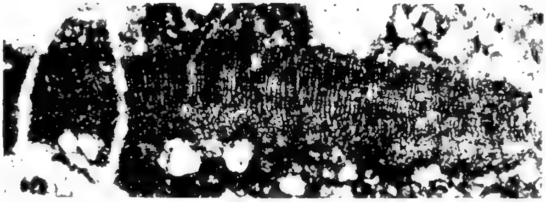

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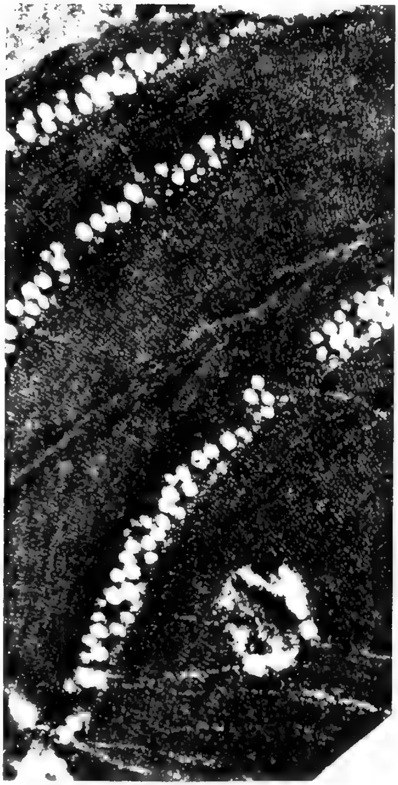


PLATE 2

(All ×50)

Fig. 1. ***Archaeolithothamnium saipanense*** Johnson. Vertical section, Middle Oligocene. V.51763.

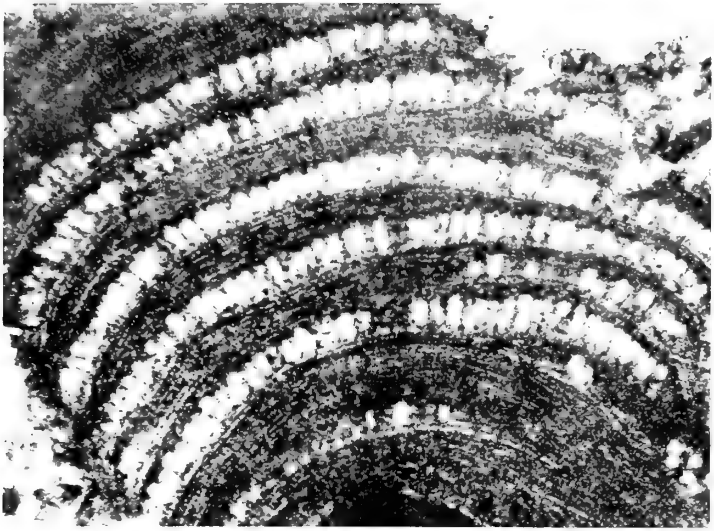
Fig. 2. ***Lithothamnium cantabricum*** Lemoine. Vertical section showing hypothallus and perithallus. Paleocene. V.51766.

Fig. 3. ***Archaeolithothamnium sociabile*** Lemoine. Nearly vertical section. Middle Oligocene. V.51764.

Fig. 4. ***Lithothamnium*** cf. ***caucasicum*** Maslov. Slightly oblique section of a small branch. Paleocene. V.51767.

Fig. 5. ***Archaeolithothamnium sarawakense*** n. sp. Holotype. Vertical section. Paleocene. V.51762.

Fig. 6. ***Lithoporella melobesioides*** (Foslie). Paleocene. V.51766.



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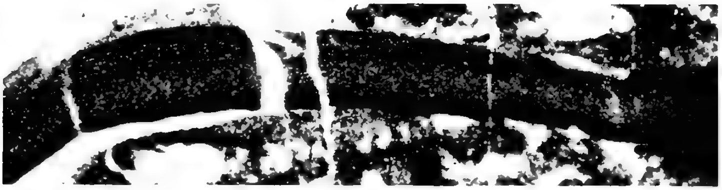

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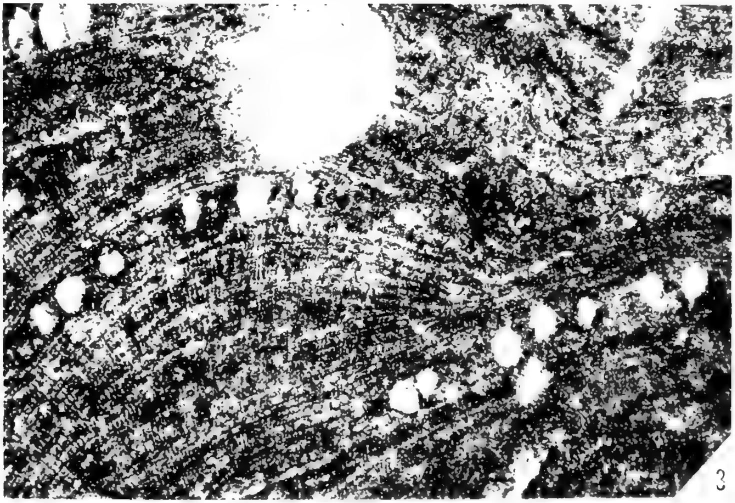

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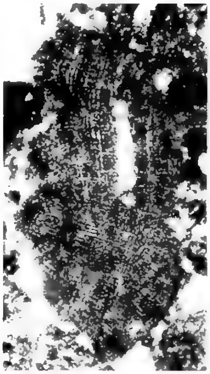

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PLATE 3

(All ×50)

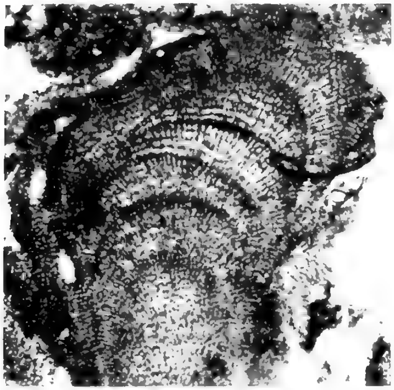
FIGS. 1, 2. ***Mesophyllum*** cf. ***pfenderae*** (Lemoine). Sections of small branches. Fig. 2 shows a conceptacle with sporangia. Paleocene. V.51768.

FIG. 3. ***Mesophyllum curtum*** Lemoine. Vertical section of a branch, badly recrystallized. Lower Miocene. V.51769.

FIG. 4. ***Archaeolithothamnium macrosporangium*** n. sp. Holotype. Vertical section showing tissue and sporangia. Lower Oligocene. V.51765.

FIG. 5. ***Lithoporella*** cf. ***minus*** Johnson. Badly recrystallized. A conceptacle chamber to right. Paleocene. V.51760.

FIGS. 6, 7. ***Corallina*** cf. ***abundans*** Lemoine. Fig. 6 shows a terminal conceptacle chamber. V.51778. Fig. 7, Fragment of a segment. Lower Oligocene. V.51779.



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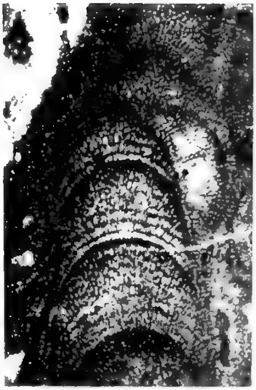

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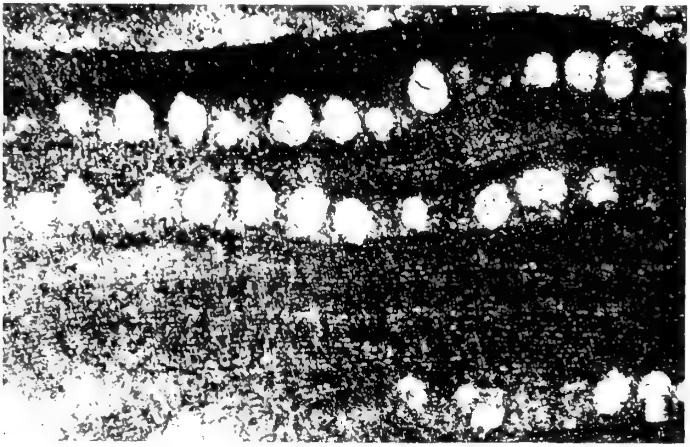

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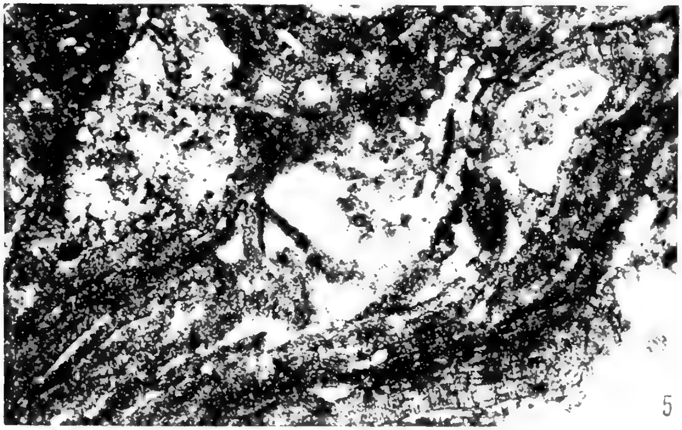

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PLATE 4

(All ×50)

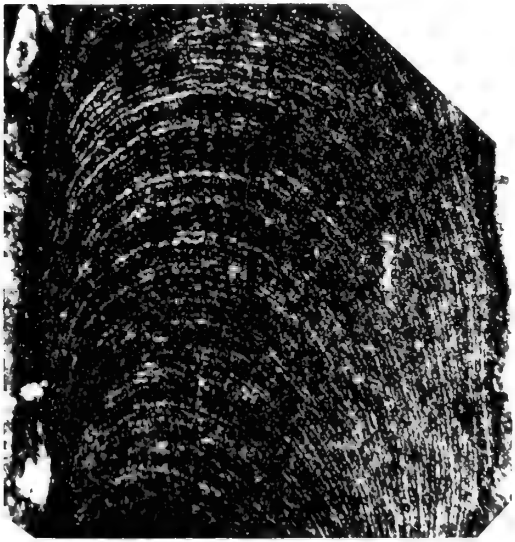
FIGS. 1, 6. ***Mesophyllum vaughanii*** (Howe) var. ***sarawakense*** nov. Fig. 1, A nearly vertical section, Holotype. Middle Oligocene. V.51772. Fig. 6, An oblique section. Middle Oligocene. V.51759.

FIG. 2. ***Jania vetus*** Johnson. Lower Miocene. V.51758.

FIG. 3. ***Mesophyllum vaughanii*** (Howe). Lower Oligocene. V.51771.

FIG. 4. ***Lithophyllum quadrangulum*** Lemoine. Section of a long thin crust mainly hypothallus. Middle Oligocene. V.51774.

FIG. 5. ***Lithophyllum*** cf. ***obliquum*** Lemoine. Vertical section. Miocene. V.51773.



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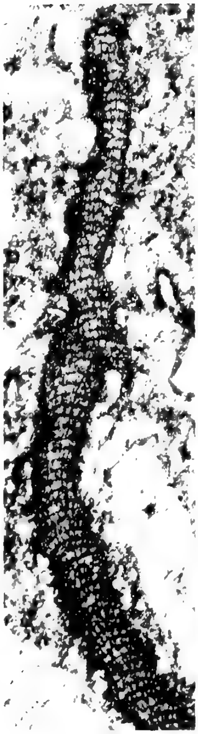

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PLATE 5

FIG. 1. **"Solenomeris"** sp. Vertical section of a fragment, ×40. Paleocene. V.51784.

FIG. 2. **Pycnoporidium sinuosum** Johnson & Konishi (×50). Paleocene. V.51785.

FIG. 3. **Jania miocenica** Johnson (×50). Lower Miocene. V.51758.

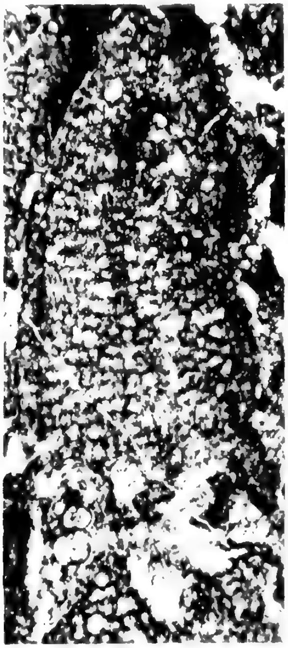
FIG. 4. **Corallina neuschelorum** Johnson. A partial segment, ×50. Lower Miocene. V.51758.

FIG. 5. **Mesophyllum vaughanii** (Howe). Fragment showing conceptacle chambers, ×50. Lower Oligocene. V.51770.

FIG. 6. **Lithophyllum capederi** Lemoine. Several crusts, ×50. Lower Miocene. V.51775.

FIG. 7. **Distichoplax biserialis** (Dietrich). Sections of two fragments, ×40. Paleocene, Borneo. V.51783.

FIG. 8. **Lithophyllum densum** Lemoine. Slightly oblique long section of a branch, ×50. Paleocene. V.51767.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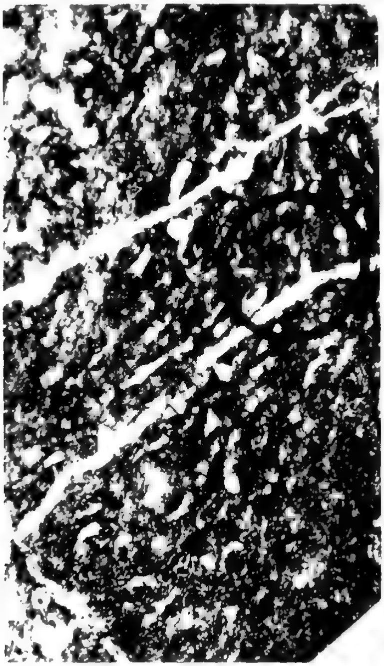
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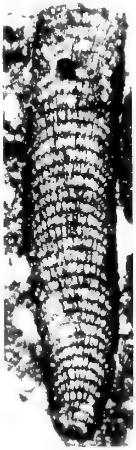
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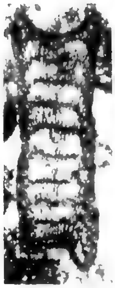
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PLATE 6

(All ×50)

FIGS. 1, 2. ***Subterraniphyllum thomasi*** Elliott. Fig. 1, An oblique long section. Lower Oligocene. V.51782. Fig. 2, Longitudinal section of a worn fragment. Lower Oligocene. V.51782.

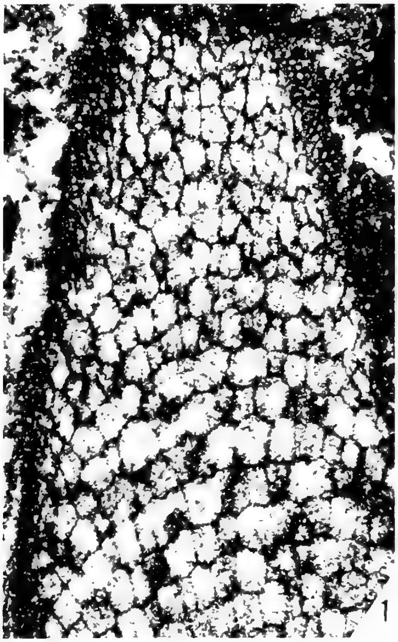
FIG. 3. ***Lithoporella antiquitas*** Johnson. Two conceptacle chambers shown. Lower Miocene. V.51776.

FIG. 4. ***Dermatolithon saipanense*** Johnson. Lower Miocene. V.51758.

FIG. 5. ***Jania*** cf. ***nummulitica*** Lemoine. Lower Oligocene. V.51780.

FIG. 6. ***Thaumatoporella parvovesiculifera*** (Raineri). Paleocene. V.51777.

FIG. 7. ***Amphiroa*** cf. ***fortis*** Johnson. Slightly oblique vertical section. Paleocene. V.51781.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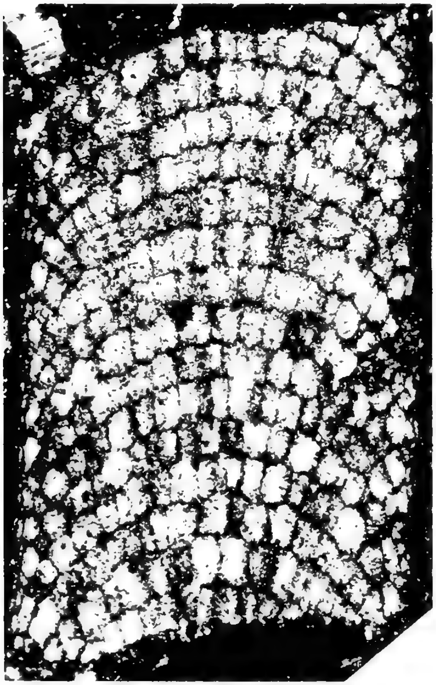
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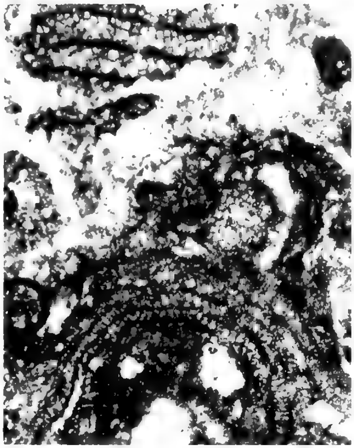
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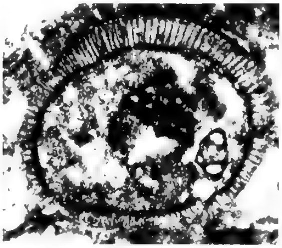
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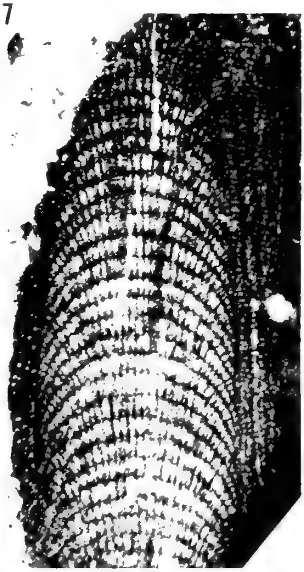
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BRITISH WEALDEN SHARKS

C. PATTERSON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 11 No. 7
LONDON: 1966

BRITISH WEALDEN SHARKS

BY

COLIN PATTERSON, Ph.D.

Pp. 281-350; 5 *Plates*; 31 *Text-figures*

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THE BRITISH MUSEUM (NATURAL HISTORY)
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THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

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TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

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BRITISH WEALDEN SHARKS

By COLIN PATTERSON

CONTENTS

SYNOPSIS

New material, consisting mainly of abundant isolated teeth from bone-beds, allows more detailed and precise definition of the known sharks of the British Wealden and Purbeck, and contains five new species : *Hybodus brevicostatus*, *Lonchidion breve* (with three new subspecies), *L. striatum*, *L. rhizion* and *L. heterodon*. Samples from successive horizons allow the interrelationships of the various species to be worked out in some detail. *Hylaeobatis* is shown to belong in the family Ptychodontidae and to lie near the ancestry of *Ptychodus* : the Ptychodontidae are probably derived from the hybodontid genus *Lonchidion*. The Wealden shark fauna is unusual in being from fresh water and in containing only hybodontoids : it is suggested that the hybodonts were able to escape from competition with more advanced selachians by entering fresh water : the radiation which they underwent there parallels their marine radiation at their first appearance, and explains the similarity between the shark fauna of the Wealden and of the marine Triassic. Certain of the more specialized Wealden forms seem to have returned to the sea and given rise to the Upper Cretaceous hybodonts and ptychodonts.

I INTRODUCTION

This paper has been prompted by the arrival in the British Museum (Natural History) of two sets of new Wealden material. Between 1960 and 1962 Drs. W. A. Clemens and K. A. Kermack of University College, London, were searching the bone-beds of the British Wealden for mammalian remains. In the course of this work large quantities of bone-bed were broken down with formic acid, and the bone separated by bromoform flotation. The mammalian finds resulting from the work have already been described (Clemens 1960, 1963; Kermack, Lees & Mussett 1965), and Dr. Kermack and his colleagues were kind enough to present the residue of the treated bone-beds to this museum. This material is rich in fish remains, though the majority are rolled and water-worn. In 1961 Mr. J. F. Wyley of Richmond, Surrey, discovered a bone-bed in the Weald Clay in the Henfield Brick Company's pit at Henfield, Sussex, and in many visits to the pit he has collected a quantity of fish material which he has generously presented to this museum. The material from Henfield is normally excellently preserved.

Knowledge of British Wealden sharks is due almost entirely to Smith Woodward. Agassiz (1837) described several hybodont fin spines under various names, and Egerton (1845) described *Hybodus basanus* from the Weald Clay of the Isle of Wight and (1854) a fin spine from Tilgate as *Asteracanthus granulosus*. In 1889 Smith Woodward briefly redescribed these species, referred several teeth to *Hybodus*, and described *Acrodus ornatus* from the Upper Wealden. Later (Smith Woodward 1916), in his monograph on the fishes of the British Wealden and Purbeck, he gave more detailed descriptions of all these species and added two new species of *Hybodus*, *H. ensis* and *H. parvidens*, and a new genus and species, *Hylaeobatis problematica*, all based on isolated teeth. No new material of any of these species has since been described (*H. basanus* has been incorrectly recorded from the Cretaceous of Japan by Yabe & Obata 1930).

In this paper a new species of *Hybodus* and four new species, one with three subspecies, of the hybodont genus *Lonchidion* Estes (1964) are described, and *Acrodus ornatus* and *Hylaeobatis problematica* are shown to be synonymous. The total list of British Wealden sharks known at present is therefore:

Hybodus basanus Egerton
**H. ensis* Smith Woodward
**H. parvidens* Smith Woodward
H. brevicostatus sp. nov.
†*H. striatulus* Agassiz
**Lonchidion breve* sp. nov.
**L. striatum* sp. nov.
**L. rhizion* sp. nov.
**L. heterodon* sp. nov.
†*Asteracanthus granulosus* Egerton (doubtfully *Asteracanthus*, see p. 310)
**Hylaeobatis ornata* (Smith Woodward)

* Species known only by isolated teeth.
† Species known only by isolated fin spines.

II LOCALITIES

The bulk of the new material described here is from four horizons, the Cliff End bone-bed, the Telham bone-bed, the Paddockhurst bone-bed and the Weald Clay of Henfield, Sussex.

(*a*) Cliff End Bone-bed

The Cliff End bone-bed, exposed on the foreshore at Cliff End, near Hastings, Sussex, the source of the mammal teeth discovered early in the century by Teilhard de Chardin and Pelletier, has recently been described by Allen (1960 : 11) and Clemens (1963 : 58), the latter also describing the method used to concentrate the vertebrate remains. The bone-bed is within the Ashdown Beds (of Valanginian age according to Hughes 1958), but its precise horizon is not yet established*. The Ashdown Beds are interpreted by Allen (1959) as a deltaic deposit, the delta flowing into a freshwater lake. The great majority of the vertebrate remains are strongly rolled and abraded. Of the recognizable fragments about 45% are shark teeth, 50% are teeth and fragments of dermal bones of actinopterygians (mainly *Lepidotes*), and 5% or less are reptilian.

The shark fauna includes :

Hybodus ensis (common)
H. parvidens (common)
H. brevicostatus (rare)
Lonchidion breve breve (moderately common)
L. rhizion (uncommon)
L. heterodon (rare)

(*b*) Telham Bone-bed

The Telham bone-bed is exposed at a number of localities in the south-eastern Weald (Allen 1949 : 279, text-fig. 45). The sample described here was collected by Mr. P. J. Whybrow from the exposure at Teigh Farm, Stone, Kent (GR TQ 937268). The bone-bed lies in the Wadhurst Clay, near the base (Upper Valanginian according to Hughes 1958), and is interpreted by Allen as the result of river water flooding over a delta plain. The vertebrate remains are in much the same condition as at Cliff End, rolled and abraded. Of the recognizable fragments, about 30% are shark teeth and the remaining 70% are almost entirely actinopterygian, mainly *Lepidotes* : reptiles account for only about 1% of the sample. The shark fauna includes :

Hybodus ensis (rare)
H. parvidens (common)
Lonchidion breve breve (moderately common)
L. rhizion (rare)

This locality is referred to in the text as Telham bone-bed, Stone, Kent.

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* In a paper published while this work was in press, Kermack, Lees & Mussett (1965: 536) give further information on the Cliff End bone-bed, pointing out that the bed cannot now be located in the cliff or on the foreshore, and that the scattered blocks found on the beach probably come from an off-shore reef, which would place the bone-bed "well down in the Fairlight Clays", near the base of the Wealden. Kermack, Lees & Mussett also publish a comment on the Cliff End fauna which I wrote on first seeing the material. I would not now infer brackish conditions from the abundant hybodont selachians: I think it probable that all the species present were capable of life in fresh water.

(*c*) Paddockhurst Bone-bed

Clemens (1960, 1963 : 63) has given this name to a bone-bed in the Grinstead Clay (Hauterivian according to Hughes 1958) at Paddockhurst Park, near Turner's Hill, Sussex. Allen (1959) interprets the Grinstead Clay as a fresh-water lake deposit. The vertebrate remains in the Paddockhurst bone-bed are neither so broken up nor so badly rolled as they are at Cliff End, and sharks are less common : shark teeth make up about 15% of the recognizable elements, reptiles about 10%, and the remaining 75% is actinopterygian, mainly scales and teeth of *Lepidotes*.

The shark fauna includes :

Hybodus ensis (common)
H. parvidens (common)
H. brevicostatus (rare)
Lonchidion breve breve (moderately common)
L. breve crenulatum (moderately common)
L. rhizion (rare)

(*d*) Henfield

The Henfield Brick Company's pit (GR TQ/218143) at Henfield, Sussex, is a large pit in the Weald Clay which is being actively worked (Milbourne 1961 : 135). The beds dip northwards at about 5 degrees (Reeves 1947 : 83). The highest beds exposed, in the north wall of the pit, are red and yellow clays without obvious fossils. These beds pass down into brown and grey clays. About 3 ft. below the red and yellow clays there is a band of '*Paludina*' limestone, 3–8 in. thick. Fishes occur in the clay immediately above the limestone. Below the limestone there is 10 ft. of brown sandy clay, and below this about 25 ft. of grey clay in which six minor cyclothems, 3–4 ft. thick, are recognizable by increasing sand content giving a brownish tinge towards the top of each. Each of these cyclothems contains fish fragments, often concentrated into more or less well marked bone-beds which are occasionally cemented into a phosphatic limestone (Pl. 1, fig. 1). Below these cyclothems the floor of the pit is occupied by grey clay containing *Iguanodon*, lignite and occasional tree trunks, passing down in the south wall of the pit into barren red and yellow clays and sands, the lowest beds exposed. This sequence lies in Reeve's Group II (1958 : 11), the middle division of the Weald Clay (Barremian according to Allen 1955 and Hughes 1958), probably near the top : Dr. F. W. Anderson has examined samples of ostracods collected from the various fish horizons and places the '*Paludina*' limestone at about 550 ft. below the top of the Weald Clay.

Associated with the fishes there are abundant ostracods, all non-marine according to Dr. Anderson, and occasional charophyte oogonia, another indication of fresh water conditions. The fish material, although consisting almost entirely of dissociated fragments, is well preserved. There is no significant difference in the fish fauna of the various fish horizons, but in the minor cyclothems the fauna varies widely within the bone-beds: the block of bone-bed shown in Pl. 1, fig. 1 shows abundant shark teeth of five species (teeth of *Lonchidion breve* and *L. striatum* are too small to show on the photograph), but the other side of the block, which is only 14 mm.

thick, shows only two or three teeth of *Lonchidion*, and is made up almost entirely of teleostean remains. Sharks make up less than 10% of the material, the bulk of which is teleostean. Actinopterygians identified include:

Lepidotes mantelli Agassiz
Coelodus mantelli Agassiz
Caturus tenuidens Smith Woodward (Pl. 1, fig. 2: not previously recorded above the Purbeck)
Pachythrissops sp.
Clupavus sp.

The shark fauna includes:

Hybodus basanus (common)
H. parvidens (rare)
H. brevicostatus (moderately common)
Lonchidion breve breve (common)
Lonchidion striatum (common)
Hylaeobatis ornata (common)

(*e*) Other localities

Small but valuable samples from two other localities are also described here. The first was collected by Mr. I. M. West of the University of Southampton from a limestone above the Broken Shell Limestone in the Upper Purbeck exposed 100 yards east of Friar Waddon farm, near Upwey, Dorset (GR SY/643858) (see Anderson 1958: 119, 129, text-figs. 21, 22). Mr. West thinks this horizon is equivalent to the *Unio* Bed of the type Purbeck. The second sample was collected by Mr. P. J. Whybrow from a limestone in the Wadhurst Clay exposed in a cutting on the east side of the road 200 yards north of Homeland, Ashurstwood, Sussex (GR TQ/419363). These two localities are referred to in the text as Friar Waddon and Ashurstwood respectively.

III SYSTEMATIC DESCRIPTIONS

Class *SELACHII*

Order HYBODONTIFORMES

Family **HYBODONTIDAE** Owen 1846

DIAGNOSIS. See Berg (1955: 61)

Genus ***HYBODUS*** Agassiz 1837: 41

DIAGNOSIS. See Smith Woodward (1916: 3), but delete 'palatoquadrate not articulated with the postorbital region of the skull'.

TYPE SPECIES. *Hybodus reticulatus* Agassiz.

H. basanus Egerton, *H. ensis* Smith Woodward and *H. parvidens* Smith Woodward, the three species of the genus known by teeth in the British Wealden, are easily distinguished in the type material described by Smith Woodward but appear to be linked by intermediate forms in the new material. *H. basanus* is the only species of the three in which the complete dentition is known, and will be described first.

Hybodus basanus Egerton

(Pl. 1, fig. 1; Text-figs. 1–3)

1845 *Hybodus basanus* Egerton : 197, pl. 4.
1889 *Hybodus basanus* Egerton ; Smith Woodward : 273, pl. 12, figs. 1–5.
1891 *Hybodus basanus* Egerton ; Smith Woodward : 63, pl. 1, pl. 2, fig. 1.
1898 *Orthybodus basanus* (Egerton) Jaekel : 139.
1916 *Hybodus basanus* Egerton ; Smith Woodward : 5, pl. 1, figs. 1, 2 ; pl. 2, fig. 1 ; text-figs. 3–5.
1919 *Hybodus basanus* Egerton ; Smith Woodward : 139, pl. 26, fig. 3.

Amended diagnosis. *Hybodus* known by skull, dentition, fin spines and fragments of postcranial skeleton ; nine or ten files of teeth in each ramus of the jaws, symphysial file present in lower jaw, dentition weakly heterodont ; teeth reaching 15 mm. in length, central cusp high, slender (ratio of height above root/crown junction to length 1·0–2·0) and arched lingually ; three or (rarely) four pairs of lateral cusps ; labial face of crown with rather numerous fine striae, often bifurcated basally, reaching tips of lateral cusps and covering from one-third to two-thirds of central cusp ; lingual face of crown with similar but longer striae almost reaching tip of central cusp ; teeth without accessory cusps on the labial or lingual margins ; root low, bent lingually ; a single pair of cephalic spines with terminal barb ; fin spines slender, compressed, not much arched, reaching about 20 cm. in length, lateral faces with 8–12 fine, sharp ridges, posterior denticles in two series, small and closely set.

Holotype. GSM No. 27973, Geological Survey & Museum, London, from the Weald Clay of Atherfield, Isle of Wight.

Material. In addition to the holotype, about twenty skulls, fragments of vertebral column, fin spines and isolated teeth in the British Museum (Natural History) and the Geological Survey & Museum.

Horizon and localities. Weald Clay : Atherfield, Isle of Wight ; Pevensey Bay, Sussex ; Henfield, Sussex ; Bexhill, Sussex.

Description. *Hybodus basanus* is the only species of the genus in which the skull is well known. Smith Woodward (1916) has given a good description of the skull based on several well preserved heads in the British Museum (Natural History). Of the palato-quadrate he writes ' it can scarcely have articulated with the postorbital prominence of the neurocranium '. Smith (1942 : 701) has questioned this, noting that in the Liassic *H. hauffianus* Fraas the skull is said to be amphistylic by Jaekel, and that it is amphistylic in *Synechodus*. Berg (1955 : 62) has also suggested that Smith Woodward's observation needs checking. I have examined all of the skulls of *H. basanus* in the British Museum (Natural History). The palatoquadrate and hyomandibular are best shown in P.2082*a* and P.6103. There can be no doubt that Smith Woodward's reconstruction (1916, text-fig. 3) is accurate in showing the hyomandibular as being large and much higher than the postorbital part of the palatoquadrate. In this *H. basanus* differs from typical amphistylic sharks such as *Hexanchus*, where the hyomandibular is slender and no higher than the otic process

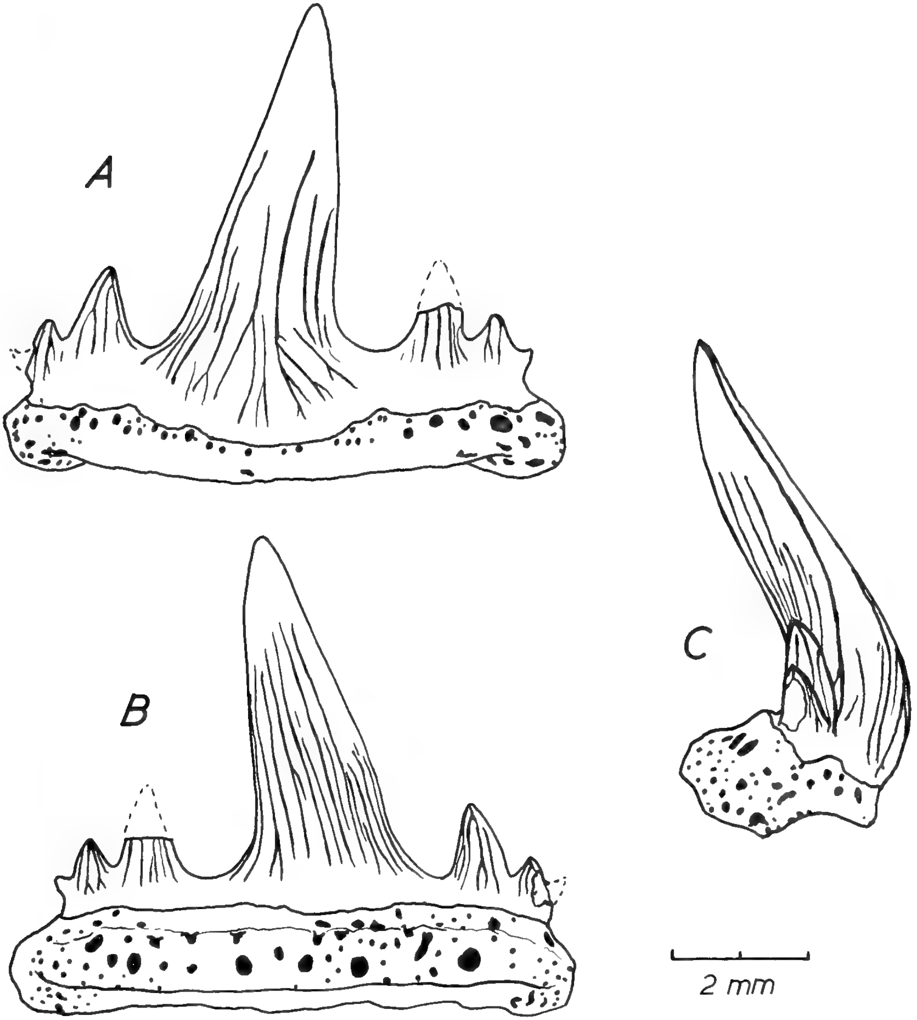

FIG. 1. *Hybodus basanus* Egerton. Tooth from the first or second file of the upper jaw, right side, in labial (A), lingual (B) and medial (C) view. P.11871, Weald Clay; Pevensey Bay, Sussex.

of the palatoquadrate, and from *Heterodontus* and *Hybodus hauffianus* (Jaekel 1906) in which the hyomandibular is stout but equal in height to the otic process of the palatoquadrate. I do not think it is possible, however, to decide whether the palatoquadrate of *H. basanus* had a post-orbital articulation or not. The otic process was certainly tucked well up below the postorbital process of the neurocranium, but there is no sign of an articular facet or condyle on the otic process.

It is possible that the suspension was amphistylic, but the long, large hyomandibular shows that the species tends towards the hyostylic condition.

Smith Woodward describes the dentition of *H. basanus* as consisting of ten or eleven paired files of teeth in each jaw, with a symphysial file in the mandible. The teeth (Text-fig. 1) have a high, slender central cusp and three pairs of lateral cusps which are well separated from the central cusp. The height of the central cusp (above the root/crown junction) is only slightly less than the length of the tooth in anterior teeth, but the height decreases posteriorly.

The central cusp curves lingually rather strongly, but the tip curves labially again, giving a weakly sigmoid outline to the cusp in medial view (Text-fig. 1B). Of the three pairs of lateral cusps, the innermost is sharply pointed, striated to its tip, and normally about one-third as high as the central cusp. The second pair of lateral cusps is shorter but similarly ornamented. The outermost cusps are normally very small and almost smooth. A minute fourth lateral cusp is occasionally present.

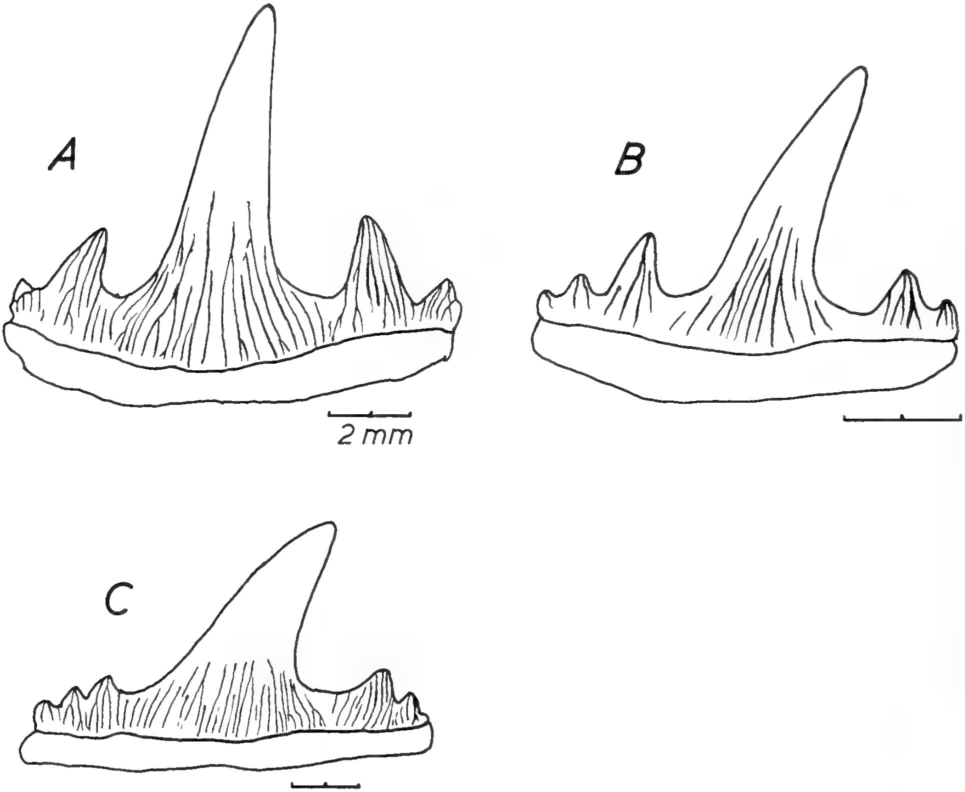

FIG. 2. *Hybodus basanus* Egerton. A. Tooth from the first file of the upper jaw, right side, in labial view. P.2082. B. Tooth from the sixth file of the lower jaw, left side, in labial view. P.6356. C. Tooth from the eighth file of the lower jaw, left side, in labial view. P.2082*b*. All from the Weald Clay of Pevensey Bay, Sussex.

The base of the labial face of the crown is ornamented with moderately fine, parallel or sub-parallel vertical striae, often bifurcating basally, which extend to the tips of the lateral cusps and to about one-third or half of the height of the central cusp. There is a good deal of variation in the strength, number and length of these striae: they are closely packed, weak and short in some fish (P.2082*b*, Text-fig. 2C), and coarse, well spaced and long, covering more than half the labial face of the central cusp, in others (P.11871, Text-fig. 1A). On the lingual face of the crown the ridges are stronger, and extend almost to the tip of the central cusp (P.2082*a*, P.11871, Text-fig. 1B). The root is low, and is turned lingually, with the labial face of the root lying almost at right angles to the axis of the central cusp. This description is based on the teeth of the complete skulls from the Weald Clay of Pevensey Bay, Sussex, and Atherfield, Isle of Wight.

It is difficult to match these teeth exactly in material from any other Wealden horizon or locality. In the new material from the Weald Clay of Henfield, which is approximately contemporary with the type material of *H. basanus*, there is a number of teeth of the type shown in Pl. 1, fig. 1 and Text-fig. 3. In these teeth the crown is lower than in those from the complete skulls of *H. basanus*, with a ratio of height (above the root/crown junction) to length of little less than 2·0, the striae are less numerous and are longer, reaching well over half the height of the central

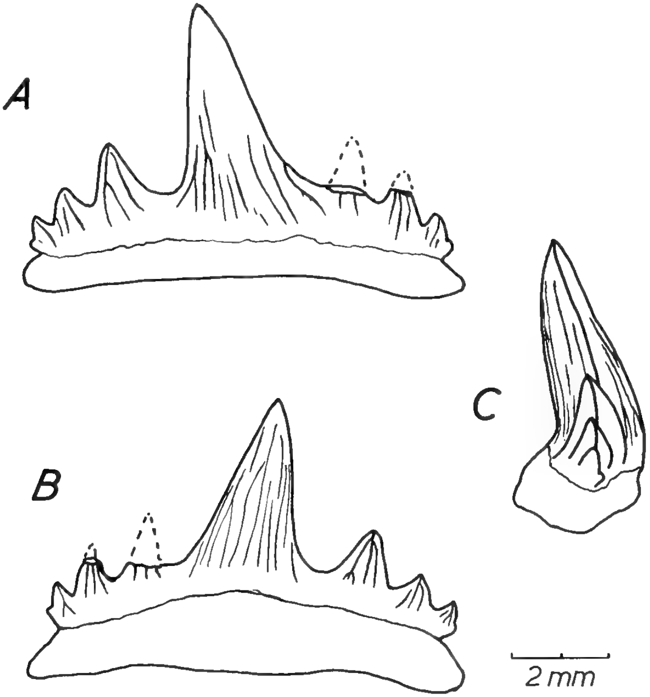

FIG. 3. *Hybodus basanus* Egerton. Lateral tooth in lingual (A), distal (B) and labial (C) view. P.46921, Weald Clay; Henfield, Sussex.

cusp on the labial face (the tooth shown in Text-fig. 3 has shorter striae than most teeth from Henfield) and to the tip of the cusp on the lingual face, and both the central cusp and the root are not turned lingually so strongly as they are in typical *H. basanus* (cf. Text-figs. 1C, 3C). In all these features the teeth from Henfield are intermediate between typical *H. basanus* from Atherfield and Pevensey, and typical teeth of *H. parvidens* from the Ashdown Beds and Wadhurst Clay (Text-figs. 6, 7). The Henfield teeth are referred to *H. basanus* rather than *H. parvidens* because they never show the knob or accessory cusp at the base of the labial face of the central cusp which is common in *H. parvidens*, because the striae are almost as numerous as they are in *H. basanus* and only rarely reach the tip of the central cusp, and because there is a difference in the extent of the striae on the labial and lingual faces of the central cusp (in *H. parvidens* the length of the striae is similar on the two faces of the central cusp).

No teeth referable to *H. basanus* are known from horizons above or below the Weald Clay. The tooth from the Lower Cretaceous of Japan referred to *H. basanus* by Yabe & Obata (1930 : 4, pl. 2, fig. 3) differs from this species in the longer and more slender central cusp and in the almost complete lack of striae on the labial face : it is possibly a *Synechodus*. Leriche (1911 : 457, pl. 6, fig. 2) has referred to *H. basanus* a fragment of fin spine from the Lower Neocomian of the Paris Basin, but this identification is very doubtful : the fragment could as well belong to another species.

AFFINITIES. Smith Woodward (1916 : 10) considered that teeth and spines from horizons in the lower part of the Wealden showed resemblances to *H. basanus* without being referable to the species. These forms (see p. 294) are here included in *H. ensis* which in the Wealden seems to trend towards *H. basanus* in the form of the teeth, but is probably not related. Teeth of *H. basanus* from Henfield are intermediate in a number of characters between more typical teeth of the species from Pevensey and the Isle of Wight, and teeth of *H. parvidens* from lower horizons. This, together with the trend towards *H. basanus* shown by *H. parvidens* in the Grinstead Clay (see p. 299), leaves little doubt that *H. basanus* is a species confined to the Weald Clay (probably to the upper part alone) which evolved directly from *H. parvidens* by increase in size, in crown height and in the number of striae.

Hybodus ensis Smith Woodward

(Text-figs. 4, 5)

1889 *Hybodus* sp. inc. (? *strictus* Agassiz) Smith Woodward : 275.
1889 *Hybodus* sp. inc. (? *striatulus* Agassiz) Smith Woodward : 276, pl. 11, figs. 14, 15.
1916 *Hybodus ensis* Smith Woodward : 11, pl. 2, figs. 2–6 ; *non* fig. 7.

AMENDED DIAGNOSIS. *Hybodus* known only by isolated teeth : teeth large, up to 2 cm. in length, central cusp high (ratio of height above root/crown junction to length 1·0–1·5), broad at base, evenly tapering and moderately compressed, not much arched lingually ; two pairs of lateral cusps, inner lateral cusps moderately high, slender, pointed, well marked off from central cusp but close to it ; labial face of crown with many fine, parallel striae reaching tips of lateral cusps but covering only basal quarter or fifth of central cusp; lingual face of crown with coarser striae extending about half way up central cusp; root low, bent lingually.

Holotype. BMNH No. 21349 (Smith Woodward, 1916, pl. 2, fig. 6), tooth without root, Middle Purbeck; Swanage, Dorset.

Material. In addition to the holotype, about one hundred isolated and fragmentary teeth.

Horizons and localities. Middle Purbeck: Swanage, Dorset. Upper Purbeck: Friar Waddon, Dorset. Ashdown Beds: Cliff End, Sussex. Wadhurst Clay: Teigh Farm, Stone, Kent; Hastings, Sussex. Grinstead Clay: Paddockhurst Park, Sussex; Tilgate Forest, Sussex.

Description. Smith Woodward based this species on incomplete teeth from the Middle Purbeck of Dorset, but also recorded it from the Wealden of Tilgate Forest (Grinstead Clay—see p. 294). All the specimens labelled as *H. ensis* by Smith Woodward are from the Purbeck.

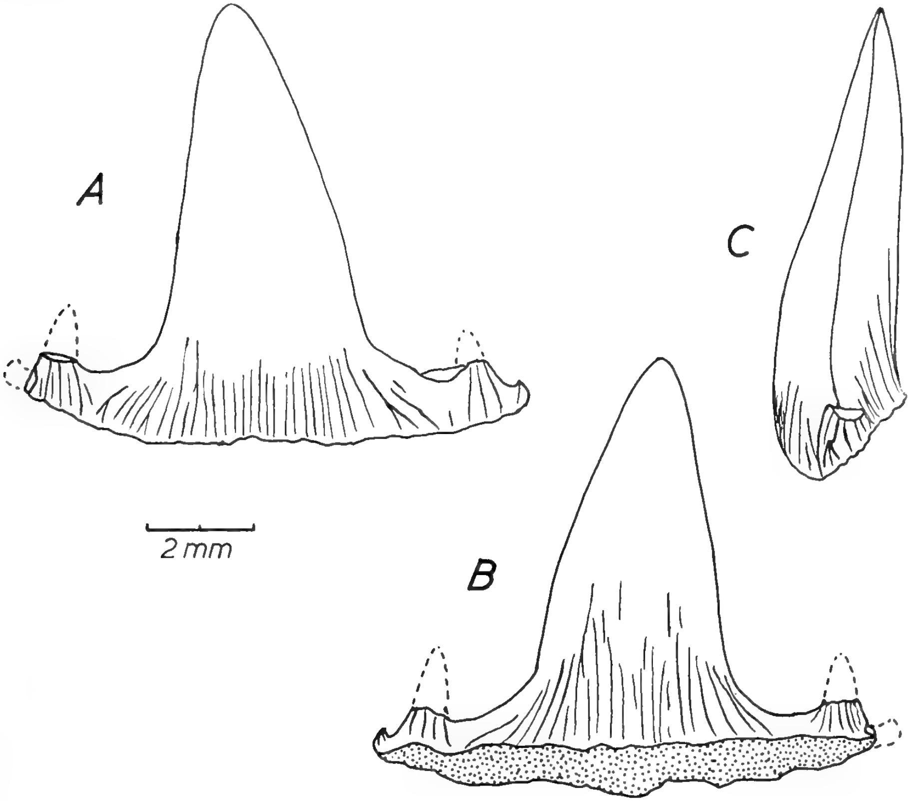

Fig. 4. *Hybodus ensis* Smith Woodward. Tooth in labial (a), lingual (b) and medial (c) view. 21349*c*, Middle Purbeck; Swanage, Dorset.

The species is poorly known, the Purbeckian type material consisting of teeth without roots exposed in labial view. One of these teeth, 21349*c*, has been removed from the matrix to expose the lingual face (Text-fig. 4). In the Purbeck material of *H. ensis* the crown is about as high as in *H. basanus*, with the ratio of length to height (above the root/crown junction) about 1·0, but the central cusp is much broader, the ratio of the breadth at its middle point to its height ranging from 2·8 to 3·0, compared with 4·0 to 5·0 in *H. basanus*. In no specimen of *H. ensis* are there more than two pairs of lateral cusps (21349*b*, Smith Woodward 1916, pl. 2, fig. 7, has three pairs of lateral cusps but does not belong in *H. ensis*—see *H. parvidens*, p. 297). In *H. ensis* the labial face of the crown (Text-fig. 4A) bears fine, close packed, parallel striae which extend almost to the tips of the inner lateral cusps but cover only the basal one-fifth or quarter of the central cusp. On the lingual face of the crown (Text-fig. 4B) the striae are less numerous, a little coarser and cover almost one-third of the height of the central cusp. The central cusp curves lingually less strongly than it does in *H. basanus* (cf. Text-figs. 1C, 4C). Other apparent differences between *H. ensis* and *H. basanus* suggested in Smith Woodward's original description—that the inner lateral cusps are higher and closer to the central cusp in *H. ensis*, and that the ratio of height to length of the tooth is greater in this species—are not confirmed by measurement of the teeth.

In 1889 (p. 276) Smith Woodward catalogued as '*Hybodus* sp. inc. (? *striatulus* Agassiz)' about thirty teeth from the Wealden of Tilgate Forest,[1] noting the high, moderately broad central cusp, the high, slender inner lateral cusps, and the striae 'rarely extending more than half the height of the median cone'. In 1916 (p. 10) he referred to these teeth as 'of the same general type as those of *H. basanus* . . . but not sufficiently similar to be referred with certainty to this species'. Most of these teeth are more or less rolled and waterworn, and many are quite indeterminable. Some, such as 48377 (Tilgate Forest) and P.6353 (Hastings, unknown horizon) agree exactly with the Purbeck specimens of *H. ensis*, and leave no doubt that this species extended into the Wealden. But the majority of these teeth do not agree exactly with the type material of *H. ensis* : 2693 (Tilgate Forest, Text-fig. 5, Smith Woodward 1889, pl. 11, fig. 14) is the best preserved of these, and is typical in shape. These teeth differ from *H. ensis* in the more slender, sharply pointed central cusp (ratio of breadth measured at the middle point to height *c.* 3·5), but they agree with *H. ensis* and differ from *H. basanus* in their large size, weakly arched central cusp (Text-fig. 5B), two pairs of lateral cusps, in the short, fine striae on the labial face of the crown, rarely reaching more than one-third of the height of the central cusp, and in the short striae on the lingual face of the crown. The striae on the lingual face of the central cusp extend about as far as they do in typical *H. ensis*, and are characteristically longer near the margins of the cusp than they are in the centre. In my opinion these teeth should be included in *H. ensis*. Some of these Wealden teeth (26026 ; Smith Woodward 1889, pl. 11, fig. 14 : 26024, both from Tilgate Forest)

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[1] Mantell's horizon at Tilgate Forest, previously thought to lie in the Upper Tunbridge Wells Sand, directly below the Weald Clay (Topley 1875 : 92), has recently been re-identified as in the Cuckfield Stone, in the middle part of the Grinstead Clay (Stubblefield 1963 : 37).

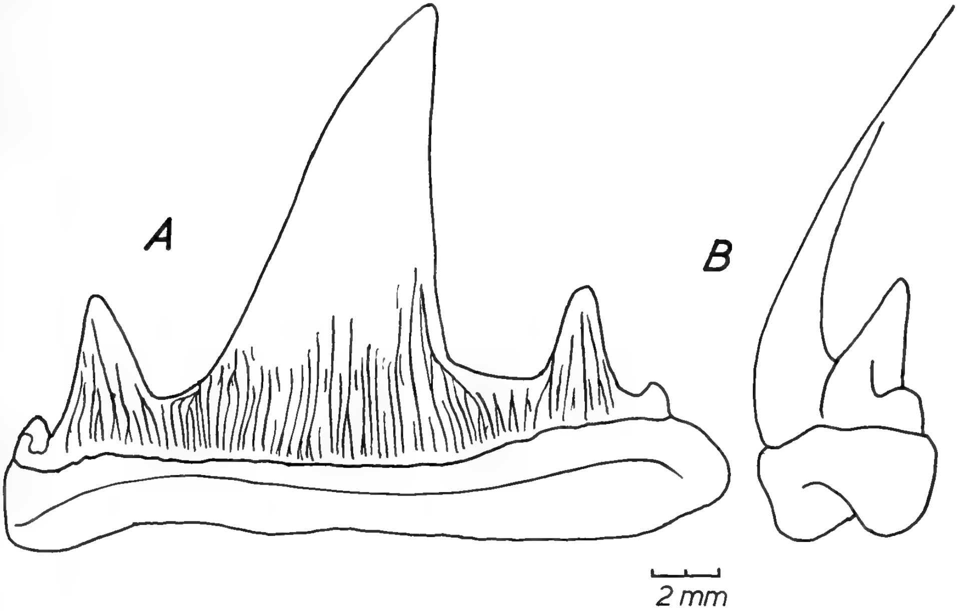


FIG. 5. *Hybodus ensis* Smith Woodward. Tooth in labial (A) and medial (B) view. 2693, Grinstead Clay; Tilgate Forest, Sussex.

tend towards *H. basanus* in having a more slender central cusp with rather coarse striae covering almost half of the labial face, but they have only two pairs of lateral cusps: 26024 is particularly like the typical Weald Clay *H. basanus*, but it seems probable that it is not an early example of this species but a tooth of *H. ensis* in which the evident trend towards narrowing of the central cusp and extension and coarsening of the ornament has gone farther than in other examples.

Among the new material from the Cliff End and Paddockhurst bone-beds there are no complete large teeth, but isolated central cusps and imperfect crowns are very common. All of these large teeth can be referred to *H. ensis*: they show a range in breadth of the central cusp from stout forms like the Purbeck *H. ensis* to slender forms approaching the proportions of *H. basanus*, but the striae on the labial face are always short, fine and closely packed, and on the lingual face they are always shorter than in *H. basanus* and are longer at the margins of the central cusp than in the centre.

No examples of *H. ensis* are known from horizons above the Grinstead Clay.

AFFINITIES. *H. ensis* is a species which ranges from the Middle Purbeck to the Grinstead Clay (Paddockhurst bone-bed and Tilgate Forest). In the Wealden the teeth show a trend towards narrowing of the central cusp, sometimes accompanied by coarsening and lengthening of the striae which may produce teeth closely similar to those of *H. basanus* in shape.

Smith Woodward (1916 : 11) noted the similarity between the Purbeck forms of *H. ensis* and the Middle and Upper Jurassic *H. grossiconus* Agassiz. Extremely similar to *H. ensis* is *H. songaensis* Saint-Seine (1962 : 4, pl. 6, fig. 6), a species based on a single tooth from the Songa Beds of the Congo, probably marine and of Kimmeridgian age, which could well be synonymous with *H. ensis*. *H. ensis* is possibly derived directly from these marine Jurassic forms.

Hybodus parvidens Smith Woodward

(Text-figs. 6–9)

1889 *Hybodus* sp. inc. Smith Woodward : 276, pl. 11, fig. 16.
1916 *Hybodus ensis* Smith Woodward : pl. 2, fig. 7 (*errore*).
1916 *Hybodus parvidens* Smith Woodward : 12, pl. 2, figs. 8–14.
1949 *Hybodus parvidens* Smith Woodward ; Allen : 277 (name only).

Amended diagnosis. *Hybodus* known only by isolated teeth : teeth small, less than 10 mm. in length ; central cusp moderately high, not much compressed, lower and broader in posterior teeth ; ratio of height of central cusp (above root/crown junction) to length of tooth between 1·5 and 3·0 ; three or four pairs of lateral cusps ; labial face of crown with few coarse striae, often bifurcating basally, which reach the tips of the lateral cusps and commonly reach the tip of the central cusp except in some high anterior teeth, striae on lingual face similar ; knob or accessory cusp frequently present at base of labial surface of central cusp, no other accessory cusps ; root moderately deep, turned lingually a little.

Holotype. BMNH P.11877, tooth without root, Wadhurst Clay, Hastings.

Material. About two hundred isolated teeth.

Horizons and localities. Middle Purbeck : Swanage, Dorset. Upper Purbeck : Friar Waddon, Dorset. Ashdown Beds : Cliff End, Sussex ; Fairlight, Sussex. Wadhurst Clay : Teigh Farm, Stone, Kent ; Hastings, Sussex ; Rye, Sussex. Grinstead Clay : Paddockhurst Park, Sussex ; Tilgate Forest, Sussex. Weald Clay : Henfield, Sussex.

Description. Smith Woodward based this species on incomplete teeth from the Wadhurst Clay, in none of which was the root preserved. The holotype and two of the paratypes are shown in Text-fig. 6. Among the new material from the Cliff End bone-bed there are several more or less complete and unworn teeth (Text-fig. 7). The high-crowned teeth (Text-figs. 6, 7A) are presumably anterior, the low-crowned (Text-fig. 7B) posterior.

In this typical material from the Ashdown Beds and Wadhurst Clay, the central cusp is moderately high in anterior teeth, with a ratio of height of cusp to length of tooth of about 1·8–2·0. In posterior teeth the central cusp becomes much lower, the ratio of height to length reaching about 3·0. The central cusp is not compressed as it is in *H. ensis* and *H. basanus*, and does not curve lingually. There are always three pairs of lateral cusps, and often four. On the labial face of the crown the striae are coarse, sparse, and often bifurcated basally. They reach the tips of the lateral cusps

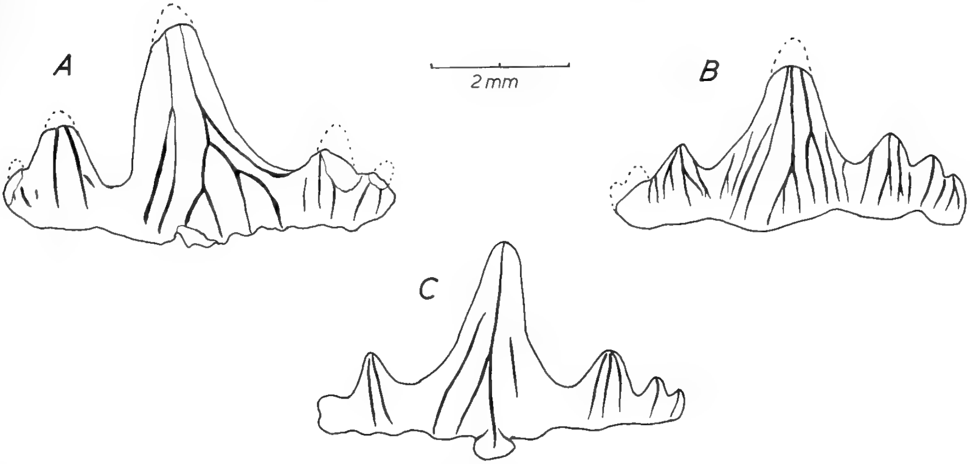


FIG. 6. *Hybodus parvidens* Smith Woodward. Teeth from the Wadhurst Clay of Hastings, Sussex, in labial view. A. P.11877, the holotype. B. P.11878 (paratype). C. P.11880 (paratype).

and commonly reach the tip of the central cusp: in a sample of 37 teeth from Cliff End, the central cusp is striated to its tip in 22; it is striated to the tip in 10 of 13 posterior teeth and in 12 of 24 anterior teeth. On the lingual face of the crown the ornament is very similar. It is interesting to note that in low-crowned posterior teeth, the striae on the lingual face of the crown tend to anastomose basally and form a reticular pattern (Text-fig. 7B) approaching the pattern found in this region in low-crowned species like *H. delabechei* and *H. brevicostatus* (Text-fig. 10). At the base of the labial face of the central cusp a knob or accessory cusp is very commonly present. This accessory cusp is larger and more sharply defined in posterior teeth than in anterior (cf. Text-fig. 7A, B). In the Cliff End material this accessory cusp is present in more than half the teeth (in 28 of a sample of 40), and is commoner in posterior teeth (present in 13 of 16 posterior teeth and in 15 of 24 anterior teeth). The root in *H. parvidens* is typically hybodont, with foramina irregularly distributed on both surfaces, is moderately deep, and is turned lingually a little (Text-fig. 7).

The above description is based on teeth from the Lower Wealden Ashdown Beds and Wadhurst Clay. Smith Woodward (1916: 12) also recorded the species from the Weald Clay of Berwick, Sussex, but I have been unable to trace the specimen on which this record was based: it was probably an example of *H. brevicostatus*. *H. parvidens* also occurs in the Purbeck, as is shown by a sample of sixteen incomplete teeth from Friar Waddon, Dorset, and by 21349*b* and 21349*d*, two teeth from the Middle Purbeck of Swanage, the first figured as *H. ensis* by Smith Woodward (1916, pl. 2, fig. 7). The picture presented by these Purbeck teeth (Text-fig. 8) is rather different from that in the Wealden material described above. The Purbeck teeth agree with the Wealden forms in size, but in most of them the crown is rather high, and where the ratio of crown height to tooth length is measurable (21349*b*, *d*) it is

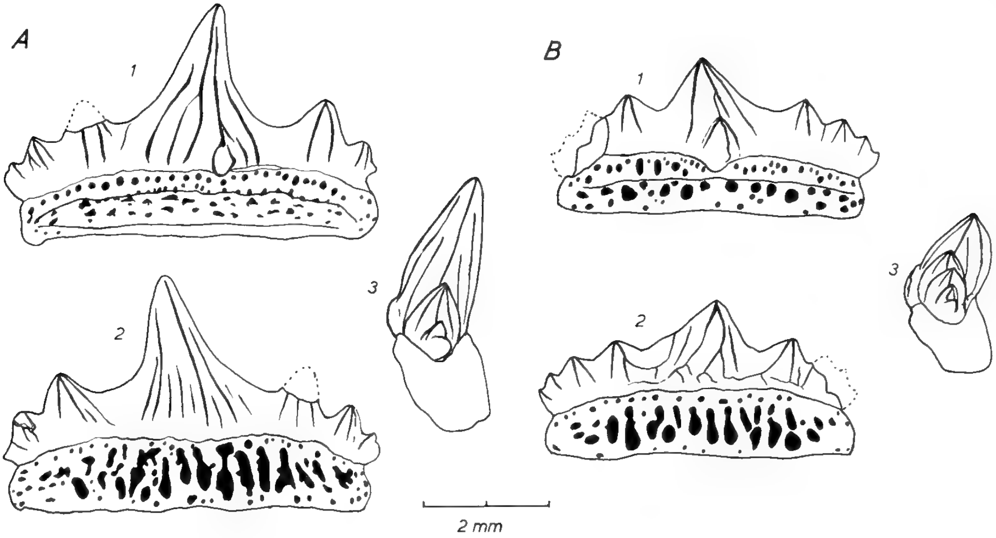


FIG. 7. *Hybodus parvidens* Smith Woodward. An anterior (A) and a posterior (B) tooth in labial (1), lingual (2) and medial (3) view. P.46930–31, Ashdown Beds, Cliff End Bone-bed; Cliff End, Sussex.

lower (1·5–1·7) than is usual in Wealden teeth. The striae on the labial face of the central cusp reach the tip in only four of the eighteen teeth: in six they cover between two-thirds and three-quarters of the cusp, in four about half the cusp, and in four less than half. Also, there is no accessory cusp at the base of the central cusp in any of the teeth, though there is an incipient cusp in two of them (Text-fig. 8B). But in spite of these differences, I have little doubt in referring these teeth to *H. parvidens*: the examples with lower crowns exactly match those typical *H. parvidens* in which the accessory cusp is absent.

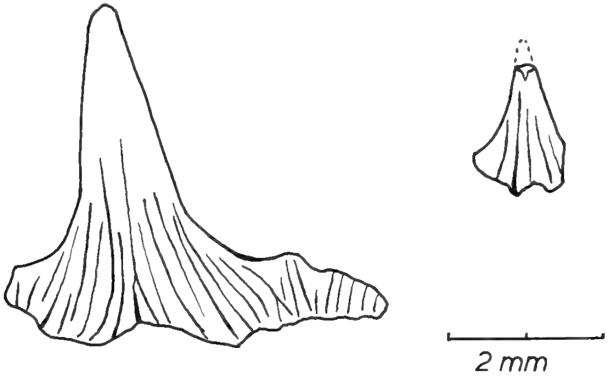


FIG. 8. *Hybodus parvidens* Smith Woodward. Fragmentary teeth in labial view. A. 21349*d*, Purbeck; Swanage, Dorset. B. P.46959, Upper Purbeck; Friar Waddon, Dorset.

Among the material from the Paddockhurst bone-bed (Grinstead Clay) complete teeth are rare, but small central cusps and incomplete teeth (Text-fig. 9A) are common. Teeth of *H. parvidens* which agree with the typical forms from the Ashdown Beds and Wadhurst Clay occur, but are rather rare. In a sample of 37 teeth, four are typical low-crowned posterior teeth of *H. parvidens*, the other 33 are high-crowned forms. Of these 33 teeth, only three are striated to the tip of the central cusp (cf. 12 out of 24 in high-crowned teeth from Cliff End), and only three have an accessory cusp (cf. 15 out of 24 at Cliff End). The striae in these teeth also tend to be finer and more numerous than in typical *H. parvidens*.

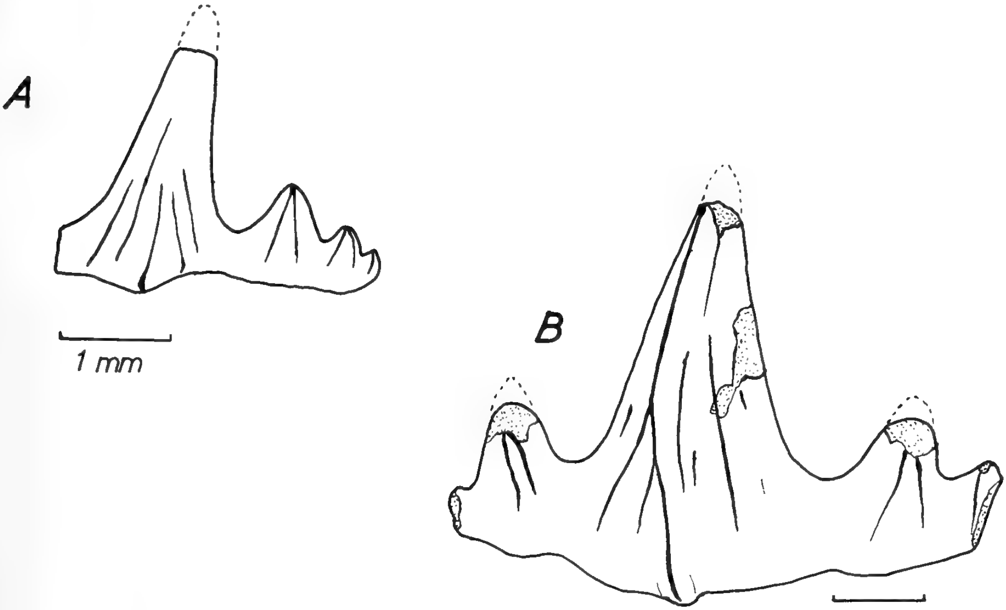


FIG. 9. *Hybodus parvidens* Smith Woodward. Teeth in labial view. A. P.46944, Grinstead Clay, Paddockhurst Bone-bed; Paddockhurst Park, Sussex. B. P.46971, Weald Clay; Henfield, Sussex.

Among the material from Tilgate Forest (Grinstead Clay) small teeth are very rare, but there are two examples of *H. parvidens*, 2850 and 3146.

Among the material from the Weald Clay of Henfield I can find only two teeth which are referable to *H. parvidens* (Text-fig. 9B); these are typical examples, very like teeth from the Grinstead Clay. Apart from these two specimens, all the high-crowned teeth from Henfield are of the type shown in Text-fig. 3, which are assigned to *H. basanus* for the reasons given on p. 292. The smaller low-crowned teeth (Text-fig. 13) are placed in *H. brevicostatus* for the reasons given on p. 306. *H. parvidens* is not known from any other locality in the Weald Clay or from any higher horizon.

AFFINITIES. The various samples of teeth of *H. parvidens* described above suggest that the history of the species was as follows. The species first appeared in the

Middle Purbeck. Purbeckian teeth are rather high-crowned, with no accessory cusp and with rather short, fine striae. In the Lower Wealden (Ashdown Beds and Wadhurst Clay) the species reached its typical and most distinctive form, with a crown which is of moderate height and has both striae to its tip and an accessory cusp in the majority of teeth. In the Grinstead Clay the species seems to trend towards the Purbeck form again, with an increase in crown height, a reduction in the height and an increase in the number of the striae on the central cusp, and a reduction in the incidence of the accessory cusp. Only two undoubted examples of *H. parvidens* are known above the Grinstead Clay. It seems very probable that the species did not become extinct, but evolved into *H. basanus* by a further increase in crown height and in the number of striae, coupled with an increase in size. The increase in size which marks the transition to *H. basanus* in the Weald Clay is perhaps correlated with the apparent extinction of the large-toothed *H. ensis* shortly before the Weald Clay was deposited.

It is shown below (p. 308) that the Wealden (Ashdown Beds to Weald Clay) species *H. brevicostatus* is also probably an offshoot of *H. parvidens* which originated near the base of the Wealden.

Smith Woodward (1916 : 12) suggested a possible relationship between *H. parvidens* and the Upper Jurassic *H. obtusus*, a species in which the crown is moderately high, coarsely striated, and in which accessory cusps are very common. But the form of the earliest examples of *H. parvidens* in the Purbeck, where there is no accessory cusp and where the crown is higher and less strongly striated than it is in the typical forms, suggests that the species did not originate from *H. obtusus* but from some unknown small, high-crowned species in the Upper Jurassic.

Hybodus brevicostatus sp. nov.

(Pl. 1, fig. 3 ; Pl. 2 ; Pl. 3, figs. 1–3 : Text-figs. 10–13)

DIAGNOSIS. *Hybodus* known by almost complete dentition and fin spines: nine paired files and a median symphysial file probably present in each jaw, dentition moderately heterodont ; teeth ranging (in one individual) from 8·0–18·5 mm. in length ; crown low and long, ratio of crown height (above the root/crown junction) to tooth length 3·25–6·25, crown not deeper than the root ; central cusp low, lateral cusps four or more, sometimes not recognizable in posterior and lateral teeth ; several accessory cusps often present on both labial and lingual margins of the crown, especially in the lower jaw ; crown with longitudinal occlusal crest and many coarse striae, often bifurcating basally, which reach the tips of the cusps and are interspersed in larger teeth with finer striae which fail to reach the tips of the cusps ; at the base of the lingual face of the crown the striae anastomose in a reticular pattern ; root deep, not turned lingually. Fin spines reaching about 18 cm. in length ; anterior edge keeled, lateral faces with 8–10 narrow, well spaced, discontinuous striae, posterior face with raised band bearing recurved denticles which lie in a single irregular series with occasional doubling, denticles extending proximally beyond the limit of the striae on the lateral surfaces.

HOLOTYPE. BMNH no. P.46973 (Pl. 2; Pl. 3, figs. 1, 3), sixty-six teeth, fragments of calcified cartilage and an incomplete dorsal fin spine, the remains of a single individual, from the Weald Clay of Henfield, Sussex.

MATERIAL. In addition to the holotype, thirty isolated teeth and a fin spine.

HORIZONS AND LOCALITIES. Ashdown Beds: Cliff End bone-bed, Sussex. Wadhurst Clay: Hastings, Sussex. Grinstead Clay: Paddockhurst bone-bed, Sussex; Tilgate Forest, Sussex. Weald Clay: Henfield, Sussex; Bookhurst, Surrey. Wealden Shales; Atherfield Point and Cowleaze Chine, Isle of Wight.

DESCRIPTION. The holotype was found in 1962 by Mr. J. F. Wyley immediately above the '*Paludina*' limestone in the north-east corner of the Henfield pit. The teeth, calcified cartilage and fin spine were collected from an area of about two square feet: the bulk of the material was collected at one time but a few teeth have been found at the same point by Mr. Wyley in subsequent visits to the pit. There can be no doubt that this material represents the remains of a single individual. Since this is the first specimen of *Hybodus* in which it is possible accurately to reconstruct the dentition with teeth free from matrix, and in which the upper and lower teeth can be distinguished, it will be described in some detail.

1. *The Dentition*

The teeth of the holotype were not found in natural association, but it has proved possible to reconstruct at least the anterior parts of the dentition with some accuracy. The teeth can be sorted into 'left' and 'right' (treating all the teeth as if they are from one jaw) by the asymmetry of the cusps, which point away from the symphysis in *Hybodus*, and by the asymmetry of the root. Many of the teeth can be matched with others to reconstruct successional files, and these files can be placed approximately in their position in the mouth by the degree of asymmetry of the crown, and by the relative height and length of the teeth. When this had been done, of the fifty-seven more complete teeth four were median, twenty-three 'left' and thirty 'right', and there appeared to be fourteen successional files, containing from two to eight teeth. Fourteen teeth could not be matched with any others. In these fourteen 'series', the measurements length of crown, length of root, depth of tooth, depth of crown, depth of root, breadth of crown and breadth of root were taken on each tooth (Table I), and the range of each measurement in each series was plotted against the inferred position in the mouth. The fourteen unmatched teeth were then measured and allocated their position in the mouth by reference to the plot. When this had been done it was clear that in each of the better represented tooth series there were two types of teeth: these represent the upper and lower jaws (see p. 303).

General Features of the Dentition

The dentition of *H. brevicostatus* (Text-fig. 10, Pl. 2) consists of a symphysial file of teeth in each jaw and probably nine paired files in each jaw. The largest teeth are the fifth paired file. In general features, the teeth are very like those of the Lower

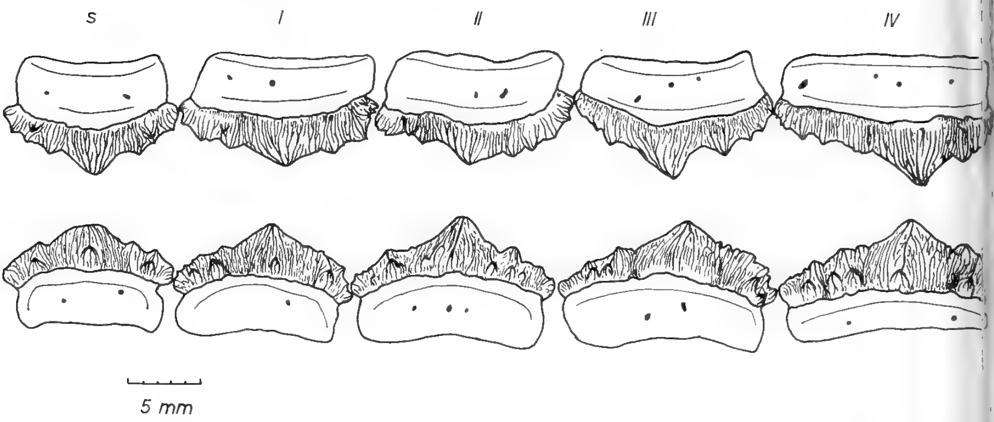


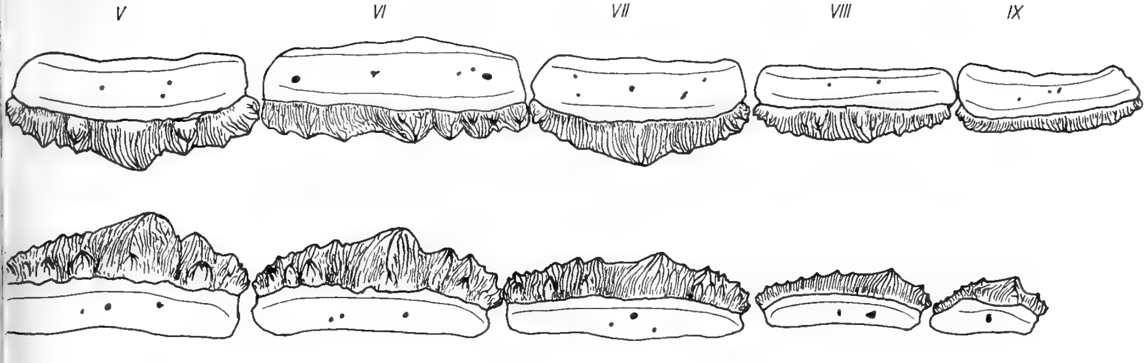
FIG. 10. *Hybodus brevicostatus* sp. nov. Restoration of the dentition of the left side in labi
VII and VIII in the upper jaw and III, VII and IX in the lower jaw are reversed drawing

Liassic *H. delabechei* Charlesworth (Smith Woodward 1889, pl. 10, figs. 1–5), with which they share a low crown, hardly exceeding the root in depth, a central cusp and four or more less conspicuous pairs of lateral cusps, and the ornament of very numerous prominent striae. The central cusp lies at or near the centre of the tooth in all but the most posterior files (Text-fig. 10, VIII and IX; Pl. 2, figs. 5, 6), where it may be strongly eccentric or unrecognizable. The number of lateral cusps is normally four on each side, but in the lateral and posterior teeth the lateral cusps may be more numerous or not recognizable. Accessory cusps occur very commonly on both the lingual and labial margins of the crown, particularly on the labial face of the mandibular teeth (see p. 305).

There is a sharp occlusal crest running the length of the tooth from which strong striae pass to the base of the crown. These main striae often bifurcate basally, and between them there are weaker striae which fail to reach the occlusal crest. There is no significant difference between the strength of the striae on the labial and lingual faces of the crown: in some teeth they are stronger on the lingual face, in others on the labial. At the base of the lingual face of the crown the ridges anastomose in a reticular pattern. There is a good deal of variation in the ornament of the crown from one tooth to another, but this variation seems to have no significance between one jaw and the other or between tooth files.

The roots of the teeth are typically hybodontoid (Casier 1947*a*: 9). In all the teeth the root is moderately compressed, approximately equal to the crown both in depth and breadth, with a concave labial face and a flat or weakly convex lingual face. In all the teeth the root is without specialized foramina but has a large number of irregular foramina on both the lingual and labial faces.

In histological structure (Pl. 3, fig. 3) the teeth are again typical of *Hybodus* (Jaekel 1889, pl. 7, figs. 1, 4). The crown is covered by a well marked and rather thick layer of enamel which contains fine fibrils in its basal part. Below the enamel there is a



view. ' s ', symphysial file, I–IX, paired files. All teeth drawn from the holotype ; V, VI,
of teeth from the right side. P.46973, Weald Clay ; Henfield, Sussex.

layer of very regular pallial dentine which makes up about one-fifth of the thickness of the crown. Below the pallial dentine the tooth consists of normal osteodentine. In the crown the osteodentine is dense, with many slender vascular canals : in the root it is much more spongy, with large, anastomosing vascular canals.

Distinction between Upper and Lower Teeth

As noted above, when the teeth of the holotype had been assigned to their positions in the jaws, among the better represented series (the symphysial and first five paired series) teeth of two types could be recognized. These clearly represent the upper and lower jaws. The upper and lower teeth can normally be distinguished by features of both the root and the crown, but the most reliable characters are in the root. In one type of tooth (Text-fig. 11A) the labial face of the root is strongly concave, the base of the root is rounded, and there is normally a well marked furrow between root and crown on both labial and lingual faces of the tooth. In the second type of tooth (Text-fig. 11B) the labial face of the root is less strongly concave, the base of the root is flattened in a well marked oblique shelf, and there is normally a very weak furrow at the junction of root and crown. The flattening of the base of the root is

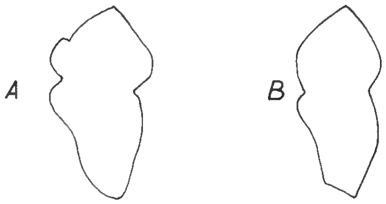


FIG. 11. *Hybodus brevicostatus* sp. nov. Diagrammatic transverse sections of teeth from the lower (A) and upper (B) jaws. ×3.

TABLE I

The dimensions (in mm.) of the teeth of P.46973, the holotype of *Hybodus brevicostatus* sp. nov. Weald Clay, Henfield, Sussex

File		Number of teeth preserved	Length of crown-Range	Length of crown-Mean	Length of root-Mean	Total depth-Range	Total depth-Mean	Depth of crown-Mean	Depth of root-Mean	Breadth of crown-Range	Breadth of crown-Mean	Breadth of root-Mean	Length of crown / Total depth	Length of crown / Breadth of crown
Symphysial	upper	2	12·0–12·1	12·05	10·8	6·9–7·7	7·3	3·55	3·8	3·5–4·0	3·75	4·2	1·6	3·2
	lower	2	11·7–12·0	11·85	10·15	7·3–7·5	7·4	3·75	3·55	4·0–4·7	4·35	3·85	1·6	2·7
First	upper	4	12·1–13·8	13·05	11·8	7·9–8·0	7·95	3·85	4·0	3·5–3·9	3·7	4·15	1·6	3·5
	lower	7	12·1–13·5	12·8	11·7	7·6–8·2	7·9	3·8	3·95	3·8–4·3	4·05	4·05	1·6	3·1
Second	upper	6	13·8–14·3	14·1	12·6	7·5–8·3	7·9	4·0	4·05	3·2–4·0	3·7	4·05	1·8	3·8
	lower	4	13·9–14·8	14·2	13·05	8·0–8·3	8·15	4·2	3·95	4·1–4·5	4·25	4·05	1·7	3·3
Third	upper	2	13·8–14·7	14·25	13·75	8·2–8·5	8·35	4·4	4·0	3·6	3·6	4·05	1·7	4·0
	lower	5	14·8–15·2	15·05	13·85	7·8–8·5	8·2	4·25	4·1	4·0–4·6	4·2	4·5	1·8	3·6
Fourth	upper	3	15·7–16·8	16·25	15·35	8·0–9·0	8·5	4·4	4·2	3·6–3·9	3·8	3·9	1·9	4·3
	lower	4	15·7–16·4	16·0	14·7	7·6–8·7	8·0	4·5	4·0	4·1–4·6	4·35	4·0	2·0	3·7
Fifth	upper	5	17·7–18·3	18·0	16·7	7·6–8·0	7·8	4·05	3·9	3·1–4·3	3·9	4·0	2·3	4·6
	lower	1	18·6	18·6	17·3	8·6	8·6	4·6	4·1	4·8	4·8	4·6	2·2	3·9
Sixth	upper	2	19·0	19·0	18·3	7·6–7·8	7·7	3·9	3·8	3·8–3·9	3·85	4·0	2·5	4·9
	lower	2	17·8–18·1	17·95	17·15	8·0	8·0	3·95	4·2	4·0–4·3	4·15	3·95	2·3	4·3
Seventh	upper	2	15·2	15·2	14·95	6·0–7·1	6·55	3·2	3·45	3·1–3·5	3·3	3·45	2·3	4·6
	lower	1	16·9	16·9	16·3	6·0	6·0	3·0	3·1	3·2	3·2	3·1	2·8	5·3
Eighth	upper	3	13·7–13·9	13·8	13·35	4·5–5·9	5·1	2·5	2·7	2·1–2·9	2·4	2·4	2·7	5·7
	lower	1	12·0	12·0	11·0	4·0	4·0	2·0	2·0	1·9	1·9	2·2	3·0	6·3
Ninth	upper	1	12·5	12·5	12·2	4·2	4·2	2·0	2·1	2·0	2·0	2·8	3·0	6·2
	lower	1	7·8	7·8	7·2	3·8	3·8	1·9	2·1	2·3	2·3	2·6	2·0	3·4

the most reliable method of distinguishing between the two types of teeth (Pl. 2, cf. figs. 1*a*, 2*a*, and 3*a*, 4*a*). In the crown, those teeth with a rounded base to the root have significantly more accessory cusps on the margin of both labial and lingual faces. Taking only the teeth of the symphysial and first six paired files, accessory cusps are present on the labial face of all the teeth with a rounded base to the root. The number of accessory cusps on this face ranges from one to six, the mean being 4·1. On the lingual face of these teeth accessory cusps are present in seventeen teeth out of twenty-six (65%), with a range of 1–3 and a mean of 1·1. In teeth with a flattened base to the root, accessory cusps are present on the labial face in sixteen out of nineteen teeth (84%), with a range of 1–6 cusps and a mean of 1·7. On the lingual face of these teeth accessory cusps are present in six out of nineteen teeth (32%), with a range of 1–2 and a mean of 0·6. The presence of an accessory cusp at the base of the labial face of the central cusp is particularly characteristic of teeth with a rounded base to the root, and there is very rarely an accessory cusp in this position in teeth with a flattened base to the root. This is reflected in the maximum breadth of the crown (Table I) which is the only dimension in which there is a significant difference between the two types of teeth.

There is no absolutely reliable criterion by which these two types of teeth can be assigned to the upper or lower jaw, but comparison with associated dentitions of *Hybodus obtusus* from the Oxford Clay and with various species of *Hybodus* and *Acrodus* from the Lower Lias suggests that the teeth with the more numerous accessory cusps and the rounded base to the root are mandibular. The roots are visible in very few of the teeth in these associated dentitions, but comparison with isolated Jurassic teeth shows that the characters discussed above will serve to assign most teeth of *Acrodus* and low-crowned species of *Hybodus* to the appropriate jaw.

Variation in Teeth with Position in the Jaws

The main variations in the teeth from different parts of the jaws are clear from Text-fig. 10, Pl. 2 and Table I. The length and depth of both root and crown increase to a maximum in the middle of each jaw ramus, the length reaching a maximum at the fifth paired file in the lower jaw and the sixth in the upper, the depth at the fourth file in the upper jaw and the fifth in the mandible. The depth of the root exceeds that of the crown in the symphysial, first, seventh, eighth and ninth files. The maximum breadth of the crown exceeds that of the root in all but the last two files in the mandible, while in the upper jaw the breadth of the root is always greater than that of the crown.

Other Material

Teeth of *H. brevicostatus* first appear in the Ashdown Beds, and range through to the Wealden Shales, at the extreme top of the Wealden, but the species is rare throughout this time.

Among the material from the Cliff End bone-bed (Ashdown Beds) there are six more or less complete teeth of the species, the best preserved of which is shown in

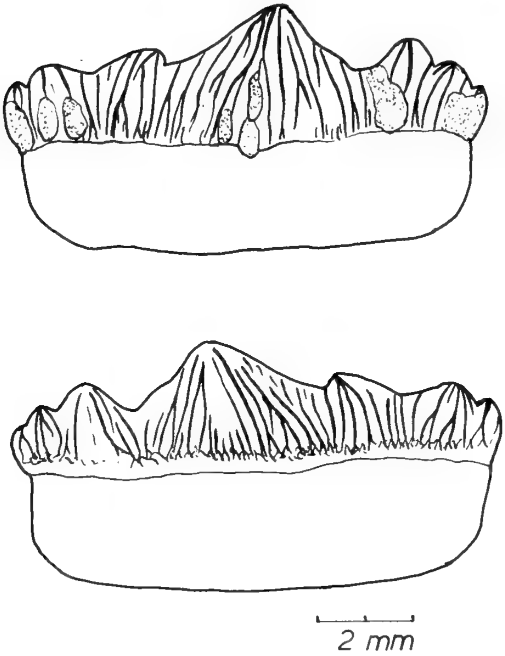


FIG. 12. *Hybodus brevicostatus* sp. nov. Tooth in labial (above) and lingual view. P.11891, Ashdown Beds, Cliff End Bone-bed ; Cliff End, Sussex.

Text-fig. 12. All these teeth are smaller than those of the holotype, with a maximum length of about 10 mm., and they have fewer striae and fewer accessory cusps.

In the Wadhurst Clay *H. brevicostatus* is represented by a fragment of a small tooth (P.11875) and by P.11876 (Pl. 1, fig. 3), a large tooth, 15 mm. in length, probably a parasymphysial from the upper jaw, in which the crown is unusually high.

In the Grinstead Clay there are thirteen teeth of *H. brevicostatus* among the material from the Paddockhurst bone-bed. These are all small (less than 9 mm. in length), low-crowned forms. 26027 from Tilgate Forest is a larger (11 mm.) example, again a low-crowned posterior tooth.

Among the material from the Weald Clay of Henfield there is a number of teeth of *H. brevicostatus* in addition to the holotype. Most of these are normal teeth, as large as or a little smaller than those of the holotype, but two are very small examples (Text-fig. 13), P.46984, less than 6 mm. in length and P.46989, 4 mm. long. These small teeth agree with those of the holotype in shape and in the numerous accessory cusps, but in the few, coarse striae on the crown and in the clearly marked lateral cusps they resemble *H. parvidens*. One anterior tooth of *H. brevicostatus* (P.12812) is also known from the Weald Clay of Bookhurst, Surrey.

The latest occurrence of *H. brevicostatus* teeth is P.13341, an incomplete parasymphysial tooth from the Wealden Shales of Atherfield Point, Isle of Wight.

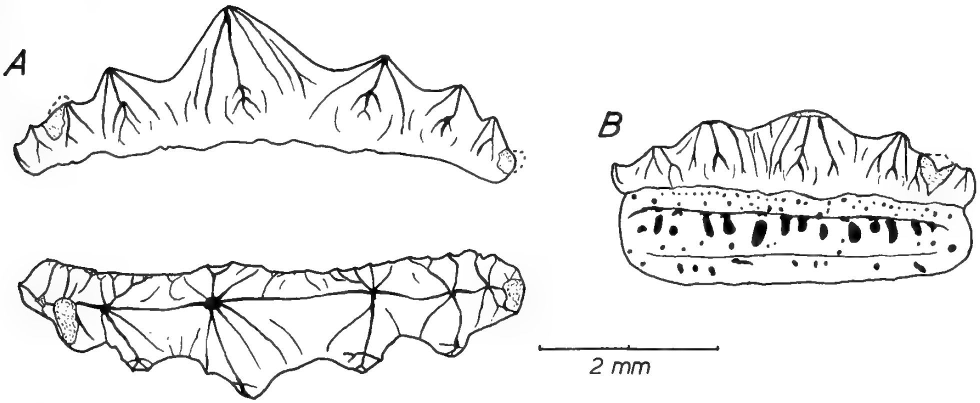


FIG. 13. *Hybodus brevicostatus* sp. nov. ? Juvenile teeth from the Weald Clay of Henfield, Sussex. A. P.46984 in labial (above) and occlusal view. B. P.46989 in labial view.

2. *Calcified Cartilage*

Together with the teeth of the holotype Mr. Wyley collected a number of fragments of heavily calcified cartilage. These include recognizable parts of the jaws and branchial arches, but they show nothing worthy of description.

3. *Fin Spines*

Found with the teeth and calcified cartilage of the holotype was a single incomplete fin spine (Pl. 3, fig. 1). The British Museum (Natural History) contains one spine which agrees with this, P.13268 from the Wealden Shales overlying the *Hypsilophodon* Bed, Cowleaze Chine, Isle of Wight (Pl. 3, fig. 2). These two spines agree almost exactly in size; each must have had a total length of about 20 cm. Although they agree well in most characters, the angle of insertion of the Isle of Wight spine (inferred from the extent of the enamel ridges on the surface and the obliquity of the growth lines) was probably less than that of the Henfield spine. This suggests that the Isle of Wight specimen is an anterior fin spine and the Henfield is posterior, since in those hybodonts known by complete specimens the anterior fin spine lies more obliquely than the posterior (Brough 1935).

The most striking feature of these fin spines, and the one which differentiates them from all other species of *Hybodus*, is that the enamel ridges on the distal part of the spine are very short, ending at or above the level of the lowermost denticles on the posterior face of the spine, and well above the apex of the groove on the posterior face of the proximal part of the spine which housed the basal cartilage of the fin. The trivial name of the species refers to these short ribs on the fin spine.

The spines are not strongly arched, the anterior edge curving through about 35°, the posterior through 25°, and are strongly compressed. The anterior edge is keeled and there is a well marked angle between the lateral and posterior faces. On the lateral face the ridges of enamel are well spaced. In both specimens a median enamel ridge forms the keel on the anterior edge. In the Henfield spine (?posterior) there are ten ridges on each side, five reaching the tip of the spine and five being confined to the proximal part. In the Isle of Wight spine there are eleven ridges on each side, seven of which extend to the tip. In the Henfield spine all the ridges end above the level of the lowermost denticle on the posterior face, the longest ribs being the first and second on the right side and the third on the left side. In the Isle of Wight spine the longest ridges are the first on each side, and they alone extend beyond the level of the lowest denticle on the posterior face.

The denticles on the posterior face of the spine are in a single median series. This single series is clearly the result of unequal development of paired denticles, for occasionally the denticles are double (Pl. 3, figs. 1*a*, 2*a*), and in other cases at the base of a fully developed denticle there is the rudiment of a second. The side on which these rudimentary denticles occurs is variable, showing that the single series of denticles is not the result of suppression of either the left or right series of denticles, but of apparently random suppression of one of each pair. In the Isle of Wight spine, which is complete to the tip, there is a total of 27 denticles, of which two show doubling and eight show rudiments of a second denticle, six on the right side and two on the left of a fully developed denticle. In the Henfield spine sixteen denticles are preserved, one is doubled, and one has a rudiment on its left side. The denticles are very variable in shape : some are strongly hooked, either to the left or the right, some are straight, and while the majority are smooth, some, particularly towards the base of the spine, bear striae like those on the teeth.

Lack of material at present prevents the preparation of thin sections of the spines, but broken surfaces show that in structure the spine agrees with *H. aschersoni* Stromer (1927 : 20, pl. 3, fig. 9, text-fig. 13) from the Cenomanian of Libya, in that in the exserted part of the spine the pulp cavity is surrounded by a zone of lamellar tissue which makes up about half the thickness of the wall of the spine, the outer part of the wall consisting of osteodentine. Passing back towards the base of the spine the zone of lamellar tissue becomes thinner until it disappears below the apex of the groove in the hind edge of the spine. Below this level the spine consists of osteodentine alone.

AFFINITIES. Teeth of *H. brevicostatus* from horizons below the Weald Clay suggest that in the history of the species between the Ashdown Beds and the Weald Clay there was an increase in size accompanied by an increase in the number of striae on the crown and in the number of accessory cusps. Small teeth from the Weald Clay of Henfield show that in the ontogeny of the species increase in size was accompanied by increase in the number of striae on the crown and reduction in the individuality of the lateral cusps. Both these facts suggest that the ancestor of *H. brevicostatus* was a rather small, low-crowned species, extant during or before the deposition of the Ashdown Beds, with sparse, coarse striae on the crown, three or four pairs of lateral cusps and a tendency to develop accessory cusps. These conditions are met by *H. parvidens*, and it seems very probable that *H. brevicostatus* is an offshoot of this species, probably originating near the base of the Wealden.

The increase in ornamentation and reduction in the individuality of the lateral cusps which occur with increased size is an interesting feature of this species. In the holotype it results in some of the teeth, especially the more posterior ones, having a very *Acrodus*-like crown, sometimes without distinguishable lateral cusps or with very numerous small ones. These conditions are just those found in some Upper Cretaceous species such as *Synechodus illingworthi* (Dixon) (Smith Woodward 1911 : 220, pl. 46, figs. 5–7) from the Cenomanian zones of the English Chalk; *Hybodus brabanticus* Leriche (1929 : 225, text-figs. 4, 5; 1930 : 105) and *Acrodus dolloi* Leriche (1929 : 228, text-figs. 6, 7) from the Lower Senonian of Belgium; *Hybodus grewingki* Dalinkevičius (1935 : 256, pl. 1, figs. 36–38) and *Acrodus guedroyii* Dalinkevičius (1935 : 256, pl. 1, figs. 34, 35) from the Cenomanian of Lithuania; *Acrodus affinis* Reuss (1845 : 1, pl. 2, figs. 3, 4), *Hybodus bronnii* Reuss (1845 : 97, pl. 24, fig. 26, pl. 42, fig. 7) and *Hybodus cristatus* Reuss (1845 : 2, pl. 2, fig. 20), all from the Turonian Plänerkalk of Bohemia; and the teeth from the Upper Sononian of Aachen, Germany, described as *Hybodus* ? sp. and *Acrodus* ? sp. by Albers & Weiler (1964 : 4, 5, text-figs. 3, 8, 9, 42). These species are also the only marine hybodonts known by teeth in the Upper Cretaceous. The best known of them is *Acrodus illingworthi* Dixon, a species transferred to the heterodontid genus *Synechodus* by Smith Woodward (1891 : 66). But there is no real evidence that this species is not a hybodont: all the teeth have typical hybodontoid roots, without the development of enlarged central foramina which is characteristic of *Synechodus* and other heterodontids (Casier 1947*b* : 2). The absence of hybodont fin spines in the English Chalk is not evidence against the species being hybodont, for only about twenty teeth are known, and judging by the conditions in *H. brevicostatus* an individual would produce well over two hundred teeth in its life but only two spines. It is also quite possible that these Upper Cretaceous hybodonts should have lost their fin spines. The syntypes and other material of *A. illingworthi* in the British Museum (Natural History) show a strong resemblance to *H. brevicostatus*, and with Leriche (1929 : 227) I believe the species should be named *Hybodus illingworthi* (Dixon). *H. brabanticus* Leriche is almost certainly a synonym of *H. illingworthi*, for Leriche included in his species some specimens figured by Smith Woodward (1911, pl. 46, fig. 7) as *S. illingworthi*, but these teeth (43511) occur in association with other teeth which are undoubtedly *H. illingworthi*. There seems little to distinguish *H. grewingki* Dalinkevičius from *H. illingworthi*, and Dalinkevičius noted the resemblance between his material and Leriche's *H. brabanticus*. Reuss's species from the Turonian of Bohemia are large teeth of the same type as *H. illingworthi* and *H. brevicostatus*. The Upper Senonian *Hybodus* teeth described by Albers & Weiler are compared by them with *H. illingworthi* and *H. brabanticus*, which they closely resemble. *Acrodus dolloi* Leriche and *A. guedroyii* Dalinkevičius are based on large teeth which resemble Lower Lias species such as *A. curtus* (=*A. anningiae*) and *A. nobilis*; the *Acrodus* teeth described by Albers & Weiler are very like *A. dolloi* but smaller. There is no other evidence of *Acrodus* of this type in the Cretaceous, but these teeth, in size, shape and ornamentation, bear considerable resemblance to the large postero-lateral teeth of *H. brevicostatus*, and could be derived from this species by further increase in size, in the number of striae and in the loss of individuality of the lateral cusps.

Fin Spines of Hybodus

Only in *H. basanus* and *H. brevicostatus* among Wealden and Purbeck sharks have fin spines been found in association with teeth. Smith Woodward (1916) suggested relationships between the various spines and teeth known from the British Wealden and Purbeck. His conclusions may be summarized as follows:

Tooth	Horizons	Spine
H. basanus	Weald Clay	? *H. sulcatus* Agassiz
' teeth of the same general type as *H. basanus* '	Wadhurst Clay Grinstead Clay	*H. subcarinatus* Agassiz
H. ensis	Middle Purbeck	' almost identical with *H. dorsalis* Agassiz '
H. parvidens	Wadhurst Clay	?
?	Grinstead Clay	*H. striatulus* Agassiz
?	Middle Purbeck	*H. strictus* Agassiz

Of the spines which Smith Woodward did not associate with species based on teeth, he compared *H. striatulus* with the Purbeck spines assigned to *H. ensis*, and *H. strictus* with *H. subcarinatus* and *H. basanus*.

We now have more complete information on the ranges and relationships of the Wealden and Purbeck teeth of *Hybodus*. *H. parvidens* is a species which ranged from the Middle Purbeck to the Weald Clay, giving rise to *H. basanus* in the Weald Clay, the evolution of *H. basanus* involving an increase in size of the teeth. We should therefore expect the fin spines of *H. parvidens* to be similar to those of *H. basanus* but smaller, and to range from the Middle Purbeck to the Lower Weald Clay. These conditions are met by *H. strictus* Agassiz in the Purbeck (12–13 cm. long) and *H. subcarinatus* Agassiz in the Wadhurst and Grinstead Clay (14–17 cm. long).

The ' teeth of the same general type as *H. basanus* ' with which Smith Woodward associated *H. subcarinatus* Agassiz are shown above (p. 294) to belong in *H. ensis*: one would therefore expect them to be associated with spines of the same type as *H. dorsalis* Agassiz—this condition is met by *H. striatulus* Agassiz.

A revised scheme of the (hypothetical) relationships between hybodont teeth and fin spines in the Wealden and Purbeck is as follows:

Tooth	Horizons	Spine
H. ensis	Middle Purbeck–Grinstead Clay	cf. *H. dorsalis* (Purbeck) *H. striatulus* (Wealden)
H. parvidens	Middle Purbeck–Weald Clay	*H. strictus* (Purbeck) *H. subcarinatus* (Wealden)
H. basanus	Weald Clay	? *H. sulcatus*
H. brevicostatus	Ashdown Beds–Weald Clay	*H. brevicostatus*

In the Wealden and Purbeck there occur tuberculated fin spines which have been described as *Asteracanthus* (*A. verrucosus* Egerton 1854, Middle Purbeck, Swanage; *A. semiverrucosus* Egerton 1854, Middle Purbeck, Swanage; *A. granulosus* Egerton, 1854, Wealden, Sussex). A spine from the Lower Neocomian of the Paris Basin is described as *A.* cf. *acutus* Agassiz by Leriche (1911 : 456, pl. 6, fig. 1), and *A. granulosus* has also been recorded from the Lower Neocomian of Switzerland, where it occurs in the same beds as teeth of '*Strophodus*' (=*Asteracanthus*) which according to Peyer (1946 : 54) are not derived fossils. But although *Asteracanthus* occurs in the marine Lower Cretaceous, it seems very unlikely that the British spines are true *Asteracanthus*—that is, that they are from a fish with '*Strophodus*' teeth, like the better known Jurassic species, for the large and conspicuous teeth could hardly have escaped notice, particularly since about a dozen spines of this type are known and in any individual there will be at least fifty teeth to each spine. The preservation of the spines is such that they can hardly be derived from older formations. The answer is probably that these spines are *Hybodus* in which the normal enamel ridges have broken up into separate tubercles as a stage in the reduction of the spine. This argument is supported by the presence of normal ridges on the distal (and first formed) parts of the spines, by the Wealden *H. striatulus* Agassiz (suggested above to belong to *H. ensis*) where the ridges are partially broken up into tubercles, and by the tendency in many Wealden *Hybodus* spines for the ridges to become fragmented proximally.

Remarks on Hybodont Teeth

This study has shown that where abundant isolated teeth of *Hybodus* from successive horizons are available, the distinctions between species become very difficult to maintain. A great deal of parallelism and convergence is bound to occur in the evolution of sharks' teeth, and further uncertainty arises from the degree of heterodonty of species (usually unknown) and from variability within a species. It is clear that the erection of new species of hybodont sharks on one or two isolated teeth is an extremely hazardous procedure.

The changes which occur in the teeth of Wealden hybodont sharks from species to species and horizon to horizon allow one to draw some general conclusions about the correlation between various dental characters in hybodonts. These can be summarized as follows :

(*a*) Characters which increase with increasing height of crown and decrease with decreasing height of crown.

1. lingual curvature of crown
2. compression of crown
3. lingual curvature of root
4. difference between ornament on labial and lingual faces of crown.

(*b*) Characters which decrease with increasing height of crown and increase with decreasing height of crown.

1. degree of heterodonty
2. number of lateral cusps
3. number and size of accessory cusps
4. depth of root
5. height of striae on crown
6. bifurcation of and anastomosis between striae

(*c*) Characters which increase with increasing size of tooth.

1. number of striae on crown.

This list of characters showing correlation with the height of the crown or the size of the tooth includes almost all those commonly used to distinguish hybodont species. If all these characters are correlated with an obviously adaptive feature like crown height it is clear that it will often be impossible to distinguish on teeth alone between relationship, parallelism and convergence. There is therefore little likelihood of any worthwhile subdivision of the genus *Hybodus*, now so large both in number of species and in range, on characters of the dentition. Jaekel's (1889, 1898) attempt at a subdivision was largely based on features of the teeth which are obviously adaptive or are correlated with adaptive features : of the four genera which he proposed, only *Polyacrodus*, distinct on histological characters (thickness of pallial dentine), has been generally accepted.

We are forced to look for other characters on which species of *Hybodus* may be grouped, but if the earliest (Lower Lias—*H. delabechei* etc.) and latest (Upper Wealden —*H. basanus*) species in which the anatomy is well known are compared, the only differences seem to be reduction of the cephalic spines (present in males only) from two pairs to one, the appearance of symphysial teeth, and slight changes in the fin spines (increase in thickness of the lamellar tissue, reduction in the strength of the enamel ridges, reduction in the distance between the paired denticles on the hind edge, culminating in suppression of one of each pair in *H. brevicostatus*). The first two of these differences are suitable for generic subdivision, but until their distribution is known in many more species no useful purpose is served by such division.

Genus ***LONCHIDION*** Estes 1964 : 7

AMENDED DIAGNOSIS. Small fresh-water hybodonts, weakly or strongly heterodont, known only by isolated teeth, cephalic spines and fin spines. Teeth low-crowned, elongated, crown not much deeper than root ; tricuspid anterior teeth present in some forms ; crown smooth or with sparse vertical striae, large labial projection or buttress below central cusp, lateral cusps absent or small and irregular ; root hybodontoid except in supposed tricuspid anterior teeth of advanced forms, where it is squatinoid ; pallial dentine of crown very thick, as in *Polyacrodus*. Fin spines with or without enamel ridges on lateral faces, with a single series of posterior denticles. Cephalic spines of normal hybodont type, without terminal barb.

TYPE SPECIES. *Lonchidion selachos* Estes (1964 : 7, text-figs. 1–4), Lance Formation, Wyoming.

Lonchidion breve sp. nov.

(Pl. 5, fig. 3 ; Text-figs. 14–20, 29E)

DIAGNOSIS. *Lonchidion* known only by isolated teeth, 3·5 mm. or less in length ; no tricuspid anterior teeth, dentition weakly heterodont ; crowns of teeth rather short, with maximum breadth between half and one-quarter of the length ; crown smooth or very feebly striated, lateral and accessory cusps very small and irregular when present, labial process strong.

Holotype. P.47024 (Text-fig. 14), complete tooth from the Paddockhurst bone-bed (Grinstead Clay) ; Sussex.

Material. About one hundred and sixty teeth, mostly without roots.

Horizons and localities. Ashdown Beds : Cliff End bone-bed, Cliff End, Sussex. Wadhurst Clay : Telham bone-bed, Stone, Kent ; top of cliff near Hastings harbour, Sussex ; Ashurstwood, Sussex. Grinstead Clay : Paddockhurst bone-bed, Sussex. Weald Clay : Henfield, Sussex. Atherfield Clay : *Perna* Bed, Sandown Bay, Isle of Wight (probably derived from Wealden Shales—see p. 319).

The teeth which are assigned to this species fall into three types which intergrade both morphologically and stratigraphically : they will be described separately as three subspecies.

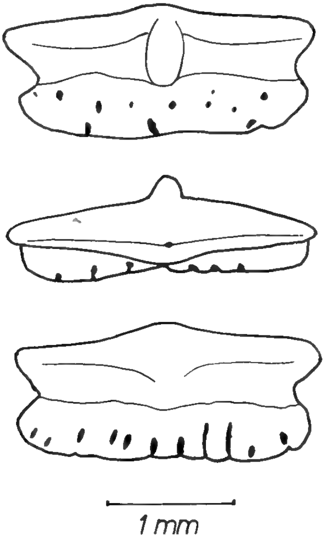


Fig. 14. *Lonchidion breve breve* sp. et ssp. nov. P.47024, the holotype, a lateral tooth in labial (above), occlusal (centre) and lingual view. Grinstead Clay, Paddockhurst Bone-bed ; Paddockhurst Park, Sussex.

Lonchidion breve breve sp. et ssp. nov.

(Pl. 5, fig. 3 ; Text-figs. 14–16, 29E)

Diagnosis. *Lonchidion breve* in which the crown of the tooth is normally smooth, without lateral or accessory cusps or striations.

Holotype. P.47024, complete tooth (Text-fig. 14) from the Paddockhurst bone-bed.

Material In addition to the holotype, about 120 teeth, mostly without roots.

Horizons and localities. Ashdown Beds : Cliff End bone-bed. Wadhurst Clay : Telham bone-bed, Stone, Kent; Hastings, Sussex ; Ashurstwood, Sussex.

Grinstead Clay: Paddockhurst bone-bed. Weald Clay: Henfield. Atherfield Clay: *Perna* Bed, Sandown Bay, Isle of Wight.

DESCRIPTION. This subspecies, the typical and commonest form of the species, occurs throughout the Wealden. In the majority of specimens only the crown is preserved, and in many examples, especially those from the Cliff End and Paddockhurst bone-beds, the teeth have undergone a good deal of *post mortem* abrasion. None of the teeth exceeds 3·5 mm. in length. The crown is normally completely smooth, without ornament or any indication of lateral cusps. There is a single, very low cusp which lies at or near the centre of the crown. The occlusal edge of the tooth is compressed into a more or less sharp ridge. Below the central cusp there is a strong rounded process or buttress on the labial face of the crown. The root plays no part in the formation of this process, and is overhung by it. A ridge normally runs on to the labial process from the central cusp. On the lingual face of the crown there is a gentle swelling opposite the central cusp and the labial process. The occlusal surface of the crown is much longer than its base, so that the tooth is strongly waisted at the junction of root and crown.

The root is preserved in few specimens, and is always somewhat worn. It is typically hybodontoid (Casier 1947*a* : 9), with no specialized vascular foramina. On the lingual face of the root there is a row of vertically elongated foramina and on the labial face irregularly scattered foramina (Text-fig. 14). The root is almost as deep as the crown and only slightly shorter.

In the type species of *Lonchidion*, the Late Cretaceous *L. selachos* Estes (see p. 330),

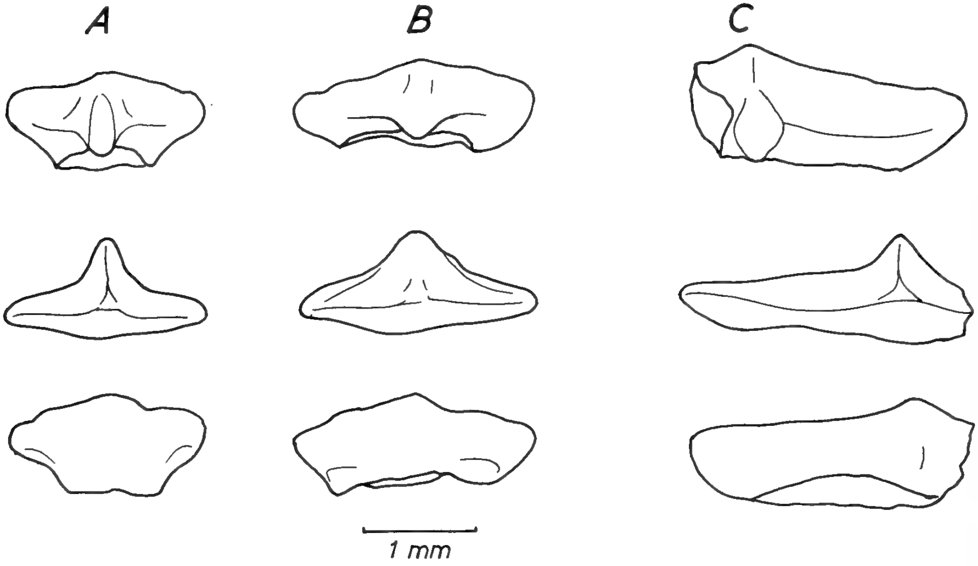


FIG. 15. *Lonchidion breve breve* sp. et ssp. nov. Three teeth from the Ashdown Beds, Cliff End Bone-bed; Cliff End, Sussex, in labial (above), occlusal (centre) and lingual view. A. P.46993; B. P.46995; C. P.47005.

the histological structure of the crown is described (Estes 1964 : 8, text-fig. 2D) as a fan-shaped radiation of dentine tubules from one central cavity which originated along a central longitudinal axis. The tooth crowns of *L. breve breve* (Pl. 5, fig. 3; Text-fig. 29E) agree with this description. Below a rather thick layer of enamel the crown is made up of pallial dentine containing long, subparallel, much branched tubules which arise from the tips of vascular canals which end shortly after entering the centre of the base of the crown. Estes compares this structure with that seen in teeth of the Triassic hybodont *Palaeobates* (Jaekel 1889, pl. 10, fig. 2; Seilacher 1943, text-figs. 22, 29, 34), especially with *P. nodosus* Seilacher. But in *Palaeobates* (Pl. 5, fig. 2) the dentine tubules are longer, parallel and more regularly branched than they are in *Lonchidion,* and they arise not from the tips of vascular canals but from a single open pulp cavity running the length of the tooth. The pallial dentine of *Lonchidion* is much more like that in the Triassic *Polyacrodus*, particularly in small species like *P. minimus* (Seilacher 1943, text-figs. 7–10; Pl. 5 fig. 1), where there are just the same wavy, irregularly branched dentine tubules arising from short vascular canals near the base of the crown. In *Polyacrodus* the pallial dentine is a little thinner than it is in *Lonchidion,* perhaps because of the greater size of the teeth, but in other respects the correspondence is exact.

The worn condition and absence of roots in most examples of this sub-species make it difficult to arrive at any clear idea of the variation in shape. The length of the crown ranges from 1·4–3·4 mm., the maximum breadth of the crown (at the labial process) from 0·4–1·2 mm. In five complete teeth the depth ranges from 1·0–1·35 mm., the ratio of depth to length from 1·5–2·5. The crown is normally broader than deep, the ratio of maximum breadth to length ranging from 1·9–3·8, and of maximum depth to length from 2·7–4·2. The shorter, deeper teeth, in which the labial process is large (Text-figs. 15A, 16A) are probably anterior; longer teeth, still with a strong labial process (Text-fig. 15B), antero-lateral; the longest teeth

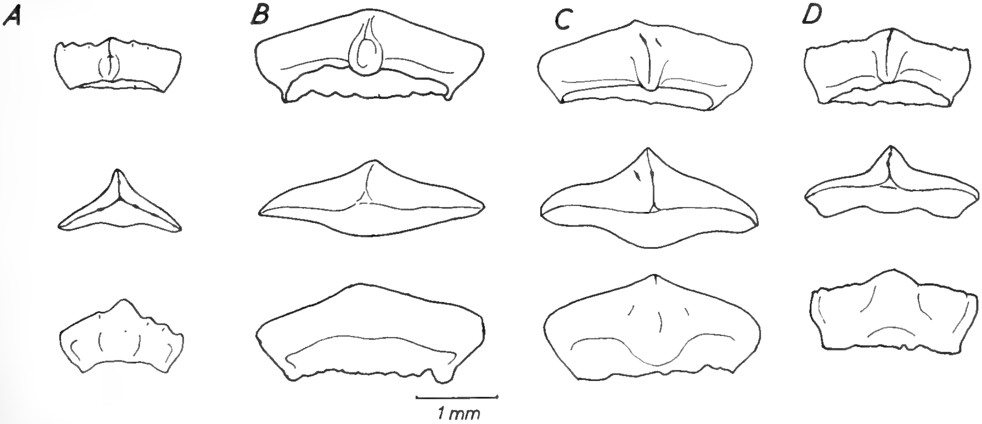


FIG. 16. *Lonchidion breve breve* sp. et ssp. nov. Teeth in labial (above), occlusal (centre) and lingual view. A, B. P.47324, P.47047 from the Weald Clay of Henfield, Sussex. C, D. P.39015, P.39011 from the *Perna* Bed, Atherfield Clay; Sandown Bay, Isle of Wight.

(Text-figs. 14, 15C) lateral, and shallow teeth with a weak labial process are probably posterior (Text-fig. 16B).

At lower horizons there is no difficulty in distinguishing between *L. breve breve* and the other subspecies of the species, but at higher horizons, the Weald Clay of Henfield and the *Perna* Bed in the Atherfield Clay, examples occur in which there are weak accessory cusps (Text-fig. 16C) or lateral cusps (Text-fig. 16A, D). These specimens tend towards *L. breve pustulatum*, to which most of the *Perna* Bed teeth belong, and also towards *L. selachos* Estes, from the Upper Cretaceous of America (see p. 330).

Lonchidion breve crenulatum sp. et ssp. nov.

(Text-figs. 17, 18)

DIAGNOSIS. *Lonchidion breve* in which the occlusal margin of the tooth crown is irregularly crenulate, and in which the lingual and labial faces of the crown are weakly and sparsely striated.

HOLOTYPE. P.47060 (Text-fig. 17B), tooth without root from the Paddockhurst bone-bed.

MATERIAL. In addition to the holotype, twenty-five teeth, all without roots.

HORIZONS AND LOCALITIES. Wadhurst Clay: Ashurstwood, Sussex. Grinstead Clay: Paddockhurst bone-bed.

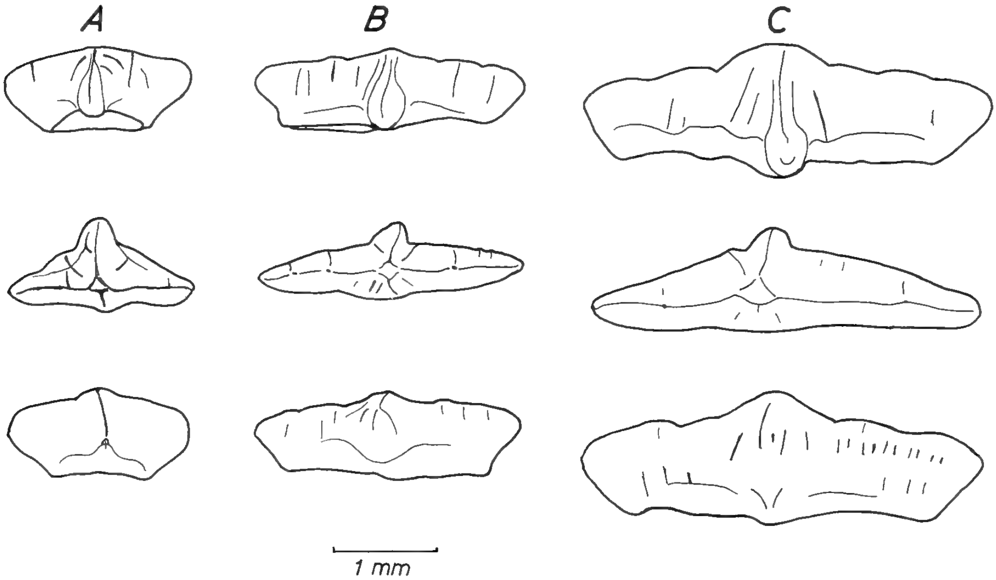


FIG. 17. *Lonchidion breve crenulatum* sp. et ssp. nov. Three teeth from the Grinstead Clay, Paddockhurst Bone-bed; Paddockhurst Park, Sussex, in labial (above), occlusal (centre) and lingual view. A. P.47059. B. P.47060, the holotype. C. P.47066.

DESCRIPTION. In this subspecies the form and proportions of the teeth do not differ significantly from those in *L. breve breve*. The largest tooth (Text-fig. 17C) is 3·5 mm. long, similar in size to the largest *L. breve breve*. The occlusal crest of the teeth is produced into a number of small and irregular lateral cusps or beads. Both the lingual and labial faces of the crown bear a number of weak, parallel, vertical striae, the striae being strongest at the central cusp. Both the beading of the occlusal crest and the striation of the crown are weakest in the short, deep anterior teeth (Text-fig. 17A), strongest in the longer, lower lateral and posterior teeth.

REMARKS. This subspecies is commonest in the Paddockhurst bone-bed, where it accounts for about half of the specimens of *Lonchidion breve*, the other half being *L. breve breve*. The fact that teeth of *L. b. crenulatum* from this horizon exhibit the same range of size and shape as those of *L. b. breve* (cf. Text-figs. 15, 17) and the absence of *L. b. crenulatum* at Cliff End and in the Telham bone-bed show that the two subspecies are distinct forms, not teeth from different parts of the mouth of the same fish. *L. b. crenulatum* is not known above the Grinstead Clay. In a sample of four teeth of *Lonchidion* from the Wadhurst Clay at Ashurstwood, Sussex, three are *L. b. crenulatum* (Text-fig. 18) and one is *L. b. breve*. *L. b. crenulatum* does not occur in the large sample of *Lonchidion* from the Cliff End bone-bed in the Ashdown Beds or the Telham bone-bed at the base of the Wadhurst Clay, nor is it known in the Purbeck, although the posterior teeth of *L. heterodon* (Text-fig. 25C) are very like it. In spite of this resemblance, it seems probable that *L. b. crenulatum* is a subspecies which evolved from *L. b. breve*, probably early in Wadhurst Clay time.

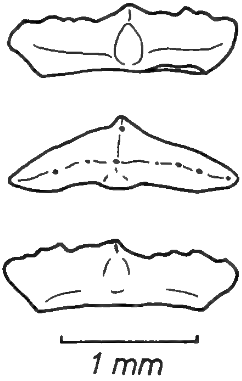


FIG. 18. *Lonchidion breve crenulatum* sp. et ssp. nov. P.47081, a tooth from the Wadhurst Clay; Ashurstwood, Sussex, in labial (above), occlusal (centre) and lingual view.

Lonchidion breve pustulatum sp. et ssp. nov.

(Text-fig. 19)

DIAGNOSIS. *Lonchidion breve* in which the occlusal crest of the crown is weakly, irregularly and finely crenulate, and in which the labial face of the crown bears a number of minute accessory cusps but no striations.

Holotype. P.47085, (Text-fig. 19B), tooth without root from the *Perna* Bed, Atherfield Clay, Sandown Bay, Isle of Wight (? derived from the Wealden Shales—see below).

Material. In addition to the holotype, fourteen teeth, all without roots.

Horizon and locality. *Perna* Bed, Atherfield Clay: Sandown Bay, Isle of Wight.

Description. In this subspecies the form and proportions are again very similar to those in *L. breve breve*. The teeth range in length from 1·8–3·6 mm., in breadth from 0·6–1·3 mm., and in the ratio of breadth to length from 2·0–3·6. The occlusal crest of the teeth is produced into irregular lateral cusps or beads, and these are more numerous than they are in *L. breve crenulatum*. The labial and lingual faces of the crown are without striae. The labial process, below the central cusp, is not so well marked off from the body of the crown as it is in the other subspecies (Text-fig. 19B, C), and the ridge on its occlusal surface bears one or sometimes two small cusps. Level with the more labially placed of these cusps on the labial process there is a series of very small accessory cusps on the labial surface of the crown, which extends as a shallow shelf at this level. The strength and number of these accessory cusps seem to be correlated with the breadth of the tooth (Text-fig. 19), but not with its length, and no real distinction between anterior and posterior or lateral teeth can be made.

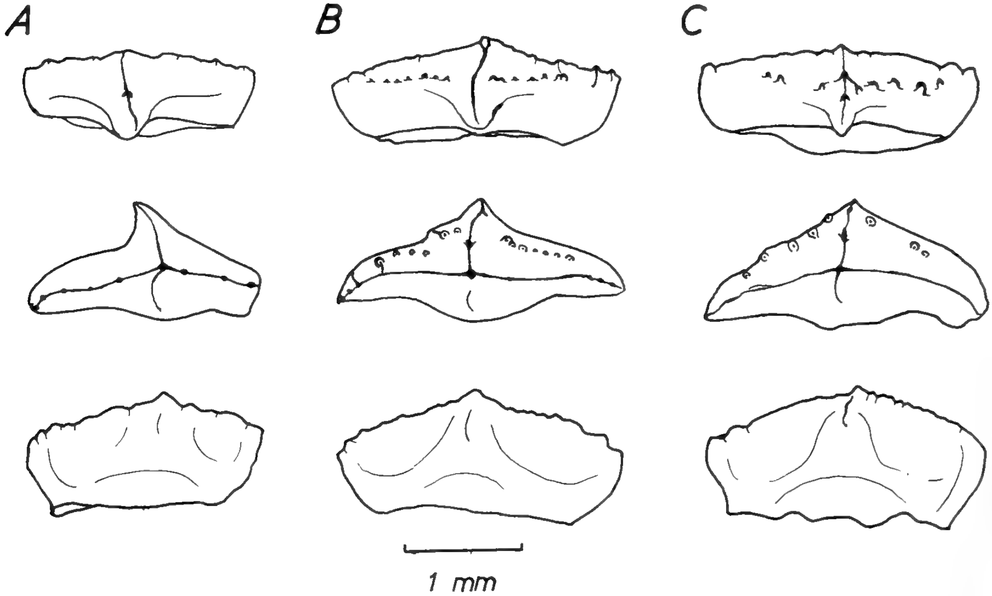


Fig. 19. *Lonchidion breve pustulatum* sp. et ssp. nov. Teeth from the *Perna* Bed, Atherfield Clay; Sandown Bay, Isle of Wight, in labial (above), occlusal (centre) and lingual view. A. P.47088. B. P.47085, the holotype. C. P.47089.

REMARKS. This subspecies is known only in the *Perna* Bed, at the base of the Lower Greensand. Most of the fish teeth from this horizon are derived from the underlying Wealden Shales (Casey 1961 : 505), and this is probably true of the specimens of *Lonchidion*, a genus otherwise unknown in marine beds. The teeth are not much rolled or waterworn, but their small size will probably account for this. Together with *L. b. pustulatum* in the *Perna* Bed there occur teeth which are referred to *L. b. breve* but which show faint traces of the lateral and accessory cusps which characterize *L. b. pustulatum* (Text-fig. 16C, D) : Similar examples also occur at Henfield (Text-fig. 16A). These forms leave little doubt that *L. b. pustulatum* has evolved directly from *L. b. breve* by extension of the labial face of the crown into a shelf bearing accessory cusps. Teeth of *L. b. pustulatum* are very like the smallest posterior teeth of the ptychodont genus *Hylaeobatis*, suggesting a possible relationship which is discussed on p. 341.

The Arrangement of the Teeth

Many of the teeth of *Lonchidion breve* have a strong wear facet on the occlusal margin of the crown, the occlusal crest and central cusp being planed off into a level surface. This indicates, as one would deduce from the form of the teeth, that *L. breve* was a durophagous form, grinding its food by rubbing the upper and lower teeth across one another. In many specimens of *L. breve* there is also a vertical groove or scar in the centre of the lingual face of the crown : this is a pressure scar formed by the tip of the labial process of the succeeding tooth, which shows that successive teeth in each file were in contact or nearly so. If the tip of the labial process of each tooth touched the centre of the lingual face of the crown of the preceding tooth, there would be a space between the tapering lateral parts of the teeth—such spaces are disadvantageous in durophagous forms, and they must have been filled by the lateral parts of the teeth of the adjacent file (Text-fig. 20). It follows that in *L. breve* there was overlap between the files of teeth, and that there must therefore have been regular alternation between the teeth in adjacent files : this is an advanced character recalling the rays, which does not normally occur in hybodonts

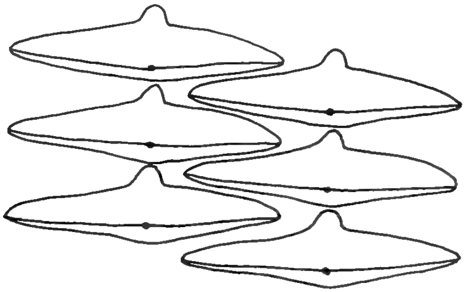


FIG. 20. *Lonchidion breve* sp. nov. Diagram showing the probable arrangement of adjacent files of teeth in occlusal view, × 15. Based on the holotype (Text-fig. 14).

and heterodontids (Casier 1953 : 40), although it is present in the Triassic fresh-water form *Lissodus africanus* (Brough 1935, pl. 2, figs. 2, 3), at least in the anterior and lateral parts of the jaw.

Lonchidion striatum sp. nov.

(Text-figs. 21, 22)

DIAGNOSIS. *Lonchidion* known only by isolated teeth, 4·5 mm. or less in length ; no tricuspid anterior teeth, dentition weakly heterodont ; crowns of teeth elongated, maximum breadth rarely less than one-quarter of the length ; occlusal crest of teeth strong, lateral cusps very weak and irregular ; both labial and lingual faces of crown with strong vertical striae, occasionally bifurcated basally, which diverge from the occlusal crest but do not reach the base of the crown ; labial process small and weak.

HOLOTYPE. P.47103 (Text-fig. 21C), a complete tooth from the Weald Clay of Henfield, Sussex.

MATERIAL. In addition to the holotype, one hundred teeth, of which nine are complete.

HORIZON AND LOCALITY. Weald Clay : Henfield, Sussex.

DESCRIPTION. The teeth of this species from Henfield are all well preserved, with little or no wear, but the root is present in only nine of the one hundred examples. The teeth range in length from 1·1 to 4·2 mm. In shape and proportions the teeth are similar to those of *L. breve breve* and *L. b. crenulatum* except that they are more elongated. Only in two teeth out of fifty does the ratio of maximum breadth to length of the crown fall below 4·0, the mean ratio being 5·9 (compared with about 2·7 in *L. b. breve*). The longitudinal occlusal crest of the crown is strongly marked,

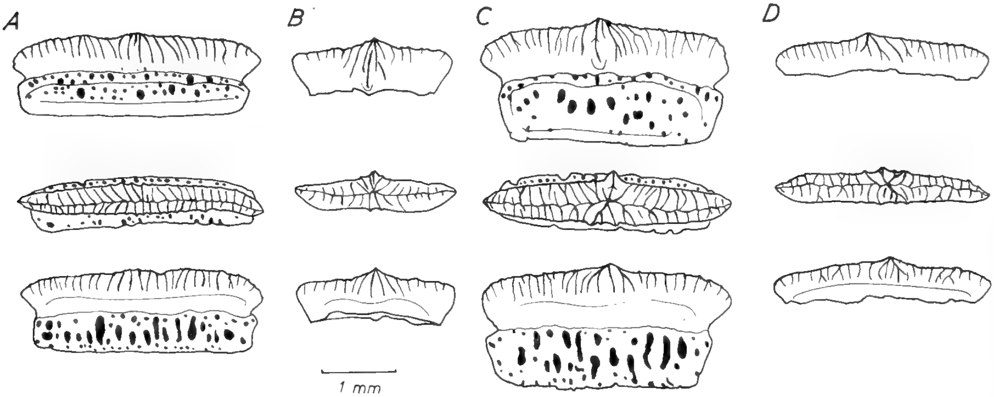


FIG. 21. *Lonchidion striatum* sp. nov. Teeth from the Weald Clay of Henfield, Sussex, in labial (above), occlusal (centre) and lingual view. A. P.47094. B. P.47095. C. P.47103, the holotype. D. P.47106.

and there is a low central cusp. The occlusal crest is roughened and jagged, as in *L. b. crenulatum*, but distinct lateral cusps are not recognizable. Diverging from the occlusal crest there are well marked vertical striae on both labial and lingual faces of the crown, the striae being stronger and more numerous than in *L. b. crenulatum*. The striae are occasionally bifurcated basally, especially at the central cusp, where they are longest and strongest. The striae do not reach the base of the crown. The labial process is weaker than in *L. breve*, particularly in the more elongated teeth, where it may almost disappear (Text-fig. 21A). The striae are weakest in the smaller and shorter teeth (Text-fig. 22A).

The root is about as deep as the crown, and is hybodontoid, without specialized foramina, just as in *L. breve*. In histological structure the crown agrees with that of *L. breve* in being made up almost entirely of pallial dentine.

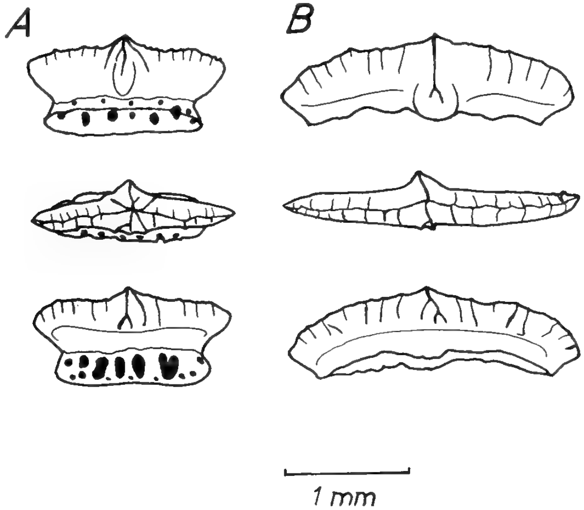


FIG. 22. *Lonchidion striatum* sp. nov. Teeth from the Weald Clay of Henfield, Sussex, in labial (above), occlusal (centre) and lingual view. A. P.47130. B. P.47138.

There is little variation in the shape of the teeth, and the dentition must have been weakly heterodont. The shorter, broader teeth, with the weakest striae (Text-figs. 21B, 22A), are probably anterior, longer teeth (Text-figs. 21C, 22B) lateral, and long, slender teeth, with a very small labial process (Text-fig. 21A, D), posterior, similar variations being evident in *L. breve crenulatum* (Text-fig. 17).

AFFINITIES. *Lonchidion striatum* differs from *L. breve crenulatum* only in the greater length of the teeth (ratio of breadth to length usually well over 4·0, always less than 4·0 in *L. b. crenulatum*), stronger and more numerous striae, and weaker labial process. There can be little doubt that *L. striatum*, known only in the Weald Clay, has evolved directly from *L. breve crenulatum*, which is unknown above the Grinstead Clay, by elongation of the teeth and strengthening of the surface ornament. The reduction of the labial process in the lateral and posterior teeth of *L. striatum* means that there would be little space between the lateral parts of successive teeth (cf. Text-fig. 20) and little or no overlap between adjacent files of teeth, producing a more *Hybodus*-like dentition than in *L. breve*.

In shape, teeth of *L. striatum* are similar to some of the Triassic species of *Acrodus* and *Polyacrodus* such as the Spitzbergen species *Polyacrodus pyramidalis* Stensiö (1921, pl. 2, figs. 21–26), *Acrodus spitzbergensis* Hulke (Stensiö 1921, pl. 2, figs. 1–19), *A. vermiformis* Stensiö (1921, pl. 2, figs. 20, 21) and *A. oppenheimeri* Stensiö (1921, pl. 3, figs. 1–11) though the teeth of all these species are larger than those of *L. striatum*.

Lonchidion rhizion sp. nov.

(Text-figs. 23, 24)

DIAGNOSIS. *Lonchidion* known only by isolated teeth less than 2 mm. in length; no tricuspid anterior teeth, dentition strongly heterodont; crowns of teeth very short and broad, maximum breadth more than half of the length; occlusal surface of teeth formed entirely by labial surface of crown and of labial process, which is much enlarged and probably overlapped the crown of preceding tooth; crown smooth, without ornament or lateral cusps; lingual surface of crown with pair of depressions or sockets separated by central crest which probably articulated with pulp cavity of succeeding tooth; pulp cavity small, root absent or very small.

HOLOTYPE. P.47144, tooth without root (Text-fig. 23B), Cliff End bone-bed, Cliff End, Sussex.

MATERIAL. In addition to the holotype, thirty-five teeth, all without roots.

HORIZONS AND LOCALITIES. Ashdown Beds: Cliff End bone-bed, Cliff End, Sussex, (25 teeth). Wadhurst Clay: Telham bone-bed, Stone, Kent (5 teeth). Grinstead Clay: Paddockhurst bone-bed, Paddockhurst Park, Sussex (5 teeth).

DESCRIPTION. The teeth assigned to this species vary from examples which do not differ much from *L. breve breve* (Text-fig. 23A) to extremely specialized types which

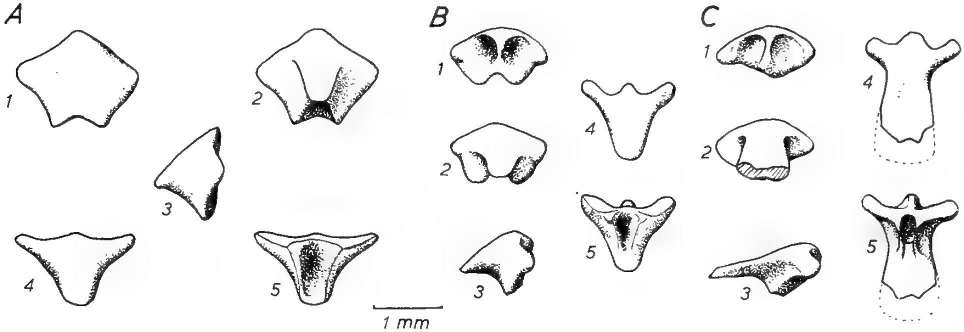


FIG. 23. *Lonchidion rhizion* sp. nov. Teeth from the Ashdown Beds, Cliff End Bone-bed; Cliff End, Sussex, in lingual (1), labial (2), medial (3), occlusal (4) and basal (5) view. A. ? anterior tooth P.47143. B. ? lateral tooth, P.47144, the holotype. C. ? posterior tooth, P.47150.

would hardly be interpreted as sharks' teeth were they not linked by intermediate forms with the more recognizable specimens. All the teeth are very small, ranging in length from 1·0 to 1·9 mm., and they are broad and deep; the ratio of maximum breadth to length ranges from 0·75 to 2·0, that of depth to length from 1·0 to 2·4.

The deeper, narrower teeth (Text-fig. 23A) are similar to the (presumed) anterior teeth of *L. breve breve* (Text-fig. 15A). In these teeth the crown is almost as deep as long, and is deeper than broad. The crown is pentagonal in lingual and labial view, two sides of the pentagon forming the occlusal crest and meeting in a rounded central cusp, two sides sloping inwards towards the base, and one side forming the base. The lingual face of the crown is almost smooth, with a slight swelling below the central cusp and a shallow depression on each side of this. In occlusal view the crown is triangular, the longest side being the occlusal crest and the apex the labial process. The labial process is much broader than it is in *L. breve*, and its flat upper surface merges with the upper part of the labial face of the crown to form the smooth, sloping occlusal surface of the tooth. There is no ridge running on to the labial process from the central cusp as there is in *L. breve*. The underside of the labial process is hollowed out, this hollow being continuous basally with the small pulp cavity of the crown.

More specialized, but linked by intermediate forms with the teeth described above, are teeth of the type shown in Text-fig. 23B. In these the crown is shallower but broader, and is almost as broad as long. The lingual face of these forms bears a central vertical crest with a well marked, circular depression on each side of it. The occlusal margin of the crown is lower and more gently rounded, the central cusp hardly recognizable in labial or lingual view but showing in occlusal view as a knob at the top of the central crest on the lingual surface. The labial process is longer than in the forms described above, and the occlusal surface formed by its upper surface is much larger. In medial view, the labial process curves labially and basally well beyond the rest of the crown. The pulp cavity in the basal surface of the crown is very small, and extends only into the proximal part of the labial process.

The most highly specialized teeth (Text-fig. 23C) have the crown shallower, the occlusal margin flatter and more gently rounded, and the crest and paired depressions on the lingual surface more strongly marked. In these forms the depressions on the lingual face are in the form of rounded sockets. The labial process is enormously enlarged, so that the breadth of the tooth is greater than its length (ratio of breadth to length as low as 0·75). The process projects labially in a long, tongue-like flange. The pulp cavity in the basal surface of the crown is very small, and hardly extends into the base of the labial process.

In none of the teeth of this species is any trace of a root preserved. The basal surface of the crown and the wall of the small pulp cavity are always quite smooth and without the foramina usually present in teeth where the root has been broken or abraded off. In the more specialized teeth the pulp cavity and basal surface of the crown are both so small that if a root were present its value as an anchor would be negligible. The form of the teeth and of the basal surface and pulp cavity suggest that there may have been no root in this species, especially in the shallower, more specialized teeth. This conclusion is supported by the inferred mode of articulation of the teeth (see below), which seems to allow no room for a root.

The Arrangement of the Teeth

As shown in Text-fig. 23, there is a great deal of variation in the teeth of *L. rhizion*, involving the depth of the tooth, the length of the labial process, and the symmetry of the tooth. I can find no correlation between these characters, except that the labial process is normally longer in shallower teeth, but deep, asymmetrical teeth with rather long labial processes do occur. As yet, there is therefore no means of assigning the different teeth to a position in the mouth, but it is clear that the dentition of *L. rhizion* must have been strongly heterodont.

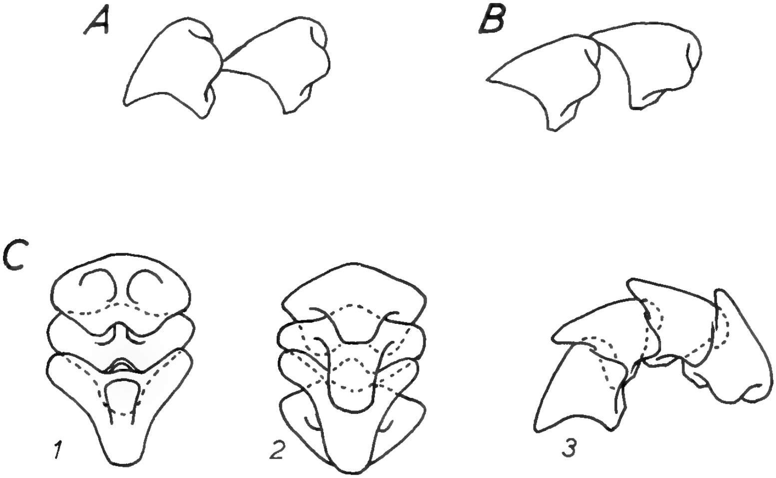


FIG. 24. *Lonchidion rhizion* sp. nov. Diagram showing possible modes of arrangement of the teeth, × 15 approx. For explanation see text. Based on the holotype (Text-fig. 23*b*). A, B, C_3 in medial view; C_1 in basal view; C_2 in occlusal view.

In none of the teeth of *L. rhizion* is there any well marked wear facet on the occlusal surface of the tooth. In *L. breve* there is often a vertical pressure scar in the centre of the lingual surface of the crown, caused by the tip of the labial process of the succeeding tooth: in *L. rhizion* there is never such a scar, but instead there is a central crest and a pair of depressions. These depressions are very weak in the deepest teeth with the largest pulp cavity (Text-fig. 23A), but become stronger as the depth of the tooth and the size of the pulp cavity decrease, until in the shallowest teeth (Text-fig. 23C) they are deep sockets. The apparent correlation (Text-fig. 23) between length of the labial process and strength of the lingual depressions does not hold good for all specimens. The shape and position of these lingual depressions and the crest between them suggest that they served for articulation between the teeth, and this is supported by the fact that they are strongest in teeth in which the pulp cavity (and basal surface of attachment) is smallest.

There are three possible ways in which the successive teeth in *L. rhizion* might have been arranged.

1. As in *L. breve* (Text-fig. 20), the teeth might have been arranged in a simple file, but without contact between successive teeth (since there is never a pressure scar on the lingual face which might be caused by the tip of the labial process of the succeeding tooth). This scheme is shown in Text-fig. 24A. It is very unlikely that the teeth were arranged in this way because it allows no function for the paired depressions and central crest on the lingual face of the crown of the shallower teeth ; because the enlargement of the labial process in the shallower teeth would also be without apparent function, and because the teeth with very long, slender labial processes (Text-fig. 23C) would give an unsatisfactory dental series.

2. The teeth might have been arranged as in Text-fig. 24B, with the labial surfaces forming the occlusal surface and the tip of the labial process of each tooth ending at the central cusp of its predecessor. Although this scheme gives a satisfactorily smooth occlusal surface to the dental series, it is open to the same objections as the scheme outlined above. The only function for the paired depressions on the lingual surface of the crown in this scheme would be to receive a pair of processes from the root of the succeeding tooth : this is unlikely, for if the roots were large enough to abut against the preceding tooth it is probable that they would be preserved in some specimens.

3. The teeth might have been arranged as in Text-fig. 24C, with the labial process of each tooth overlapping the central cusp of its predecessor. Manipulation of plasticine models of the teeth shows that in this type of arrangement the boss at top of the crest in the centre of the lingual surface would have fitted in the labial part of the pulp cavity of the succeeding tooth, and that the paired depressions would have articulated with the ridge or knob on each side of the pulp cavity at the base of the labial process. In this arrangement the radius of the tooth whorl would have been rather small, since a satisfactory fit between successive teeth is only obtained if their axes differ by about forty degrees. This scheme gives a function to the crest and paired depressions on the lingual face of the crown, gives a functional explanation of the elongation of the labial process, and gives each tooth series a radula-like occlusal surface which should be highly efficient. It does not give an entirely satisfactory fit between either the deep teeth with a short labial process (Text-fig. 23A) or the shallow teeth with a very long labial process (Text-fig. 23C), but with most of the specimens it is satisfactory. If the teeth were arranged in this way, part of the pulp cavity was occupied by the lingual crest of the preceding tooth and not by a root. In the shallowest teeth with the longest labial process the pulp cavity is so small that the articulation between the teeth would have left only a narrow channel lingually, through which nerves and vessels could have passed into the pulp cavity.

It is suggested, pending the discovery of more complete material, that *Lonchidion rhizion* was a shark in which a flattened but serrated grinding dentition was evolved by the labial process of each tooth overlapping the crown of its predecessor ; that this overlapping entailed drastic reduction and eventual loss of the root, and that this was compensated for by the development of complex interlocking articulations between successive teeth.

Affinities. *Lonchidion rhizion* is known only from the Ashdown Beds (Cliff End bone-bed), where it is not common, and from the Wadhurst Clay (Telham bone-bed) and Grinstead Clay (Paddockhurst bone-bed), where it is rare. The least specialized teeth are very like the (presumed) anterior teeth of *L. breve breve*, and it is probable that the species evolved from *L. breve*, primarily by flattening and broadening of the labial process. *L. rhizion* is the only known shark in which some, at least, of the teeth were without roots.

Lonchidion heterodon sp. nov.

(Text-fig. 25)

Diagnosis. *Lonchidion* known only by isolated teeth, less than 4·0 mm. in length ; tricuspid symphysial teeth probably present, dentition heterodont ; crowns of teeth moderately elongated, ratio of breadth to length 2·5–4·5 (except in the presumed symphysial teeth, where the ratio is less than 2·0), crown shallower than broad in lateral teeth, deeper than broad in anterior and posterior teeth ; teeth *Hybodus*-like, with low central cusp and three pairs of lateral cusps (one pair in symphysial teeth), with striae diverging from occlusal crest, striae few and weak in anterior and posterior teeth, numerous and strong in large lateral teeth ; labial process strong in anterior and posterior teeth, weak in lateral teeth.

Holotype. P.47188 (Text-fig. 25a), a lateral tooth without root from the Upper Purbeck, Friar Waddon, Dorset.

Material. Twelve teeth, all without roots.

Horizons and localities. Upper Purbeck : Friar Waddon, Dorset (6 teeth). Ashdown Beds : Cliff End bone-bed, Cliff End, Sussex (5 teeth). Wadhurst Clay : Hastings, Sussex (1 tooth).

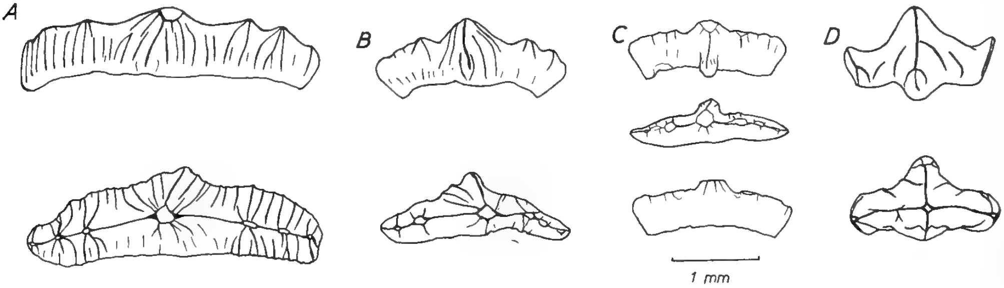


Fig. 25. *Lonchidion heterodon* sp. nov. Teeth in labial (above) and occlusal view, c also in lingual view (below). a. P.47188, lateral tooth, the holotype. b. P.47189, antero-lateral tooth. c. P.47192, posterior tooth. d. P. 47197, symphysial tooth tentatively referred to this species. a, b, c from the Upper Purbeck ; Friar Waddon, Dorset ; d from the Ashdown Beds, Cliff End Bone-bed ; Cliff End, Sussex.

Description. The holotype is a broad, low-crowned tooth which is *Hybodus*-like in appearance, with a low central cusp and three pairs of lateral cusps. The occlusal crest is well marked. Both labial and lingual faces of the crown bear strong striae which reach the occlusal crest at the central and lateral cusps but fail to do so between the cusps. The striae are occasionally bifurcated basally, and are stronger and longer on the labial face than on the lingual. The labial process, below the central cusp, is poorly marked. Both the basal surface of the crown and the lingual surface are concave, and the tooth is strongly asymmetrical. The material contains seven teeth of this type, ranging in length from 2·5 to 4·0 mm., and in the ratio of breadth to length from 3·0–4·5. The asymmetry and curvature of the basal surface and occlusal crest are particularly characteristic of these teeth. Smaller teeth of this type grade into the type shown in Text-fig. 25B. which are about 2 mm. in length and have the crown higher and narrower. In these teeth the central cusp is stronger and the lateral cusps weaker than in the larger teeth, while the labial process is larger and the striae fewer and shorter. These teeth are still weakly asymmetrical, and have the basal surface and the labial surface concave. In the small tooth shown in Text-fig. 25C these trends go further : the crown is higher and narrower, the central cusp and labial process are accentuated, the lateral cusps and striae reduced. There is little difference between this tooth and examples of *Lonchidion breve crenulatum* (Text-fig. 17) from the Grinstead Clay.

Tentatively included in this species is the tooth shown in Text-fig. 25D. This is bilaterally symmetrical and must be a symphysial tooth. There is a large central cusp, a single pair of sharp lateral cusps, a large labial process, and a few coarse striae. In this tooth (length 1·7 mm.) the breadth and depth are almost equal, and the ratio of breadth to length is about 1·7, much less than in the other teeth of the species.

The material of this species, though very limited, suggests that the dentition was strongly heterodont and consisted of small, high-crowned symphysial teeth (Text-fig. 25D), large, broad, low-crowned lateral teeth (Text-fig. 25A), smaller, narrower antero-lateral and postero-lateral teeth (Text-fig. 25B), and posterior teeth which are very like *Lonchidion breve crenulatum* (Text-fig. 25C).

The root is not preserved in any specimen. In histological structure (seen in peels taken from ground, etched surfaces of a fragment of a lateral tooth from the Upper Purbeck) the crown of this species agrees exactly with *Lonchidion* : the crown is made up entirely of pallial dentine, the long, branched dentine tubules radiating from vascular canals at the base of the crown.

Affinities. This species, though poorly known, is of interest and importance as the only record of *Lonchidion* in the Jurassic. The smallest teeth of the species, presumably posterior, are almost identical with those of *L. breve crenulatum* from the Grinstead Clay, but are linked by a series of intermediate forms with teeth like the holotype (Text-fig. 25A) which are very *Hybodus*-like (cf. *H. parvidens*—Text-fig. 7B ; *H. brevicostatus*—Text-fig. 13B) though still retaining the very thick pallial dentine which is typical of *Lonchidion*. *L. heterodon* is rare at Cliff End, in the Ashdown Beds ; and is known above this only by a single lateral tooth from the Wadhurst

Clay. If we assume that *L. heterodon*, as the earliest known species of *Lonchidion* shows the most primitive condition, the genus must have originated as a heterodont, low-crowned, *Hybodus*-like form with very thick pallial dentine. The more homodont species, *L. breve*, would then have evolved by adoption in all the teeth of the slender, high-crowned, almost smooth form of the posterior teeth in *L. heterodon*, and by increasing the overlap between adjacent files of teeth.

Fin Spines and Cephalic Spines of Lonchidion

In the late Cretaceous species *Lonchidion selachos*, Estes (1964 : 9) was able to include fragmentary fin spines and cephalic spines from localities at which teeth of the species occur. There is little doubt of the association between the teeth and the spines since *L. selachos* is the only hybodont known from the deposits. In the British Wealden and Purbeck the matter is complicated by the presence of small and immature hybodonts of other species.

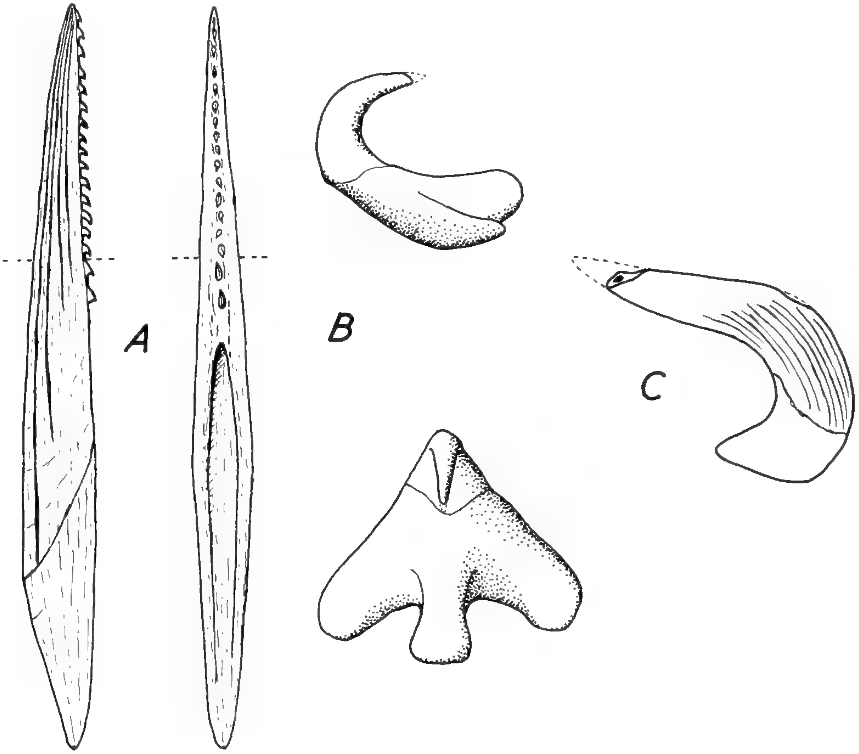


FIG. 26. *Lonchidion* sp. A. Dorsal fin spine, a restoration based mainly on P.29995, Wealden; Isle of Wight, P.12815, Weald Clay; Bookhurst, Surrey, and P.47208, Weald Clay; Henfield, Sussex, in lateral (left) and posterior view, ×1½ approx. The broken line marks the plane of the section shown in Pl. 3, fig. 4. B. Cephalic spine, P.11895 from the Wadhurst Clay; Brede, Hastings, Sussex, in dorsal (below) and lateral view, ×3·5 approx. C. Incomplete cephalic spine in lateral view, P.47207, Weald Clay; Henfield, Sussex. ×6·5.

In *L. selachos* the cephalic spine (Text-fig. 27E) has a weakly lobed root, no barb at the tip, and is ornamented with small tubercles which are drawn out into ridges distally and are pointed anteriorly. The spine is about 10 mm. in length, roughly 2·5 times as long as the average lateral tooth of the species. Among the material from the Cliff End bone-bed there are several worn and incomplete cephalic spines of small size : a complete spine of this type from the Wadhurst Clay was figured by Smith Woodward (1916, pl. 1, fig. 4). These spines (Text-fig. 26B) differ from the cephalic spine assigned to *L. selachos* in that the root is much wider and more sharply divided into three lobes, and the enamelled exserted part of the spine lies at a much shallower angle to the root and does not curve back so far. In all the specimens from Cliff End the enamelled part of the spine is perfectly smooth, but this could well be due to abrasion, for in a similar spine (P.12813) from the Weald Clay of Bookhurst, Cranley, Surrey, there are vertical striae at the base (the only part preserved) of the exserted portion. These cephalic spines are tentatively referred to *Lonchidion* : probably they belong to *L. breve*, the commonest species at Cliff End.

A single cephalic spine from the Weald Clay of Henfield (P.47207, Text-fig. 26C) is also probably a *Lonchidion*. The root is almost entirely missing but the crown curves back in just the same way as in *L. selachos*, much more strongly than in the Cliff End and Wadhurst Clay spines. The tip of the spine is smooth and without a barb, but the proximal part of the crown is ornamented with about twelve sub-parallel striae, quite a different form of ornamentation from *L. selachos*. This cephalic spine is perhaps from *L. striatum*, the dominant species of *Lonchidion* at Henfield.

The fin spines of *L. selachos* (Text-fig. 27F) are all incomplete, so that the total length cannot be measured, but they reached at least 5 mm. in breadth, and were probably about 5 cm. long. The surface is apparently without enamel ridges and is marked only by the weak striations of the texture of the superficial osteodentine. There is a single series of denticles on the posterior face.

There are no complete fin spines among the bone-bed material described here, and the fragments of spines from Cliff End and Paddockhurst are too worn for description. But fragmentary spines from the Weald Clay of Henfield and Bookhurst, Cranley, Surrey, and from an unknown horizon (? *Perna* Bed) in the Isle of Wight seem to be referable to *Lonchidion*, although it is only in the few examples where part of the inserted base is preserved that one can distinguish with certainty between small spines and the tips of large spines of *Hybodus*. From these fragments one can reconstruct the fin spine of Wealden *Lonchidion* (Text-fig. 26A). The spines reached about 7 cm. in length and were almost straight, the posterior border of the spine showing a slight curvature in its distal part. The exserted part of the spine is ornamented with enamel ridges. One ridge forms a keel on the anterior border of the spine. On the proximal part of the spine there are two or three ridges near the anterior border, the posterior part of the lateral surface being smooth. Towards the tip, the number of ridges increases to about five, equally spaced on the lateral surface. The ridges are straight and do not anastomose or bifurcate. The denticles on the posterior face of the spine are in a single series, although towards the base they may be placed alternately to the right and left of the mid-line, indicating their origin from paired series.

I have seen no examples of the double or rudimentary paired denticles of the type described in *H. brevicostatus* (p. 308). The denticles are smooth and without striae: at the tip of the spine they are low and long based, proximally the bases are shorter and the denticles higher and recurved. In no specimen is a complete series of denticles preserved, but there cannot have been more than about twenty or twenty-five. In histological structure (Pl. 3, fig. 4) the spines consist of the usual outer layer of osteodentine with an inner layer of lamellar tissue in the exserted part of the spine. The lamellar tissue makes up from half to two-thirds of the wall of the spine at about the middle of its length.

These spines agree with those which Estes (1964 : 11) assigns to the late Cretaceous *L. selachos*, particularly in the lack of curvature and the form and position of the posterior denticles, but they differ in retaining a few enamel ridges on the lateral surfaces.

The Affinities of **Lonchidion**

The only other species of *Lonchidion* known is *L. selachos* Estes (1964) from freshwater deposits of late Cretaceous age in Wyoming, where isolated teeth are fairly common at a number of localities. The lateral teeth of *L. selachos* (Text-fig. 27A) are very like those of *L. breve breve* in the smooth crown, large hybodontoid root,

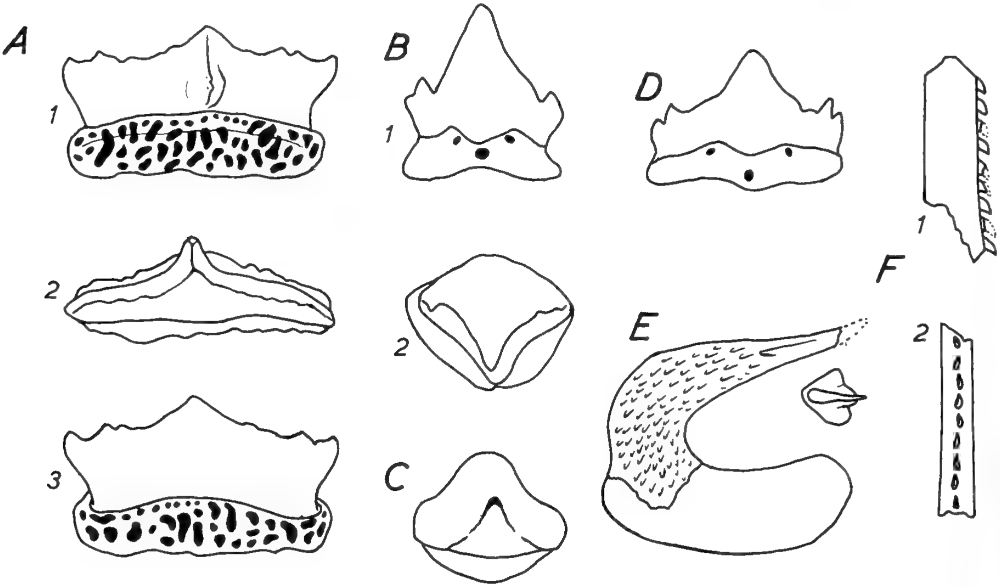


FIG. 27. *Lonchidion selachos* Estes. A. Lateral tooth (the holotype) in labial (1), occlusal (2) and lingual (3) view, ×9. B. Symphysial tooth in lingual (1) and occlusal (2) view, ×11. C. Symphysial tooth in basal view, ×11. D. Parasymphysial tooth in lingual view, ×11. E. Cephalic spine, the base restored, in lateral view, ×3·5, and (inset) in dorsal view, ×$\frac{2}{3}$. F. Fragment of dorsal fin spine in lateral (1) and posterior (2) view, ×2. All from the Lance Formation; Wyoming, U.S.A. After Estes (1964).

waisted root/crown junction, labial process, and histological structure, but they have the occlusal crest produced into fairly well marked cusps: teeth of *L. breve breve* tending towards this type occur high in the Wealden (see p. 316). In size they range from 2–6 mm., a little larger than *L. breve*. Estes suggests that this type of tooth occupied only the lateral and posterior parts of the mouth, and that the anterior teeth were of the type shown in Text-fig. 27B, C, D, high-crowned teeth with one or two pairs of lateral cusps, no labial process, and squatinoid roots (Casier 1947*a* : 10) with a central canal. In the British Wealden and Purbeck, although several hundred teeth of *Lonchidion* have been examined, no teeth of this type have been found. Although it is possible that in *Lonchidion* the anterior teeth could, by the Upper Cretaceous, have evolved a squatinoid root, in parallel with the heterodontids, it seems equally probable that the teeth described by Estes belong to a squatinid or orectolobid, perhaps to his species *Squatirhina americana* or a related form.

Estes compares the lateral teeth of *L. selachos* with teeth from the German Keuper described as *Palaeobates spinosus* by Seilacher (1943, text-figs. 27, 28). The lateral teeth of *P. spinosus* are typical of the genus, flattened *Heterodontus*-like teeth which bear little resemblance to *Lonchidion* except in their histological structure. But Seilacher assigns to the posterior part of the jaws of *P. spinosus* very small teeth (less than 1 mm. in length) which are very like those of *Lonchidion*, with a strong labial process, a waisted root/crown junction and a smooth crown. As Estes notes, no teeth of this type occurred in Stensiö's (1921 : 35) material of associated *Palaeobates* teeth from the Trias of Spitsbergen, and the systematic position of these small teeth is by no means certain. Teeth of this type are clearly fairly abundant in the German Trias: acid treatment of a small block of bone-bed from the Muschelkalk of Crailsheim (28466) has yielded several isolated crowns which are almost indistinguishable from *Lonchidion breve breve*. Until more complete information on these Triassic forms is available it is impossible to decide whether they are related to *Lonchidion* or are convergent, particularly since no Lower Jurassic teeth resembling *Lonchidion* are known. Estes also draws attention to the resemblance between the teeth of *Lonchidion* and those of the only other freshwater hybodont, the Triassic *Lissodus africanus* (Broom) (Brough 1935, pl. 2).

Glikman (1964) has recently proposed a radical reclassification of selachians. He divides the sharks and rays among two infraclasses, Orthodonta and Osteodonta, mainly on the basis of the histological structure of the teeth. In Orthondota the crown of the tooth consists of orthodentine, in Osteodonta of osteodentine surrounded by pallial dentine. Glikman finds these two groups to have been distinct since their first appearance in the Devonian. He places the hybodontids and ptychodonts in the Osteodonta, and makes a new family Polyacrodontidae, order Polyacrodontida and superorder Polyacrodonti within the Orthodonta for *Polyacrodus* and *Palaeobates*. Thus Glikman believes that *Polyacrodus* and *Palaeobates* on the one hand and the hybodonts on the other represent lines which have evolved independently since the Devonian and are only very distantly related. Because of the structure of the teeth, both *Lonchidion* and *Lissodus* would be placed in the Orthodonta, presumably in the Polyacrodonti, though the regular alternation of the teeth in adjacent series which occurs in *Lissodus* and in some species of *Lonchidion* (see p. 319) is not a character of Polyacrodonti according to Glikman. Thus Glikman's major subdivision of the sharks makes it necessary to believe that *Lissodus* and *Lonchidion* are only related to the well known Jurassic and Lower Cretaceous species of *Hybodus* in so far as the Orthodonta and Osteodonta shared a hypothetical common ancestry in the Lower Devonian. Yet *Lissodus* and *Hybodus* share such characters as fin spines of exactly similar form and structure, the anterior spine lying more obliquely than the posterior (Brough 1935), a posteriorly placed anal fin, the presence above the eyes, in males only, of two pairs of cephalic spines of similar form, etc. That such features as these should have been acquired independently and roughly simultaneously in two unrelated groups seems extremely unlikely. Another selachian group in which teeth composed either of osteodentine or orthodentine occur in closely related forms is the Upper Cretaceous sub-family Ganopristinae of the pristid sawfishes (Schaeffer 1963). In the ganopristines the rostral teeth of forms like *Onchopristis*, *Sclerorhynchus* and *Ganopristis* have a crown of orthodentine, while *Onchosaurus* and *Pucapristis* (like the Tertiary and living Pristinae) have a crown of osteodentine. Close relationship between these various genera seems beyond doubt. I am therefore unable to accept Glikman's Orthodonta and Osteodonta, at least so far as the Mesozoic sharks are concerned. I believe that the thickness of the pallial dentine and the presence or absence of osteodentine are features which have changed a good deal in the history of the sharks, that these characters cannot be used to define major subdivisions, and that there are as yet no satisfactory grounds on which forms such as *Polyacrodus*, *Palaeobates*, *Lissodus* and *Lonchidion* can be separated from the Hybodontidae. At present, all that can be said of the origins of *Lonchidion* is that the fin spines and cephalic spines ally it with the Hybodontidae, the histological structure of the teeth is like *Polyacrodus*, and that the teeth in the earliest known species, *L. heterodon*, are more like those of *Hybodus* than they are in later species. Similar forms (*Lissodus*) were already present in fresh water in the Trias.

Lonchidion is evidently a genus of hybodont which became adapted to life in fresh water in or before the Upper Jurassic, and underwent considerable radiation there, producing *Polyacrodus*-like forms (*L. striatum*) and highly specialized forms in which the roots of the teeth were lost (*L. rhizion*), both these being short-lived, while the more generalized types (*L. breve*, *L. selachos*) continued through almost to the end of the Cretaceous as the last survivors of the hybodonts. The relationships between the species of *Lonchidion* are summarized in Text-fig. 31.

Family **PTYCHODONTIDAE**

AMENDED DIAGNOSIS. Hybodont sharks in which there are no fin spines or cephalic spines; vertebral centra possibly calcified; jaws elongated, with teeth confined to their broad symphysial region; teeth flattened and crushing, dentition heterodont; nine or less paired files of teeth and an unpaired symphysial file in each jaw; largest and most specialized teeth, which are rhombic or rectangular, at or near the symphysis, teeth decreasing in size posteriorly ; crowns of teeth with strong ridges or crests of enamel ; crown made up mainly of osteodentine ; roots of teeth hybodontoid.

Genus ***HYLAEOBATIS*** Smith Woodward 1916 : 19

Amended diagnosis. Ptychodont sharks known only by isolated teeth ; jaws probably very broad, dentition probably similar in both jaws ; a symphysial file and eight paired files of teeth in each jaw ; symphysial teeth rectangular, three or four times as long as broad, parasymphysial teeth rectangular, about two-and-a-half times as long as broad ; second paired lateral teeth rhomboid, remaining teeth more or less ovoid and *Acrodus*-like, not so closely apposed as anterior teeth ; crowns of teeth with occlusal crest near labial margin in anterior teeth, central in posterior teeth ; fine bifurcating and anastomosing striae radiating from occlusal crest ; histological structure of crown like that in *Acrodus*, vascular canals less regularly arranged than in *Ptychodus*.

Type species. *Hylaeobatis ornata* (Smith Woodward), the only species.

Hylaeobatis ornata (Smith Woodward)

(Pl. 4 ; Pl. 5, figs. 4–7 ; Text-figs. 28–30)

1889 *Acrodus ornatus* Smith Woodward : 296, pl. 13, fig. 10.
1916 *Acrodus ornatus* Smith Woodward ; Smith Woodward : 14, pl. 2, figs. 15–18.
1916 *Hylaeobatis problematica* Smith Woodward : 19, pl. 5, figs. 1–5, text-fig. 10.

Diagnosis. As for genus ; symphysial teeth reaching about 15 mm. in length.

Holotype. P.5275, posterior tooth without root, probably from the Wealden Shales, Brixton, Isle of Wight.

Material. In addition to the holotype, about 300 teeth, all but ten without roots.

Horizons and localities. Weald Clay : Henfield, Sussex ; Crowhurst, Surrey ; Bexhill, Sussex ; Meadvale, Redhill, Surrey ; Hastings, Sussex ; Sevenoaks, Kent. Wealden Shales : Brook, Brixton, Yaverland and Atherfield Point, Isle of Wight. Lower Greensand : *Perna* Bed, Sandown, Isle of Wight ; Sandgate Beds, Godalming, Surrey (derived).

Description. The new material of this species from Henfield, consisting of almost three hundred teeth (mostly without roots), allows one to attempt a restoration of the dentition and shows that the two species *Acrodus ornatus* and *Hylaeobatis problematica* are synonymous, the first having been established for the small posterior teeth and the second for the large anterior teeth.

The material from Henfield includes nine complete teeth in which the roots are preserved : the dimensions of these teeth are shown in Table II. Among these nine complete teeth, seven distinct types are present, the two pairs P.47212, P.47218 and P.47213, P.47217 being of the same type. Two more types of tooth are represented among the incomplete teeth.

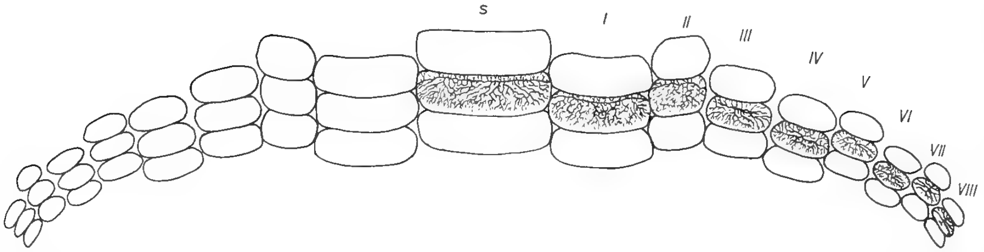


FIG. 28. *Hylaeobatis ornata* (Smith Woodward). Restoration of the dentition of one jaw in occlusal view, × 1·5 approx. 's', symphysial file; I–VIII, paired files. The surface pattern of one tooth in the symphysial file and each of the right hand files is drawn from examples from the Weald Clay of Henfield, Sussex.

1. Symphysial teeth. The largest and broadest of the complete teeth, P.47211, (Pl. 4, fig. 1; Text-fig. 28 'S') is perfectly bilaterally symmetrical and has a clearly marked ridge in the centre of the basal surface of the root: this must be a symphysial tooth, and the ridge marks the symphysis between the two rami of the jaw. In shape the tooth agrees with a worn specimen figured by Smith Woodward (1916, pl. 5, fig. 3), and among the teeth from Henfield there are nine rootless examples of this type, ranging in length from 7–15 mm., and in the ratio of breadth to length from 2·8–3·5. The labial face of the crown is strongly convex in the vertical plane, weakly concave in the horizontal. The lingual face is strongly concave vertically and weakly convex horizontally. The lateral ends of the crown are rounded in P.47211, but in other specimens they may show two pressure scars, giving a hexagonal coronal surface. In P.47211 the crown is quite unworn. The coronal surface is divided into a narrow labial zone and a broad lingual zone by a clearly marked longitudinal ridge. Comparison with the less specialized posterior teeth shows that this ridge is the occlusal crest. The labial zone, which makes up about a quarter of the surface of the crown, slopes sharply downwards, and is ornamented with bifurcating ridges which pass out from the occlusal crest to end about half way between this crest and the root/crown junction. The lower half of this sloping labial surface of the crown fitted in life in the hollow on the lingual face of the crown of the preceding tooth. The broad lingual zone of the crown is almost flat, and formed the occlusal surface of the tooth. It is ornamented with striae which originate at the occlusal crest and which bifurcate and anastomose frequently as they pass lingually, so that the lingual half of the crown has a reticular surface. The strongly concave lingual face of the crown is separated from the coronal surface by a sharp angle, and is smooth except for coarse irregularities near the root/crown junction.

2. Parasymphysial teeth. P.47212 (Pl. 4, fig. 2; Text-fig. 28, I) is a tooth in which the crown is elongated, broad and flat, as in the symphysial teeth, but is clearly asymmetrical and is shorter and proportionally broader than in the symphysial teeth. As one would expect, teeth of this type are about twice as common as the symphysial teeth: there are about twenty incomplete examples among the material from Henfield. The tooth figured by Smith Woodward (1916) in Pl. 5, fig. 4, is a worn

TABLE II

The dimensions (in mm.) of nine complete teeth of *Hylaeobatis ornata* from the Weald Clay of Henfield, Sussex

Specimen	Length of crown	Length of root	Total depth	Depth of crown	Depth of root	Breadth of crown	Breadth of root	$\frac{\text{Length of crown}}{\text{Breadth of crown}}$	$\frac{\text{Length of crown}}{\text{Total depth}}$	File to which assigned
P.47211	14·0	12·7	6·9	2·8	3·6	4·0	3·2	3·5	2·2	S
P.47212	10·6	9·3	5·5	2·7	2·3	4·1	3·0	2·6	2·0	I
P.47218	9·4	8·0	5·0	2·5	2·2	4·2	2·6	2·2	1·9	I
P.47213	5·8	5·3	5·3	3·0	2·1	4·2	3·0	1·4	1·1	II
P.47217	3·9	3·1	4·0	1·7	2·0	2·7	1·8	1·4	1·0	II
P.47214	6·7	6·1	3·9	2·0	1·7	3·3	2·2	2·0	1·7	IV
P.47219	5·3	4·9	2·4	1·0	1·0	1·8	1·2	2·9	2·2	V
P.47215	4·7	4·9	2·8	1·3	1·2	2·3	1·6	2·0	1·7	VI
P.47216	3·0	3·2	2·0	1·0	0·7	1·1	0·9	2·7	1·5	VIII

example of this type. These teeth range from 6–12 mm. in length, and in the ratio of breadth to length from 2·6 to 3·0. The crown is shaped like that of the symphysial teeth, being weakly concave labially and convex lingually in the horizontal plane, with the occlusal crest near the labial margin, a steeply sloping labial zone, and similar ridged and reticulate ornament. The crown is deeper at one end than at the other, and the deeper end of the crown commonly bears a pair of pressure scars caused by contact with the teeth in the adjacent file. The lower end of the crown is often without pressure scars, as in the specimen figured by Smith Woodward. These teeth are almost certainly parasymphysial teeth from the first paired files in the jaws, the deeper end of the crown being medial and the pressure scars at this end being caused by contact with the large symphysial teeth.

3. Antero-lateral teeth. P.47213 (Pl. 4, fig. 3 ; Text-fig. 28, II) is an example of a third and very distinctive type of tooth, in which the crown is short and very broad, with a ratio of breadth to length often less than 1·5, and the total depth almost equal to the length of the crown. The crown of this type of tooth is strongly asymmetrical. The material from Henfield contains about twenty-five teeth of this type, ranging in length from 4–8 mm. and in the ratio of breadth to length from 1·3–1·8. The holotype of *H. problematica* (Smith Woodward, 1916, pl. 5, fig. 1) and two more of Smith Woodward's figured specimens of this species (1916, pl. 5, figs. 2, 4) are of this type. In these teeth the ornamentation of the crown is very like that in the symphysial and parasymphysial teeth, but the occlusal crest does not lie so near to the labial margin of the crown, and there is often an area of reticulate ornamentation lying labial to this ridge, a feature which is not seen in symphysial and parasymphysial teeth. As in the parasymphysial teeth, one end of the crown is deeper than the other : this deeper end is commonly marked by pressure scars whereas the shallow end is almost always without pressure scars. The concavity on the lingual face of the crown, in which the labial margin of the succeeding tooth fitted, is much stronger at the deeper end of the crown than at the shallower. These facts show that the deeper end of the crown is medial, that these teeth were in close contact medially with their neighbours in both the same and the adjacent file, but that laterally these contacts, particularly with teeth in the adjacent file, were less close. The teeth are probably members of the second paired files in the jaws, next to the parasymphysials, the two types of teeth being equally common. These antero-lateral teeth show the strongest asymmetry of all the teeth.

4. Lateral and posterior teeth. The three types of teeth described so far, the symphysial, parasymphysial and antero-lateral, all have the crown approximately rectangular or rhomboid in shape, with a broad, flat coronal surface and with the occlusal crest near the labial margin. The remainder of the teeth from Henfield do not show these features : the crown is ovoid in shape, its surface is more or less rounded, and the occlusal crest lies at or near the centre of the crown. The distinction between these two classes of teeth is not absolute, intermediates between the two being found in some of the antero-lateral teeth, where the crown may be moderately rounded and have the occlusal crest some distance from the labial margin, and in some of the larger lateral teeth. These intermediate forms and the relative

abundance of the different types of teeth leave little doubt that the two classes of teeth are correctly placed in the same species. The symphysial, parasymphysial and antero-lateral teeth, interpreted as representing five files (one median and two paired) make up a little less than one-third of the sample from Henfield (68 out of 215 teeth) : this proportion gives some support to the conclusion, reached on morphological grounds, that there was a total of seventeen files of teeth in each jaw.

P.47214 (Pl. 4, fig. 4 ; Text-fig. 28, IV) is an example of one of the larger lateral teeth. The crown is approximately ovoid in outline. The occlusal crest of the crown, though not strongly marked in this specimen, lies nearer to the centre of the crown than to the labial margin. The ornamentation of the crown consists of bifurcating and anastomosing striae, diverging from the occlusal crest and forming a reticulum towards the margins of the crown, including a reticular area towards the labial margin, as in the antero-lateral teeth. The material from Henfield contains about fifty teeth agreeing with this specimen, ranging in length from 4·0–7·5 mm. and in the ratio of breadth to length from 1·9–2·7. Like the parasymphysial and antero-lateral teeth, these specimens are asymmetrical, with the medial end of the crown a little higher than the lateral. Pressure scars on the ends of the teeth are rare, and these teeth were evidently not closely associated with the neighbouring files. These teeth are interpreted as forming the third and fourth paired files of teeth in each jaw.

Among the remaining teeth from Henfield, two more distinct types can be easily recognized, a long, narrow type, and a short, broad type, both including only small teeth. The long, narrow teeth (P.47216, Pl. 5, fig. 6 ; Text-fig. 28, VIII) range in length from 3·0–5·0 mm., with a ratio of breadth to length between 2·7 and 3·2. The crown is an elongate ovoid in shape. In the larger examples the ornamentation of the crown is irregular, though an occlusal crest in the centre of the crown can normally be recognized, from which bifurcating and anastomosing ridges diverge, forming a reticular pattern towards both lingual and labial margins of the crown. The occlusal crest curves lingually at each end of the crown. In smaller teeth of this type the ornamentation is more regular, with a strongly marked occlusal crest which curves lingually at the ends of the crown and forms a weak central cusp in the centre. The lingual half of the coronal surface is almost smooth in the smallest teeth, but usually bears a ridge, running parallel to the occlusal crest, which is joined to the central cusp and curves lingually without reaching the ends of the crown. The labial half of the crown bears two or three similar longitudinal ridges, joined to the central cusp and turning labially before reaching the ends of the crown. The holotype of *Acrodus ornatus* Smith Woodward (P.5275 ; 1889, pl. 13, fig. 10) is a worn tooth of this type, and among the material from Henfield there are about twenty-five examples.

The short, broad teeth (Text-fig. 28, VII) in none of which is the root preserved, agree with the long narrow teeth described above in all features of ornamentation, but are typically 3–4 mm. in length and 1·6–2·1 mm. in breadth, with a ratio of breadth to length of 1·6–1·9. They show the same increasing regularity of ornamentation with decreasing size, with the appearance in small forms of ridges running parallel to the occlusal crest. The crown in these teeth is almost semicircular in shape, with a flat lingual margin and a strongly arched labial one. A tooth of this type is figured as *Acrodus ornatus* by Smith Woodward (1916, pl. 2, fig. 18), and there are about thirty examples among the material from Henfield.

There remain undescribed about fifty teeth from Henfield, which are intermediate in shape and ornament between the large lateral teeth (III, IV) and the small teeth of short, broad (VII) and long, narrow (VIII) type. In these teeth (P.47215; Pl. 5, fig. 7) the crown is ovoid in shape, 3·0–7·0 mm. in length, and with a ratio of breadth to length of 1·9–3·0. The larger of these, 4·5–7·0 mm. in length, are narrower, with the ratio of breadth to length usually between 2·5 and 3·0, while the smaller teeth, 3·0–4·5 mm. in length, are broader, with the ratio of breadth to length from 2·0 to 2·5. The labial margin of the crown is usually more strongly curved than the lingual. An occlusal crest is normally recognizable in the centre of the crown, with bifurcating and anastomosing striae diverging to form a reticular pattern at both lingual and labial margins. One specimen figured as *Acrodus ornatus* by Smith Woodward (1916, pl. 2, fig. 17) is a worn tooth of this type. Of each of the paired types of teeth described above, the material from Henfield normally contains between twenty and thirty examples. This material contains about fifty of these ovoid teeth, and they probably represent two paired files in the postero-lateral part of the jaw (Text-fig. 28, V–VI).

5. The Root. There is no significant variation in the shape or structure of the root between the small posterior teeth and the large symphysial teeth. In all the teeth the root is typically hybodontoid (Casier 1947*a* : 9) in structure : porous and trabecular, with an irregular series of large foramina in both the lingual and labial surfaces (Pl. 4). The labial face of the root is concave, and is clearly marked off from the flat basal surface, which slopes lingually. The lingual face of the root is strongly convex, its upper part sloping out in a ledge which is largest in the anterior teeth, where it fitted against the concavity on the labial face of the root of the succeeding tooth. The root is shorter and narrower than the crown in all but the smallest posterior teeth (Pl. 5, figs. 6, 7). In the posterior teeth the root is shallower than the crown, but in the large anterior teeth it may be as deep as or deeper than the crown.

6. Histological Structure. Smith Woodward (1916 : 20, text-fig. 10) has given a brief account of the histological structure of the crown, which he compares with that of *Ptychodus*. Sections of the crowns of a large anterior tooth and a small posterior one are shown in Pl. 5, figs. 4, 5. The structure of the crown seems to be closer to that of *Acrodus* (Owen 1840, pl. 14), with which it agrees in the rather sparse and irregularly arranged vascular canals and the ' bunching ' of the tubules of the thin pallial dentine where they arise from the vascular canals. In *Ptychodus* the vascular canals are more regularly and closely arranged, and are parallel throughout the distal part of their length, as they are in the teeth of rays (Casier 1953, pls. 1, 2).

7. Other remains. There are no shark vertebrae associated with the abundant teeth of *Hylaeobatis* at Henfield, suggesting that the notochord was uncalcified, as in the hybodontids, or that the centra were very weakly calcified. As all the fin spines from Henfield are of normal hybodont type and seem to belong either to *Hybodus basanus* or to *Lonchidion*, there is no evidence that fin spines were present in *Hylaeobatis*.

Restoration of the dentition. On the basis of the morphology and relative abundance of the various types of teeth described above, a tentative reconstruction of the jaw of *Hylaeobatis ornata* has been made (Text-fig. 28). This reconstruction is largely hypothetical in that there is, as yet, no means of distinguishing between teeth from the upper and lower jaws, and one cannot discover whether there was any difference between the arrangement of the teeth in the two jaws, as there was in *Ptychodus*. But since only one type of symphysial tooth has been found, which when worn has a single, centrally placed wear facet, any variation between the two jaws is unlikely to be of the type seen in *Ptychodus*, where the symphysial teeth are large in one jaw and small in the other (Smith Woodward 1888 : 296). Smith Woodward (1916 : 21, pl. 5, fig. 4) has described one antero-lateral tooth of *Hylaeobatis* as showing signs of having been opposed by two teeth in life, but this is not true of any of the teeth from Henfield, and at present there is no good evidence of dissimilarity between the two jaws.

Since the symphysial teeth are the largest teeth, with the flattest crowns, the most labially displaced occlusal crest, and the closest fit with their neighbours in the same and adjacent files, the very broad, weakly curved dentition suggested in Text-fig. 28 seems the most reasonable interpretation of the material. As the crowns of the symphysial and parasymphysial teeth are slightly concave forwards, the medial part of the dentition must have been transversely placed and without appreciable posterior curvature. The strongly asymmetrical antero-lateral teeth (II) must mark the transition between the transversely placed, pavement-like dentition of the front of the mouth and the more *Acrodus*-like teeth of the last six files, which were probably curved back towards the articular region of the jaws. The asymmetry of the antero-lateral teeth and the close fit with the parasymphysial teeth which is indicated by the pressure scars on their medial faces show that these teeth must have curved forwards, as shown in Text-fig. 28. Because of this, it is difficult to see how the curvature of the posterior part of the jaw could have been greater than that shown in the figure, if the files of teeth were in reasonably close contact. All this suggests that the jaws of *Hylaeobatis* were very broad anteriorly, and that the dentition was largely confined to the anterior, transverse part of the jaw, as more complete remains show that it was in *Ptychodus* (Smith Woodward 1904). The transition between the small, *Acrodus*-like posterior teeth and the large, flattened teeth at the symphysis shows how a ray-like dentition can be produced in a hybodont by specializations which include the shifting labially of the occlusal crest, so that the occlusal surface is formed by the lingual face of the crown, the hollowing out of the lingual face of the crown to give increased contact between successive teeth, and the development of a rough surface by anastomosis between the surface striae. The variability in the occurrence and size of the pressure scars on the lateral and medial surfaces of the crowns of the anterior teeth suggests that in *Hylaeobatis*, just as in *Ptychodus*, the teeth in adjacent files did not alternate regularly in position as they do in the rays.

The Affinities of **Hylaeobatis**

Smith Woodward (1916 : 19) placed *Hylaeobatis* in the Myliobatidae, but compared it with *Ptychodus* (which he then included in the same family) and suggested that it might be intermediate between *Ptychodus* and the cestracionts (including hybodonts). Later (1932 : 83) he included the genus in the Ptychodontidae. Casier (1953) has discussed the origin and affinities of the ptychodonts in some detail, and has shown that they are almost certainly specialized derivatives of the hybodonts or heterodontids, probably the former. He considered (p. 34) *Hylaeobatis* to be as close to the heterodontids as to the ptychodonts, and saw in it ' une forme intermédiaire, au point de vue de la morphologie dentaire, entre les Hybodontiformes et les Ptychodontes '. More recently (1961 : 45, pl. 5, fig. 1), in describing as *Hylaeobatis?* sp. a tooth from the Neocomian of the Congo, Casier revised this opinion and concluded that *Hylaeobatis* is probably a pycnodont. The tooth described by Casier seems to bear little resemblance to *Hylaeobatis*, particularly in the ornamentation of the occlusal surface and the flat, ornamented lingual face, and is probably a pycnodont tooth.

The new material described here seems entirely to confirm Smith Woodward's and Casier's (1953) opinions on the affinities of *Hylaeobatis*. *Hylaeobatis* shows unmistakable signs of hybodont relationships in the *Acrodus*-like posterior teeth and histological structure of the crown, and in the hybodontoid roots of the teeth. On the other hand, there are equally important indications of relationship with *Ptychodus*. Casier (1953 : 25) considers that the ptychodont type of dentition evolved from hybodonts with undifferentiated dentition by specialization of the anterior teeth and reduction in the number of files of teeth (in contrast to the heterodontids, where the lateral teeth are specialized, the anterior teeth remaining small). *Hylaeobatis* exhibits the most important character of the ptychodonts, the enlargement and specialization of the anterior teeth, with the symphysials and parasymphysials the most specialized. As to the number of files of teeth, *Ptychodus decurrens*, which seems to be the least specialized of the well known species (see below), has only five or six paired files in addition to the symphysials, but in later species the number of paired files rises (perhaps secondarily) to eight in *P. mortoni* (Williston 1900 : 238) and to nine in the Upper Senonian *P. mediterraneus* (Canavari 1916 : 37). *Hylaeobatis*, with eight paired files and a symphysial, agrees with *P. mortoni* and with hybodontids such as *Acrodus curtus* (=*A. anningiae*) (Smith Woodward 1889, text-fig. 10). The number of paired files is rather variable in hybodontids (9 or 10 in *H. basanus*, 9 in *H. brevicostatus*, six in *Asteracanthus*), and too much importance should not be attached to it. In the apparent absence of fin spines *Hylaeobatis* agrees with *Ptychodus* and differs from the hybodontids, in the apparent absence of calcified centra it agrees with the hybodontids (the evidence for the presence of calcified centra in *Ptychodus* is not conclusive—see below).

There seems little doubt that *Hylaeobatis* is intermediate between the hybodontids and *Ptychodus*. The genus is placed in the Ptychodontidae because it already exhibits the specialization of the anterior teeth which is characteristic of this family. There are two further points to be considered : the origin of *Hylaeobatis* and the ptychodontids, and the nature of the relationship between *Hylaeobatis* and *Ptychodus*.

The Origin of **Hylaeobatis**

Casier argues that forms with a ptychodont dentition, with the anterior teeth the largest and most specialized, must have evolved from hybodontoids in which the dentition was homodont, without the enlargement of the lateral teeth which is characteristic of most hybodontids and of heterodontids. Also, since the anterior teeth of *Hylaeobatis* are the most specialized, it seems reasonable to assume that the small posterior teeth will retain most resemblance to the ancestral form. In the Weald Clay at Henfield, where teeth of *Hylaeobatis* are very abundant, there is an almost perfect gradation between the smaller posterior teeth of this genus and teeth of *Lonchidion breve breve*, a hybodontid species in which the dentition was probably almost homodont (see p. 314). In the smallest teeth of *Hylaeobatis* (Text-fig. 29C), possibly juvenile, the surface ornamentation is reduced to a single central occlusal crest with a few weakly marked cusps along it, and a single labial accessory cusp overlying a broad labial process. Such teeth are similar in shape to but broader than teeth of *Lonchidion breve*: they are particularly like *L. breve pustulatum* (Text-fig. 19), a subspecies known only from the *Perna* Bed at the base of the Atherfield Clay. The histological structure of the teeth of *Lonchidion breve*, with their very thick

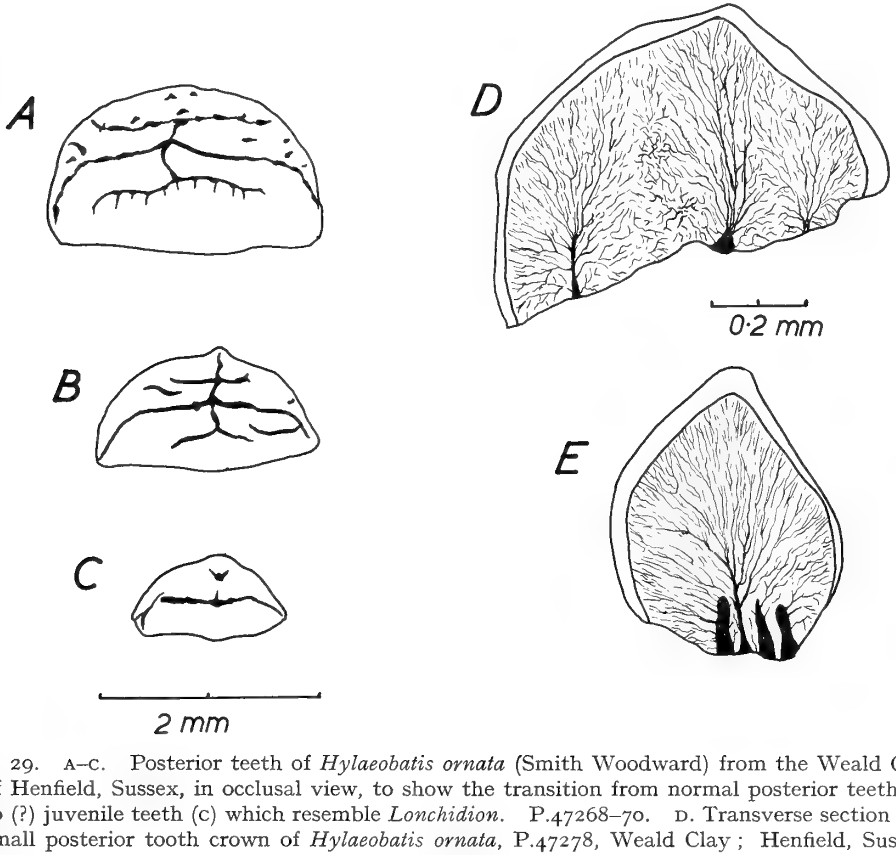


FIG. 29. A–C. Posterior teeth of *Hylaeobatis ornata* (Smith Woodward) from the Weald Clay of Henfield, Sussex, in occlusal view, to show the transition from normal posterior teeth (A) to (?) juvenile teeth (C) which resemble *Lonchidion*. P.47268–70. D. Transverse section of a small posterior tooth crown of *Hylaeobatis ornata*, P.47278, Weald Clay; Henfield, Sussex. E. Transverse section of a tooth crown of *Lonchidion breve breve* sp. nov., P.47279, Ashdown Beds, Cliff End Bone-bed; Cliff End, Sussex.

pallial dentine, seems at first to be against any relationship with *Hylaeobatis*, in which the crown consists mainly of osteodentine with a rather thin layer of pallial dentine whose tubules arise in bunches from the terminal parts of the vascular canals of the osteodentine (see p. 331 for discussion of Glikman's (1964) views on the differences between these types of tooth structure). But the differences here seem to be due largely to the greater size and thickness of the crown in *Hylaeobatis*. In *Lonchidion* the tubules of the pallial dentine arise from the tips of vascular canals, just as in *Hylaeobatis*, but the crown is so low and narrow that there is normally only a single row of vascular canals at the base of the crown : other vascular canals are sometimes present (Text-fig. 29E), from which a few short dentine tubules are given off into the basal parts of the crown. In the smallest teeth of *Hylaeobatis* (Text-fig. 29D) the structure may be very like that of *Lonchidion* : in these teeth the vascular canals only enter the base of the crown, there giving off sprays of pallial dentine tubules which make up the bulk of the crown. The type of structure seen in the teeth of *Hylaeobatis* can be derived from that of *Lonchidion* by increase in the breadth of the crown, making more vascular canals and tufts of pallial tubules necessary, and increase in the depth of the crown without increase in the thickness of the pallial dentine, allowing the basal part of the crown to be formed by osteodentine laid down around the vascular canals.

At present, I would suggest that *Hylaeobatis* (and the Ptychodontidae) arose from a homodont species of the hybodontid genus *Lonchidion*, primarily by reduction in the labial process, by increase in the surface ornament, by specialization in the anterior teeth, and by loss of fin and cephalic spines.

Relationships within the Ptychodontidae

The Ptychodontidae contains only the three genera *Ptychodus*, *Hylaeobatis* and *Heteroptychodus*. *Heteroptychodus* Yabe & Obata (1930 : 6), type species *H. steinmanni* Yabe & Obata (1930 : 7, pl. 2, figs. 6–8), is known only by a single tooth crown from the basal Cretaceous of Japan. This tooth is quite unlike *Hylaeobatis* and rather unlike *Ptychodus*, but the genus is so poorly known that nothing is to be gained from discussing it. I agree with Smith Woodward (1912 : 245) that the separate genus *Hemiptychodus* Jaekel (1894 : 137) for *P. mortoni* Mantell, in which the striae radiate from the centre of the tooth crown, is not justified.

Since *Hylaeobatis* is unknown above the base of the Aptian and *Ptychodus* does not appear until the Cenomanian there is a long gap in the history of the Ptychodontidae, and the two genera are not necessarily closely related. There is a number of characters in which *Ptychodus* is more specialized than *Hylaeobatis*, including :

1. Differences between the dentition of the two jaws in *Ptychodus*, one having very small symphysial teeth and large parasymphysials, the other having the largest teeth on the symphysis. Smith Woodward (1904), on the basis of a specimen in the Willett Collection in Brighton Museum in which the greater part of the cartilage of one jaw and fragments of the other are preserved, interpreted the jaw with the small symphysial teeth as the upper, but Canavari (1916 : 92) has shown that these small symphysial teeth were sunk beneath the level of the parasymphysials so that

they were not functional but formed the floor of a median groove in the dentition. He argues that such a groove would be without function in the upper jaw, but that in the lower it would serve as a gutter down which masticated food would be washed to the oesophagus. This interpretation seems reasonable and may provide an explanation for this difference between *Ptychodus* and *Hylaeobatis*, in which there is no evidence of differentiation between the upper and lower dentition.

2. Differences in the histological structure of the teeth. In *Ptychodus* (Owen 1840, pls. 18, 19; Casier 1953, pl. 1) the vascular canals of the crown are long, straight, and parallel through the greater part of their length, producing a tissue which resembles the tubular dentine of holocephalans and dipnoans. This type of tissue is an adaptation to a durophagous diet (Radinsky 1961 : 79) which has arisen independently in a number of groups, including rays, *Ptychodus* and *Asteracanthus* among selachians. The type of structure seen in *Ptychodus* can probably be derived from that in *Hylaeobatis* by alignment of the ascending vascular canals which give off the pallial dentine, in just the same way as the teeth of the hybodontid *Asteracanthus* (*Ptychodus*-like in structure) are probably derived from those of *Acrodus* (*Hylaeobatis*-like in structure).

3. *Ptychodus* is thought to have had calcified vertebral centra, while there is no evidence for such structures in *Hylaeobatis*. Direct evidence for the presence of calcified centra in *Ptychodus* rests on two specimens, one from the English Chalk (39436, *P. decurrens*; Smith Woodward 1912, pl. 52, figs. 1–6) in which two centra are preserved in association with fragments of calcified cartilage and twenty-three scattered teeth, and one from the Italian Upper Senonian, the holotype of *P. mediterraneus* Canavari (1916), in which an impression of a single centrum is preserved in association with an almost complete dentition. In my opinion there is still considerable doubt as to the weight to be attached to these specimens. In favour of the centra belonging to the same animal as the teeth is the fact that both the centra and the teeth in the two specimens are of approximately the same size (the centra *c.* 50 mm. in diameter in both, parasymphysial teeth from the lower jaw *c.* 35 × 29 mm. in Canavari's specimen, 34 × 31 mm. in the English specimen): it is unlikely that this should be so if the teeth and centra were associated either by chance or by the ingestion of *Ptychodus* by a shark with calcified centra. Against the centra belonging to *Ptychodus* there are several points. First, as Smith Woodward (1912 : 229) noted, the centra are very like those found in association with teeth of *Squalicorax* in the Kansas Chalk, where there is no doubt that the teeth and vertebrae are from the same animal: I have been unable to find any significant differences between the two types of centra in external or internal structure. Secondly, a considerable number of associated dentitions of *Ptychodus* has been collected in the English and American Chalk: it seems strange that only in one of these (one of the least complete) are centra preserved. Thirdly, calcified centra are not known in any other hybodontiform shark. It appears that there is not enough evidence to regard the presence of centra as a genuine difference between *Hylaeobatis* and *Ptychodus*.

The earliest well-known species of *Ptychodus* is *P. decurrens* Agassiz, the only species known in the Cenomanian zones of the English Chalk (Dibley 1911 : 273).

This species is more like *Hylaeobatis* than are later species in that there is no broad, flat, marginal zone on the crown, and it is therefore probably primitive. As the symphysial teeth of *Ptychodus* are the most specialized, one may expect that, as in *Hylaeobatis*, the small posterior teeth will show most resemblance to the ancestral form. A posterior tooth of *P. decurrens* is shown in Text-fig. 30A. Although larger and more strongly ornamented than posterior teeth of *Hylaeobatis*, it shows the same relative proportions of crown and root, and has an approximately similar surface

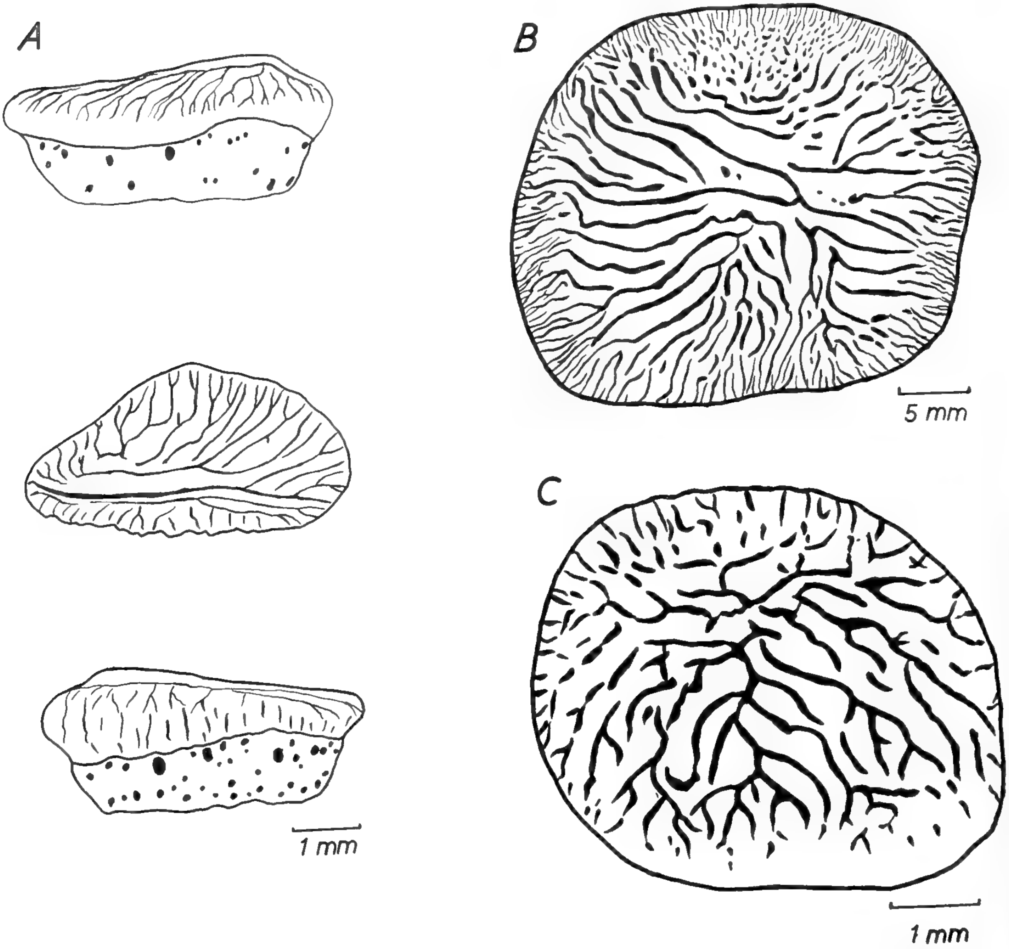


Fig. 30. A. *Ptychodus decurrens* Agassiz. Posterior tooth in labial (above), occlusal (centre) and lingual view. 4361, Lower Chalk; Lewes, Sussex. B. *Ptychodus decurrens* var. *oweni* Dixon. Parasymphysial tooth, probably from the first paired file of the upper jaw, right side, in occlusal view (symphysis to the right, labial margin uppermost). 39125, Lower Chalk; Halling, Kent. C. *Hylaeobatis ornata* (Smith Woodward). Antero-lateral tooth from the second paired file in occlusal view (symphysis to the left, labial margin uppermost). P.47230, Weald Clay; Henfield, Sussex.

ornamentation, a longitudinal occlusal crest from which bifurcating striae diverge. The arrangement of the striae tends towards the parallel ridges characteristic of anterior teeth in *Ptychodus*, but parallel transverse ridges also tend to develop in posterior teeth of *Hylaeobatis* (p. 337). Differences between teeth of *P. decurrens* and *Hylaeobatis* include :

1. The striae on the crown in *Ptychodus* extend almost to the root/crown junction on all surfaces of the tooth : this seems to be true of all except the smallest posterior teeth (Text-fig. 30A). In *Hylaeobatis* the lingual face of the crown is always smooth or nearly so, and on the other faces the striae end well above the root/crown junction.

2. In *Hylaeobatis* the whole of the lingual face of the crown is occupied by a concavity in which the labial surface of the succeeding tooth fits : this is true even of the smallest teeth. In the small posterior teeth of *Ptychodus* there may be no cavity at all, as in Text-fig. 30A, while in the anterior teeth the cavity is always rather small and often appears to be more a pressure scar caused by the succeeding tooth rather than a real feature of the tooth. In *Ptychodus* the surface of the lingual cavity is always ornamented, like the rest of the crown, while in *Hylaeobatis* it is smooth. This seems to imply that in *Ptychodus* the fit between successive teeth was not so close as it was in *Hylaeobatis*.

3. In *Ptychodus* the crowns of the anterior teeth are almost square or only slightly longer than broad. There is no counterpart in *Ptychodus* of the transversely elongated symphysial and parasymphysial teeth of *Hylaeobatis*, nor is there any sign in *Ptychodus* of the labial shifting of the main occlusal crest which is characteristic of these anterior teeth in *Hylaeobatis*. But the antero-lateral teeth of *Hylaeobatis* (II, Text-fig. 28) are almost identical in shape with parasymphysial teeth of *P. decurrens*, and in the ornamentation of the crown they are very close to *P. decurrens* var. *oweni* (Smith Woodward 1912, pl. 52, figs. 9–11) a form in which the striae are more irregular than they are in typical examples of the species. The teeth shown in Text-fig. 30B, C demonstrate this very close similarity, the only difference between the two being the finer and more extensive ornamentation of *P. decurrens*, a feature which could well be due simply to the much larger size of the latter.

In summary, there are some characters in which *Ptychodus* is more advanced than *Hylaeobatis*, particularly the histological structure of the teeth and the different form of the symphysial teeth in the upper and lower jaws, but both these characters could have evolved from the conditions in *Hylaeobatis*. In *Ptychodus* the crown is more heavily and extensively ornamented than in *Hylaeobatis*, and there was a less close fit between successive teeth—in the first of these characters *Ptychodus* is probably more advanced than *Hylaeobatis*, in the second more generalized, but again these conditions could be derived from those in *Hylaeobatis*. In *Ptychodus* there is no counterpart of the specialized elongated symphysial and parasymphysial teeth of *Hylaeobatis*, but there is a close similarity between the antero-lateral teeth of the second paired file in *Hylaeobatis* and the parasymphysial teeth of *P. decurrens*. This suggests that *Ptychodus* did not evolve direct from *Hylaeobatis*, or at least not from the only known species of that genus, but from a similar form in which the symphysial and parasymphysial teeth were less specialized.

IV ECOLOGY AND RELATIONSHIPS OF THE FAUNA

It now seems certain that the bulk of British Wealden (excepting the upper part of the Weald Clay and the Wealden Shales: Anderson 1963; Casey 1961 : 490) and the greater part of the Middle and Upper Purbeck (Anderson 1958) were laid down in fresh water (Allen 1959). At Henfield this is confirmed for the fish horizons by the ostracods and charophytes (see p. 286). The abundance and variety of the shark fauna is therefore surprising, for shark remains are normally taken as evidence of marine or estuarine conditions, since among living elasmobranchs only some species of *Carcharhinus*, potamotrygonid rays and pristids have become adapted to life in fresh or brackish water. As for the hybodonts, Casier (1961 : 77) is of the opinion that they were all marine while Estes (1964 : 167) notes that *Lonchidion selachos* is only the second freshwater form known, the other being *Lissodus africanus* (Brough 1935). It is notable that none of the more advanced selachian groups is present in the British Wealden and Purbeck, although notidanids, heterodontids, orectolobids scyliorhinids, squalids, squatinids and rhinobatids were already present in Upper Jurassic seas: this provides additional evidence that the deposits were laid down in fresh water. The moderately large and varied hybodont fauna of the English Wealden and Purbeck shows that by the end of the Jurassic (if not before) some hybodont sharks had become euryhaline and entered fresh waters. This move was clearly advantageous: it removed the hybodonts from competition with more advanced forms, some of which (particularly notidanids, heterodontids, orectolobids, rhinobatids) must have occupied very similar niches, and allowed them free rein as almost the only aquatic predators among the rich teleostean, molluscan and arthropodan fauna of the Wealden lakes and rivers. The hybodonts were here able to undergo a new adaptive radiation, analogous to their marine radiation at their first appearance in the Triassic. This radiation, taking place in the absence of other selachian competitors, is almost certainly responsible for the similarity between the Cretaceous freshwater selachian fauna and the Triassic marine fauna which emerges from a list of the species most resembling the Wealden forms. The high-crowned Wealden *Hybodus* species, *H. basanus*, *H. ensis* and *H. parvidens*, resemble similar forms which occur throughout the Triassic and Jurassic. The low-crowned *H. brevicostatus* is most like the larger Triassic *Polyacrodus* species and low-crowned Liassic *Hybodus* such as *H. delabechei*. *Lonchidion breve* resembles the Triassic *Lissodus* and Triassic teeth assigned to *Palaeobates*; *L. striatum* resembles the smaller Triassic *Polyacrodus* species; *L. heterodon* is another form resembling Triassic *Palaeobates*. *Lonchidion rhizion* and *Hylaeobatis* are the only entirely novel forms in the Wealden, the first apparently unique, the second leading on to the Upper Cretaceous ptychodonts. Other specialized Lower Cretaceous hybodonts include the ' hybodontoïde de position systematique indeterminée ' described by Casier (1961 : 18, pl. 3, figs. 3–6, text-figs. 2, 3) from the Congo, in which there is a very deep root with two large canals in the centre and a low, crescentic crown of *Acrodus*-like histological structure. This form, known by isolated teeth from a number of localities, is quite possibly another freshwater hybodont. It occurs in

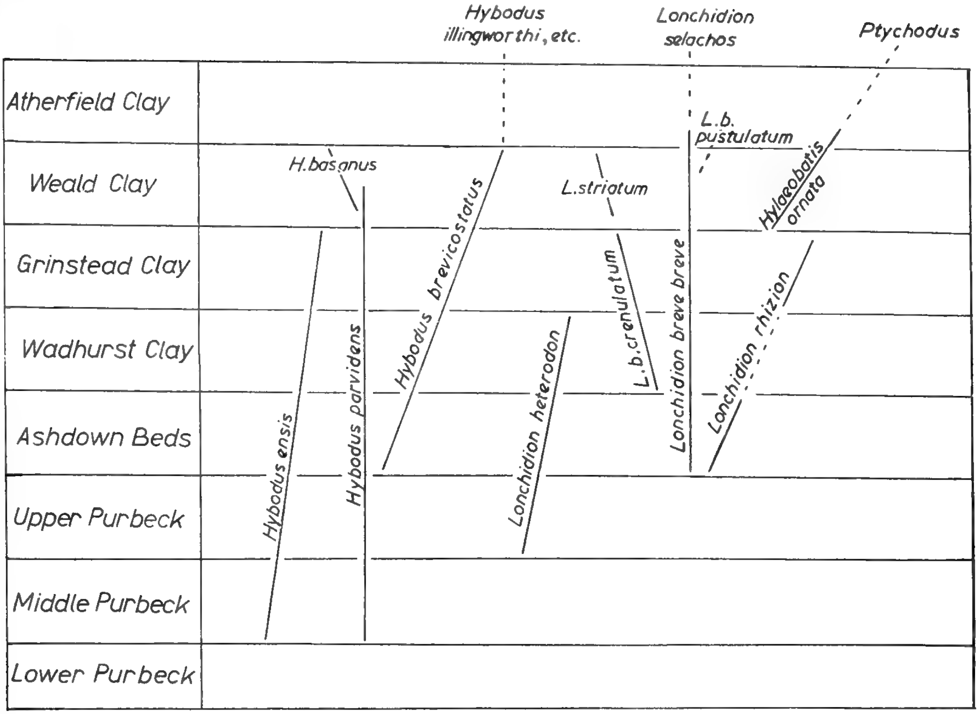


FIG. 31. Diagram showing the probable interrelationships of the sharks of the British Wealden and Purbeck and certain Upper Cretaceous species. Lines converging upwards indicate convergent evolution, lines converging downwards indicate phylogenetic relationship. Only those formations from which sharks are known are included.

beds of freshwater character (Casier 1961 : 73) which Casier finds to be marine largely because *Hybodus*, which he thought to be exclusively marine, is present (p. 77).

It seems probable that the hybodonts successful invasion of fresh water in the Lower Cretaceous was not permanent : some euryhalinity was retained, and in the Upper Wealden some of the more specialized forms were able not only to accommodate to the influx of salt water at the end of the Wealden, but to compete successfully with the more advanced selachians present in the sea. The last of the marine hybodontids (*Hybodus illingworthi*, *Acrodus dolloi*, etc., Cenomanian to Senonian) are probably derived from the Wealden *H. brevicostatus*, and the ptychodonts, highly successful and widely distributed in the Upper Cretaceous, seem to have evolved from near the Wealden *Hylaeobatis*.

Within the Wealden and Purbeck, fairly large samples of teeth from successive horizons give an unusually complete and well documented account of the evolution of the various species. These changes are summarized in Text-fig. 31, the details being given in the descriptions of the species. I have no doubt that this diagram is a gross simplification of the true picture, and that further sampling will produce additions to the fauna and to the complexity of the dendrogram.

This work has been made possible by those who have collected and presented the bulk of the new material described : Dr. K. A. Kermack and his colleagues at University College and Messrs J. F. Wyley, I. M. West, P. J. Whybrow and B. H. Newman. I am most grateful to all these gentlemen, in particular to Mr. Wyley for his careful collecting at Henfield and for allowing me to accompany him on visits to the pit. My thanks are also due to Dr. F. W. Anderson of H.M. Geological Survey, who has kindly examined samples of ostracods from Henfield, to Mr. H. A. Toombs for his help, and to Mr. P. J. Green, who took the photographs.

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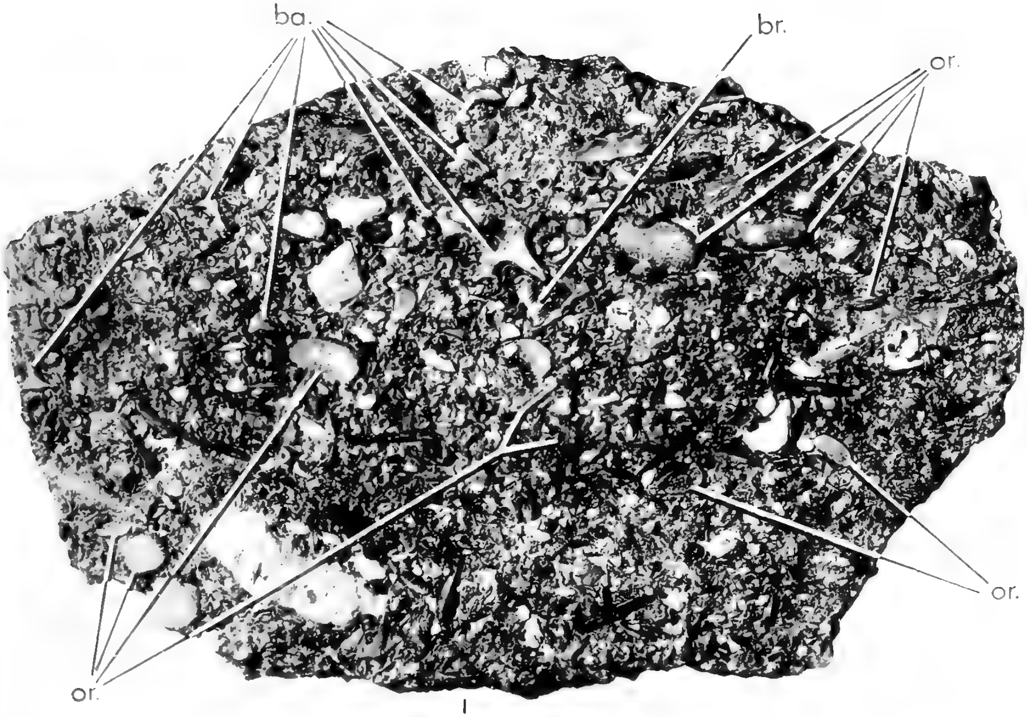
PLATE 1

FIG. 1. A block of bone-bed from the Weald Clay, Henfield Brick Co. pit, Henfield, Sussex. Teeth of *Hybodus basanus*, *H. brevicostatus* and *Hylaeobatis ornata* are indicated by ' ba.', ' br.' and ' or.' respectively. P.46920. × 1·5.

FIG. 2. *Caturus tenuidens* Smith Woodward. A fragment of right dentary in lateral view. Weald Clay; Henfield, Sussex. P.46837. × 4.

FIG. 3. *Hybodus brevicostatus* sp. nov. Upper anterior tooth in labial (*a*) and lingual (*b*) view. Wadhurst Clay; Hastings, Sussex. P.11876. × 3.



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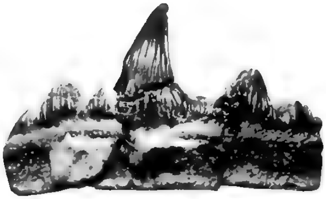


3a

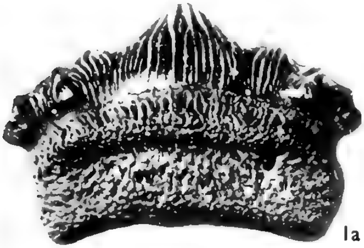
3b

PLATE 2

Hybodus brevicostatus sp. nov.

Teeth of the holotype, P.46973, Weald Clay; Henfield, Sussex. All ×4.

FIG. 1. Upper symphysial tooth in labial (*a*) and lingual (*b*) view.
FIG. 2. Tooth from the fifth file of the right upper jaw in labial (*a*) and occlusal (*b*) view.
FIG. 3. Tooth from the first file of the left lower jaw in labial (*a*) and occlusal (*b*) view.
FIG. 4. Tooth from the sixth file of the left lower jaw in labial (*a*) and lingual (*b*) view.
FIG. 5. Tooth from the eighth file of the left lower jaw in labial (*a*) and occlusal (*b*) view.
FIG. 6. Tooth from the ninth file of the left upper jaw in labial (*a*) and lingual (*b*) view.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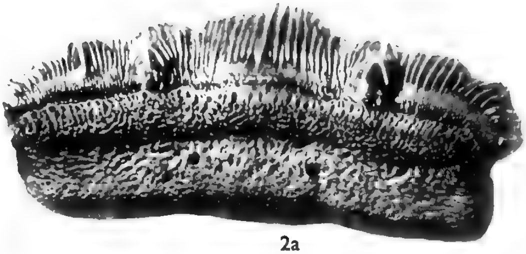
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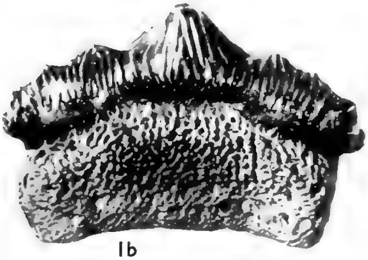
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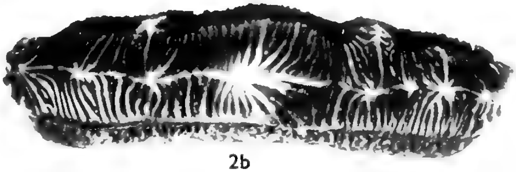
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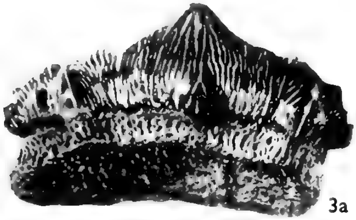
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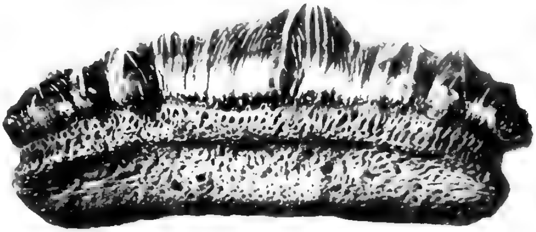
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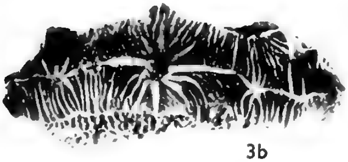
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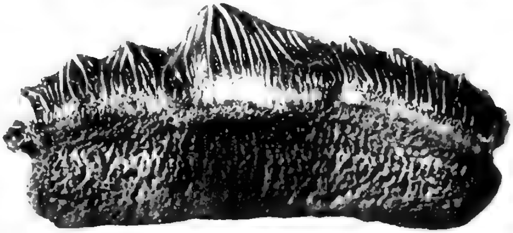
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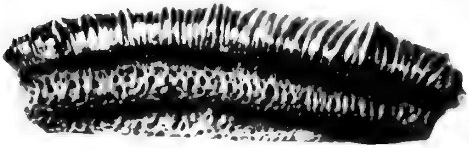
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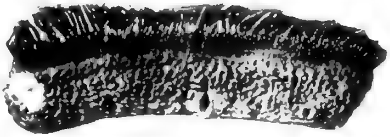
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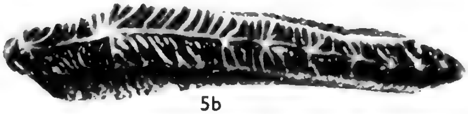
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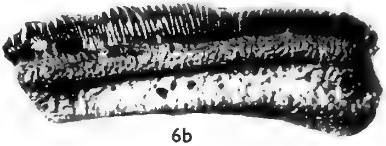
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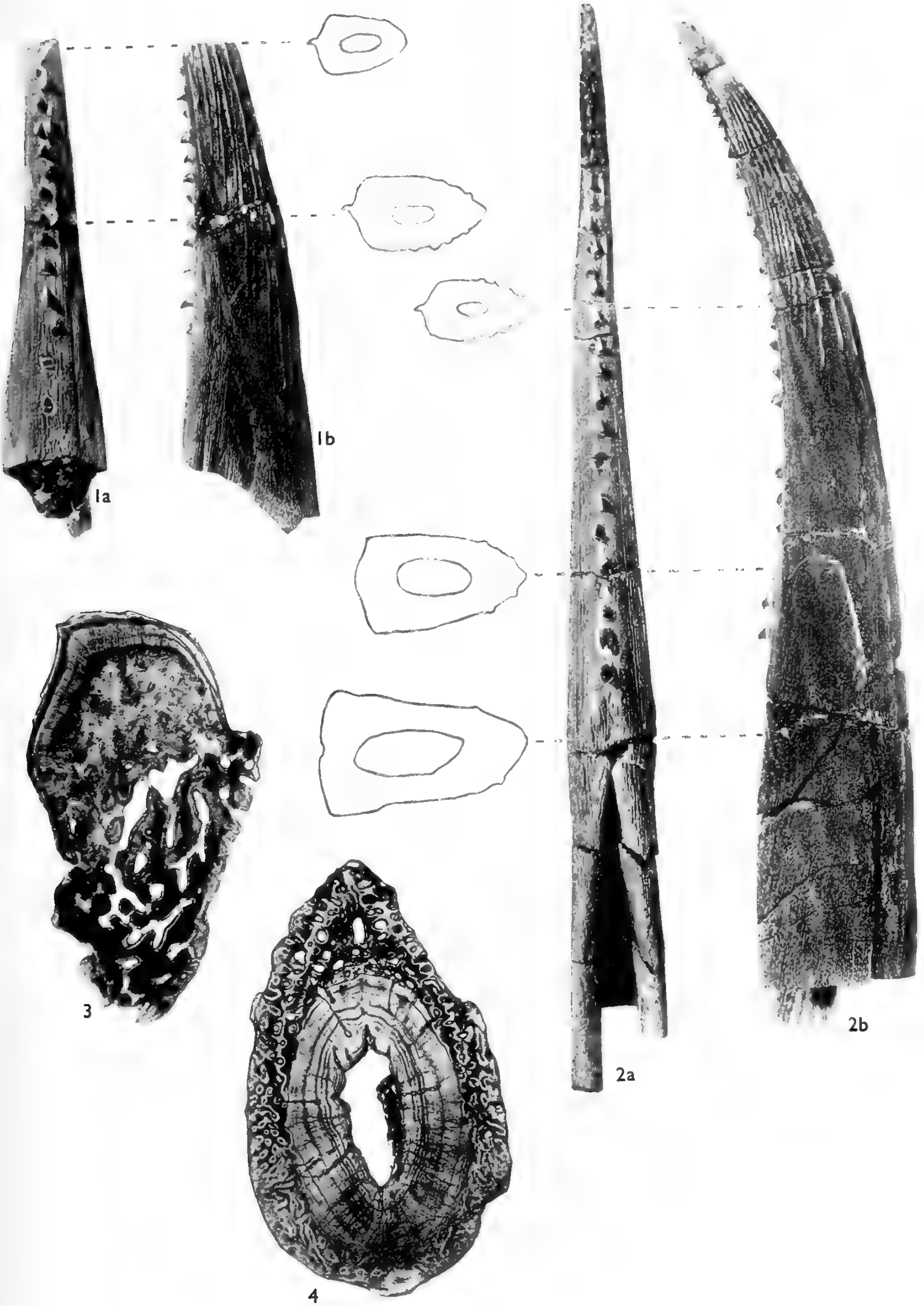
PLATE 3

FIGS. 1, 2. *Hybodus brevicostatus* sp. nov. Dorsal fin spines in posterior (*a*) and right lateral (*b*) view, natural size, with outline sections (× 1·5) at the points marked. Fig. 1, the holotype, P.46973, Weald Clay; Henfield, Sussex. Fig. 2, P. 13268, Wealden Shales (overlying *Hypsilophodon* Bed); Cowleaze Chine, Isle of Wight.

FIG. 3. *Hybodus brevicostatus* sp. nov. Thin section of a tooth from the holotype, P. 46973, Weald Clay; Henfield, Sussex. × 12.

FIG. 4. *Lonchidion* sp. Thin section of a dorsal fin spine, cut at the level marked in Text-fig. 26A. P.47208, Weald Clay; Henfield, Sussex. × 12.


1a
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4

PLATE 4

Hylaeobatis ornata (Smith Woodward)

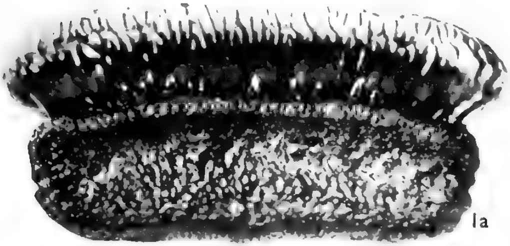
Teeth from the Weald Clay of Henfield, Sussex. ×5.

FIG. 1. Symphysial tooth in labial (*a*), occlusal (*b*), lingual (*c*) and lateral (*d*) view. P.47211.

FIG. 2. Parasymphysial (first paired file) tooth in labial (*a*) and lingual (*b*) view. P.47212.

FIG. 3. Antero-lateral (second paired file) tooth in labial (*a*), occlusal (*b*), lingual (*c*) and lateral (*d*) view. P.47213.

FIG. 4. Lateral tooth (probably fourth paired file) in labial (*a*), occlusal (*b*) and lingual (*c*) view. P.47214.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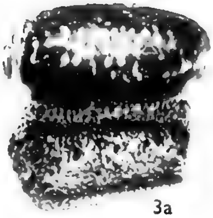
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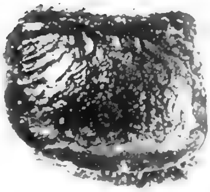
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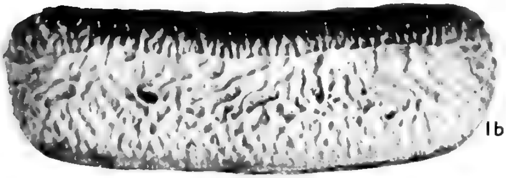
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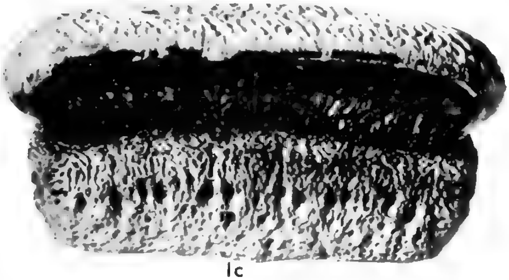
3d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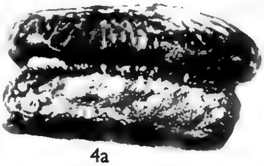
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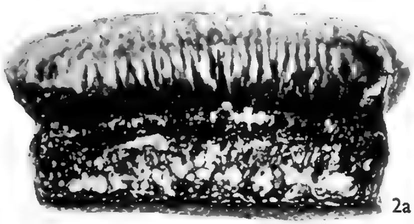
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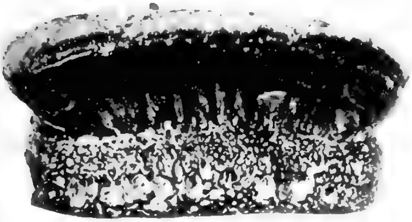
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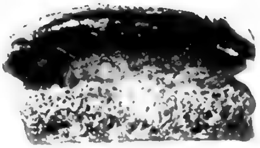
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PLATE 5

FIG. 1. *Polyacrodus minimus* (Agassiz). Vertical section of tooth crown. P.47271, Rhaetic ; Holwell, Frome, Somerset. × 30.

FIG. 2. *Palaeobates angustissimus* (Agassiz). Vertical section of tooth, P.47272, Muschelkalk ; Crailsheim, Germany. × 20.

FIG. 3. *Lonchidion breve breve* sp. & ssp. nov. Vertical section of tooth crown cut through the labial process. P.47275, Ashdown Beds, Cliff End bone-bed ; Cliff End, Sussex. × 50.

FIGS. 4, 5. *Hylaeobatis ornata* (Smith Woodward). Vertical sections of crowns of a parasymphysial tooth (Fig. 4, P.47276, × 20) and a posterior tooth (Fig. 5, P.47277, × 40), Weald Clay ; Henfield, Sussex.

FIGS. 6, 7. *Hylaeobatis ornata* (Smith Woodward). Teeth in labial (*a*), occlusal (*b*) and lingual (*c*) view, Weald Clay ; Henfield, Sussex. Fig. 6. Posterior tooth (probably eighth paired file), P.47216, × 10. Fig. 7. Postero-lateral tooth (probably sixth paired file), P.47215, × 5.


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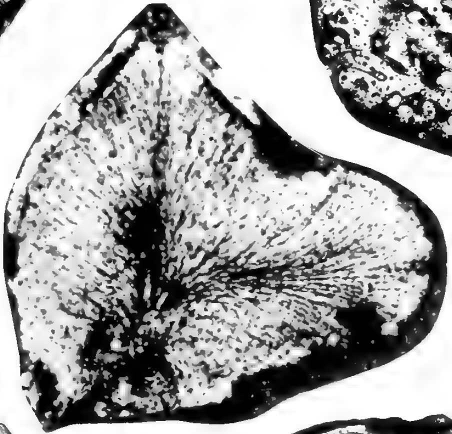
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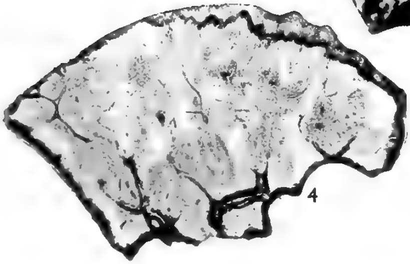
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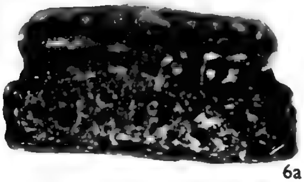
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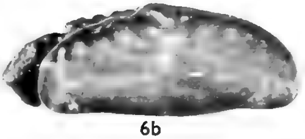
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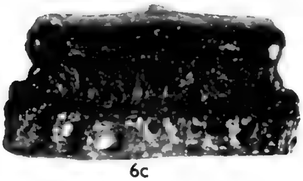
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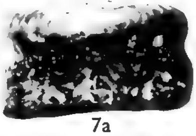
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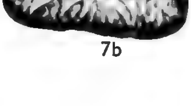
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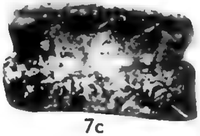
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O. NYBELIN

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GEOLOGY Vol. 11 No. 8
LONDON: 1966

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BY

ORVAR NYBELIN
(Professor, Natural History Museum, Gothenburg, Sweden)

Pp. 351–432 ; 15 *Plates* ; 16 *Text-figures*

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ON CERTAIN TRIASSIC AND LIASSIC REPRESENTATIVES OF THE FAMILY PHOLIDOPHORIDAE S. STR.

By ORVAR NYBELIN

SYNOPSIS

This paper is a revision, based mainly on the exoskeleton of the head and trunk, of a number of Upper Triassic and Liassic species formerly included in the genus *Pholidophorus* Agassiz. Special attention is paid to the shape of the preoperculum, the preopercular sensory canal and the squamation. Four species of *Pholidophorus*, including the type species, *Ph. bechei*, are redescribed. In the genus *Pholidophoroides* Woodward two species are redescribed. A new genus *Pholidophoropsis* is made for *Pholidophorus caudalis* Woodward and *Pholidophoropsis maculata* sp. nov. is described. A new genus and species, *Pholidolepis dorsetensis*, is made for part of the material previously included in *Ph. caudalis*. Relationships between the various species and genera of Pholidophoridae s. str., and between the Pholidophoridae and the Parasemionotidae and Leptolepidae are discussed.

I. INTRODUCTION

The fundamental requisite for any discussion regarding the origin of the teleostean fishes is a knowledge of the species belonging to the family Pholidophoridae. Because of the vague definition of the genus *Pholidophorus* Agassiz 1832 many varied species have been attributed to it with the result that it has become one of the most extensive holostean genera, obviously containing many heterogeneous elements of dubious affinity. Consequently a revision of the genus *Pholidophorus* has long been highly desirable.

In 1941 Woodward took up the question. Besides the genus *Pholidophorus* s. str., with *Ph. bechei* Agassiz as type species, he created three new genera : *Pholidophoroides* with *Ph. crenulatus* Egerton as type species and with *Ph. caudalis* Woodward as probably belonging to the same genus, *Pholidophoristion* with *Ph. ovatus* Agassiz as type species and *Ph. micronyx* Agassiz as second member, and *Ichthyokentema* for the two species *Ph. purbeckensis* Davies and *Ph. brevis* Davies. The last named genus has recently been treated in an excellent manner by Griffith & Patterson (1963), and its differences from *Pholidophorus* have proved to be so striking that a new family, Ichthyokentemidae, has been erected for it. The genera *Pholidophoroides* and *Pholidophoristion* have, however, not yet been thoroughly investigated and their validity consequently not proved.

A rather large number of specimens referred to the species *Ph. caudalis* Woodward and belonging to the British Museum (Natural History) attracted my attention because some of them showed a striking similarity to members of the genus *Leptolepis*. Because of this I have tried to study this material in more detail and have arrived at the conclusion that the specimens labelled as *Ph. caudalis* represent numerous different species. As *Ph. caudalis* was considered by Woodward as probably belonging to his new genus *Pholidophoroides* I have also found it necessary to take the type species *Ph. crenulatus* into consideration, and have tried to make a redescription of this species based on the excellent material in the British Museum (Natural History). From Woodward's (1895) description of *Pholidophorus limbatus* Agassiz it seemed to me not unlikely that the species could have some relationship to the genus *Pholidophoroides*. It is therefore included here.

A definition of the genus *Pholidophoroides* required a comparison with the type species of the genus *Pholidophorus*. It is, however, not obvious which species should be considered as the type species of this genus. The genus *Pholidophorus* was erected by Agassiz (1832) for the two species *Ph. latiusculus* and *Ph. pusillus* from the Upper Trias of Seefeld, Tyrol. The diagnoses for the genus and for the two species are rather scanty and meaningless : " *Pholidophorus* Ag. Häringsgestalt. Grosse rautenförmige Schuppen. Schwanzflosse ziemlich gleichlappig, indessen ziehen sich die Schuppen noch an den obern Lappen hinauf. Rückenflosse den Bauchflossen gegenüber. Afterflosse sehr klein.

" 1. *Ph. latiusculus* Ag. Grössere Schuppen. Im Verhältniss breiter als der folgende.

" 2. *Ph. pusillus* Ag. Beide von Seefeld in Tyrol. In der Sammlung meines Freundes Dr. *Alex. Braun*, und letztere auch im Museum in Carlsruhe."

In his later work Agassiz (1833, 2 : 9) mentions the genus *Pholidophorus* for the first time, with the following five species :

" 1. *Pholidophorus limbatus* Agass. Ecailles frangées à leur bord postérieur. Corps très-allongé. Lias : Lyme Regis.

" 2. *Pholidophorus dorsalis* Agass. Caractérisé par de longs chevrons sur le bord du premier rayon de la dorsale. Lias : Seefeld.

" 3. *Pholidophorus latiusculus* Agass. Plus court ; écailles plus grandes. Seefeld.

" 4. *Pholidophorus pusillus* Agass. Ecailles très-petites. Seefeld.

" 5. *Pholidophorus microps* Agass. Tête petite ; écailles en scie fine à leur bord postérieur, plus hautes que larges. Sohlenhofen."

A more exhaustive description of the genus and its twenty species follows on p. 271 of the same volume (1844) ; the first one treated is *Ph. bechei* Agassiz. *Ph. latiusculus* is only mentioned on p. 287 as the second species (after *Ph. dorsalis*) among those which were not figured for want of space but which the author intended to describe later on. The short note on *Ph. latiusculus* runs as follows : " Du lias de Seefeld et de Lyme Regis. Espèce très-voisine de la précédente, mais plus petite, ayant la dorsale moins reculée ; elle n'a guère que deux à trois pouces de long."

The first species ascribed to the genus *Pholidophorus* is thus *Ph. latiusculus*, but Agassiz never named a type species of the genus nor a holotype of *latiusculus*, and never gave a figure of it ; the diagnoses cited above are too meagre and meaningless to allow an exact identification of the species. In his treatment of the fossil fishes from the Upper Trias of Seefeld, Kner (1866) tried to identify the three *Pholidophorus* species *dorsalis*, *latiusculus*, and *pusillus*, but says regarding the proposed identification : " Ich hoffe hiedurch wenigstens anderen Paläontologen festere Anhaltspunkte zur Unterscheidung der Arten zu bieten und ihnen anschaulich zu machen, welche Formen mindestens mir den drei Arten von Agassiz zu entsprechen scheinen ; ob meine Deutung die richtige sei, darüber mögen sie selbst dann entscheiden." Woodward (1895) obviously accepted the identification proposed by Kner and I cannot find any objection to this.

Regarding the type species of the genus *Pholidophorus* Woodward did not choose the first named *latiusculus* but *bechei*, the first species described and figured by Agassiz (1837, 2, pl. 39, figs. 1–4 ; 1844, 2 : 272). Woodward (1895 : 450–451) gives a good diagnosis of the latter species, which has more recently been investigated by Miss Rayner (1941, 1948), who was, however, principally interested in the study of the endocranium ; her description of the exoskeletal cranial bones and the accompanying text-figures are thus rather schematic and do not allow a detailed comparison with other, closely related species. Consequently I have found it necessary to attempt a redescription and a new reconstruction of the exoskeletal cranial bones, based on some specimens belonging to the Department of Palaeontology, British Museum (Natural History).

The descriptions of *Ph. latiusculus* given by Kner (1866) and Woodward (1895) are also quite insufficient today. During a visit to Innsbruck in November 1963 I had the opportunity to see in the Univ.-Institut für Geologie und Paläontologie some specimens from Seefeld, identified as *Ph. latiusculus*, among them a rather well preserved specimen figured by Kner (1866, pl. 3, fig. 3). As *Ph. latiusculus* seems to be closely related to *Ph. bechei* I find it convenient to append a short description of this species also, partly based on the specimens loaned from Innsbruck, partly on specimens belonging to the British Museum (Natural History), as well as of another interesting species, *Pholidophorus caffii* Airaghi, the holotype of which has been kindly placed at my disposal by the Director of the Museo Civico di Scienze Naturali " E. Caffi ", Bergamo, Italy. The description of a specimen probably belonging to *Pholidophorus pusillus* has also been included.

Unless otherwise stated all the registered numbers given in the text refer to specimens in the British Museum (Natural History) collections.

II. SYSTEMATIC DESCRIPTIONS

Genus ***PHOLIDOPHORUS*** Agassiz

1832 *Pholidophorus* Agassiz : 145.

Preliminary diagnosis. Pholidophoridae of small to medium size. Exoskeletal cranial bones and scales with ganoin covering. Nasal well developed and well separated from its antimere by the frontals. Two well-developed supraorbitals. Maxillary not markedly stout and deep, posterior margin evenly rounded. Two supramaxillaries, overlapping dorsal margin of maxillary ; supramaxillary 2 without a marked process at antero-dorsal corner. Antorbital rather small ; five infraorbitals. Preoperculum with preopercular sensory canal running nearer to anterior than to posterior margin. Lower jaw not markedly deep, its greatest depth being in the posterior third of its length ; dentary with a smooth dental part, separated from ornamented splenial part by strong ridge. Dorsal fin above base of ventral fins. Fulcra present along anterior margin of at least dorsal, pectoral and ventral fins ; caudal fin hemi-heterocercal with dorsal and ventral margins fulcrated. Scales rather thick with articulating pegs and with their posterior margin smooth ; anterior lateral line scales much deeper than broad.

Type species. *Pholidophorus bechei* Agassiz.

Remarks. The diagnosis given above for the genus *Pholidophorus sensu stricto* must at present be regarded as a preliminary one, and this mainly for two reasons. Firstly, it is based on two species only, the type species of the genus and *Ph. latiusculus* Agassiz ; only after a thorough study of the remaining species earlier ascribed to *Pholidophorus* or at least of a good number of them, can the limits of this genus be made out and the common features of all its known species be established. Secondly, the present investigation only deals with external features, mainly the exoskeletal cranial bones ; an investigation of the endocranium and the visceral skeleton will undoubtedly reveal further characteristics of value for a definitive diagnosis.

Pholidophorus bechei Agassiz

(Pls. 1, 2, 3; Text-figs. 1, 2)

1837 *Pholidophorus bechei* Agassiz, **2**, pl. 39, figs. 1–4.
1837 *Pholidophorus onychius* Agassiz, **2**, pl. 39, figs. 5–7.
1844 *Pholidophorus bechei* Agassiz, **2**, 1 : 272.
1844 *Pholidophorus onychius* Agassiz, **2**, 1 : 274.
1895 *Pholidophorus bechei* Agassiz ; Woodward : 450, pl. 12, figs. 1, 2.
1941 *Pholidophorus* Rayner : 230, text-fig. 10.
1948 *Pholidophorus bechei* Agassiz ; Rayner : 318, pl. 21, fig. 45, text-figs. 24–29.
1963 *Pholidophorus bechei* Agassiz ; Griffith & Patterson : 31.

PRELIMINARY DIAGNOSIS. *Pholidophorus* of medium size, up to about 200 mm. in total length. Nasal very large, anteriorly rounded and reaching beyond the anterior tip of the frontal. Posterior margin of preoperculum deeply notched. Preopercular sensory canal with about 17–19 tubules.

HOLOTYPE. The first known specimen of this species is the one described and figured by de la Beche (1822) who, however, did not propose a scientific name for it ; according to Agassiz (1844, Vol. 2, pt. I : 273) this specimen was preserved in the collection of the Geological Society, London, but the specimen could not be found (March, 1965) in the collection of the Geological Survey Museum, London, where the British part of the Geological Society's collection is now housed. The specimen figured by Agassiz (1837, pl. 39, fig. 1) belonged at that time to Miss Philpot, Lyme Regis.

MATERIAL. The specimens used for the following description are Nos. 25276, 38107, 38109, 39859, P.154, P.1051, P.1052*d*, P.3586*c*, and P.3589*a*, all belonging to the British Museum (Natural History), London. Unfortunately they are all more or less defective, especially in the ethmoidal region.

DESCRIPTION. This species may attain a total length of about 200 mm. according to Woodward (1895 : 450), who also states that the length of the head with opercular apparatus is somewhat less than the maximum depth of the trunk and occupies one-fifth of the total length of the fish. As the main purpose of my investigation is to study the exoskeletal cranial bones of the type species of *Pholidophorus*, I have not examined the whole material in the British Museum (Natural History) but only some specimens showing these details. The largest of them, 25276, has a total length of about 164 mm., a standard length of about 140 mm. and a length of the head of about 37 mm., thus somewhat more than one-fifth of the total length (*ca.* 22·5%) and about one quarter of the standard length (*ca.* 26%). These values correspond rather well with those given by Woodward. Of the other larger specimens P.1051 is defective but seems to be a little larger than 25276, while P.1052*d* is a little smaller than that specimen. 38107 and 38109 have a standard length of 113 mm. and about 125 mm. respectively. The remaining three specimens are, however, much smaller with a standard length of about 80 mm. (P.3589*a*), 76 mm. (P.154), and 64 mm. (39859), respectively.

Regarding the exoskeletal cranial bones no differences of taxonomic value can be observed between the larger and the smaller specimens, as far as their preservation allows a comparison. There exists, however, a marked difference regarding the development of the ganoin layer on the cranial bones as well as on the scales. In the largest specimens (Pl. 2, fig. 3) there is a continuous, thick layer of ganoin, more or less richly ornamented, on all exposed parts of the exoskeletal cranial bones and all the scales are thick. In the smaller specimens (64–80 mm. standard length ; Pl. 2, figs. 1, 2) the ganoin covering is much thinner, on the exoskeletal cranial bones appearing as streaks, spots or small tuberculations, and the ganoin covering on the body scales seems to be remarkably thin in the anterior part of the body, gradually becoming thicker posteriorly. Even in 38107 (standard length 113 mm.) the scales on the anterior part of the body look thinner than in the posterior part. Perhaps this may be an indication of the beginning of the reduction of the ganoin covering which must have taken place in the phylogenetic development from the holostean to the teleostean stages of evolution.

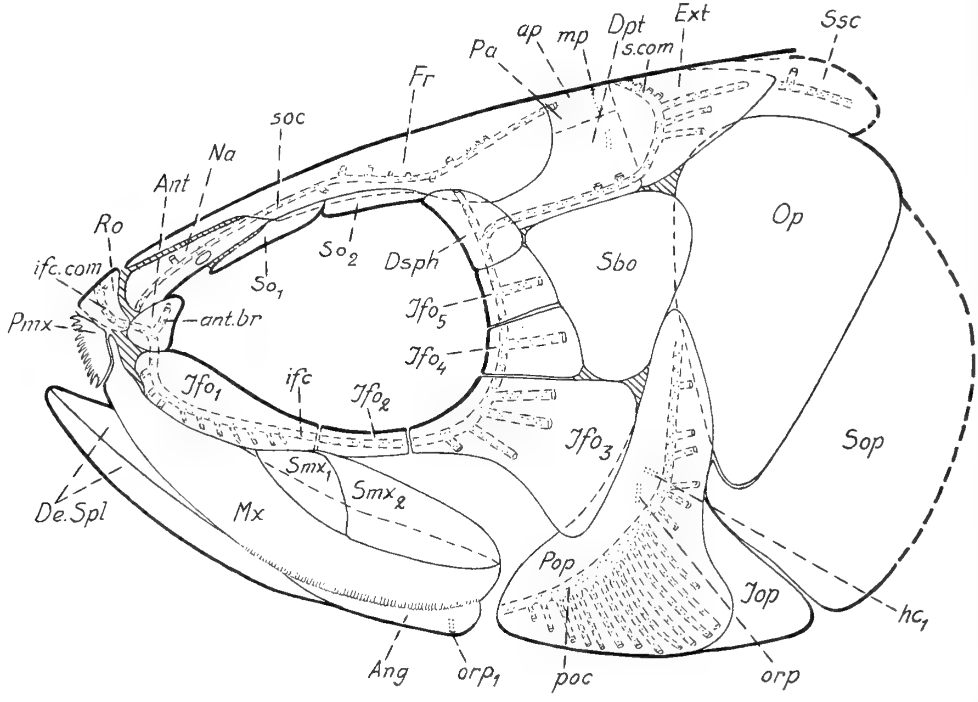

FIG. 1. *Pholidophorus bechei* Agassiz. Attempted restoration of head in lateral view. × 3.3. *Ang*, angular ; *Ant*, antorbital ; *De. Spl*, dentary ; *Dpt*, dermopterotic ; *Dsph*, dermosphenotic ; *Ext*, extrascapular ; *Fr*, frontal ; Ifo_1–Ifo_5, infraorbitals 1 to 5; *Iop*, interoperculum ; *Mx*, maxillary ; *Na*, nasal ; *Op*, operculum ; *Pa*, parietal ; *Pmx*, premaxillary ; *Pop*, preoperculum ; *Ro*, rostral ; *Sbo*, suborbital ; Smx_1, Smx_2, anterior and posterior supramaxillaries ; So_1, So_2, anterior and posterior supraorbitals ; *Sop*, suboperculum ; *Ssc*, suprascapula ; *ap*, anterior pit-line ; hc_1, anterior division of supramaxillary pit-line ; *ifc*, infraorbital sensory canal ; *ifc. com*, ethmoidal commissure ; *mp*, middle pit-line ; *orp*, postmaxillary pit-line ; orp_1, oral pit-line ; *poc*, preopercular sensory canal ; *s. com*, supratemporal commissure ; *soc*, supraorbital sensory canal.

Exoskeletal skull roof

The *premaxillary* (*Pmx*, Pl. 1 ; Pl. 2, figs. 1, 2 ; Pl. 3, figs. 3, 4 ; Text-fig. 1) has the form of an equilateral triangle with the dorsal margin almost straight, the postero-dorsal margin weakly S-shaped to fit the margin of the maxillary, and the antero-ventral margin a little convex and carrying a single row of 15 or more curved teeth. The slightly bulging outer surface carries a few ganoin tuberculations.

The *rostral* (*Ro*, Pl. 2, figs. 2, 3 ; Text-figs. 1, 2) is best preserved in the small specimen P.3589*a*. Its median, bulging part is ornamented with a few ganoin spots, its ventro-lateral parts are, however, very defective and nothing can be made out with accuracy regarding the outline of the bone. In P.1052*d* parts of the rostral can also be observed.

The *nasal* (*Na*, Pl. 2, figs. 1–3 ; Text-figs. 1, 2) is comparatively very large. Anteriorly it is evenly rounded ; in its posterior part it tapers gradually backwards. In the smallest specimen investigated, 39859, its lateral margin has an almost semicircular notch for the posterior nasal opening (Pl. 2, fig. 1), in the largest specimen P.1052*d*, this opening is entirely surrounded by the bone (Pl. 2, fig. 2) just as figured by Miss Rayner (1941, text-fig. 10). In these two specimens as well as in P.3589a the nasals of both sides are well separated by the anterior tip of the frontals ; nothing indicates that the nasals meet in the mid-line as figured by Miss Rayner. In the smallest specimen the dorsal surface of the nasal is quite smooth but in the two other specimens mentioned it is provided with a few ganoin spots, principally on the ridge indicating the course of the supraorbital sensory canal.

The *frontal* (*Fr*, Pl. 2, figs. 1–3 ; Text-figs. 1, 2) is pointed in its anterior part, mesial to the nasal, and from this region backwards it becomes progressively broader and has its broadest part posteriorly. Above the orbit the frontal margin is slightly concave, posterior to it the margin is almost straight and posteriorly directed. The postero-lateral corner of the frontal is rounded off and its posterior margin seems to be slightly wavy. The suture between the frontals of both sides is straight anteriorly but in the middle of its course it is irregularly sinuous, its path varying from specimen to specimen. The dorsal surface of the frontal is practically smooth in the smallest specimen (Pl. 2, fig. 1) ; in P.3589*a* there are smaller and larger, partly confluent ganoin spots (Pl. 2, fig. 2) and in the large specimen, P.1052*d*, the whole dorsal surface of the frontal is covered with ganoin forming radiating ridges of tuberculations on the lateral part of the anterior half of the bone (Pl. 2, fig. 3).

There are two well-developed *supraorbitals*. The anterior one, supraorbital 1 (So_1, Pl. 2, figs. 1–3 ; Text-figs. 1, 2), is situated in the angle between nasal and frontal ; its posterior half is rather broad and posteriorly rounded off, antero-laterally it tapers considerably. In the smallest specimen, 39859, its surface is smooth, in P.3589*a* and especially in the large specimen, P.1052*d*, the surface is ornamented with ganoin tuberculations. Posterior to supraorbital 1 there is an elongate supraorbital 2 in P.3589*a* (So_2, Pl. 2, fig. 3 ; Text-figs. 1, 2) ; its mesial margin is slightly convex, fitting the concave margin of the frontal, anteriorly its margin is concave, fitting the posteriorly rounded supraorbital 1 and posteriorly it tapers gradually. Its dorso-lateral surface is covered with a rather thick ganoin

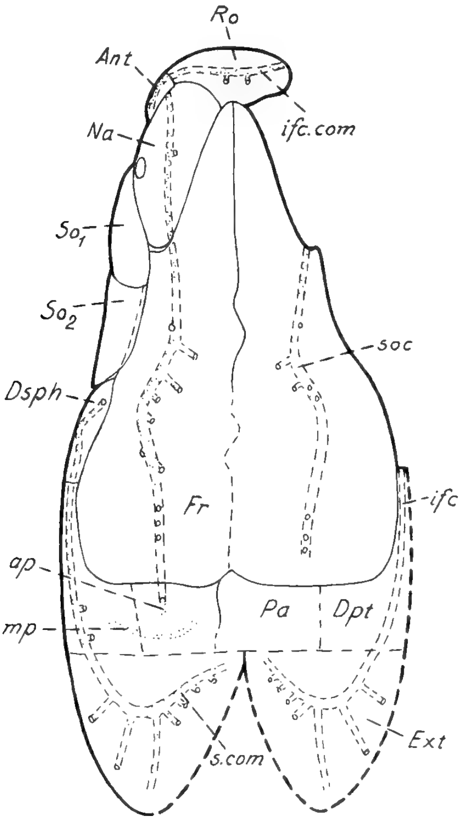

FIG. 2. *Pholidophorus bechei* Agassiz. Attempted restoration of head in dorsal view. × 3·3. Lettering as in Fig. 1.

layer. In P.1052*d* there is posterior to supraorbital 1 a small, rounded supraorbital 2; it seems not to be broken off posteriorly ; some bone fragments posterior to it may be other parts of the same bone, perhaps fragmented during an early stage in the ontogenetic development (*So*, Pl. 2, fig. 2).

The *dermosphenotic* (*Dsph*, Pl. 1 ; Pl. 2, fig. 2 ; Text-figs. 1, 2) is missing in most specimens, and in P.1052*d* only fragments of it are visible. In 38107, however, a rather well-preserved, roughly triangular dermosphenotic is present with its dorso-posterior margin convex and with its slightly concave and thickened anterior margin constituting the postero-dorsal border of the orbit.

The shape of the exposed surface of the *parietal* (*Pa*, Text-figs. 1, 2) is difficult to determine because of the poor preservation of this part of the skull roof, but it seems to be roughly square.

The *dermopterotic* (*Dpt*, Pl. 2, figs. 1–3 ; Text-figs. 1, 2) is comparatively narrow in its anterior part lateral to the posterior part of the frontal, but it broadens posterior to that bone on the dorsal surface of the skull, where it meets the parietal.

The *extrascapular* (*Ext*, Pl. 1; Pl. 2, fig. 2; Text-figs. 1, 2) is heavily crushed in all specimens investigated by me, but it seems to have the usual triangular shape.

Dermal bones of cheek and opercular apparatus

The *maxillary* (*Mx*, Pl. 1; Pl 2, figs. 1, 2; Pl. 3, figs. 3, 4; Text-fig. 1) is anteriorly pointed but it deepens ventrally, posterior to the premaxillary, so that a notch is formed for the premaxillary. The maxillary then becomes deeper with its greatest depth near its evenly rounded posterior margin; its ventral margin is evenly convex. The dorsal margin, on the whole slightly concave, is overlapped by infraorbital 1 (lachrymal) and the two supramaxillaries; anteriorly, at the deepening of the maxillary, its dorsal margin shows a shallow but marked concavity for the antero-ventral part of infraorbital 1. The lateral surface of the maxillary is ornamented with a longitudinal striation which is parallel to the dorsal and ventral margins in the larger specimens; however, in the smallest specimen, 39859, this ornamentation is only feebly marked (Pl. 2, fig. 1), in the somewhat larger specimens, P.154 and P.3589*a*, the ganoin streaks are broader and more irregularly arranged. Regarding the dentition along the ventral margin of the maxillary nothing can be said with accuracy because of the defective state of preservation; in 38107 and 38109 the posterior part of the ventral margin shows, however, some markings which suggest a feeble dentition, and in P.3589*a* the same part carries a delicate, comb-like dentition as in *Leptolepis*.

The two *supramaxillaries* (Smx_1, Smx_2, Pl. 1; Pl. 2, fig. 1; Pl. 3, fig. 4; Text-fig. 1) are situated dorsal to the posterior part of the maxillary, partly overlapping its dorsal margin. The anterior one, supramaxillary 1, is comparatively small and roughly semicircular with its ventral margin straight. Its lateral surface has a ganoin ornamentation of irregular patches in the smaller specimens; in the larger specimens they are confluent. In 38109 and P.1051 the anterior tip of the bone carries a well marked <-shaped crest parallel to its margins (Pl. 3, figs. 4, 5). The posteriorly situated supramaxillary 2 is much larger than supramaxillary 1 and almost triangular in shape with its greatest depth anteriorly; its ventral margin is straight, its dorsal margin convex, and its anterior margin concave to fit the convex margin of supramaxillary 1. Its antero-dorsal tip is slightly produced, and is apparently more pronounced in the smaller specimens. The lateral surface of supramaxillary 2 is ornamented with irregular ganoin spots in the smaller specimens: in the larger ones the entire surface is covered by a layer of ganoin with feebly marked tuberculations.

The six bones of the infraorbital series (antorbital—five infraorbitals) are rather well preserved.

The *antorbital* (*Ant*, Pl. 2, fig. 1; Pl. 3, fig. 2; Text-figs. 1, 2), well exposed in 25276, 39859 and P.3586*c*, is comparatively small, almost triangular in shape with the angles rounded off. Its anterior and ventral margins are slightly convex and its posterior margin is straight or moderately concave.

Infraorbital 1 (*lachrymal*) (Ifo_1, Pl. 2, fig. 1; Pl. 3, figs. 3–5; Text-fig. 1) is well preserved in 38109. It is elongate and deepest anteriorly. Its convex ventral margin has anteriorly a shallow notch, its postero-dorsal margin is not entirely visible but seems to be slightly concave.

Infraorbital 2 (Ifo_2, Pl. 1; Text-fig. 1), clearly visible in 38107, has the usual elongate shape with the dorsal margin slightly concave. The ventral margin is slightly convex.

Infraorbital 3 (Ifo_3, Pl. 1; Pl. 2, fig. 1; Text-fig. 1) is by far the largest bone in the series, stretching from the orbit to the anterior margin of the preoperculum, which it slightly overlaps. Its antero-dorsal and antero-ventral margins are concave, its dorsal margin is straight and its posterior margin is slightly convex.

Infraorbitals 4 and 5 (Ifo_4, Ifo_5, Pl. 1; Pl. 2, fig. 1; Text-fig. 1) are almost square with their anterior margins slightly concave and their posterior margins slightly convex. Infraorbital 5 is not entirely exposed in any of the specimens investigated but it seems to be a little smaller than infraorbital 4.

A comparatively large *suborbital* (*Sbo*, Pl. 1; Text-fig. 1) is situated posterior to infraorbitals 4 and 5 and seems to overlap the antero-dorsal part of the operculum. It is, however, generally crushed in the specimens available and in consequence of this, its outline can only be made out in part.

The *preoperculum* (*Pop*, Pl. 1; Pl. 2, figs. 1, 2; Pl. 3, figs. 4, 5; Text-fig. 1) has a very characteristic shape. The dorsal, almost vertical limb broadens continuously ventrally. The antero-ventrally directed limb is remarkably broad. The posterior margin of the bone is deeply notched below the angle between the two limbs, the postero-ventral corner projects backwards but is rounded off, not pointed as in Miss Rayner's reconstruction, the ventral margin is almost straight or slightly convex and the anterior margin shows a rather marked convexity below the middle of the bone.

The *operculum* (*Op*, Pl. 1; Pl. 2, fig. 1; Text-fig. 1) is roughly triangular; the straight anterior, vertical margin and the straight postero-ventral margin meet at a low angle, the dorsal margin is evenly rounded. The anterior margin seems to be a little thickened.

The *suboperculum* (*Sop*, Pl. 1; Pl. 3, figs. 4, 5; Text-fig. 1) is comparatively large, but it is not entirely preserved in any of the specimens investigated and consequently its outline cannot be made out with accuracy. The antero-dorsal process anterior to the ventral tip of the operculum is comparatively strong.

The posterior part of the *interoperculum* (*Iop*, Pl. 1; Pl. 3, figs. 4, 5; Text-fig. 1) is well exposed in 38107, 38109, and P.1051; its anterior part is not visible in any of the specimens investigated.

Branchiostegal rays and gular plate

Branchiostegal rays are exposed in 38107, 38109, and P.1051. In 38107 there are at least 12 branchiostegal rays on the right side (*R. Br*, Pl. 1), in P.1051 at least 13 rays may be distinguished, the six anterior ones still attached to the large ceratohyal 2 (Ch_2, Pl. 3, fig. 5), which is unfenestrated but provided with a deep groove for the hyoid artery.

An elongate, anteriorly keeled, detached but not entirely exposed bone in P.3589*a* may be interpreted as the *gular plate* (*Gu*, Pl. 3, fig. 1). A fragment of a gular plate is probably visible also in P.154.

Lower jaw

The lower jaw is more or less exposed in most specimens; in P.1051 it is almost entirely free from overlying bones (Pl. 3, fig. 5); it is a little defective but the outline of the defective parts can be followed through the impression in the rock.

The dental and splenial parts of the *dentary* (*De. Spl*, Pl. 1; Pl. 2, figs. 1, 2; Pl. 3, figs. 4, 5; Text-fig. 1) are separated by a prominent ridge on the lateral surface of the bone; the anterior part of its dorsal margin is only gently ascending; at about the limit between the first and second third of the length of the lower jaw the dorsal margin of the dentary is abruptly thickened and ascends postero-dorsally. The boundary between the dentary and the angulo-supra-angular cannot be made out. The lateral surface of the splenial part is ornamented with thick striations and rugosities, whereas that of the dental part is quite smooth. In 38109 there are, as already stated by Miss Rayner (1948 : 319), some delicate teeth a little distance from the anterior tip of the dentary (Pl. 3, fig. 4); as far as I can see there are seven.

The *angulo-supra-angular* (*Ang*, Pl. 1; Pl. 2, fig. 1; Pl. 3, figs. 4, 5) constitutes the posterior part of the lower jaw; its depth equals about one-third of the length of the jaw. The lateral surface of the angulo-supra-angular has ventrally a conspicuous ganoin ornamentation.

No true dermarticular can be seen. The *articular* (*Art*, Pl. 1; Pl. 2, fig. 1; Pl. 3, figs. 4, 5) is partly visible in 38109.

Sensory canal system of head

The sensory canal system of the head is well developed, but because of the bad state of preservation of certain bones it cannot be described in every detail; in particular the lack of a specimen with the bones of the snout in natural position makes the interpretation uncertain.

The *supraorbital sensory canal* (*soc*, Pl. 2, fig. 1; Text-figs. 1, 2) pierces the nasal, the frontal and the parietal.

The nasal part of the canal is clearly visible in 39859, P.1052*d* (Pl. 2, fig. 3), and P.3589*a* (Pl. 2, fig. 2); it runs in a gentle arch from the antero-lateral to the postero-mesial margin of the bone, where it enters the frontal. In the large specimen, P.1052*d*, there is a single pore visible on the dorso-mesial side of the canal a little anterior to the fenestra for the nostril. In the smaller specimen, P.3589*a*, a corresponding pore may be traced on the dorso-lateral side of the canal; in the smallest specimen no pores can be observed.

The frontal part of the supraorbital sensory canal is very difficult to see because of the crushed state of the frontal in all specimens at my disposal. In the anterior part of the bone it runs, however, at first almost directly backwards, then it curves postero-laterally parallel to the lateral margin of the frontal and finally continues postero-mesially to the posterior margin of the bone. Pores or short tubules can only be observed in P.1052*d*, and there the state of preservation does not allow any certain conclusions. According to Rayner (1948) there is great variability regarding the number and position of tubules and pores in this part of the supraorbital sensory canal ; my interpretation of the arrangement in P.1052*d* is given in Text-figs. 1, 2. On the left side where the canal can be followed practically without interruption, except for its hindmost part, I have observed only a single short, laterally directed tubule in the posterior part of the anterior straight course of the canal ; at the curve there issue two somewhat longer, postero-mesially directed tubules from the mesial side of the canal and behind them two very short tubules on the same side of the canal ; on the postero-mesially directed part of the canal there are five very short tubules or pores. On the right side, where the canal is more defective, the tubules and pores seem to have on the whole the same arrangement, as far as they are discernible.

The parietal part of the supraorbital sensory canal is visible on the left parietal ; the canal itself is very short, apparently without tubules or pores. It continues backwards as a well-marked groove, the anterior pit-line (*ap*, Pl. 2, fig. 2 ; Text-figs. 1, 2).

The *infraorbital sensory canals* (*ifc*, Pl. 3, fig. 4 ; Text-figs. 1, 2) of both sides are joined anteriorly by a slightly arched ethmoidal commissure in the rostral. In P.1052*d* a short, posteriorly directed tubule can be seen on each side of the mid-line of the bone.

The small antorbital contains in its ventral half the curved anterior part of the infraorbital sensory canal. From its convex dorsal side the canal gives off a short antorbital branch, ending with a comparatively large pore ; no more pores can be observed on this part of the canal except in 25276, where a pore seems to be present at the anterior angle between the canal and the antorbital branch (Pl. 3, fig. 2). According to Rayner (1941, text-fig. 10B ; 1948, text-fig. 25) the antorbital branch joins the supraorbital sensory canal " to form a closed circuit around the eye ". I cannot, however, share this opinion. As already mentioned above no specimen seen by me has the exoskeletal bones of the snout preserved in natural articulation, but when trying to reconstruct this part of the skull I have not been able to arrive at a solution other than that given in Text-fig. 1. Only much better preserved material regarding the mutual position of the bones in question can decide which solution is correct.

Passing into infraorbital 1 (lachrymal) the infraorbital sensory canal pierces this bone on the whole parallel to its convex anterior and ventral margins. Judging from 38109 (Pl. 3, fig. 4) the canal gives off from its anterior side three short, antero-ventrally directed tubules and from its ventral side at least seven ventrally to postero-ventrally directed tubules, the middle ones being the largest ; as the bone is apparently not complete in its posteriormost part there might, consequently, exist one or more tubules in infraorbital 1 in addition to the ten observed by me.

In infraorbital 2, only preserved in 38107, the sensory canal is not visible.

In infraorbital 3 the sensory canal runs parallel to the concave anterior margin of the bone. In P.154 it gives off two postero-ventrally directed tubules, the anterior one rather short, and two posteriorly directed tubules. In 38107 there seem to be only three tubules, only one of them posteriorly directed ; in the other specimens the state of preservation does not allow any observations regarding the tubules.

In infraorbitals 4 and 5 the sensory canal gives off a single, posteriorly directed tubule in each bone.

In the dermosphenotic, well preserved in 38107, the infraorbital sensory canal curves posteriorly ; from its convex dorsal side the canal gives off a rather wide, dorsally directed tubule, ending in a pore ; this pore is also visible on the defective dermosphenotic in P.1052*d*.

From the dermosphenotic the canal enters the dermopterotic, piercing it along its lateral margin. To what extent the canal in the dermopterotic belongs to the sensory canal system of the head and to the cephalic division of the main lateral line, respectively, must be left unanswered. Judging from P.3589*a* the posterior part of the canal gives off two dorsally directed short tubules, and the preopercular sensory canal seems to issue at the postero-lateral corner of the bone.

Cephalic division of main lateral line

A well-marked middle pit-line is visible in P.1052*d* on the left parietal posterior to the anterior pit-line ; it extends laterally over the broad posterior part of the dermopterotic.

The cephalic division of the main lateral line passes over from the dermopterotic into the extrascapular, where it gives off mesially the supratemporal commissure, and continues posteriorly into the suprascapular. Because of the preservation of the extrascapular the canal and its tubules can be only partly observed ; in P.1052*d* two rather long tubules are given off from the lateral side of the canal, and at least four short tubules issue from the posterior side of the supratemporal commissure. In 38107 also, four short tubules are given off from the posterior side of the supratemporal commissure decreasing in length mesially, but in this specimen only one large tubule can be observed with accuracy lateral to the main canal.

The *preopercular sensory canal* runs on the whole parallel to the curved anterior margin of the preoperculum, about midway between its anterior and posterior margins in the dorsal limb but decidedly nearer to its anterior margin in its antero-ventral limb. From its posterior side the canal gives off a series of tubules the number and arrangement of which are difficult to determine with precision in the largest specimens because of the thickness of the bone, especially in the dorsal limb of the bone ; in the small specimens the preoperculum is too defective to allow any detailed analysis of number and position of the tubules, but their arrangement seems to be generally the same as in the larger specimens. In the antero-ventral limb of the preoperculum there are in 25276, 38107, and 38109 thirteen postero-ventrally directed, curved tubules increasing in length from the anterior small one to the twelfth ; the thirteenth tubule is shorter and does not reach the postero-lateral margin of the bone. In P.1051 there is the same characteristic arrangement of the tubules, but their number cannot be counted with accuracy. Dorsal to this group of tubules the tubules are shorter and seem to vary a little in number and position. 25276 clearly shows six rather short tubules, in 38109 only five tubules can be observed, but the dorsalmost part of the bone is defective ; in 38107 and P.154 at least 4 short tubules are present, but also here their exact number is difficult to determine. In P.1051, in which the preoperculum is remarkably thick and, moreover, broken in its dorsal part, only three short tubules can be seen. The real number of small tubules in the dorsal part of the preoperculum may be estimated as five or six and the total number of tubules belonging to the preopercular sensory canal may consequently be given as 18–19.

On the lateral surface of the preoperculum at about its middle and anterior to the preopercular sensory canal two short grooves are clearly visible in most specimens, the dorsal one more or less horizontal, the ventral one on the whole vertical. It seems most likely that the horizontal groove represents the posterior portion of the anterior division of the supramaxillary line and the vertical one the post-maxillary line according to the nomenclature proposed by Stensiö (1947). In P.154, however, no supramaxillary line can be observed on the preoperculum, but on infraorbital 3 an oblique groove is present, which may be interpreted as the anterior portion of the anterior division of the supramaxillary line. This difference in the development of the supramaxillary line may merely be an individual variation rather than a feature of taxonomic importance.

The *mandibular sensory canal* and its tubules are not visible, only the openings of some separate tubules may be observed, but their total number cannot be determined.

In the largest specimen investigated, 25276, as well as in the small specimens 39859 and P.154, there is a small vertical groove on the lateral surface of the angular near its ventral margin ; this groove obviously represents the oral line according to Stensiö (1947).

Exoskeletal shoulder girdle and squamation

The *suprascapula* (*Ssc*, Pl. 1) is partly visible in 38107 and P.1052*d*, but in neither case can its outline be determined ; it is, however, a rather large bone. In 38107 a smaller, reniform bone postero-ventral to the suprascapula may be the *supracleithrum*, but no sensory canal can be observed in it.

The *cleithrum* is only to a small extent exposed in the material studied by me and no description can be given.

The *scales* are, according to Woodward (1895), arranged in approximately 40 transverse rows ; in none of the specimens seen by me is the squamation uninterrupted but in 38107 there may be about 45 transverse rows reckoned from the posterior margin of the operculum to the middle of the caudal fin. On the body there are about four longitudinal rows of scales which are deeper than broad, the lateral line scales being the deepest. All scales have an even posterior margin.

Lateral line

The parts of the lateral line piercing the suprascapula and the supracleithrum are not visible in any of the specimens exhibiting these bones, and in the supracleithrum no tubules can be observed. In the suprascapula two rather wide tubules are clearly visible, the anterior one mesially, the posterior one postero-mesially directed.

The lateral line runs almost straight along the sides of body and tail, ending at the base of the middle caudal rays. Each lateral line scale has a pore at about the middle of its lateral surface.

Paired and unpaired fins

The fins are as a rule more or less defective in all specimens investigated by me and consequently little can be added in this respect to the facts given by Woodward (1895 : 451).

The *pectoral fin* seems to be of moderate size and with a moderate number of lepidotrichia, about 18 according to my counts, i.e. the same number as given by Woodward for the pectoral. The first lepidotrichium is rather stout and is provided with some fulcra.

The *ventral fin* has a rather high number of lepidotrichia, about 14 or 15 (14 according to Woodward), the innermost ones rather delicate and branched almost to their bases. The first two lepidotrichia are comparatively short and undivided, the third one (the first branched lepidotrichium) carries some fulcra.

The *dorsal fin* has, according to Woodward, about 12 lepidotrichia ; in my material no dorsal fin is complete. In P.154 the anterior part of the fin is rather well preserved and shows anteriorly three undivided lepidotrichia followed by a long divided lepidotrichium with few but rather long fulcra.

Regarding the *anal fin* Woodward gives no number of lepidotrichia, and in my material all anal fins are damaged and incomplete. On none of them have I observed any traces of fulcra, but as Woodward mentions the presence of fulcra on all fins, he must have seen some on the anal fin also.

The *caudal fin* is hemi-heterocercal and provided with densely set fulcra on its dorsal as well as on its ventral margin.

REMARKS. Woodward (1895 : 450) considers *Ph. onychius* Agassiz to be identical with *Ph. bechei*. I have had no opportunity to see the holotype of *Ph. onychius*, belonging to the Oxford Museum, but 38109, originally labelled as *Ph. onychius* is, as far as I can see, in all respects a quite typical *Ph. bechei*, which supports Woodward's opinion.

HORIZON AND LOCALITY. Lower Lias ; Lyme Regis, Dorset.

Pholidophorus latiusculus Agassiz

(Pl. 4; Pl. 5; Pl. 15, figs. 1, 2, 6, 7; Text-figs. 3, 4)

1832 *Pholidophorus latiusculus* Agassiz : 145.
1833 *Pholidophorus latiusculus* Agassiz; Agassiz, **2** : 9.
1844 *Pholidophorus latiusculus* Agassiz; Agassiz, **2**, 1 : 271, 287.
1866 *Pholidophorus latiusculus* Agassiz; Kner : 328, pl. 3, figs. 2, 3.
1867 *Pholidophorus latiusculus* Agassiz; Kner : 903, pl. 2, fig. 1.
1895 *Pholidophorus latiusculus* Agassiz; (*partim*?) Woodward : 454, ? pl. 14, fig. 3.

PRELIMINARY DIAGNOSIS. *Pholidophorus* of small size, up to about 85 mm. in total length. Nasal not very large, anteriorly pointed. Posterior margin of preoperculum with a shallow notch. Preopercular sensory canal with about 14–15 tubules.

NEOTYPE. As already mentioned in the introduction, Agassiz did not name a holotype for this species. A species with this name is, however, described and figured by Kner (1866); the best preserved of his specimens, figured on Pl. 15, fig. 2, is still present in the collections of the Univ. Institut für Geologie und Paläontologie, Innsbruck, Austria, and may conveniently be chosen as neotype of *Pholidophorus latiusculus*. The correctness of the identification is beyond doubt as can be seen by a comparison between the figure given by Kner (represented on Pl. 15, fig. 1) and a photograph in natural size of the same specimen (Pl. 15, fig. 2).

MATERIAL. The description given below is based on the following specimens: Three specimens, F.123 (neotype), Lit. F and No. 1028, all belonging to the Univ. Institut für Geologie und Paläontologie, Innsbruck, and two specimens, 33987 (in counterpart) and P.1063, both belonging to the Department of Palaeontology, British Museum (Natural History); further, a rather disarticulated specimen, P.11780, showing a number of scales and some isolated cranial bones may also belong to this species or perhaps to *Ph.* cf. *pusillus*.

DESCRIPTION. All the specimens, except P.11780, show the same characteristic shape, with the head and forepart of the body bent dorsally. The three Innsbruck specimens are of about the same size with a length without caudal (standard length) of *ca.* 75 mm.; in the neotype the caudal fin is defective, in the two other specimens the caudal fin has a length of *ca.* 10 mm.; the total length may consequently attain *ca.* 85 mm. Specimens 33987 and P.1063 are smaller; the first with a total length of *ca.* 75 mm. and a standard length of *ca.* 65 mm., P.1063 with a standard length of *ca.* 57 mm. The greatest depth of the body cannot be given as all specimens are more or less flattened through pressure. The length of the head seems to be roughly one quarter of the standard length.

Exoskeletal skull roof

The snout region is defective in all specimens available and the premaxillary and rostral bones are missing.

The *nasal* (*Na*, Pl. 4; Pl. 5, fig. 1; Text-figs. 3, 4) is preserved only in the neotype and in P.1063; it is comparatively large but its anterior part is pointed, not broadly

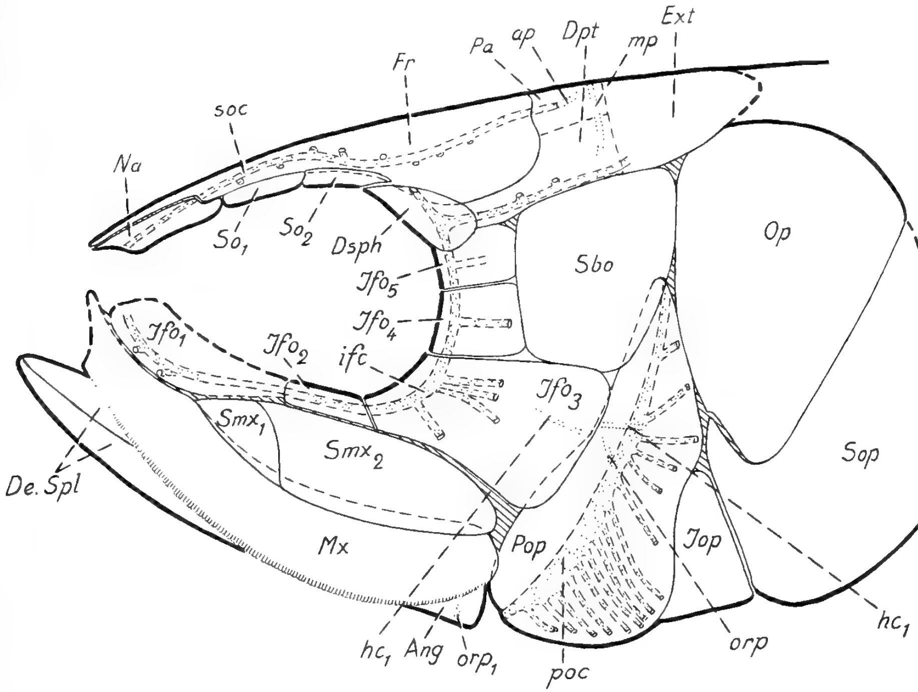

FIG. 3. *Pholidophorus latiusculus* Agassiz. Attempted restoration of head in lateral view. ×7 approx.

Ang, angular ; *De. Spl*, dentary ; *Dpt*, dermopterotic ; *Dsph*, dermosphenotic ; *Ext*, extrascapular ; *Fr*, frontal ; *Ifo*$_1$–*Ifo*$_5$, infraorbitals 1 to 5 ; *Iop*, interoperculum ; *Mx*, maxillary ; *Na*, nasal ; *Op*, operculum ; *Pa*, parietal ; *Pop*, preoperculum ; *Sbo*, suborbital ; *Smx*$_1$, *Smx*$_2$, anterior and posterior supramaxillaries ; *So*$_1$, *So*$_2$, anterior and posterior supraorbitals ; *Sop*, suboperculum ; *ap*, anterior pit-line ; *hc*$_1$, anterior division of supramaxillary pit-line ; *ifc*, infraorbital sensory canal ; *mp*, middle pit-line ; *orp*, postmaxillary pit-line ; *orp*$_1$, oral pit-line ; *poc*, preopercular sensory canal ; *soc*, supraorbital sensory canal.

rounded as in *Ph. bechei* and the bone is not pierced by the posterior nasal opening. Its dorso-lateral surface is ornamented with irregular streaks and tuberculations.

The *frontal* (*Fr*, Pl. 4 ; Pl. 5, figs. 1, 2 ; Text-figs. 3, 4) has on the whole the same shape as in *Ph. bechei*, but its anterior part, mesial to the nasal, seems to be comparatively more slender. As in that species the suture between the frontals of both sides is straight anteriorly but in the middle of its course somewhat sinuous ; in P.1063 (Pl. 5, fig. 1) it curves at first a little to the left, then to the right and then again to the left. The entire dorsal surface of the frontal carries small ganoin rugosities which form low radiating ridges in its antero-lateral part.

The two *supraorbitals* (*So*$_1$, *So*$_2$, Pl. 4 ; Pl. 5, fig. 1 ; Text-figs. 3, 4) are of about the same size. The anterior one, supraorbital 1, is situated posterior to the nasal ; in P.1063 its anterior part is hidden below the posterior part of the nasal, but judging from the neotype its anterior part is rounded off, not drawn out into an antero-lateral projection as in *Ph. bechei*. The mesial margin of supraorbital 2 slightly overlaps the lateral margin of the frontal; posteriorly its lateral margin is concave, fitting the antero-dorsal margin of the dermosphenotic. Both supraorbitals are ornamented with low ganoin ridges and rugosities.

The *dermosphenotic* (*Dsph*, Pl. 5, fig. 1; Text-figs. 3, 4) is, judging from P.1063, a rather small bone, pointed anteriorly and rounded posteriorly with its dorsal margin a little convex and its antero-ventral margin a little concave.

The *parietal* (*Pa*, Pl. 5, fig. 1; Text-figs. 3, 4) and the *dermopterotic* (*Dpt*, Pl. 4; Pl. 5, figs. 1, 2; Text-figs. 3, 4) cannot be described in detail because of the bad state of preservation which does not allow a determination of their boundaries.

Only the lateral part of the *extrascapular* is preserved in P.1063 (*Ext*, Pl. 5, fig. 1). Apparently it is pushed over the posterior part of the dermopterotic, and consequently nothing can be made out with regard to its general shape.

Dermal bones of cheek and opercular apparatus

The *maxillary* (*Mx*, Pl. 4; Pl. 5, fig. 1; Text-fig. 3) is defective in all specimens but to judge from 33987 it is pointed anteriorly, rather as in *Ph. bechei*, and then deepens with its deepest part at its posterior rounded end. Its dorsal margin is slightly concave and is overlapped by infraorbital 1 (lachrymal) and the two supramaxillaries. The lateral surface of the maxillary is provided with a dense longitudinal striation. Along the whole slightly convex ventral margin there is a feeble dentition like that in *Leptolepis*.

The two *supramaxillaries* (Smx_1, Smx_2, Pl. 4; Pl. 5, fig. 1; Text-fig. 3) overlap the posterior part of the dorsal margin of the maxillary. The anterior one, supramaxillary 1, best preserved in the neotype (Pl. 4), is comparatively small, semicircular to almost triangular in shape; its lateral surface is ornamented with well-marked concentric ridges or streaks. Among the few cranial bones preserved in P.11780 there is a small semi-circular bone with a marked striation, which agrees rather well with supramaxillary 1 in the neotype. Supramaxillary 2 is fairly large and elongate with its dorsal and ventral margins slightly convex; posteriorly it is rounded off; its antero-ventral margin is concave, fitting the postero-dorsal margin of supramaxillary 1. The antero-dorsal tip of supramaxillary 2 is slightly thickened but not markedly produced. Its lateral surface is ornamented with numerous well-marked striations running parallel to its dorsal and ventral margins; they are partly confluent in the middle of the bone.

Unfortunately, of the bones of the infraorbital series, the antorbital is missing in all specimens investigated.

Infraorbital 1 (*lachrymal*) (Ifo_1, Text-fig. 3) is present only in 33987 and there only as a fragment of its anterior part; nothing therefore can be made out with regard to its general shape.

Infraorbital 2 (Ifo_2, Pl. 5, fig. 1; Text-fig. 3) is preserved in P.1063; it is, as usual, a small elongate bone which is situated below the orbit; its posterior margin is postero-ventrally directed.

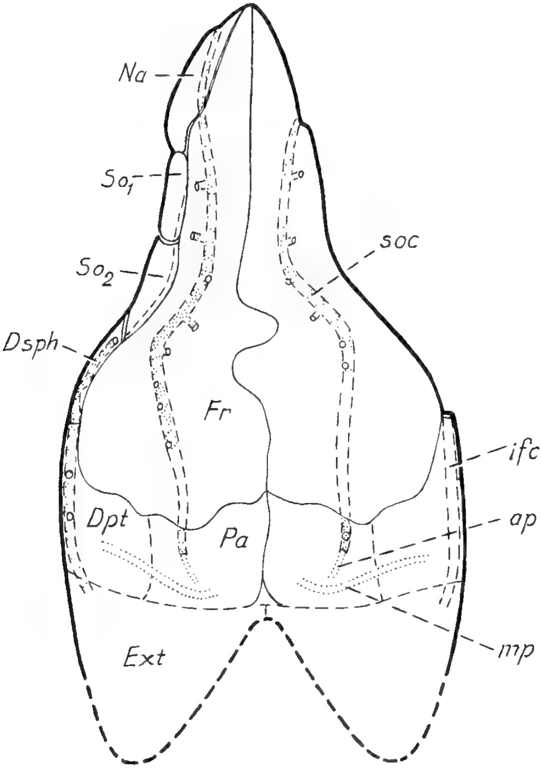

FIG. 4. *Pholidophorus latiusculus* Agassiz. Attempted restoration of head in dorsal view (possibly somewhat flattened). ×7 approx. Lettering as in Fig. 3.

Infraorbital 3 (*Ifo*$_3$, Pl. 4; Pl. 5, figs. 1, 3; Text-fig. 3) stretches from the orbit to the anterior margin of the preoperculum, which it overlaps as in *Ph. bechei*; its general shape is also almost as in that species.

Infraorbital 4 (*Ifo*$_4$, Pl. 4; Pl. 5, figs. 1, 3; Text-fig. 3) has its anterior, dorsal and ventral margins almost straight whereas its posterior margin is slightly convex; it is about half as broad as infraorbital 3.

Infraorbital 5 (*Ifo*$_5$, Pl. 4; Pl. 5, figs. 1, 3; Text-fig. 3) can only be seen in part in the neotype, in P.1063 and, in impression, in Innsbruck Lit. F; it seems to have about the same general shape as infraorbital 4.

The *suborbital* (*Sbo*, Pl. 4; Pl. 5, fig. 1; Text-fig. 3) seems to be a little broader than in *Ph. bechei*. Judging from the neotype its anterior margin lies almost vertical, whereas its posterior margin is slightly curved in the antero-ventral direction.

The *preoperculum* (*Pop*, Pl. 4; Pl. 5, figs. 1, 3; Text-fig. 3) is best preserved in the neotype, where it is partly hidden below infraorbital 3 and the suborbital, in P.1063 and, in impression, in Innsbruck Lit. F, where its postero-ventral part is lost. In 33987 it is rather defective. Its general shape resembles that of the preoperculum in *Ph. bechei*, but its dorsal limb is broader and its postero-ventral part does not protrude posteriorly as in that species ; the notch in its posterior margin is consequently much shallower. It is not possible to determine the course of the anterior margin of the preoperculum because of the overlying bones, but judging from the impression in Innsbruck Lit. **F**, the anterior margin has a slight convexity ventral to the middle of its length (Pl. 5, fig. 3). In P.11780 there is a fragmentary bone which I interpret as the left preoperculum ; its anterior margin is rather well preserved and shows the same convexity as in the specimen just mentioned.

The *operculum* (*Op*, Pl. 4 ; Pl. 5, fig. 1 ; Text-fig. 3) has, on the whole, the same general shape as in *Ph. bechei*, but its dorsal part seems to be broader and its ventral tip is more obtuse ; its anterior margin is a little thickened except ventrally where the margin is slightly notched for the antero-dorsal process of the suboperculum.

The *suboperculum* (*Sop*, Pl. 4 ; Pl. 5, fig. 1 ; Text-fig. 3) seems to be proportionately as large as in *Ph. bechei* but its posterior margin is defective in all specimens except P.11780, possibly belonging to this species ; in this specimen its posterior, well-preserved part shows a shallow concavity high on the posterior margin.

Of the *interoperculum* (*Iop*, Pl. 4 ; Pl. 5, fig. 1 ; Text-fig. 3) only the posterior part is visible in the neotype, in P.11780 and, in impression, in Innsbruck Lit. F.

Branchiostegal rays and gular plate

The branchiostegal rays and the gular plate cannot be seen in any of the available specimens.

Lower jaw

The lower jaw is only partly exposed in the neotype and in 33987 and P.1063 ; in Innsbruck Lit. F. the left lower jaw is exposed but very defective (Pl. 15, fig. 6) and in P.11780, possibly belonging to this species, an isolated right lower jaw is present but partly crushed (Pl. 15, fig. 7). These specimens suggest that the lower jaw in *Ph. latiusculus* has about the same shape as in *Ph. bechei* (Pl. 13, fig. 5).

In all the specimens of *Ph. latiusculus* the ventral, splenial part of the *dentary* is separated from the dorsal, dental part by a well-marked ridge and its lateral surface is ornamented with thick ganoin rugosities and irregular striations. The dental part is anteriorly only gently ascending but further back it bends dorsally to form a small process, and then runs postero-dorsally ; its lateral surface is without ornamentation. No teeth can be observed.

The limit between the dentary and the *angulo-supra-angular* (*Ang*, Pl. 15, fig. 7) is not clearly visible. The postero-ventral part of the lateral surface of the last named bone carries a well developed ornamentation.

Sensory canal system of head

The sensory canal system of the head seems to follow the same general pattern as in *Ph. bechei*, as far as the preservation of the material allows a comparison.

The *supraorbital sensory canal* (*soc*, Pl. 5, fig. 1 ; Text-figs. 3, 4) pierces the nasal, the frontal and the parietal.

In the nasal the canal runs almost straight from the antero-lateral to the postero-mesial part of the bone in P.1063; no tubules or pores can be observed. In the neotype this part of the canal is not clearly visible.

In the frontal the supraorbital sensory canal is rather well-marked as a slight ridge on the dorsal surface of the bone. Its course is on the whole the same as in *Ph. bechei*: an anterior part running almost straight posteriorly is followed by a curved part corresponding to the broadening of the frontal; the posterior part runs at first in postero-mesial direction, then straight back to the middle of the posterior margin of the bone. P.1063 has the following arrangement of tubules and pores (Text-figs. 3, 4): from its anterior straight part the left canal gives off laterally two short tubules; from its curved part three short tubules are given off from the mesial side; the straight postero-mesially directed part has on its lateral side three very short tubules or pores; the posteriormost part of the sensory canal is damaged and the presence of pores or tubules in that part cannot be made out. On the right side corresponding tubules are given off from the anterior and the curved parts of the canal, but further back only a single pore or tubule on the mesial side of the canal can be observed. In Innsbruck Lit. F. (Pl. 5, fig. 2) there seem to be three laterally directed tubules issuing from the anterior straight part of the canal but only two pores from the curved part can be observed; along the lateral side of the posterior, postero-mesially directed part of the canal there are four pores.

The parietal part of the supraorbital sensory canal is well exposed in P.1063 (Pl. 5, fig. 1). It is comparatively much longer than in *Ph. bechei* and on the right parietal there is a small shallow concavity on the dorsal surface of the canal which may be a pore, but its interpretation as a true pore is questionable. The sensory canal continues posteriorly as a well-marked groove, the anterior pit-line (*ap*, Pl. 5, fig. 1; Text-figs. 3, 4).

The *infraorbital sensory canal* (*ifc*, Text-fig. 3) is quite unknown in its anterior parts because of the absence of the rostral and antorbital bones.

Only in 33987 is infraorbital 1 (lachrymal) present, and there only in its antero-ventral part; it shows the anterior curved part of the canal in this bone with two antero-ventrally directed, pore-like tubules. For the rest the sensory canal and its tubules in infraorbital 1 are unknown.

In infraorbital 2 the sensory canal is not visible.

In infraorbital 3 the sensory canal pierces the bone parallel to its concave anterior margin. From its morphologically posterior side it gives off some tubules, the number of which is not easy to determine because of the thickness of the bone. In the neotype (Pl. 4) there seem, however, to be three rather long posteriorly directed tubules situated close together; antero-ventral to these tubules a short postero-ventrally directed tubule is present. In P.1063 (Pl. 5, fig. 1) only two long, posteriorly directed tubules can be seen with certainty; a short postero-ventrally directed tubule in the anterior part of the bone seems to be present but cannot be observed in detail.

In infraorbital 4 the sensory canal gives off posteriorly a single tubule in the neotype. In infraorbital 5, which is only partly visible, no tubule can be observed with accuracy.

Judging from 33987, in which the posterior part of the dermosphenotic is preserved, the posteriorly curving sensory canal pierces this bone in its posterior part; from the anterior side of the curve a rather wide tubule is given off in antero-dorsal direction. In P.1063 the canal itself cannot be followed exactly, but the tubule is partly visible and seems to end in a pore at the dorsal margin of the bone.

The sensory canal passes over into the dermopterotic and runs along its lateral margin. Judging from specimen Innsbruck Lit. F it seems to give off dorsally two short tubules. As in *Ph. bechei* the preopercular sensory canal seems to be given off near the postero-lateral corner of the bone.

Cephalic division of main lateral line

The middle pit-line (*mp*, Pl. 5, figs. 1, 2; Text-figs. 3, 4) is well developed, stretching from the postero-mesial part of the parietal to near the lateral margin of the dermopterotic.

The cephalic division of the main lateral line passes over from the dermopterotic to the extrascapular, but as this bone is very badly preserved or missing nothing can be made out regarding this part of the canal and its tubules.

The preopercular sensory canal runs, as in *Ph. bechei*, on the whole parallel to the anterior margin of the preoperculum. The tubules given off from its morphologically posterior side show the same general pattern as in *Ph. bechei*. In the neotype, the best preserved specimen in this respect, there seem to be three short, almost straight tubules dorsal to the angle on the posterior margin of the bone, the dorsalmost difficult to observe with accuracy as it is hidden below the suborbital, and ventral to the angle two shorter, slightly curved tubules; these five dorsal tubules obviously correspond to the four to six shorter dorsal tubules in *Ph. bechei*. Ventral to these shorter tubules there is, as in *Ph. bechei*, a rather long tubule which, however, does not reach the posterior margin of the bone. Anteriorly it is followed by nine curved tubules which decrease in length antero-ventrally; there are thus ten openings belonging to this group of tubules, but it seems as if the fourth tubule reckoned from the antero-ventral tip of the preoperculum is only a branch of the following tubule. The ten antero-ventral tubules in question obviously correspond to the thirteen antero-ventral tubules in *Ph. bechei*. In P.1063 the shorter dorsal tubules are likewise five in number but the ventral part of the preoperculum is too damaged to allow a count of the tubules. The preopercular impression in Innsbruck Lit. F shows five dorsally situated shorter tubules and ventral to them about nine tubules. The total number of tubules belonging to the preopercular sensory canal in *Ph. latiusculus* is consequently 14–15 against 17–19 in *Ph. bechei*.

In P.1063 (Pl. 5, fig. 1) the lateral surface of the preoperculum shows one almost horizontal (*hc_1*) and one vertical (*orp*) groove, obviously the posterior portion of the anterior division of the supramaxillary line and the postmaxillary line respectively as described above in *Ph. bechei*. An oblique, posteriorly directed groove on the lateral surface of infraorbital 3 may represent the anterior portion of the anterior division of the supramaxillary line. In the neotype (Pl. 4) the postmaxillary line is hidden below infraorbital 3, but the other two lines are clearly visible, that on infraorbital 3, however, is not continuous but divided into two parts. In Innsbruck Lit. F. (Pl. 5, fig. 3) all the three lines mentioned can be traced on the impression. As compared with the corresponding lines in *Ph. bechei* the two lines on the preoperculum are proportionately much longer and the line on infraorbital 3 seems to occur normally in all specimens.

The mandibular sensory canal can partly be seen in the neotype and in P.1063; the openings of separate tubules, marked by ganoin thickenings, are visible here and there ventral to the ridge separating the dental and splenial parts of the dentary; their total number cannot be made out.

In 33987, the only one in which the lateral surface of the angular is clearly exposed, a small vertical groove representing the oral line is visible on the angular near its ventral margin.

Exoskeletal shoulder-girdle and squamation

A suprascapula cannot be identified in any of the specimens investigated. In the neotype an almost triangular bone with strongly marked ganoin ridges on its lateral surface may be a *supracleithrum* (*Scl*, Pl. 4). In the smaller specimen, 33987, the same bone is visible but the ganoin ridges are not as marked as in the neotype; in P.1063 (Pl. 5, fig. 1) a fragment of the same bone is present. In the last named specimen much of the *cleithrum* (*Cl*, Pl. 5, fig. 1) is exposed, and shows a large, deep notch above the insertion of the pectoral fin.

The squamation (Pl. 4) is only partly preserved, but in the neotype about 38 transverse scale rows can be observed, reckoned from the posterior margin of the operculum to the middle of the caudal fin base. The lateral line scales are the deepest, but also the rows immediately above and below the lateral line scales seem to be deeper than broad. All the scales are comparatively thick and have an even posterior margin.

Lateral line

Nothing can be made out regarding that part of the lateral line piercing the suprascapula and the supracleithrum. The lateral line scales are arranged in an almost straight row along the side of the body (*l.l*, Pl. 4; cf. also Pl. 15, fig. 2).

Paired and unpaired fins

Very little can be said regarding the fins in this species.

The *pectoral fin* is partly preserved in all specimens investigated but only in P.1063 can the number of lepidotrichia be counted with accuracy (Pl. 5, fig. 1); there seem to be about 19 lepidotrichia, the first one carrying some small fulcra.

Only a few lepidotrichia belonging to the *ventral fin* are preserved in specimen 33987, in others the ventral fin is missing.

The *dorsal* and *anal* fins are lacking in all specimens seen by me, but according to Kner (1867, pl. 2, fig. 1) the dorsal fin is situated approximately above the ventral fins as in *Ph. bechei*.

The *caudal fin* is hemi-heterocercal and carries well-developed fulcra on its dorsal and ventral margins.

REMARKS. Apart from small differences, mainly in the ornamentation of the exoskeletal cranial bones, all the specimens mentioned above except P.11780 are so similar that they may be considered to belong to one and the same species. Whether the specimens from Italian localities attributed to *Ph. latiusculus* by authors such as de Alessandri, Bassani, Costa, Mariani etc., are identical with the specimens described above is a question which at present must be left open, as I have had no opportunity to see them.

HORIZON AND LOCALITY. Upper Trias; Seefeld, Tyrol, Austria.

Pholidophorus (?) ***caffii*** Airaghi

(Pl. 6, fig. 1; Text-fig. 5)

1908 *Pholidophorus Caffii* Airaghi: 3, text-fig. 2.
1914 *Pholidophorus latiusculus* Agassiz; (*partim*) Bassani: 379.
1920 *Pholidophorus latiusculus* Agassiz; (*partim*) Alessandri: 96.
1937 *Pholidophorus latiusculus* Agassiz; Boni: 132, pl. 4, fig. 4, pl. 5, fig. 3, text-figs. 9, 10.

DIAGNOSIS. *Pholidophorus* (?) of small size, up to 58 mm. in total length. Greatest depth of body about one quarter of the standard length or slightly more. Depth of caudal peduncle about one-tenth of the standard length. Maxillary and lower jaw rather short. Infraorbitals 3 and 4 deeper than broad. Preoperculum broad, its posterior margin without a marked notch. Preopercular sensory canal running nearer to posterior than to anterior margin of bone in dorsal limb, in ventral limb at about the middle, and with about eight tubules. Scales thick, not serrated posteriorly, arranged in about 35 transverse rows counted from posterior margin of operculum to middle of caudal fin base. A few longitudinal rows of body scales deeper than broad.

HOLOTYPE. Specimen originally described by Airaghi (1908) and belonging to the Museo Civico di Scienze Naturale di Bergamo, Italy. The only specimen.

DESCRIPTION. The total length of the holotype is 58 mm., the length from the tip of the snout to the hindmost lateral line scale (standard length) is 49 mm. The estimated depth of the body is slightly more than one quarter (26·5%) of the standard length and the depth of the caudal peduncle is about one-tenth of that length. The length of the head is estimated to be slightly less than one quarter of the standard length. The maxillary and lower jaw are, comparatively, a little shorter than in *Ph. bechei* and *Ph. latiusculus*.

The position of the paired and unpaired fins is clearly visible. The base of the ventral fin is situated a little nearer to the hindmost lateral line scale than to the tip of the snout, and the distance between the base of the ventral and the origin of the anal is about 75% of the distance between the bases of the pectoral and ventral fins. The dorsal fin begins above the ventral fin base. A good figure of the entire fish is given by Boni (1937, pl. 5, fig. 3).

The cranial bones are, unfortunately, partly defective ; most bones belonging to the exoskeletal skull roof are lacking and many of the other cranial bones are poorly preserved. Consequently the following description is rather incomplete.

Exoskeletal skull roof

The premaxillary, rostral, nasal, frontal, supraorbital, dermosphenotic and dermopterotic bones are missing or represented by insignificant fragments. Parts of the parietal and the extrascapular seem to be present (*Pa*?, *Ext*?, Pl. 6, fig. 1), but their shape cannot be made out.

Dermal bones of cheek and opercular apparatus

Only the posteriorly directed lateral part of the comparatively short *maxillary* is present ($Mx + Smx_1$, Pl. 6, fig. 1 ; Text-fig. 5). It is, however, very defective, almost the entire ventral part is missing and consequently nothing can be made out

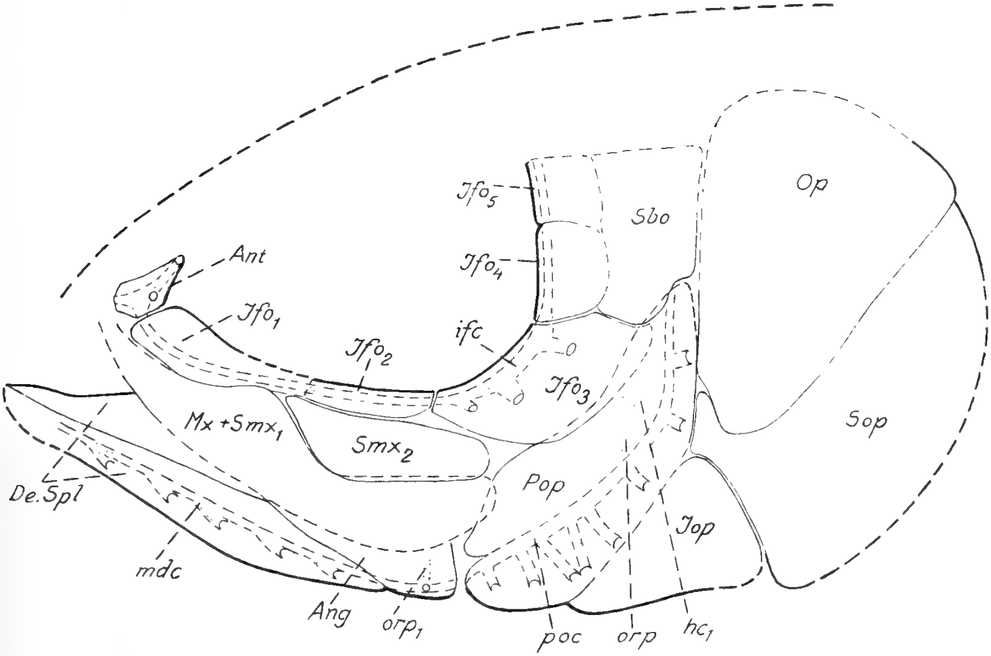

FIG. 5. *Pholidophorus* (?) *caffii* Airaghi. Holotype. Attempted restoration of head in lateral view. × 10·5.

Ang, angular ; *Ant*, antorbital ; *De. Spl*, dentary ; Ifo_1–Ifo_5, infraorbitals 1 to 5 ; *Iop*, interoperculum ; $Mx + Smx_1$, maxillary and anterior supramaxillary ; *Op*, operculum ; *Pop*, preoperculum ; *Sbo*, suborbital ; Smx_2, posterior supramaxillary ; *Sop*, suboperculum ; hc_1, anterior division of supramaxillary pit-line ; *ifc*, infraorbital sensory canal ; *mdc*, mandibular sensory canal ; *orp*, postmaxillary pit-line ; orp_1, oral pit-line ; *poc*, preopercular sensory canal.

regarding the depth of the maxillary or of the dentition. The lateral surface of the preserved part is, however, ornamented with longitudinal streaks and, posteriorly, with some short oblique ridges. The posterior end of the maxillary is broken off, and thus its shape, if rounded or notched, cannot be stated. According to Boni (1937, text-fig. 9) the posterior part of the maxillary is wedged between infraorbital 3 and the antero-ventral limb of the preoperculum, but the part in question is, as far as I can see, the antero-dorsal part of the ventral limb of the preoperculum, and not part of the maxillary.

Boni's text-fig. 9 shows only a single *supramaxillary*, obviously corresponding to supramaxillary 2 in other species ; anterior to it the figure shows, however, a roughly triangular or semicircular elevation on the dorsal margin of the maxillary, corresponding to supramaxillary 1 in other forms. At first I was inclined to consider this eminence as not belonging to that bone, but as soon as I had the opportunity of examining the holotype I could confirm that there was no division between this elevation and the rest of the maxillary. Whether this is a secondary, perhaps individual, fusion of the two bones or a primitive stage of development, characteristic of *Ph. caffii*, is a question which must be left open until more specimens of this species are available for study. Supramaxillary 2 (*Smx*$_2$, Pl. 6, fig. 1 ; Text-fig. 5) is rather well preserved ; it is almost rectangular, its antero-dorsal corner forms a blunt short process, and its lateral surface is ornamented with rather dense, horizontal striations.

All the bones of the infraorbital series, an antorbital and five infraorbitals, are present.

The *antorbital* (*Ant*, Pl. 6, fig. 1 ; Text-fig. 5) is rather well preserved but its outline cannot be made out in detail ; it is large in comparison with the antorbital in *Ph. bechei* and tapers postero-dorsally.

Infraorbital 1 (*lachrymal*) (*Ifo*$_1$, Pl. 6, fig. 1 ; Text-fig. 5) was exposed by preparation ; it is rounded anteriorly, its ventral margin is convex, its dorsal margin concave and the exposed dorso-lateral surface is slightly concave.

Infraorbital 2 (*Ifo*$_2$, Pl. 6, fig. 1 ; Text-fig. 5) is well preserved but broken into two pieces ; it has a generally elongate shape with the dorsal margin slightly concave, the ventral margin slightly convex.

Infraorbital 3 (*Ifo*$_3$, Pl. 6, fig. 1 ; Text-fig. 5) is likewise well preserved except that its postero-dorsal corner is broken off ; it is markedly deeper than broad and its dorsal margin constitutes an obtuse angle so as to fit the ventral margins of infraorbital 4 and the suborbital.

Infraorbital 4 (*Ifo*$_4$, Pl. 6, fig. 1 ; Text-fig. 5) is partly incomplete but seems to be a little deeper than broad.

Infraorbital 5 (*Ifo*$_5$, Pl. 6, fig. 1 ; Text-fig. 5) is better preserved and seems to be almost square and only a little smaller than infraorbital 4.

Posterior to infraorbitals 4 and 5, the ventral part of the *suborbital* (*Sbo*, Pl. 6, fig. 1 ; Text-fig. 5) is clearly visible but it is broken into two pieces on to the lateral crest of the hyomandibular ; regarding its outline it can only be said that its posterior margin seems to be straight and vertical, thus probably not overlapping the anterior margin of the operculum, and that its postero-ventral margin is a little convex.

The *preoperculum* (*Pop*, Pl. 6, fig. 1 ; Text-fig. 5) is, comparatively, very broad, especially in its antero-ventral limb, the antero-dorsal margin of which shows a rather pronounced convexity ; the postero-ventral margin of the preoperculum is damaged but it seems to have been almost straight or only slightly concave and thus without the notch characteristic of the preoperculum in *Ph. latiusculus* and especially in *Ph. bechei*. The uppermost end of the preoperculum is defective.

The *operculum* (*Op*, Pl. 6, fig. 1 ; Text-fig. 5) seems to have the usual almost triangular shape, but as its anterior and dorsal margins are damaged its shape cannot be made out exactly. Its ventral tip is rounded, about as in *Ph. latiusculus*, and as in that species the anterior margin of the operculum is slightly notched ventrally to receive the antero-dorsal process of the suboperculum.

The *suboperculum* (*Sop*, Pl. 6, fig. 1 ; Text-fig. 5) is only partly preserved ; its antero-dorsal process is well developed.

The *interoperculum* (*Iop*, Pl. 6, fig. 1 ; Text-fig. 5) seems to be roughly triangular with the posterior margin slightly convex ; its lateral surface carries a few striations parallel to its margins.

Branchiostegal rays and gular plate

The posteriorly situated, rather short but broad *branchiostegal rays* (*R. Br*, Pl. 6, fig. 1) are visible ventral to the preoperculum and the interoperculum.

The *gular plate* is not visible.

Lower jaw

The lower jaw is, like the maxillary, comparatively short. Anteriorly the dorsal margin of the dental part of the *dentary* (*De. Spl*, Pl. 6, fig. 1 ; Text-fig. 5) is only gently ascending, but as most of the dorsal margin of the lower jaw is covered by overlying bones, its outline cannot be followed. No teeth could be observed on the exposed dorsal margin of the dentary. The lateral surface of the dental part is smooth and that of the splenial part is only feebly ornamented but shows clearly the tubules of the mandibular sensory canal ; the ridge separating the two parts of the dentary seems to be comparatively weak.

The ventral part of the *angular* (*Ang*, Pl. 6, fig. 1 ; Text-fig. 5) is well exposed ; its lateral surface is practically smooth.

Sensory canal system of head

Regarding the sensory canal system of the head, almost nothing of the *supraorbital sensory canal* can be determined because the nasal and frontal bones are lacking. On the fragment thought to belong to the parietal a single short canal is visible. This might be interpreted as the posteriormost part of the supraorbital sensory canal, but as it is not followed by a pit-line this interpretation is rather uncertain. No canals, tubules or pores can be observed in the bone fragment considered as part of the extrascapular.

The *infraorbital sensory canal* (*ifc*, Text-fig. 5) can be followed for almost its entire length; only the ethmoidal commissure and the part in the dermosphenotic and dermopterotic are missing. In the antorbital the canal describes an arch in its ventral part and gives off postero-dorsally an antorbital branch ending in a pore; at the point where the antorbital branch arises there seems to be a rather large pore. In infraorbital 1 (lachrymal) the sensory canal can be followed for most of its length but its state of preservation allows no statements regarding the number or disposition of its tubules. In infraorbital 2 the sensory canal is partly visible; an opening at the posterior end of the bone is not a real pore but an artifact due to damage. In infraorbital 3 the sensory canal gives off three postero-ventrally directed and short but strongly marked and widely separated tubules, the antero-ventral one being the shortest, the dorsal one the longest. The anterior part of infraorbital 4 is obviously pierced by the sensory canal, but no tubule can be seen with certainty. In infraorbital 5 the sensory canal can be traced but no tubule is visible.

Cephalic division of main lateral line

The *preopercular sensory canal* seems to pierce the dorsal limb of the preoperculum nearer to its posterior than to its anterior margin; in the ventral limb it runs at about the middle of its length, not nearer to its anterior margin as in *Ph. bechei* and *Ph. latiusculus*. The tubules given off from the morphologically posterior side of the canal are short but rather wide. Only eight tubules seem to be present, two in the dorsal limb of the preoperculum dorsal to and at the posterior angle of the bone respectively, one short tubule farther ventrally and five tubules in the ventral part of the ventral limb of the bone. Consequently, the general arrangement of the tubules is not unlike that in *Ph. bechei* and *Ph. latiusculus*, but the tubules in the ventral group are not long and narrow as in the two former species and the total number of tubules is only about 8 as against 17–19 in *Ph. bechei* and 14–15 in *Ph. latiusculus*.

On the lateral surface of the preoperculum there are two grooves, one horizontal and one vertical, (hc_1, *orp*, Pl. 6, fig. 1; Text-fig. 5), meeting at a right angle; the horizontal groove represents the posterior portion of the anterior division of the supramaxillary line and the vertical one the postmaxillary line according to the nomenclature proposed by Stensiö (1947).

The *mandibular sensory canal* (*mdc*, Pl. 6, fig. 1; Text-fig. 5) is exposed to a small extent in the anterior, broken portion of the splenial part of the dentary; it is impossible to say how many tubules the canal gives off in that part of the bone, but posterior to the exposed part of the canal five short tubules are visible. Near the ventral margin of the angular there is a pore belonging to that part of the mandibular sensory canal which pierces the angular, and dorsal to this pore there is a short, vertical groove, representing the oral line (orp_1, Pl. 6, fig. 1; Text-fig. 5).

Exoskeletal shoulder-girdle and squamation

Dorsal to the operculum there is a large *suprascapula* (*Ssc*, Pl. 6, fig. 1) but it is crushed and partly defective and consequently its outline cannot be determined exactly. Postero-ventral to it there is a *supracleithrum* (*Scl*, Pl. 6, fig. 1) of about the same size and shape as the suprascapula, but this bone also is crushed and defective. Almost the entire *cleithrum* is missing but its impression suggests a rather robust bone. Posterior to this impression there is a deep bony plate which may be interpreted as a *postcleithrum.*

The *scales* are arranged in about 35 transverse rows counted from the posterior margin of the supracleithrum to the middle of the caudal fin base (=lateral line scales). On the body the lateral line scales and those in the longitudinal rows immediately dorsal and ventral to them, three rows in all, are deeper than broad. All the scales are comparatively thick and, as far as can be judged, with a regular posterior margin.

Lateral line

Those parts of the lateral line piercing the suprascapula and the supracleithrum are not visible ; in the suprascapula, however, a short but rather wide, mesially directed tubule can be seen ; in the supracleithrum no tubules are visible.

The lateral line scales (*l.l*, Pl. 6, fig. 1) are arranged in a straight row from the second scale to the last one at the base of the middle caudal rays.

Paired and unpaired fins

All fins are present but at least in part more or less defective.

The *pectoral fin* is of moderate size. Boni (1937) gives the number of its lepidotrichia as 11, a remarkably low number. There are, indeed, 11 rather stout lepidotrichia clearly exposed, but ventral to the postcleithrum and easily overlooked there is a cluster of broken, more slender lepidotrichia ; these may represent the posterior rays of the pectoral fin and their number may be at least 7–8, and consequently the total number of pectoral lepidotrichia may be estimated as about 18 or about the same number as in *Ph. bechei* and *Ph. latiusculus*. The first lepidotrichium carries some very small fulcra (*Fu*, Pl. 6, fig. 1).

The *ventral fin* is rather defective. For this fin Boni gives the number of lepidotrichia as 5, which is too low ; as far as I can see there are at least two small, undivided lepidotrichia anteriorly, followed by 6 divided and branched lepidotrichia, the anterior one fulcrated. Posterior to these lepidotrichia the fin is damaged and the total number of ventral fin lepidotrichia thus remains unknown.

The *dorsal fin* is well preserved but the number of lepidotrichia is difficult to interpret. Anteriorly there are two undivided lepidotrichia, the anterior one rather short and almost scale-like ; there follows a third, rather long, apparently undivided lepidotrichium with a comparatively long and slender rod (fulcrum?) in front of it ; posterior to these three there are 8 divided and branched lepidotrichia, the anteriormost of which is richly fulcrated. Consequently, the total number of dorsal fin lepidotrichia is at least 11 as compared with 9 (10?) as stated by Boni.

The *anal fin* is not as well preserved as the dorsal fin and the number of its lepidotrichia cannot be stated with accuracy. There are, however, two short, undivided lepidotrichia anteriorly followed by at least 7 divided and branched ones, the anteriormost of which with a few, long fulcra ; thus there are at least 9 lepidotrichia as against the 5–6 as stated by Boni.

The *caudal fin* is hemi-heterocercal and its dorsal as well as its ventral margin is densely set with fulcra.

REMARKS. *Pholidophorus caffii,* described as a new species by Airaghi (1908), has been considered merely a synonym of *Ph. latiusculus* by Bassani (1914), de Alessandri (1920) and Boni (1937). It is, however, beyond doubt that the specimen on which Airaghi founded his species, redescribed above, does represent a species clearly distinguishable from *Ph. latiusculus* in the sense of Kner. Differences in the relative length of maxillary and lower jaw, the general shape of the preoperculum, the course of the preopercular sensory canal and the number of its tubules clearly separate Airaghi's *Pholidophorus caffii* from Kner's *Ph. latiusculus.* In my opinion differences in the preoperculum and the course of the preopercular sensory canal are of such a degree that the placing of *caffii* in the genus *Pholidophorus* s. str.may even be questionable. This problem will be discussed in more detail later on (p. 423).

HORIZON AND LOCALITY. Upper Trias ; Viciarola, near S. Pellegrino (Val Brembana), Italy.

Pholidophorus cf. ***pusillus*** Agassiz

(Pl. 6, fig. 2 ; Text-fig. 6)

1895 *Pholidophorus latiusculus* Agassiz ; Woodward : 455 (*partim*).

PRELIMINARY DIAGNOSIS. *Pholidophorus* of small size, up to 65 mm. in total length, similar to *Ph.* (?) *caffii* but differing from that species *i.a.* in the following features : Maxillary and lower jaw not markedly short. Infraorbitals 3 and 4 considerably broader than deep. Preoperculum similar to that of *caffii* but preopercular sensory canal with about 11 tubules, longer than those in *caffii.* Scales arranged in about 38–40 transverse rows counted from posterior margin of operculum to middle of caudal fin base.

MATERIAL. Specimen No. P.4418 in the Department of Palaeontology, British Museum (Natural History).

DESCRIPTION. The total length of the specimen is about 65 mm., the standard length is estimated as 56 mm. The greatest depth of the body cannot be determined. The depth of the caudal peduncle is about one-tenth of the standard length. The length of the head is estimated to be slightly less than one quarter of the standard length. The maxillary and lower jaw are relatively longer than in *Ph. bechei* and *Ph. latiusculus,* and even more so than in *Ph.* (?) *caffii.*

The fins are not preserved except for some lepidotrichia of the anal fin and the entire caudal fin ; the position of the dorsal fin in relation to the ventral fins is thus unknown.

The cranial bones are very defective ; all bones belonging to the exoskeletal skull roof are lacking and many of the other cranial bones are fragmentary. Thus only the following rather incomplete description can be given.

Dermal bones of cheek and opercular apparatus

Only the posteriorly directed part of the comparatively long *maxillary* (*Mx*, Pl. 6, fig. 2; Text-fig. 6) is preserved; apart from its relatively greater length it seems to have the same general shape as in *Ph. bechei* and *Ph. latiusculus*, but its ventral margin is defective and consequently nothing can be said about its real depth or about the dentition. Neither can it be determined with any accuracy whether its posterior margin is rounded or slightly notched; judging from an impression on the preoperculum behind the broken end of the maxillary it looks, however, as if its posterior margin was slightly notched. The lateral surface of the maxillary is richly ornamented with ganoin spots and irregular longitudinal streaks and ridges except along its postero-dorsal margin, indicating that supramaxillary 2 may overlap the maxillary a little.

Of the *supramaxillaries*, supramaxillary 1 (Smx_1, Pl. 6, fig. 2; Text-fig. 6) is almost semicircular; it is well separated from the maxillary, but seems not to overlap the dorsal margin of that bone; its lateral surface carries a striation approximately parallel to the convex dorsal margin of the bone, similar to the striation on the dorsal

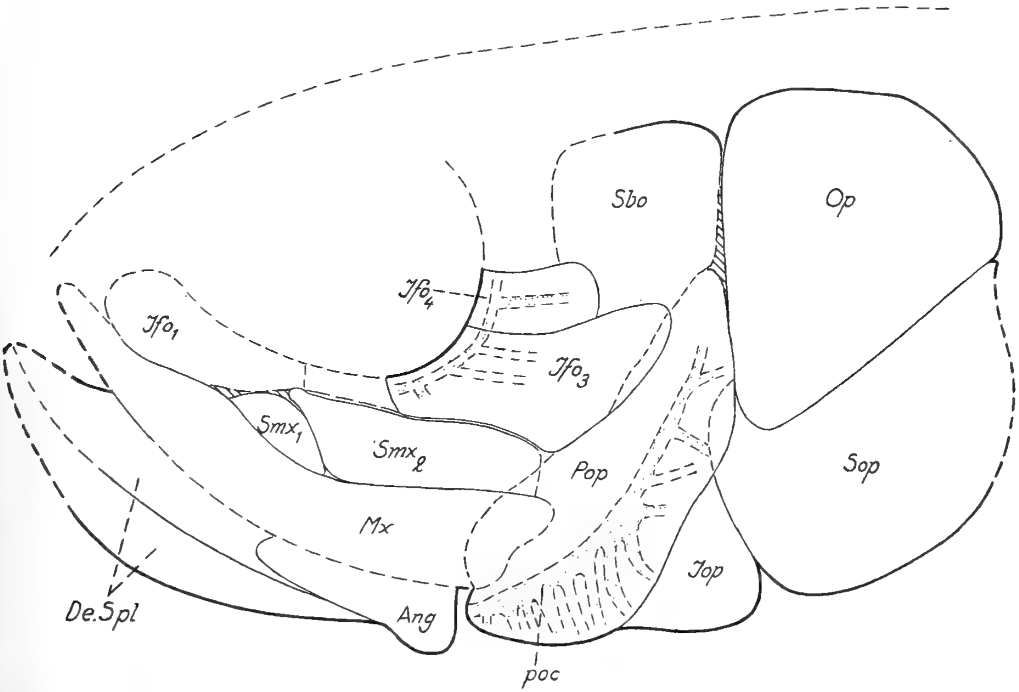

Fig. 6. *Pholidophorus* cf. *pusillus* Agassiz. Attempted restoration of head in lateral view. B.M. No. P.4418. × 10.
Ang, angular; *De. Spl*, dentary; Ifo_1, Ifo_3, Ifo_4, infraorbitals 1 and 3–4; *Iop*, interoperculum; *Mx*, maxillary; *Op*, operculum; *Pop*, preoperculum; *Sbo*, suborbital; Smx_1, Smx_2, anterior and posterior supramaxillaries; *Sop*, suboperculum; *poc*, preopercular sensory canal.

elevation of the maxillary in *Ph.* (?) *caffii.* Supramaxillary 2 (*Smx*$_2$, Pl. 6, fig. 2; Text-fig. 6) has about the same, almost rectangular shape as in that species but it is comparatively longer antero-posteriorly; its antero-dorsal corner is broken off but may have been of about the same shape as in *Ph.* (?) *caffii.* The lateral surface of supramaxillary 2 shows a horizontal striation, but this striation is by no means as dense as in *Ph.* (?) *caffii* or in *Ph. latiusculus.*

The bones of the infraorbital series are only partly preserved.

An isolated bone fragment in the snout region looks like an *antorbital* (*Ant*?, Pl. 6, fig. 2), but this interpretation is rather uncertain.

Another bone fragment dorsal to the anteriormost preserved part of the maxillary may belong to *infraorbital* 1 (*lachrymal*) (*Ifo*$_1$, Pl. 6, fig. 2) but it provides no information about the outline of this bone.

Infraorbital 2 is missing.

Infraorbital 3 (*Ifo*$_3$, Pl. 6, fig. 2; Text-fig. 6) is remarkably broad, about twice as broad as deep, its postero-dorsal part overlaps the preoperculum and its dorsal margin is slightly concave; its shape is thus quite different from that of the corresponding bone in *Ph.* (?) *caffii.*

Infraorbital 4 (*Ifo*$_4$, Pl. 6, fig. 2; Text-fig. 6) is almost complete, nearly rectangular and considerably broader than deep.

Some bone fragments dorsal to infraorbital 4 indicate the presence of an *infraorbital* 5.

Between the visible part of the hyomandibular and the anterior margin of the operculum there is a rather large bony plate which is obviously a *suborbital* (*Sbo*, Pl. 6, fig. 2; Text-fig. 6); its margins are, however, only partly visible.

The *preoperculum* (*Pop*, Pl. 6, fig. 2; Text-fig. 6) is well preserved, only its uppermost end is defective. Its shape is very similar to that of the preoperculum in *Ph.* (?) *caffii.* A shallow concavity is present ventral to the ill-defined posterior angle between the upper and lower limbs of the bone, but there is no real notch as in *Ph. bechei* and *Ph. latiusculus.*

The *operculum* (*Op*, Pl. 6, fig. 2; Text-fig. 6) seems to be remarkably broad, much broader than in the other species treated here, but this may be partly due to pressure as the bone is somewhat dislocated.

The *suboperculum* (*Sop*, Pl. 6, fig. 2; Text-fig. 6), likewise dislocated, is only partly preserved; its postero-dorsal half is missing.

Of the *interoperculum* (*Iop*, Pl. 6, fig. 2; Text-fig. 6) only the posterior part is exposed; it seems to have the same general shape as in *Ph.* (?) *caffii*, but lacks the concentric striations.

Branchiostegal rays and gular plate

As in *Ph.* (?) *caffii* only some of the posterior *branchiostegal rays* (*R. Br*, Pl. 6, fig. 2) are exposed; they are, however, relatively much longer than in that species.

The *gular plate* is not visible.

Lower jaw

The lower jaw is exposed to a certain extent, but its anterior part is lacking and its dorsal margin is covered by the maxillary bones and cannot be described. It is, however, obvious that the lower jaw is relatively much longer and stouter than in *Ph.* (?) *caffii*. The lateral surface of the dental part of the *dentary* (*De. Spl*, Pl. 6, fig. 2; Text-fig. 6) is quite smooth, whereas the splenial part, which seems to be deeper than in the three species described above, has a rich ganoin ornamentation obscuring the tubules of the mandibular sensory line; the ganoin-covered ridge separating these two parts of the dentary is very pronounced. No dentition could be observed.

The angular part of the *angulo-supra-angular* is partly visible but its posterior margin is indistinct because of damage; its lateral surface is ornamented ventrally with ganoin patches.

Sensory canal system of head

Very little of the sensory canal system of the head can be made out. All the bones containing the *supraorbital sensory canal* are absent and only some parts of the *infraorbital sensory canal* are preserved (Text-fig. 6). In infraorbital 3 the sensory canal can be traced but the tubules are difficult to observe; there are, however, traces of at least two rather long, posteriorly directed tubules, and a third, very short tubule is given off from the anterior part of the canal. In infraorbital 4 the canal itself cannot be seen with accuracy, but a single large, posteriorly directed tubule is clearly visible.

Cephalic division of main lateral line

Of this part of the sensory canal system only the *preopercular sensory canal* is visible (Text-fig. 6). The canal itself pierces the preoperculum at about the middle of its length and, on the whole, lies parallel to its anterior and posterior margins, thus not nearer to its posterior margin in the dorsal limb as it is in *Ph.* (?) *caffii* and not distinctly nearer to its anterior margin as in *Ph. bechei* and *Ph. latiusculus*. The number of tubules given off from the posterior side of the canal is difficult to determine, but two tubules are clearly visible in the dorsal limb of the bone, dorsal to and at its posterior angle respectively; ventral to this angle there is a rather short tubule followed more ventrally by about eight wide tubules in the antero-ventral third of the bone. Between the second and the third tubules reckoned from above there is a structure resembling a postero-dorsally directed tubule or rather, a sensory line; its position posterior to the preopercular sensory line may be an argument against the interpretation of it being a supramaxillary line, but as it cannot be followed anteriorly because of the damaged condition of the lateral surface of the middle part of the preoperculum the question of its real nature must be left open. The same is true of the postmaxillary line, the ventralmost part of which may perhaps be traced ventral to the damaged middle part of the bone (*orp*?, Pl. 6, fig. 2). The total number of tubules belonging to the preopercular sensory canal may consequently be eleven, perhaps twelve, that is, only a little higher than in *Ph.* (?) *caffii*; their arrangement is virtually identical in the two species but those of the ventral group are considerably longer, almost reaching the ventral margin of the preoperculum; they are, however, not as long and as numerous as in *Ph. bechei* or *Ph. latiusculus*.

The *mandibular sensory canal* is not visible and only two tubular openings can be traced posteriorly on the splenial part of the dentary.

A short vertical groove on the lateral surface of the angular is probably an oral pit-line (*orp*, Pl. 6, fig. 2).

Exoskeletal shoulder-girdle and squamation

No bones belonging to the exoskeletal shoulder-girdle are visible.

The *scales* are comparatively thick with even posterior margins. There seem to be about 38–40 transverse rows of scales, counted from the posterior margin of the operculum to the middle of the caudal fin base, but as the squamation is in part rather badly damaged, this count is somewhat uncertain. On the anterior part of the body there are some longitudinal rows of scales which are deeper than broad. The dorsal margin of each body scale is drawn out into a peg (*Sc*, Pl. 6, fig. 2).

Paired and unpaired fins

The pectoral, ventral and dorsal fins are missing and only a few lepidotrichia of the anal fin are partly visible.

The caudal fin is hemi-heterocercal; its dorsal margin carries a dense series of rather large fulcra; along the ventral margin of the caudal fin the fulcra are smaller.

REMARKS. The specimen just described, identified by Woodward (1895) as *Pholidophorus latiusculus*, cannot belong to that species, or to *Ph.* (?) *caffii*, as is evident from the descriptions given above. On the contrary it seems to me rather probable that it may be identical with the second *Pholidophorus* species originally mentioned by Agassiz (1832) from Seefeld, *Ph. pusillus*, the material of which belonged to Dr. Alex. Braun and the Karlsruhe Museum. Dr. Erwin Jörg, Landessammlungen für Naturkunde, Karlsruhe, has kindly informed me that no material of *Ph. pusillus* or of *Ph. latiusculus* now exists in this collection; it was probably destroyed in 1942. The original material of *Ph. pusillus* must also be considered lost. The identification of *Ph. pusillus* proposed by Kner (1866) refers to some small fish specimens from Seefeld; in the Univ.-Institut für Paläontologie und Geologie, Innsbruck, some material exists which can be identified as the two upper specimens figured by him on pl. 6, fig. 2 (in reality the specimen *b* on this figure is composed of two specimens!). Their preservation is, however, rather poor, and they show no details (except some branchiostegal rays) which can be directly compared with those preserved in P.4418. But there are some facts favouring the identification of this specimen with *Ph. pusillus*. The size and slender shape of the body is about the same and according to Kner the number of transverse scale-rows amounts to 38–40, just as I have found in the specimen in question. Because of this it seems to me rather improbable that two different *Pholidophorus* species of about the same size and shape should exist in the Seefeld deposits. Specimen P.4418 is most probably an unusually well-preserved, large specimen of *Ph. pusillus*. A final decision as to its relationship with that species must, however, be postponed until more extensive and better preserved material from Seefeld can be thoroughly investigated. Therefore I have only identified the specimen in question as *Ph.* cf. *pusillus* Agassiz.

HORIZON AND LOCALITY. Upper Trias; Seefeld, Tyrol, Austria.

Genus ***PHOLIDOLEPIS*** nov.

PRELIMINARY DIAGNOSIS. Pholidophoridae of rather small size, as far as known similar to *Pholidophorus* but differing in the following features. Exoskeletal cranial bones with very feeble ganoin covering. Supramaxillary 2 with rather well-marked process at antero-dorsal corner. Preoperculum with preopercular sensory canal running near to anterior margin. Fulcra as far as known absent on all fins except along dorsal margin of caudal fin. Scales thin and cycloid, with fine concentric striations.

The generic name *Pholidolepis* is a composite one derived from *Pholidophorus* and *Leptolepis*, so as to indicate the probable intermediate position of the new genus between the two other genera.

TYPE SPECIES. *Pholidolepis dorsetensis* sp. nov.

Pholidolepis dorsetensis gen. et sp. nov.

(Pl. 7; Text-figs. 7, 8)

1895 *Pholidophorus caudalis* Woodward: 458 (*partim*).

PRELIMINARY DIAGNOSIS. *Pholidolepis* of rather small size, up to about 110 mm. in total length. Body elongate, depth about one-fifth of the length without caudal (standard length). Head less than one quarter of standard length. Preopercular sensory canal with about 15 tubules.

HOLOTYPE. British Museum (Nat. Hist.) No. 38164.

MATERIAL. In addition to the holotype, Nos. 35725, 38536, P.3662, P.44708, P.44709 of the British Museum (Natural History) and P.259, of the D.M.S. Watson Collection, Cambridge, have been used for the following description, all more or less badly preserved.

Besides these specimens there is, however, in the British Museum (Natural History) a number of still more defective specimens, probably belonging to *Ph. dorsetensis*: Nos. 35562, 38537, 39862, 43007, P.939, P939*b*, P.939*c*, P.4370, and P.44707.

DESCRIPTION. The holotype has a total length of about 110 mm.; length from tip of snout to posterior margins of hypurals (standard length) about 95 mm. Specimen P.44708 has a standard length of about 98 mm., P.3662 of about 80 mm., which lengths constitute the range for the specimens investigated.

The body is decidedly more elongate than in *Ph. caudalis*, to which species the specimens in question have been referred by Woodward, but as all specimens are crushed the true depth of the body cannot be given with accuracy ; it may be estimated as about one-fifth of the standard length. The length of the skull seems to be less than one quarter of the standard length.

The dermal bones of the head are comparatively thin ; as far as can be seen only the bones of the jaws show a surface ornamentation.

Exoskeletal skull roof

Only very little can be made out regarding the bones belonging to the exoskeletal skull roof because of the bad state of preservation.

The *premaxillary* is not visible in any of the specimens investigated.

The *rostral* may be present in Watson Colln. No. P.259, but only in a defective state.

The *nasal* (*Na*, Pl. 7, fig. 3 ; Text-figs. 7, 8) is rather well preserved in the holotype. It is an elongate, comparatively large bone reminiscent of the corresponding bone in *Ph. bechei* and situated lateral to the foremost part of the lateral margin of the frontal ;

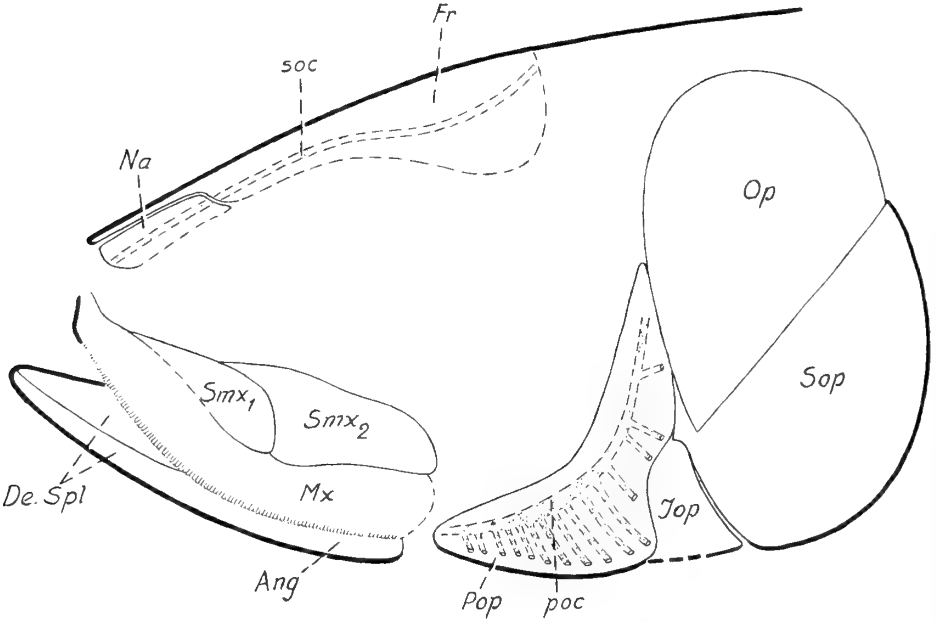

FIG. 7. *Pholidolepis dorsetensis* gen. et sp. nov. Attempted restoration of head in lateral view. ×6·3.

Ang, angular ; *De. Spl*, dentary ; *Fr*, frontal ; *Iop*, interoperculum ; *Mx*, maxillary ; *Na*, nasal ; *Op*, operculum ; *Pop*, preoperculum ; Smx_1, Smx_2, anterior and posterior supramaxillaries ; *Sop*, suboperculum ; *poc*, preopercular sensory canal ; *soc*, supraorbital sensory canal.

anteriorly it is rounded and reaches about as far forwards as the anterior tip of the frontal. Its lateral outline cannot, however, be determined exactly because of damage and consequently it is impossible to say whether a notch or fenestra for the posterior nostril is present as in *Ph. bechei*.

The *frontal* (*Fr*, Pl. 7, figs. 1, 3; Text-figs. 7, 8) is preserved in the holotype, in 38536 and in Watson Colln. No. P.259, but in all these specimens it is more or less defective because of crushing. Its anterior half is, judging from the holotype, rather broad but tapers towards the anterior rounded tip at the level of the nasal. The posterior half broadens considerably but its posterior margin cannot be accurately defined in any specimens. There are no traces of surface ornamentation on the frontal.

No *supraorbitals* can be seen clearly in any specimens but some small bone fragments lateral to the lateral margins of the frontal and nasal in the holotype (*So*, Pl. 7, fig. 3) may belong to an anterior supraorbital similar to that bone in *Ph. bechei*.

Only the sensory canal of the *dermosphenotic* seems to be present in the holotype, the rest of the bone is missing. In the other specimens investigated this bone is not visible.

The *parietal*, the *dermopterotic* and the *extrascapular* are, in all specimens, too damaged for description.

Dermal bones of cheek and opercular apparatus

The *maxillary* (*Mx*, Pl. 7, figs. 1–3; Text-fig. 7) is more or less completely preserved in the holotype as well as in 38536 and P.44708, and Watson Colln. No. P.259, but in none of them is it undamaged and its anterior, antero-mesially directed tip is not visible. Its posteriorly directed, lateral part is, as usual, evenly curved with the convexity directed ventrally. Its lateral surface is provided with a weak ornamentation, consisting of more or less oblique striations as can be seen in the holotype and particularly in P.44708 (Pl. 7, fig. 2). In the latter the ventral border of the maxillary carries a dentition similar to that in *Leptolepis*.

The *supramaxillaries* are only visible in P.44708 and Watson Colln. No. P.259. The anterior one, supramaxillary 1 (Smx_1, Pl. 7, fig. 2), is partly preserved in the first named specimen and seems to be much longer antero-posteriorly than the corresponding bone in *Pholidophorus*, thus more like that of *Leptolepis*, but as its anterior part is damaged its outline cannot be made out with accuracy. If there exists any surface ornamentation on supramaxillary 1 it must be only weakly developed. Supramaxillary 2 (Smx_2, Pl. 7, fig. 2) is also best preserved in P.44708; its antero-dorsal process is decidedly more pronounced than in *Pholidophorus* but not nearly so long as in *Leptolepis*. The lateral surface of supramaxillary 2 carries a weak longitudinal striation somewhat recalling that in *Ph. latiusculus* but much weaker. Both supramaxillaries seem to overlap the dorsal margin of the maxillary but only to a small degree.

The *bones of the infraorbital series* as well as the *suborbital* are practically missing in all specimens.

The *preoperculum* (*Pop*, Pl. 7, figs. 1, 3; Text-fig. 7) is present in most specimens but in none is it undamaged. It is best preserved in 38536 and has the same general

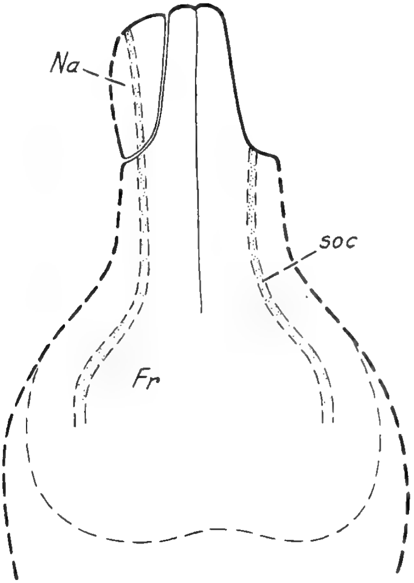

FIG. 8. *Pholidolepis dorsetensis* gen. et sp. nov. Attempted restoration of head in dorsal view. ×6·3. Lettering as in Fig. 7.

shape as in *Leptolepis*, the anterior margins of the dorsal and the antero-ventral limbs meeting to enclose an angle, but it has a deep notch on its posterior margin as in *Ph. bechei*. There is no process on its anterior margin at the angle as there is, for example, in *Leptolepis normandica*.

The *operculum* (*Op*, Text-fig. 7) is very damaged by crushing or is lacking in all specimens except Watson Colln. No. P.259. Judging from this specimen its general shape is about the same as in *Pholidophorus*.

The *suboperculum* (*Sop*, Text-fig. 7) is also only preserved in Watson Colln. No. P.259. It seems to be comparatively deep, and the process at its antero-dorsal corner is longer and more pointed than in *Ph. bechei*.

Only the posterior part of the *interoperculum* (*Iop*, Text-fig. 7) is exposed in the specimen just named and in 38536, and nothing can be said about its general shape.

Lower jaw

The lower jaw is partly visible in the holotype and in 38536 and P.44708, and Watson Colln. No. P.259. Its outline cannot be determined, but in all specimens mentioned the anterior part of the *dentary* (*De. Spl*, Pl. 7, figs. 1–3; Text-fig. 7) ascends rather gently as in *Pholidophorus*, not abruptly as in *Leptolepis*; from this it may be concluded that the general shape of the lower jaw is also almost as in *Pholidophorus*. The ridge separating the dental and the comparatively low splenial parts of the dentary is clearly visible. In specimen P.44708 (Pl. 7, fig. 2) the lateral surface of the *angular* (*Ang*, Pl. 7, fig. 2) is provided with a surface ornamentation of thin longitudinal ridges or streaks similar to those on the maxillary.

A *gular plate* is not visible in any of the specimens investigated.

Sensory canal system of head

The sensory canal system of the head is only partly visible and the description must therefore be rather incomplete.

Part of the *supraorbital sensory canal* (*soc*, Pl. 7, figs. 1, 3; Text-figs. 7, 8) can be seen in the holotype, in 38536 and in Watson Colln. No. P.259. In its foremost part, piercing the nasal bone, the canal is straight and continues straight backwards in the anterior, narrower part of the frontal. As the frontal broadens the canal bends laterally and then runs obliquely postero-mesially; its posterior part in the parietal cannot be followed. No tubules or pores can be observed with accuracy except in Watson Colln. No. P.259, where three postero-mesially directed tubules are given off from the mesial side just before and at the bend of the canal.

Almost nothing can be made out regarding the *infraorbital sensory canal*. In the holotype only a small part of a sensory canal is present, probably the canal in the dermosphenotic (*Dsph*, Pl. 7, fig. 3), with the backward bend of the main canal and the antero-dorsally directed tubule.

Cephalic division of main lateral line

The cephalic division of the main lateral line can only be followed in the preoperculum.

The *preopercular sensory canal* (*poc*, Pl. 7, fig. 3) and its tubules follow the same general pattern as in *Ph. bechei*, but the number of tubules is lower. In the ventral limb of the preoperculum there are in 38536 eleven tubules, obviously corresponding to the 13 ventrally situated tubules in *Ph. bechei*; the posterior ones are, as in that species, long, narrow and curved with the convexity anteriorly directed. Dorsal to these tubules there are four shorter tubules, corresponding to the five to six shorter tubules in *Ph. bechei*. The total number of tubules is thus 15 in this specimen; in the others investigated the preoperculum is too damaged to allow a count of the tubules, but as far as can be observed the general pattern is the same as that just described for 38536.

Exoskeletal shoulder girdle and squamation

Parts of the *cleithrum* are exposed in many of the specimens but in no case can it be studied in any detail. No other bones belonging to the exoskeletal shoulder-girdle can be identified.

The squamation consists of thin cycloid scales with delicate concentric striations.

The lateral line

No lateral line can be seen with certainty in any of the specimens available.

Axial skeleton and paired and unpaired fins

The *vertebral centra* are thin bony cylinders which are, however, crushed or displaced in all specimens investigated ; their undamaged shape cannot be described nor can their number be determined with any degree of accuracy. The neural and haemal spines are comparatively long.

The fins are in part rather well preserved but in the dorsal and anal fins the lepidotrichia are poorly preserved. No fulcra can be observed on the pectoral, ventral, dorsal or anal fins, but with regard to the two last named fins this statement needs confirmation on better preserved material.

The *pectoral fin* has a rather high number of lepidotrichia ; in P.3662 and P.44709, and Watson Colln. No. P.259 I have counted 19 rays, in P.44708 20 rays.

In the *ventral fin* the number of lepidotrichia is also rather high ; in P.44708 and P.44709 and Watson Colln. No. P.259 their number is 15 or about as in *Ph. bechei.*

The *dorsal fin* is poorly preserved in all specimens, but in P.44709 the number of dorsal radials can be determined as 12, the anterior one as usual being composed of two elements.

The *anal fin* has 8 radials in the holotype and in 38536 and P.44709.

The *caudal fin* carries along its dorsal margin rather long and stout fulcra ; no fulcra have been observed on the ventral margin of the fin.

REMARKS. There is no doubt that the specimens just described were erroneously identified as *Pholidophorus caudalis* Woodward, as can be seen from a comparison with the following description (see p. 411), and I have been unable to find another described species to which they can be referred. Consequently I have assigned them to a new species for which I propose the name *Pholidolepis dorsetensis.* Unfortunately the material on which the new species is based is rather defective, and I am not fully convinced that all specimens here referred to *Ph. dorsetensis* really belong to that species. In particular I am in doubt regarding Watson Colln. No. P.259, which shows very few details directly comparable with those exposed in the other specimens ; it is especially unfortunate that almost nothing of the characteristic preoperculum is preserved. On the other hand I have not found any differences justifying its separation from the other specimens. More complete and better preserved material is necessary for a fuller description of *Ph. dorsetensis.*

HORIZON AND LOCALITY. Lower Lias ; Lyme Regis, Dorset.

Genus ***PHOLIDOPHOROIDES*** Woodward

1941 *Pholidophoroides* Woodward : 89.

EMENDED DIAGNOSIS. Pholidophoridae of medium size. Exoskeletal cranial bones and scales with ganoin covering. Nasal well developed and well separated from its antimere by the frontals, anteriorly reaching level of anterior margin of frontals. A single, well-developed supraorbital. Maxillary rather stout and deep with more or less pronounced convexity on dorsal margin ventral to infraorbital 1 (lachrymal) and supramaxillary 1 ; posterior margin notched. Two supramaxillaries, not markedly overlapping dorsal margin of maxillary, supramaxillary 2 without marked process at antero-dorsal corner. Antorbital well developed, more than five (seven?) infraorbitals. Preoperculum with preopercular sensory canal running along middle of bone, about equidistant from anterior and posterior margins. Lower jaw not markedly deep, greatest depth in posterior third of its length ; dentary with smooth dental part, separated from splenial part by strong ridge. Dorsal fin above interspace between ventral and anal fins. Fulcra present along anterior margin of paired as well as unpaired fins. Caudal fin hemi-heterocercal with dorsal and ventral margins fulcrated. Scales moderately thick ; some longitudinal series of flank-scales higher than broad.

TYPE SPECIES. *Pholidophoroides crenulata* (Egerton).

REMARKS. When creating the new genus *Pholidophoroides* Woodward (1941 : 89) diagnosed it in the following manner : " One species from the Lower Lias, *P. crenulatus* Egerton, is distinguished from *Pholidophorus* by its smaller scales, which are less deepened on the flank. The scales are arranged in from 50 to 60 transverse rows, and those of the anterior part of the lateral line are less than twice as deep as broad. The scales are also comparatively thin, often displaying their concentric lines of growth. The fins are small like those of *Pholidophorus*. The maxilla seems to be comparatively stout. Ring vertebrae are conspicuous in the abdominal region. *P. crenulatus* may therefore be regarded as the type-species of a distinct genus, *Pholidophoroides*. . . . The Lower Liassic species, *P. caudalis* A. S. Woodw., probably also belongs to *Pholidophoroides*."

The diagnosis given above is mainly based on the taxonomic characteristics of the redescribed type species, but also taking into consideration the other species here ascribed to the genus *Pholidophoroides*.

Pholidophoroides crenulata (Egerton)

(Pls. 8, 9, 10 ; Pl. 15, figs. 3, 4, 5, 8 ; Text-figs. 9–11)

1843	*Pholidophorus crenulatus* Egerton : 184.
1852	*Pholidophorus crenulatus* Egerton ; Egerton, pl. 5.
1887	*Isopholis crenulatus* (Egerton) Zittel : 216.
1890	*Pholidophorus crenulatus* Egerton ; Woodward & Sherborn : 146.
1895	*Pholidophorus crenulatus* Egerton ; Woodward : 463, pl. 12, fig. 6.
1941	*Pholidophoroides crenulatus* (Egerton) Woodward : 89.

DIAGNOSIS. *Pholidophoroides* of medium size, at least up to 150 mm. in total length. Greatest depth of the body about one quarter of the standard length or slightly more (*ca.* 25–30% of that length). Depth of the caudal peduncle less than one-tenth (*ca.* 8–9%) of the standard length. Maxillary deep. Preopercular sensory canal with 16 or 17 tubules. Scales rather thin, in about 45–50 transverse rows reckoned from the hind margin of operculum to the middle of the caudal fin ; about four longitudinal rows of body scales somewhat deeper than broad and with the hind margin crenulated.

LECTOTYPE. British Museum (Natural History) Nos. P.572 and P.573 are the two specimens originally described and figured by Egerton (1843, 1852) and designated as " The two type specimens " by Woodward (1895 : 463). P.573 is the more complete specimen (standard length about 82 mm., height of body about 21 mm., height of caudal peduncle 7·5 mm.) and is therefore selected as lectotype.

Material. In addition to the lectotype, the specimens mainly used for the following description are P.153, P.421, P.572, P.1046*a*, *b*, P.4415, 38110, 38739, 38738 ; they agree in all comparable features with P.573.

Description. The total length of the largest specimen, P.1046*a*, is 150 mm. ; its length from the tip of the snout to the hindmost scale in the lateral line (standard length) is about 125 mm. The other specimens in the British Museum (Natural History) have a standard length from 120 to 74 mm. The greatest depth of the body is about one quarter of the standard length or slightly more (*ca.* 25–30% of this length) ; the depth of the caudal peduncle is somewhat less than one-tenth (8–9%) of the standard length. The length of the head is about one quarter of the standard length, generally slightly less (*ca.* 22–25%).

The ventral fins are situated approximately midway between the tip of the snout and the hindmost lateral line scale and the distance between the base of the ventrals and the origin of the anal is about 75–85% of the distance between the bases of the pectoral and ventral fins.

A good figure of the entire fish is given by Woodward (1895, pl. 12, fig. 6).

The specimens most thoroughly investigated are rather well preserved with the bones of the skull exposed to a great extent, and consequently they allow the following description to be made.

Exoskeletal skull roof

The *premaxillary* (*Pmx*, Pl. 10, figs. 1, 2 ; Text-fig. 9) is visible in P.1046*a*, *b*, and to some extent also in P.4415 and 38738. It is comparatively stout with the postero-dorsal margin weakly S-shaped. The straight antero-ventral margin is serrated, forming a single row of teeth. The lateral surface of the premaxillary is densely set with ganoin tuberculations.

The *rostral* (*Ro*, Pl. 9 ; Text-figs. 9, 10) is best preserved in 38110, but cannot be studied in any detail. The part pierced by the ethmoidal commissure is a little swollen dorsally ; posteriorly its lateral parts are concave and rather thin at the margin.

The *nasal* (*Na*, Pls. 8, 9 ; Text-figs. 9, 10) is also best exposed in 38110. It is an oblong, rather broad bone, situated posterior to the lateral parts of the rostral. It is, on the whole, oval but its antero-lateral and postero-lateral margins (lateral to the posterior opening for the supraorbital sensory canal) are concave, probably marking the postero-mesial and antero-mesial limits of the anterior and posterior nasal openings respectively. The nasals are separated by the narrow anterior part of the frontals.

The *frontal* (*Fr*, Pls. 8, 9 ; Pl. 10, fig. 2 ; Pl. 15, fig. 4 ; Text-figs. 9, 10) is rather narrow in its anterior part, mesial to the nasal, but it broadens considerably posterior to the nasal ; from there its lateral margin runs at first almost straight posteriorly, but behind the orbit the bone widens again and has its greatest breadth in its posterior

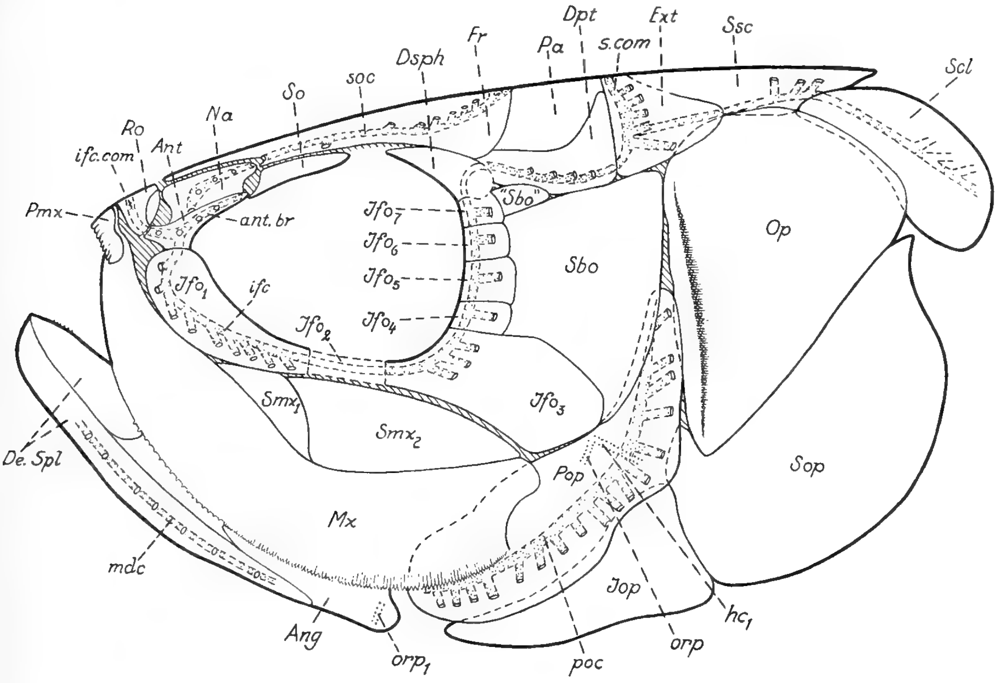

FIG. 9. *Pholidophoroides crenulata* (Egerton). Attempted restoration of head in lateral view. ×5 approx.

Ang, angular ; *Ant*, antorbital ; *De. Spl*, dentary ; *Dpt*, dermopterotic ; *Dsph*, dermosphenotic ; *Ext*, extrascapular ; *Fr*, frontal ; *Ifo*$_1$–*Ifo*$_7$, infraorbitals 1 to 7 ; *Iop*, interoperculum ; *Mx*, maxillary ; *Na*, nasal ; *Op*, operculum ; *Pa*, parietal ; *Pmx*, premaxillary ; *Pop*, preoperculum ; *Ro*, rostral ; *Sbo*, suborbital ; " *Sbo* ", "accessory suborbital" ; *Scl*, supracleithrum ; *Smx*$_1$, *Smx*$_2$, anterior and posterior supramaxillaries ; *So*, supraorbital ; *Sop*, suboperculum ; *Ssc*, suprascapula ; *ant. br*, antorbital branch of infraorbital sensory canal ; *ap*, anterior pit-line ; *ifc*, infraorbital sensory canal ; *ifc. com*, ethmoidal commissure ; *mdc*, mandibular sensory canal ; *mp*, middle pit-line ; *poc*. preopercular sensory canal ; *pp*, posterior pit-line ; *s. com*, supratemporal commissure ; *soc*, supraorbital sensory canal.

part. Its postero-lateral corner is rounded off and its posterior margin is irregularly wavy. The suture between the frontals is practically straight anteriorly ; posteriorly its course is difficult to follow, but it does not seem to be markedly sinuous.

A strong *supraorbital* (*So*, Pl. 9 ; Text-figs. 9, 10) is situated behind the posterior nasal opening and lateral to the broadened part of the frontal posterior to the nasal. Anteriorly its dorsal surface bulges a little and is ornamented with some small elevations. In dorsal aspect the lateral border of the supraorbital is almost straight, ending anteriorly in a point.

A very small bone between the lateral margin of the frontal and the anterior tip of the dermosphenotic in 38739 (*So*?, Pl. 8 ; Pl. 15, fig. 4) may perhaps be a small second supraorbital ; in P.1046*b* a similar small bone may be traced, but as I have not found a corresponding element in any of the other specimens investigated, it may perhaps be only a fragment of the anterior part of the dermosphenotic or of the lateral frontal margin.

The *dermosphenotic* (*Dsph*, Pls. 8, 9; Pl. 10, fig. 2; Pl. 15, fig. 4; Text-figs. 9, 10) is mostly more or less crushed on the underlying autosphenotic. Its anterior part, situated along the postero-lateral margin of the frontal, is pointed and a little curved and constitutes the postero-dorsal border of the orbit. Its posterior margin cannot be determined with accuracy, but according to P.1046*b* it seems to be rounded off.

The margins of the *parietal* (*Pa*, Pl. 10, fig. 2; Pl. 15, fig. 4; Text-figs. 9, 10) are difficult to determine, as the skull roof of the single specimen showing the cranial bones in dorsal view, 38110, is much crushed in its posterior part, but judging from 38739 it has a rather wide extension laterally, thus being much broader than long.

The *dermopterotic* (*Dpt*, Pls. 8, 9; Pl. 10, fig. 2; Pl. 15, fig. 4; Text-figs. 9, 10) is comparatively narrow in its anterior part between the frontal and the dermosphenotic but broadens continuously backwards, attaining its greatest breadth at its straight posterior margin.

The shape of the *extrascapular* (*Ext*, Pl. 9; Pl. 10, fig. 2; Text-figs. 9, 10) cannot be determined; its lateral part is, however, almost triangular with the postero-lateral margin a little convex and the postero-mesial margin slightly concave. The mesial part of the extrascapular is not preserved in any of the specimens investigated.

Dermal bones of cheek and opercular apparatus

The *maxillary* (*Mx*, Pls. 8, 9; Pl. 10, figs. 1, 2; Text-fig. 9) is strikingly large and stout. Its anterior, mesially directed part is only partly visible in the specimens investigated, but seems to be rather low; its dorsal margin has an arched, thickened edge with the convexity directed ventrally, fitting the concavity on the postero-dorsal margin of the premaxillary; the surface covered by the premaxillary is smooth. The lateral, posteriorly directed part of the maxillary increases rapidly in height; its ventral margin is evenly convex, but its dorsal margin, on the whole concave, has a marked convexity below infraorbital 1 and supramaxillary 1. The posterior margin of the maxillary is rather deeply notched. The anterior half of the lateral surface has, nearest to the premaxillary, an ornamentation of densely set tuberculations like those on the premaxillary; posteriorly the ornamentation becomes a longitudinal striation parallel to the margins. The posterior half of the lateral margin is smooth except for some longitudinal striations along the dorsal margin; in P.4415 there are, also, some longitudinal ganoin streaks parallel to the ventral margin. A delicate comb-like dentition, about as in *Leptolepis*, is present along the posterior half of the ventral margin, the teeth decreasing in length anteriorly. No teeth can be observed along the anterior half of the ventral margin, but whether this is the actual condition or only dependent upon the state of preservation, must remain undecided.

Two *supramaxillaries* are situated dorsal to the maxillary, not markedly overlapping its dorsal margin. The anterior one, supramaxillary 1 (Smx_1, Pls. 8, 9; Pl. 10, figs. 1, 2; Text-fig. 9), is rather small, almost semicircular, and has a well-

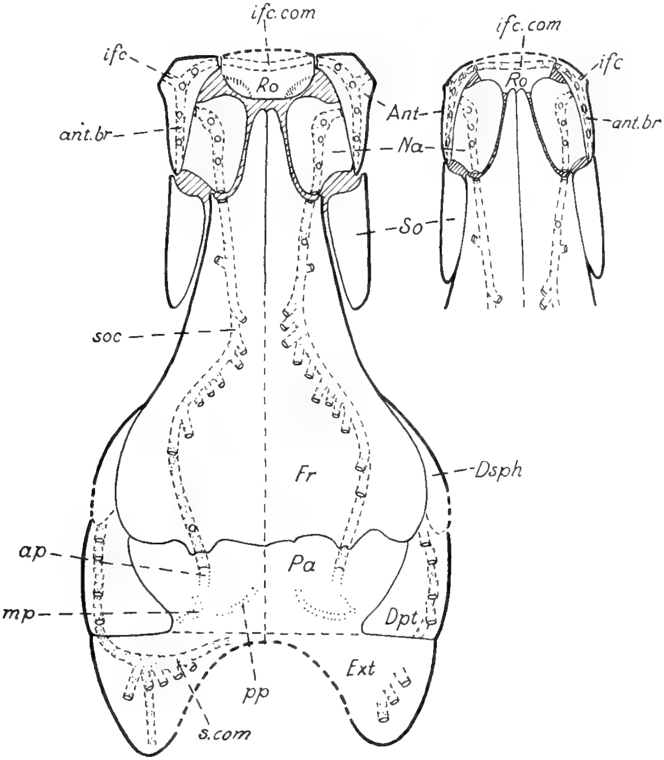

FIG. 10. *Pholidophoroides crenulata* (Egerton). Attempted restoration of head in dorsal view, the snout flattened, with (right) the probable mutual positions of the bones of the snout. ×5 approx. Lettering as in Fig. 9.

marked concentric striation on its lateral surface. The posterior one, supramaxillary 2 (*Smx*$_2$, Pl. 8 ; Pl. 10, figs. 1, 2 ; Text-fig. 9), is considerably larger ; its anterior margin is concave, fitting the convexity of supramaxillary 1, but its antero-dorsal corner is not markedly produced into a process. The dorsal and ventral margins of supramaxillary 2 are evenly convergent towards the posterior tip of the bone. Supramaxillary 2 also has a well-marked concentric striation on its lateral surface.

The bones of the infraorbital series are generally well preserved, only infraorbital 2 is lacking in all specimens investigated.

The *antorbital* (*Ant*, Pls. 8, 9 ; Pl. 10, fig. 2 ; Text-figs. 9, 10) is an almost ⊥-shaped bone situated ventro-lateral to the rostral and the nasal ; its posterior tip reaches the antero-lateral tip of the supraorbital.

Ventral to the antorbital and between it and the anterior part of the maxillary and supramaxillary 1 there is a large *infraorbital* 1 or *lachrymal* (*Ifo*$_1$, Pl. 8 ; Pl. 10, figs. 1, 2 ; Text-fig. 9). Its anterior margin is semicircular and its ventral margin is slightly convex ; its dorsal margin is not clearly visible but is probably slightly concave.

Infraorbital 3 (*Ifo*$_3$, Pls. 8, 9 ; Pl. 10, figs. 1, 2 ; Text-fig. 9) is comparatively large, stretching from the orbit to the anterior margin of the preoperculum ; its antero-ventral margin is slightly concave.

The following bones in the series, dorsal to infraorbital 3, are crushed, displaced or lacking in most specimens, but judging from 38110 and P.1046*a* and *b* there are about four small, square infraorbitals between infraorbital 3 and the dermosphenotic (*Ifo*$_4$, *Ifo*$_5$, *Ifo*$_6$, *Ifo*$_7$, Pl. 9 ; Text-figs. 9, 11) ; in 38110 there seems to exist one more element in the series on the right side (*Ifo*$_8$?, Pl. 9 ; Text-fig. 11), but here the arrangement is rather obscure.

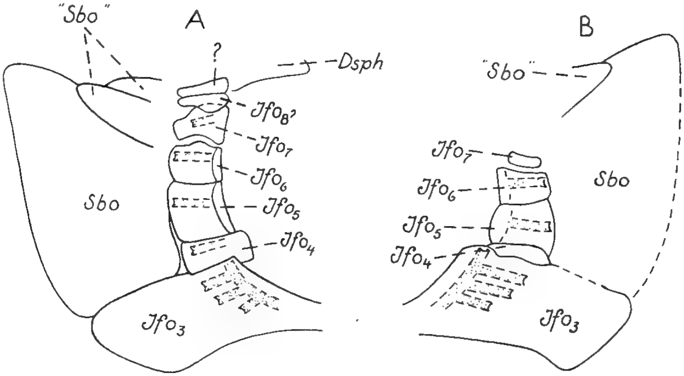

FIG. 11. *Pholidophoroides crenulata* (Egerton). Infraorbital 3, postorbital infraorbitals and suborbitals (same specimen as on Pl. 9). Lettering as in Fig. 9 ; A right side, B left side. B.M. 38110. × 5 approx.

A large *suborbital* (*Sbo*, Pls. 8, 9 ; Pl. 10, fig. 2 ; Text-fig. 9) bone is situated posterior to infraorbitals 4–7, covering the hyomandibular ; as a rule it is crushed in the middle on to the strong lateral crest of this latter bone. Dorsal to the suborbital there are in 38110 (" *Sbo* ", Pl. 9 ; Text-figs. 9, 11) two small bones on the right side and a single similar bone on the left side, tapering posteriorly and, like the suborbital, with a conspicuous concentric surface striation. A single similar bone is also seen in 38738. It is difficult to interpret these bones ; they may be homologous to the supraspiracular plates described by Stensiö (1932, text-fig. 67) in *Perleidus stoschiensis* Stensiö and by Lehman (1952, text-figs. 85, 86) in *P. madagascariensis* Piveteau. But they are more likely to be " accessory suborbitals ". In many holosteans there is a series of suborbitals posterior to the infraorbitals which may fuse or remain separate in various ways. Thus, for example the posterior part of infraorbital 3 in *Pholidophoroides* as well as in *Leptolepis* is probably the originally ventralmost suborbital, secondarily fused with infraorbital 3 (*cf.* Stensiö 1947 : 164), whereas the others as a rule fuse into a single, large suborbital. In *Ph. crenulata* the dorsalmost component or components may remain free, at least in some specimens.

The peculiar condition of the dorsalmost infraorbitals and the " accessory suborbitals " on the right side in 38110 is also difficult to interpret. It may be due to an ontogenetic disturbance or perhaps to regeneration after an injury.

The *preoperculum* (*Pop*, Pls. 8, 9 ; Pl. 10, figs. 1, 2 ; Text-fig. 9) is a weakly crescentic bone with a dorsal, more or less vertical limb and an antero-ventrally directed ventral limb, much broader than the dorsal one. Its posterior margin has, ventral to the more or less pronounced angle between the two limbs, a characteristic shallow concavity or indentation.

The *operculum* (*Op*, Pls. 8, 9 ; Pl. 10, figs. 1, 2 ; Text-fig. 9) is roughly triangular ; its anterior, vertical margin and its postero-ventral margin are straight and its dorsal margin rounded off. The anterior margin is thickened ventral to the facet for the processus opercularis of the hyomandibular.

The *suboperculum* (*Sop*, Pls. 8, 9 ; Pl. 10, figs. 1, 2 ; Text-fig. 9) is comparatively large and its antero-dorsal process anterior to the ventral tip of the operculum is remarkably broad and strong. According to 38739, P.1046*b* and P.4415 the posterior margin of the suboperculum has dorsally a shallow concavity or indentation.

The *interoperculum* (*Iop*, Pl. 8 ; Pl. 10, figs. 1, 2 ; Text-fig. 9) has a roughly triangular shape, with the posterior and ventral margins a little concave.

Branchiostegal rays and gular plate

There seems to be a rather large number of *branchiostegal rays* ; they are best exposed in P.4415 (*R. Br*, Pl. 10, fig. 1), on which 16 rays can be seen, but more small ones may exist in front of the anteriormost of the exposed rays.

P.1046*b* shows parts of a rather large median *gular plate* (*Gu*, Pl. 10, fig. 2). Its anterior tip is a little bent upwards, but as the lateral margin is broken off, nothing can be stated regarding its shape.

Lower jaw

The lower jaw is generally only partly exposed, its dorsal margin being covered by other bones in all specimens investigated except in P.153 (Pl. 15, fig. 5), where the lower jaw is isolated and its outline can be determined rather exactly ; its greatest depth is somewhat less than half of its length.

The ventral, splenial part of the *dentary* (*De. Spl*, Pl. 8 ; Pl. 10, figs. 1, 2 ; Pl. 15, fig. 5 ; Text-fig. 9) is limited dorsally by a well-marked ridge, and its lateral surface is ornamented with longitudinal ganoin striations and rugosities. The dental part is only gently ascending anteriorly and its lateral, slightly convex surface is not ornamented. In P.153 a few very small teeth can be observed on its margin. Approximately between the first and second third of the length of the lower jaw the dental part ascends abruptly and is thickened ; this thickening obviously corresponds to the dorsally directed thickening of the dentary in *Leptolepis*.

Only the ventral part of the *angular* (or more precisely *angulo-supra-angular*, though no limit between the two components can be determined) is generally exposed (*Ang*, Pl. 8 ; Pl. 10, figs. 1, 2) ; in P.153 (*Ang*, Pl. 15, fig. 5) it is, however, entirely exposed although partly crushed and defective. Because of this it is not possible to determine its anterior margin in the dorsal part ; anteriorly it is rounded. Postero-ventrally the lower jaw ends in a conical point, reminiscent of a dermarticular, but as no suture can be seen separating it from the rest of the angular, it must be only the hindmost part of that bone. The postero-ventral part of the lateral surface of the angular, obviously exposed when the mouth is closed, is ornamented with ganoin streaks and small tuberculations, for the rest the lateral surface of the bone is smooth.

In P.4415 the hindmost part of the right lower jaw is exposed in medial view, showing the *articular* (*Art*, Pl. 10, fig. 1; Pl. 15, fig. 8) with its articular fossa for the quadrate and a small but well marked ossified processus coronoideus.

No true dermarticular has been observed.

Sensory canal system of head

The sensory canal system of the head is well developed as canals embedded in the bone tissue with short tubules and pores.

The *supraorbital sensory canal* (*soc*, Pl. 9; Pl. 15, fig. 3; Text-figs. 9, 10) pierces the nasal, the frontal and the parietal. The following description is based on 38110.

In the nasal the canal describes an arch from near the anterior end of the lateral margin to near the mid-line of the bone and then passes almost straight back to the posterior tip of the nasal. At the bend it possesses an elevated, rather large pore, and further back there are two more pores or short tubules. There is no evidence of a communication between the supraorbital and the infraorbital sensory canals.

From the nasal the canal passes over into the frontal at its concave margin behind the nasal, running at first almost straight backwards and then curving in a postero-lateral direction parallel to the lateral margin of the frontal before continuing postero-medially to the posterior margin of the bone. The number of tubules issuing from the frontal part of the canal seems to vary a little on both sides. On the dorsal side of the anterior straight part of the right canal there is a small pore, and further posteriorly a short tubule seems to issue from the lateral side; where the canal bends it gives off a mesial series of 9 tubules of various lengths, and further backwards there seem to be two more, posteriorly directed tubules. On the left side a conspicuous tubule issues from the lateral side of the anterior straight part of the canal (a corresponding tubule is seen also in 38738); more posteriorly the canal gives off at least 7 postero-mesially directed tubules and at least one posteriorly directed tubule; a short distance anterior to the posterior margin of the frontal there is a conspicuous pore on the dorsal surface of the canal.

The parietal contains only a very short part of the supraorbital sensory canal without pores or tubules, ending as a short groove which represents the anterior pit-line.

The *infraorbital sensory canal* (*ifc*, Text-figs. 9, 11) begins with a slightly arched ethmoidal commissure in the rostral, joining the canals of both sides; no pores or tubules belonging to the ethmoidal commissure can be observed.

From the rostral the canal passes over into the antorbital and pierces its anterior broader part, sending out posteriorly an antorbital branch. The antorbital part of the sensory canal system possesses four dorsal pores of which two are on the main canal, one on its mesial part and one about dorsal to the point where the antorbital branch comes off, and one is in the anterior and one in the posterior part of this branch.

From the antorbital the infraorbital sensory canal passes over into infraorbital 1 (lachrymal) and runs parallel to the anterior and ventral margins of this bone. From its anterior, arched part the canal sends out two very short, forwardly directed tubules, sometimes looking like wide pores, and from the ventral side there issue about 7 postero-ventrally directed tubules.

As infraorbital 2 is missing in all specimens available, nothing can be said about the part of the canal belonging to this bone.

In infraorbital 3 the number of tubules seems to be subject to rather great individual variation. In P.1046*b* (Pl. 10, fig. 2) the somewhat defective infraorbital 3 shows three large tubules, in P.421 and 41857 there are likewise three tubules and in 38110 there are three large, well separated tubules, whereas in P.1046*a* and 38738 four tubules are situated rather close together ; in 38739 there are two groups each of three small tubules.

In the remaining small infraorbitals the sensory canal seems to give off a single, posteriorly directed tubule in each bone.

Regarding the course of the infraorbital sensory canal in the dermosphenotic nothing can be stated with accuracy because of the defective state of preservation of this bone.

In the dermopterotic the sensory canal runs along the lateral margin of the bone. Dorsally it gives off four short tubules. To what extent this canal belongs to the sensory canal system of the head and to the cephalic division of the main lateral line, respectively, is a question which must be left open. The point at which it gives off the preopercular sensory canal cannot be determined.

Cephalic division of main lateral line

On the posterior part of the parietal there is a transverse, slightly arched groove with its convexity directed postero-mesially ; this groove may represent the middle pit-line (*m.p*, Pl. 15, fig. 3 ; Text-fig. 10). A groove mesial to it may be the posterior pit-line (*pp*, Pl. 15, fig. 3 ; Text-fig. 10).

The cephalic division of the main lateral line passes over from the dermopterotic into the extrascapular and continues backwards to the suprascapular, giving off mesially the supratemporal commissure (*s. com*, Text-figs. 9, 10), but the course of these canals cannot be followed exactly. Judging from the fragmentary extrascapular on the left side in 38110 (Pl. 9) the main canal gives off laterally a large tubule, and at least four tubules are given off posteriorly from the lateral part of the supratemporal commissure ; its mesial part is missing. In the fragmentary right extrascapular of the same specimen there seem to be two tubules given off laterally from the main canal ; the supratemporal commissure and its tubules are lacking.

The *preopercular sensory canal* (Text-fig. 9) pierces the preoperculum in the middle of its length almost parallel to its anterior and posterior margins. In 38739 (Pl. 8) it gives off posteriorly 17 tubules, almost evenly distributed over the whole length of the canal, five of which are situated in the dorsal limb of the bone, dorsal to the obtuse posterior angle, but as the antero-ventral tip is not entirely exposed it is possible that one more tubule ought to be added to this number. In P.1046*b* (Pl. 10, fig. 2) there are likewise 17 tubules, four of which are situated in the dorsal limb, but between tubules 7 and 8 reckoned from the antero-ventral tip of the bone there is in addition a short tubule, probably only a branch of tubule 7; tubules 1–7 are situated close together. Specimen 48009 also shows 17 tubules issuing from the morphologically posterior side of the preopercular sensory canal, whereas in P.421 and P.3595 only 15–16 tubules could be determined with accuracy. In 38738 five tubules are clearly visible in the dorsal limb of the preoperculum.

In P.1046*b* and P.4415 the lateral surface of the preoperculum possesses a well-marked groove which may be the posterior portion of the anterior division of the supramaxillary pit-line (hc_1, Pl. 10, figs. 1, 2). A postmaxillary pit-line cannot be traced in any of the specimens investigated except in P.421; in this specimen the middle of the lateral surface of the preoperculum shows a vertical groove which I interpret as the postmaxillary pit-line.

The *mandibular sensory canal* (*mdc*, Text-fig. 9) cannot be followed because of the thickness of the splenial part of the dentary, but in P.1046*b* (Pl. 10, fig. 2) many of its short, backwardly directed tubules are discernible, their openings being accentuated by ganoin thickenings.

On the lateral surface of the angular there is postero-ventrally a short vertical groove in P.153 and P.4415 which must be the oral pit-line (orp_1, Pl. 10, fig. 1; Pl. 15, figs. 5, 8).

Exoskeletal shoulder girdle and squamation

Very little can be said about the *suprascapula* and the *supracleithrum*, which are only fragmentarily preserved in 38110 (*Ssc*, *Scl*, Pl. 9) and almost entirely destroyed by crushing in the other specimens investigated; the outline of the suprascapula and the supracleithrum as given in the attempted restoration (*Ssc*, *Scl*, Text-fig. 9) is consequently very doubtful.

The *cleithrum* and the *postcleithrum* are not sufficiently exposed in the specimens available to allow their description in any detail.

The *scales* are arranged in about 45–50 transverse rows reckoned from the hind margin of the operculum to the middle of the caudal fin; posterior to the last row there are about 8–9 rows on the body axis dorsal to the lateral line, thus in all about 55–60 rows, which accords well with Woodward's (1941) statement of about 50–60 transverse rows. On the body there are generally four, sometimes only three, longitudinal rows of enlarged scales, the deepest being about twice as deep as broad and with the posterior margin crenulated; the number of points on the posterior margin is about 8, seldom up to 10 on the largest scales, but it decreases posteriorly in accordance with the decreasing depth of the scales.

The scales are comparatively thick on the middle and posterior parts of the body as well as on the tail; on the anterior part of the body they are, however, thinner and show, as stated by Woodward, a concentric striation. In most specimens investigated this striation is visible only in a few transverse rows behind the skull; in P.1046*b*, however (Pl. 10, fig. 2), such thin striated scales cover the whole anterior part of the body and extend posteriorly almost to the level of the pelvic fin base.

Lateral line

The lateral line pierces the suprascapula, and seems to give off three short but rather wide, mesially to postero-mesially directed tubules. In the supracleithrum the course of the sensory line is not clearly visible in any of the specimens available, but it seems to give off three postero-mesially directed tubules.

The anterior lateral line scales are rather indistinct, but more posteriorly they are clearly visible, each scale having a distinct pore on its lateral surface. The course of the lateral line is almost straight, along the middle of the body, ending at the base of the middle caudal lepidotrichia.

Axial skeleton and paired and unpaired fins

The *axial skeleton* consists of rather thin ring-vertebrae, which are partly visible in some of the specimens available; in none of them, however, are the vertebrae exposed to such a degree that anything can be made out regarding their shape and number.

The *pectoral fin* is of moderate size. The number of lepidotrichia is rather high; in P.4415 not less than 26 lepidotrichia can be counted, the ventralmost ones are, however, very small and articulated almost from their bases. In the type specimens P.572 and P.573 as well as in P.1046*b* and 47461 there seem to be at least 23 or 24 lepidotrichia. The first lepidotrichium is strong and rather densely set with fulcra (*Fu*, Pl. 8).

In the *ventral fin* the number of lepidotrichia amounts to 15, which number I have counted in P.1046*b* and P.4415. As in the pectoral fin the last two or three lepidotrichia are rather delicate and easily overlooked. The first two lepidotrichia are rather short and unarticulated, the third one (the first branched lepidotrichium) is densely set with small fulcra. Lateral to the base of the ventral fin there is a large axillary scale and enlarged scales also occur between the fins of both sides.

The *dorsal fin* has, anteriorly, two unarticulated lepidotrichia, the first as a rule rather short, the second longer. The third, long lepidotrichium carries a series of small fulcra on its anterior margin. The total number of lepidotrichia is difficult to determine as in most specimens the last rays are covered by scales or are defective; in P.1046*a* there are, however, about 14–15 lepidotrichia, and in P.421 I have counted 15. The number of dorsal radials cannot be stated because of the thickness of the squamation.

The *anal fin* has, as in the dorsal fin, two unarticulated lepidotrichia anteriorly followed by a third long, fulcrated lepidotrichium; the total number of lepidotrichia is difficult to determine but seems to be at least 11–12. No anal radials are visible.

The *caudal fin* may be interpreted as hemi-heterocercal, the scaled lobe dorsal to the lateral line (the reduced body axis) reaching farther posteriorly than the scaled ventral lobe. The dorsal and ventral margins are densely set with small fulcra.

HORIZON AND LOCALITY. Lower Lias; Lyme Regis, Dorset.

Pholidophoroides limbata (Agassiz)

(Pls. 11, 12; Text-fig. 12)

1833 *Pholidophorus limbatus* Agassiz, **2**, 1 : 9.
1843 *Pholidophorus limbatus* Agassiz, **2**, pl. 37, figs. 1–5.
1844 *Pholidophorus limbatus* Agassiz, **2**, 1 : 282.
1895 *Pholidophorus limbatus* Agassiz; (*partim*) Woodward : 464, pl. 12, fig. 7.

DIAGNOSIS. *Pholidophoroides* similar to *Ph. crenulata* but somewhat larger in size, at least up to 180 mm. in total length. Greatest depth of body nearly one-third of standard length or slightly less (*ca.* 28–32% of that length). Depth of caudal peduncle one-tenth of standard length or slightly more (10–11%). Maxillary proportionately not quite as deep as in *Ph. crenulata*. Preopercular sensory canal with about 14 tubules. Scales rather thick in about 40–42 transverse rows reckoned from hind margin of operculum to middle of caudal fin; five to six longitudinal rows of body scales deeper than broad with hind margin strongly though finely serrated.

HOLOTYPE. Unknown. Agassiz says (loc. cit., p. 283): "Il en existe des exemplaires dans plusieurs collections d'Angleterre, entre autres au Musée d'Oxford, dans les collections de lord Enniskillen et de sir Philipp Egerton." None of the specimens from the two last named collections [now in the British Museum (Natural History)] agree with either of the figures (pl. 37, figs. 1, 2) given by Agassiz. I have had no opportunity to visit the Oxford Museum collection. Woodward (1895) remarks: "*Type*. Distorted specimens of trunk", but gives no information regarding the collection to which they belong. P.1047 is chosen as LECTOTYPE.

MATERIAL. The following description is based mainly on P.1047, P.1047*a*, P.3596, P.4422, 36472, 38531, and 41906. Specimens P.1047*b* and *c*, P.3632, 38532 and 27595 also belong to this species but are more defective, and from them only little could be added to the description; P.4410 is perhaps not referable to *Ph. limbata*. P.7582, an "imperfect skeleton probably of this species" according to Woodward (1895 : 466) belongs to the species described below (p. 416) as *Pholidophoropsis maculata* sp. n.

DESCRIPTION. The total length of the largest specimen, P.1047, is 180 mm., its length from the tip of the snout to the hindmost lateral line scale (standard length) is estimated at 150 mm. The other specimens have a standard length varying between about 140 and 108 mm. The greatest depth of the body is nearly one-third of the standard length or slightly less (about 28–32%), the depth of the caudal peduncle is about 10–11% of the standard length; the depth of the body and of the caudal peduncle are consequently somewhat greater in this species than in *Ph. crenulata.* The length of the head is about one quarter of the standard length or slightly less (about 23–25%), about the same as in the type species.

The ventral fins are situated approximately midway between the tip of the snout and the hindmost lateral line scale, and the distance between the base of the ventrals and the origin of the anal is about 78–88% of the distance between the bases of the pectoral and ventral fins, about as in *Ph. crenulata.*

A good figure of the entire fish is given by Woodward (1895, pl. 12, fig. 7).

All specimens available are unfortunately more or less defective with respect to the snout region and the skull roof, consequently the following description of the cranial bones is rather incomplete and provisional. Presumably it will, however, be sufficient to demonstrate the close relationship between *Ph. limbata* and the type species of the genus.

Exoskeletal skull roof

This part of the skull is more or less defective in the specimens available. In specimen P.1047 nothing of it is preserved, in 38531 only the dermosphenotic, the dermopterotic and the extrascapular are partly present, in P.4422 and 36472 some bones of the snout region can be observed, but they are partly defective and dislocated.

The *premaxillary* (*Pmx,* Pl. 12, figs. 1, 2; Text-fig. 12) is rather well exposed, after preparation, in P.4422. It is an almost square, slightly tumid bone with the lateral surface almost smooth, not tuberculated as in *Ph. crenulata.* The antero-ventral margin carries a single row of comparatively large teeth, considerably larger than in *Ph. crenulata*; they are slightly curved and increase in length posteriorly.

The *rostral* (*Ro,* Pl. 12, fig. 2; Text-fig. 12) is to a great extent visible in P.4422 as a thin, somewhat bulging bony plate, partly covering a bone which may be the mesethmoid.

The *nasal* is missing in P.4422, but in 36472 (*Na,* Pl. 11, fig. 2) there is an oblong bone, obviously pierced by a sensory canal, which I interpret as the right nasal. Its outline cannot, however, be determined in detail.

The *frontal* (*Fr,* Pl. 11, fig. 2; Text-fig. 12) is preserved, though much crushed and broken off anteriorly, in P.4422; in 36472, on the other hand, the anteriormost part of the frontal is preserved. Judging from these two specimens the frontal has on the whole the same shape as in *Ph. crenulata.*

Part of a *supraorbital* is present in P.4422, but it gives no information regarding the shape of this bone.

The *dermosphenotic* is missing or only present as fragments in all the specimens investigated; in 38531 (*Dsph,* Pl. 12, fig. 3) its anterior, pointed part is clearly visible, indicating that its shape is about the same as in *Ph. crenulata.*

The outline of the *parietal* is impossible to determine.

The *dermopterotic* (*Dpt,* Pl. 11, fig. 2; Pl. 12, fig. 3; Text-fig. 12) does not seem to differ in general from that of *Ph. crenulata*; parts of it are exposed in P.4422, 36472, and 38531.

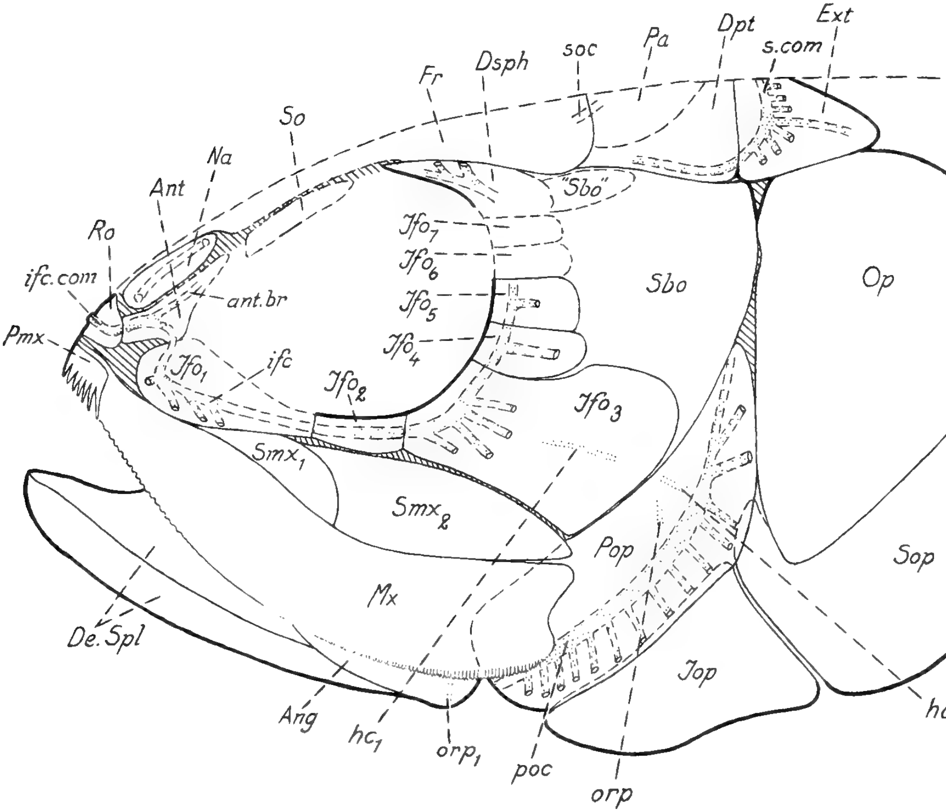

FIG. 12. *Pholidophoroides limbata* (Agassiz). Attempted restoration of head in lateral view. ×4·2.

Ang, angular; *Ant*, antorbital; *De. Spl*, dentary; *Dpt*, dermopterotic; *Dsph*, dermosphenotic; *Ext*, extrascapular; *Fr*, frontal; Ifo_1–Ifo_7, infraorbitals 1 to 7; *Iop*, interoperculum; *Mx*, maxillary; *Na*, nasal; *Op*, operculum; *Pa*, parietal; *Pmx*, premaxillary; *Pop*, preoperculum; *Ro*, rostral; *Sbo*, suborbital; "*Sbo*", "accessory suborbital"; Smx_1, Smx_2, anterior and posterior supramaxillaries; *So*, supraorbital; *Sop*, suboperculum; *ant. br*, antorbital branch of infraorbital sensory canal; hc_1, anterior division of supramaxillary pit-line; *ifc*, infraorbital sensory canal; *ifc. com*, ethmoidal commissure; *orp*, postmaxillary pit-line; orp_1, oral pit-line; *poc*, preopercular sensory canal; *soc*, supraorbital sensory canal.

The *extrascapular* (*Ext*, Pl. 12, fig. 3; Text-fig. 12) is as a rule very defective; in specimen 38531, however, its lateral part is well exposed, its antero-lateral corner being rounded and its postero-lateral and postero-mesial margins almost straight.

Dermal bones of cheek and opercular apparatus

The *maxillary* (*Mx*, Pl. 11, figs. 1, 2; Pl. 12, figs. 1, 2; Text-fig. 12) is well preserved in P.1047 and 36472, its anterior, mesially directed part is, however, not entirely visible but seems to be rather low as in *Ph. crenulata*. The lateral, posteriorly directed part is not as deep as in *Ph. crenulata*, but otherwise both species agree closely in the most important characteristics, such as the convexity of the dorsal margin below infraorbital 1 and supramaxillary 1, the deeply notched posterior margin and the longitudinal striation of its lateral surface. The posterior part of the convex ventral margin of the maxillary has, as in *Ph. crenulata*, a delicate, comb-like dentition, but anteriorly there is in P.4422 (Pl. 12, fig. 1) a single row of small tuberculations, obviously the bases of somewhat larger teeth which have been broken off. The same arrangement can also be observed on the ventral margin of the left maxillary in 36472 (Mx_S, Pl. 11, fig. 2).

The two *supramaxillaries* (Smx_1, Smx_2, Pl. 11, figs. 1, 2 ; Text-fig. 12), only well preserved in P.1047 and 36472 (in the last named specimen partly pushed in below the dorsal margin of the maxillary), are also similar to those of *Ph. crenulata* with regard to shape and the presence of a well-marked striation on the lateral surface. The antero-dorsal corner of supramaxillary 2 does not seem to be drawn out into a larger process.

The bones of the infraorbital series are only partly preserved.

In specimens P.4422 and 36472 there is a defective bone in the snout region which may be interpreted as an *antorbital* (*Ant*, Pl. 11, fig. 2 ; Pl. 12, fig. 2 ; Text-fig. 12) ; its shape seems to be about as in *Ph. crenulata* but its outline cannot be determined exactly.

Infraorbital 1 (*lachrymal*) (Ifo_1, Pl. 11, figs. 1, 2 ; Pl. 12, fig. 2 ; Text-fig. 12) is present only in P.1047, P.4422, and 36472, in all three specimens only as a fragment ; however, from what can be observed it agrees with that of *Ph. crenulata*.

An *infraorbital* 2 (Text-fig. 12) is present in P.4422 ; it is elongate antero-posteriorly, its dorsal margin is slightly concave and its ventral margin correspondingly convex.

Infraorbital 3 (Ifo_3, Pl. 11, figs. 1, 2 ; Pl. 12, fig. 3 ; Text-fig. 12) is present in P.1047, P.4422, 36472 and 38531. Its outline cannot be followed exactly in all specimens, but as compared with the corresponding bone in *Ph. crenulata* its posterior part seems to have a greater dorso-ventral extension.

Dorsal to infraorbital 3 there is in 38531 (Pl. 12, fig. 3) a well-preserved *infraorbital* 4, and further dorsally there seem to be traces of three more infraorbitals. In 36472 (Pl. 11, fig. 2) infraorbital 4 is partly exposed, infraorbital 5 is clearly visible and dorsal to it there are some fragments probably of two more infraorbitals. Consequently, as in *Ph. crenulata* there seem to be seven infraorbitals altogether.

The *suborbital* (*Sbo*, Pl. 11, figs. 1, 2 ; Pl. 12, fig. 3 ; Text-fig. 12) is partly preserved in P.1047, P.4422, 36472 and 38531. Corresponding to the comparatively great depth of infraorbital 3 in this species, the suborbital is not as deep as in *Ph. crenulata*. In both P.4422 and 36472 (" *Sbo* ", Pl. 11, fig. 2 ; Text-fig. 12) a small bone, fragmentary in P.4422, has been observed between the suborbital and the dermopterotic, which probably corresponds to the " accessory suborbital " found in some specimens of *Ph. crenulata*.

The *preoperculum* (*Pop*, Pl. 11, figs. 1, 2 ; Pl. 12, fig. 3 ; Text-fig. 12) has, on the whole, the same shape as in *Ph. crenulata*, but it is somewhat straighter, the posterior margin being more evenly arched with only a little-marked angle between the dorsal and the ventral limbs and almost without the shallow concavity or indentation ventral to the angle that is found in *Ph. crenulata*.

The *operculum*, the *suboperculum* and the *interoperculum* seem not to differ in shape from the corresponding bones in *Ph. crenulata*.

Branchiostegal rays and gular plate

Some branchiostegal rays (*R. Br*, Pl. 11, fig. 1, Pl. 12, fig. 3) are preserved in P.1047 and 38531; they show nothing of special interest. A gular plate is not visible in any of the specimens investigated.

Lower jaw

The lower jaw is partly exposed in P.1047, P.4422 and 36472. The dental part of the dentary has a smooth lateral surface and the lateral surface of the splenial part of the bone is more or less ornamented with a longitudinal ganoin striation as in *Ph. crenulata*. No dentition can be observed with certainty.

Sensory canal system of head

Due to the fragmentary preservation of the skull very little can be said about the sensory canal system of the head.

In 36472 the anterior part of the *supraorbital sensory canal* is indicated in the nasal by an anterior and a posterior opening; because of the thickness of the bone the course of the canal between the two openings cannot be observed with accuracy. In P.4422 the hindmost part of the sensory canal in the frontal and its short continuation in the parietal may be traced. For the rest the supraorbital sensory canal and its tubules and pores cannot be seen.

Of the *infraorbital sensory canal*, only the following few remarks can be given. In P.4422 the ethmoidal commissure (*ifc. com*, Pl. 12, fig. 2; Text-fig. 12) joining the infraorbital sensory canals of both sides can clearly be seen as an arched bony tube which is slightly elevated above the dorsal surface of the rostral. Laterally there seem to be one or two pores, but whether they really are pores cannot be stated with certainty.

In the antorbital the infraorbital sensory canal seems to have about the same course as in *Ph. crenulata*, but because of the defective state of this bone a more detailed description cannot be given.

In infraorbital 1 (lachrymal), partly preserved in P.1047, the sensory canal has the same course along the anterior and ventral margins of the bone as in *Ph. crenulata*; of the tubules only the ventral one of the two pore-like tubules from the anterior, arched part of the canal and the three anterior tubules from the ventral part of the canal can be seen. In P.4422 and 36472 only a small part of the sensory canal is preserved.

In infraorbital 2 the sensory canal runs parallel to the dorsal and ventral margins of the bone. Whether this part of the canal gives off a tubule may be left open.

In infraorbital 3 the sensory canal gives off, posteriorly, three rather long tubules in P.1047 (Pl. 11, fig. 1) and four tubules in 38531 (Pl. 12, fig. 3). In *Ph. limbata*, as in *Ph. crenulata*, the number and arrangement of the tubules in this bone are subject to individual variation. The canal and its tubules cannot be observed in P.4422 and 36472.

In infraorbital 4, clearly visible only in 38531 (Pl. 12, fig. 3), the canal gives off a single, posteriorly directed tubule and the same seems to be true of infraorbital 5 in 36472. In the remaining infraorbitals, both more or less defective, the sensory canal cannot be traced.

In the dermosphenotic in 38531 (Pl. 12, fig. 3) an antero-dorsally directed branch of the infraorbital sensory canal is clearly visible, giving off at least two short, dorsally directed tubules.

As in *Ph. crenulata*, nothing can be said concerning the various parts of the sensory canal in the dermopterotic and the origin of the preopercular sensory canal. In 36472 and 38531 the course of the sensory canal in the dermopterotic seems to be about the same as in *Ph. crenulata*.

Cephalic division of main lateral line

The cephalic division of the main lateral line passes over from the dermopterotic into the extrascapular. In 38531 (Pl. 12, fig. 3; Text-fig. 12) its course in this bone can be followed, in part at least, from near its antero-lateral corner to near its posterior end, mesially giving off the supratemporal commissure (*s. com*, Text-fig. 12) and laterally three postero-laterally directed tubules. The preserved lateral part of the supratemporal commissure gives off three tubules posteriorly.

The *preopercular sensory canal* (Text-fig. 12) has the same course along the middle of the preoperculum as in *Ph. crenulata*. Regarding the tubules given off from the posterior side of the canal, thirteen are clearly visible in 38531, but as the preoperculum is a little damaged at about its mid-point, there may be at least one more tubule. In P.1047 I have counted 14 tubules, but their arrangement is remarkably irregular; in 36472 at least 12 tubules are visible, but one or two more tubules may be present in the anteriormost hidden part of the preoperculum. The total number of preopercular tubules in *Ph. limbata* may consequently be estimated as about 14 against about 17 in *Ph. crenulata*.

In P.1047 and 36472 the lateral surface of the preoperculum clearly shows the two grooves representing the posterior portion of the anterior division of the supramaxillary (horizontal) pit-line and the postmaxillary (vertical) pit-line respectively (hc_1, *orp*, Pl. 11, figs. 1, 2; Text-fig. 12). As in *Pholidophorus latiusculus* an anterior portion of the anterior division of the supramaxillary line is clearly visible on the lateral surface of infraorbital 3.

Regarding the *mandibular sensory canal*, nothing can be made out.

In 36472 the lateral surface of the angular possesses a small vertical groove, obviously the oral pit-line (orp_1, Pl. 11, fig. 2).

Exoskeletal shoulder-girdle and squamation

The *suprascapula* and *supracleithrum* are preserved only in 38531, and then only as fragments which give very little information about their shape.

The *cleithrum* (*Cl*, Pl. 11, fig. 2; Pl. 12, fig. 3) is, to a certain extent, visible in 36472 and 38531; it seems to be proportionately smaller than that of *Leptolepis*. A deep, scale-like bony plate posterior to the suboperculum and cleithrum may be interpreted as a *postcleithrum* (*Pcl*, Pl. 12, fig. 3).

The *scales* are arranged in about 40 to 42 transverse rows counted from the hind margin of the operculum to the middle of the caudal fin; posterior to the last row there are about 9 rows on the body axis dorsal to the lateral line, thus in all about 50 rows. On the body there are generally five longitudinal rows of enlarged scales, the deepest more than twice as deep as broad (proportionately deeper than in *Ph. crenulata*) and with the posterior margin finely serrated; the number of small points on the posterior margin is approximately 15 on the largest scales or about as in pl. 37, fig. 4 of Agassiz (1843). All the scales, including the anterior ones, are comparatively thick, and I cannot see any concentric striations such as are present in *Ph. crenulata*.

Lateral line

Because of the defective state of the suprascapula and supracleithrum nothing can be made out regarding the lateral line in these bones. The anterior lateral line scales are also indistinct, but a few transverse rows behind the operculum the lateral line becomes very distinct and runs almost straight to the base of the middle caudal rays.

Paired and unpaired fins

The *pectoral fin* is similar to that of *Ph. crenulata*, the highest number of lepidotrichia seems to be 23, perhaps 24, thus a little lower than in the type species; it must, however, be kept in mind that the number of the small ventral lepidotrichia is difficult to determine.

The *ventral fin* has 12 clearly visible lepidotrichia in 38531, but as in *Ph. crenulata* there may have been about three more small ones; in P.3596 I have counted 14 lepidotrichia, the two innermost very small.

The *dorsal fin* has the same general shape as in *Ph. crenulata*. Also regarding the number of lepidotrichia there is no important difference. In 38531 there seem to have been about 14 lepidotrichia, the anterior ones preserved as impressions only; in the other specimens investigated the dorsal fin is more or less defective.

The *anal fin* also is similar to that in *Ph. crenulata*; the anterior part of this fin with its two anterior short lepidotrichia followed by the third long and fulcrated lepidotrichium is figured by Woodward (1919, pl. 22, fig. 6). The total number of lepidotrichia is about 13, perhaps up to 15 in P.1047*a*. In P.4422 the anal radials, 12 in number, are clearly exposed.

The *caudal fin* is hemiheterocercal as in *Ph. crenulata*.

Horizon and locality. Lower Lias; Lyme Regis, Dorset.

Genus ***PHOLIDOPHOROPSIS*** nov.

PRELIMINARY DIAGNOSIS. Pholidophoridae of medium size, as far as known similar to *Pholidophoroides* but differing in the following features. Exoskeletal cranial bones without or with only very feeble ganoin ornamentation. Scales thin and cycloid with fine concentric striations.

TYPE SPECIES. *Pholidophoropsis caudalis* (Woodward).

Pholidophoropsis caudalis (Woodward)

(Pl. 13, Text-fig. 13)

1844 ? *Leptolepis caudalis* Agassiz, **2**, 2 : 133 (*nom. nud.*).
1895 *Pholidophorus caudalis* Woodward : 457, pl. 18, figs. 1, 2 (*partim*).
1941 *Pholidophorus* (? *Pholidophoroides*) *caudalis* Woodward ; Woodward : 90.

DIAGNOSIS. *Pholidophoropsis* of medium size, at least up to 120 mm. in total length. Greatest depth of body slightly more than one quarter of standard length (*ca.* 26–27% of that length). Depth of caudal peduncle slightly more than one-tenth (*ca.* 11%) of standard length. Maxillary proportionately not as deep as in *Ph. crenulata*. Preopercular sensory canal with about 10 tubules. Scales very thin.

HOLOTYPE. British Museum (Natural History) No. P.3664.

MATERIAL. Besides the holotype, specimens P.3664*a* (paratype) and 39871 belong to this species and have been used in the following description.

DESCRIPTION. The total length of the holotype is 120 mm. ; P.3664*a* and 39871 have a total length of 95 mm. and 117 mm. respectively, but in both these specimens the tips of the caudal fin are broken, and the maximum length of the last named specimen may consequently have been at least 120 mm.[1] The standard length or length from the tip of the snout to the base of the middle caudal fin rays is about 100 mm. in the holotype, in the two other specimens 81 and 102 mm. respectively, but P.3664*a* seems to be a little shortened by pressure. The greatest depth of the body is slightly more than one quarter (26–27%) of the standard length and the depth of the caudal peduncle is about 11% of the standard length. The length of the head seems to be exactly one quarter of the standard length in the two larger specimens ; in P.3664*a* this length is slightly greater because of the shortened standard length.

The ventral fins are situated about midway between the tip of the snout and the base of the caudal fin rays, and the distance between the base of the ventrals and the origin of the anal is about 70% of the distance between the bases of the pectoral and ventral fins. As in the species of the genus *Pholidophoroides* the dorsal fin is situated above the interspace between the ventral and anal fins ; in P.3664*a* a forward displacement of the dorsal fin seems, however, to have occurred through pressure.

Good figures of the entire holotype and of P.3664*a* are given by Woodward (1895, pl. 18, figs. 1, 2).

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[1] Woodward (1895 : 457) gives the length of *Ph. caudalis* as "about 0·13" ; This obviously refers to 43055, described below (p. 416) as *Pholidophoropsis maculata* sp. nov.

All three specimens are more or less defective and the following description is consequently rather incomplete but sufficient for identifying the species and demonstrating its close affinity with members of the genus *Pholidophoroides* described above. As a general characteristic of *Ph. caudalis* it may be mentioned that the exoskeletal bones of the skull, as well as the scales, are rather thin and almost totally lack ganoin ornamentation.

Exoskeletal skull roof

A *premaxillary* (*Pmx*, Pl. 13, fig. 1 ; Text-fig. 13) is preserved in P.3664*a* ; its denticulated ventral margin is visible, but as the other parts of the bone are hidden below the antorbital, its general shape cannot be stated.

The *rostral* cannot be identified with certainty in any of the specimens available.

The *nasal* (*Na*, Pl. 13, figs. 1, 2 ; Text-fig. 13) is partly visible in P.3664*a*, but this bone too is to a great extent hidden below the antorbital ; a bone fragment anterior to the frontal in the holotype may represent the posterior part of the nasal. From these two fragments it may be concluded that the nasal of this species does not differ very much from the corresponding bone in *Ph. crenulata.*

The *frontal* (*Fr*, Pl. 13, figs. 1, 2 ; Text-fig. 13) seems to be rather broad in its anterior part and its dorsal surface bulges along the anterior part of the supraorbital sensory canal. The posterior, broad part of the frontal is defective and nothing of its posterior margin can be made out. The suture between the frontals of both sides is straight anteriorly but then makes an S-shaped bend to the left and to the right, clearly visible on the holotype.

The anterior part of a rather strong *supraorbital* (*So*, Pl. 13, fig. 2 ; Text-fig. 13) obviously similar to that in *Ph. crenulata,* is present in the holotype.

The *dermosphenotic* and the *parietal* are not discernible.

In the holotype parts of the *dermopterotic* and *extrascapular* (*Dpt*, *Ext*, Pl. 13, fig. 2 ; Text-fig. 13) are exposed but are insufficient to allow any detailed description.

Dermal bones of cheek and opercular apparatus

The *maxillary* (*Mx*, Pl. 13, figs. 1, 2 ; Text-fig. 13) is best preserved in P.3664*a* ; it has, on the whole, the same shape as in *Ph. crenulata* with the characteristic convexity on the dorsal margin, but the longitudinal striation on the lateral surface is not nearly so pronounced. The posterior margin is partly crushed, but may have been notched in the same way as *Ph. crenulata.* The main difference from that species, apart from the lesser depth of the bone, lies in the presence of a delicate dentition along the whole ventral margin, not confined to its posterior half only.

The two *supramaxillaries* (Smx_1, Smx_2, Pl. 13, fig. 1 ; Text-fig. 13) have the same general shape as in *Ph. crenulata*, but judging from P.3664*a* in which they are best preserved and well exposed, the antero-dorsal corner of supramaxillary 2 seems to be more markedly drawn out into a short process. Both supramaxillaries show a faint concentric striation on their lateral surface.

The bones of the infraorbital series are, for the most part, badly preserved.

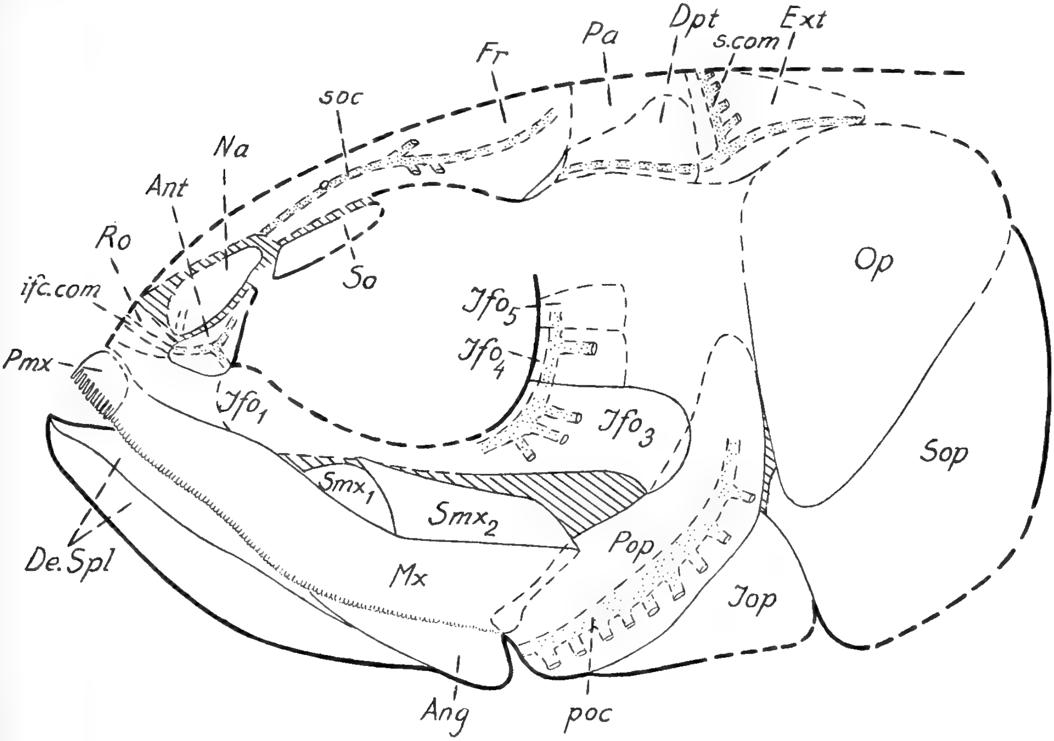

FIG. 13. *Pholidophoropsis caudalis* (Woodward). Attempted restoration of head in lateral view. ×5.

Ang, angular ; *Ant*, antorbital ; *De. Spl*, dentary ; *Dpt*, dermopterotic ; *Ext*, extrascapular ; *Fr*, frontal ; Ifo_1, Ifo_3–Ifo_5, infraorbitals 1 and 3 to 5 ; *Iop*, interoperculum ; *Mx*, maxillary ; *Na*, nasal ; *Op*, operculum ; *Pa*, parietal ; *Pmx*, premaxillary ; *Pop*, preoperculum ; *Ro*, rostral ; Smx_1, Smx_2, anterior and posterior supramaxillaries ; *So*, supraorbital ; *Sop*, suboperculum ; *ifc. com*, ethmoidal commissure ; *poc*, preopercular sensory canal ; *s. com*, supratemporal commissure ; *soc*, supraorbital sensory canal.

The *antorbital* (*Ant*, Pl. 13, figs. 1, 2 ; Text-fig. 13) is present in P.3664 and P.3664*a*, but in both the postero-dorsal part is broken off. Judging from the last named specimen it seems, however, that the antorbital in this species is shorter than in *Ph. crenulata.*

Infraorbital 1 (*lachrymal*) (Ifo_1, Pl. 13, fig. 2 ; Text-fig. 13) can be traced in the holotype only, but the fragment gives no information as to the shape of the bone.

Infraorbital 2 is missing in all the three specimens available.

An *infraorbital* 3 (Ifo_3, Pl. 13, fig. 2 ; Text-fig. 13) is present in the holotype as well as in 39871. It has the ordinary shape with the antero-ventral margin slightly concave and the posterior margin rounded.

Of the remaining bones in the infraorbital series, a small *infraorbital* 4 is present in the holotype (Ifo_4, Pl. 13, fig. 2). Two fragments in P.3664*a* may represent infraorbitals 4 and 5.

A *suborbital* bone (*Sbo*, Pl. 13, fig. 2) is visible in the holotype, but its posterior margin is not distinguishable. Dorsal to this bone there is a small tongue-like bone similar to the small bone or bones dorsal to the suborbital in *Ph. crenulata* (see p. 398).

The *preoperculum* (*Pop*, Pl. 13, figs. 1, 2 ; Text-fig. 13) is more or less defective in the specimens available ; it is best preserved in the holotype and has the same general shape as in *Ph. crenulata*, but its ventral, antero-ventrally directed limb diminishes markedly in depth towards the tip of the bone.

The *operculum*, the *suboperculum* and the *interoperculum* are partly preserved in the holotype and, as far as can be judged, they have the same general shape as the corresponding bones in *Ph. crenulata*.

Lower jaw

The lower jaw is visible to a great extent in P.3664*a* (*De. Spl, Ang*, Pl. 13, fig. 1), but as in most specimens of the two *Pholidophoroides* species described above, its dorsal margin is covered by the maxillary and therefore neither the entire outline of the lower jaw nor its depth can be determined. The lateral surface of the dentary has a longitudinal crest, obviously corresponding to the well-marked ridge between the dental and splenial parts of the dentary in *Ph. crenulata*, but ventral to this crest there are no traces of the rich ganoin ornamentation characteristic of this species and of *Ph. limbata*.

Sensory canal system of head

The *supraorbital sensory canal* (*soc*, Pl. 13, fig. 2 ; Text-fig. 13) in the nasal is partly visible in P.3664*a* as a short, laterally curving canal, representing the anteriormost part of this sensory canal. In the holotype no canal can be seen with certainty in the preserved posterior fragment of the nasal.

The frontal part of the supraorbital sensory canal has the same general course as in *Ph. crenulata* and is best exposed in the left frontal of the holotype. Its anterior, straight part is marked by a bulging of the dorsal surface of the bone, and on this part there is a small dorsal pore. At the postero-lateral curve the canal gives off from its mesial side a posteriorly directed tubule and from the lateral side at least two short, laterally directed tubules ; more posteriorly the sensory canal cannot be followed. The main difference from the supraorbital sensory canal in *Ph. crenulata* is that the tubules are given off mainly from the lateral side of the canal in *Ph. caudalis* but from the mesial side in *Ph. crenulata*.

The *infraorbital sensory canal* is clearly visible in the antorbital bone of the holotype as well as in P.3664*a* ; it gives off a posteriorly directed antorbital branch. For the rest the infraorbital sensory canal can only be traced as a slightly bent canal in infraorbital 3, giving off three postero-ventrally directed tubules in the holotype and in 39871. In the holotype infraorbital 4 shows a single tubule given off from the posterior side of the canal, for the rest the infraorbital sensory canal cannot be followed.

Cephalic division of main lateral line

In the holotype the sensory canal in the dermopterotic can be traced parallel to the dorso-lateral margin of the bone, but only a single pore on its dorsal surface can be observed. In the extrascapular the main canal and the supratemporal commissure are rather clearly visible (Pl. 13, fig. 1 ; Text-fig. 13). No tubules from the main canal are, however, discernible, but the supratemporal commissure gives off from its posterior side at least four backwardly directed tubules, decreasing in length towards the mid-line of the skull.

The *preopercular sensory canal* pierces the preoperculum in the middle of its length, as in *Ph. crenulata.* The tubules given off from its morphologically posterior side are short and straight ; their number cannot be determined exactly, but they are obviously less numerous than in *Ph. crenulata* ; in the dorsal limb of the bone only one tubule is visible dorsal to the posterior, ill-defined angle between the dorsal and ventral limbs, but as the upper part of the dorsal limb is not well exposed, there may be one or more tubules in the dorsal limb of the preoperculum. In the ventral limb, well exposed in the holotype, eight tubules are visible.

The *mandibular sensory canal* cannot be seen.

Exoskeletal shoulder girdle and squamation

Because of the bad state of the material available very little can be determined of the bones belonging to the exoskeletal shoulder girdle ; nothing seems, however, to indicate that they are of special interest as species characteristics.

The squamation consists of very thin scales forming, where they are preserved, a continuous thin layer, generally without marked boundaries between the individual scales. In the holotype some scales are, however, clearly visible ; they are thin with a delicate concentric striation, and their posterior margins are rounded and not serrated. It must, however, be noted that in P.3664*a* and 39871 some of the posteriormost scales are markedly thicker than the body scales.

A lateral line cannot be traced in any of the three specimens investigated.

Axial skeleton and paired and unpaired fins

The *axial skeleton* consists, as in *Ph. crenulata,* of rather thin ring-vertebrae. The shape and number of the abdominal vertebrae is difficult to state ; the centra of the caudal vertebrae are, judging from P.3664*a*, about twice as deep as broad.

The best preserved *pectoral fin,* that of P.3664*a*, shows 21 lepidotrichia, but it is not quite certain that the series is complete. The first, strong lepidotrichium is fulcrated.

The *ventral fin* has, in the same specimen, 15 clearly visible lepidotrichia ; the first ones are, however, defective, and no fulcra could be seen.

The *dorsal fin* is similar to the corresponding fin in *Ph. crenulata,* including the presence of fulcra ; in 39871 I have counted 15 lepidotrichia. The radials, clearly visible in this species because of the thin scale covering, in the holotype number at least 14, in P.3664*a* about 14 and in 39871 thirteen.

The *anal fin* is likewise similar to that of *Ph. crenulata*, but the number of lepidotrichia cannot be determined. The number of radials is eleven in both the holotype and P.3664*a* ; in 39871 there must have been more than the 9 radials still preserved.

The *caudal fin* is hemi-heterocercal as in *Ph. crenulata* and *Ph. limbata*, and with the dorsal and ventral margins densely set with small fulcra.

REMARKS. The two best preserved specimens of this species, the holotype and P.3664*a*, could be studied only during short visits to London and therefore it is quite possible that a closer investigation of them will reveal details not mentioned in the description given above. It is my hope, however, that this description will be sufficient for the identification of the species as well as providing a suitable basis for a discussion regarding its affinities and taxonomic position.

HORIZON AND LOCALITY. Lower Lias ; Lyme Regis, Dorset.

Pholidophoropsis maculata sp. nov.

(Pl. 14, Text-figs. 14, 15)

1895 *Pholidophorus caudalis* Woodward : 457 (*partim*).
1895 *Pholidophorus limbatus* Agassiz ; Woodward : 466 (*partim* : P.7582).

DIAGNOSIS. *Pholidophoropsis* of medium size, at least up to about 160 mm. in total length. Greatest depth of body about one quarter of standard length. Maxillary comparatively slender. Preopercular sensory canal with about 14 tubules. External bones of skull with scattered ganoin spots and streaks. Scales comparatively large, thin, with concentric striae and with posterior margin rounded ; axillary scales with ganoin spots.

HOLOTYPE. British Museum (Natural History) No. 43055.

MATERIAL. Besides the holotype, P.7582, listed by Woodward under *Pholidophorus limbatus* as " Imperfect skeleton probably of this species ", shows such striking similarities with the holotype that both undoubtedly belong to one and the same species. It has also been used for the following description, but its defective state of preservation allows only some complementary additions to the description of the holotype.

DESCRIPTION. The total length of the holotype is about 127 mm. (Pl. 14, fig. 1). Woodward's (1895 : 457) statement that the maximum length of his *Ph. caudalis* is " about 0·13 " is obviously founded on this specimen. The length from the tip of the snout to the hind margins of the hypurals (standard length) is about 109 mm. The total length of P.7582 cannot be measured ; the skull together with the vertebral column to the posterior margin of the hypurals (standard length) is about 133 mm. and the total length may be estimated as about 160 mm. The greatest depth of the body in the holotype is 27 mm. or almost exactly one quarter of the standard length ; the caudal peduncle is crushed dorso-ventrally and its depth cannot therefore be measured. The length of the head in the holotype cannot be stated with accuracy (the opercular bones seem to have been displaced backwards through pressure) but it may be a little greater than the maximum depth of the body. In P.7582 the length of the head is about one quarter of the standard length.

The position of the dorsal, ventral and anal fins is somewhat different from that in the species described above. The base of the ventral fin is situated a little nearer to the tip of the snout than to the hind margins of the hypurals, and the distance between the base of the ventrals and the origin of the anal is about 85% of the distance between the bases of the pectorals and the ventrals. The dorsal fin is situated somewhat further back, beginning about midway between the base of the ventrals and the anal origin and ending above the last named fin.

The skull is more or less defective in both specimens investigated ; consequently the following description must be considered as provisional.

Exoskeletal skull roof

A *premaxillary* is not preserved in either of the specimens available.

In the holotype the *rostral* seems to be well developed, but its shape cannot be determined in any detail.

The *nasal* (*Na*, Pl. 14, fig. 2 ; Text-figs. 14, 15), preserved only in the holotype, is a broad, almost leaf-like bone with the antero-lateral margin concave, obviously constituting the postero-mesial limit of the anterior nasal opening. The dorsal surface of the nasal is ornamented with ganoin spots.

The *frontal* (*Fr*, Pl. 14, fig. 2 ; Text-figs. 14, 15) has a typical shape, with the broadest part posterior ; its anterior, narrower part is hidden below the nasals in the holotype and defective in P.7582, but seems to be short, perhaps comparatively shorter than in *Ph. crenulata*. In the holotype the suture between the frontals of both sides is straight anteriorly and then makes an S-shaped bend to the right and to the left.

The *supraorbital* (*So*, Pl. 14, fig. 2 ; Text-figs. 14, 15) is only partly preserved in the holotype, but seems to have approximately the same general shape as in *Ph. crenulata*. In P.7582 the supraorbital is lacking.

A *dermosphenotic* is not visible in either of the specimens investigated.

The shape of the *parietal* (*Pa*, Pl. 14, fig. 2 ; Text-figs. 14, 15) cannot be determined, but as the dermopterotic is comparatively broad in the mesio-lateral direction, the exposed dorsal surface of the parietal may be smaller than in *Ph. crenulata*.

The *dermopterotic* (*Dpt*, Pl. 14, fig. 2 ; Text-figs. 14, 15) is clearly visible on the right side in the holotype and on the left side in P.7582, showing that its mesio-lateral breadth is comparatively large. The surface of the dermopterotic, like that of the frontal and the parietal, has an ornamentation of small, partly confluent ganoin spots.

The lateral part of a bone, possibly the *extrascapular*, is visible posterior to the dermopterotic in both specimens, but this interpretation is rather uncertain as no traces of a sensory canal or of tubules can be seen.

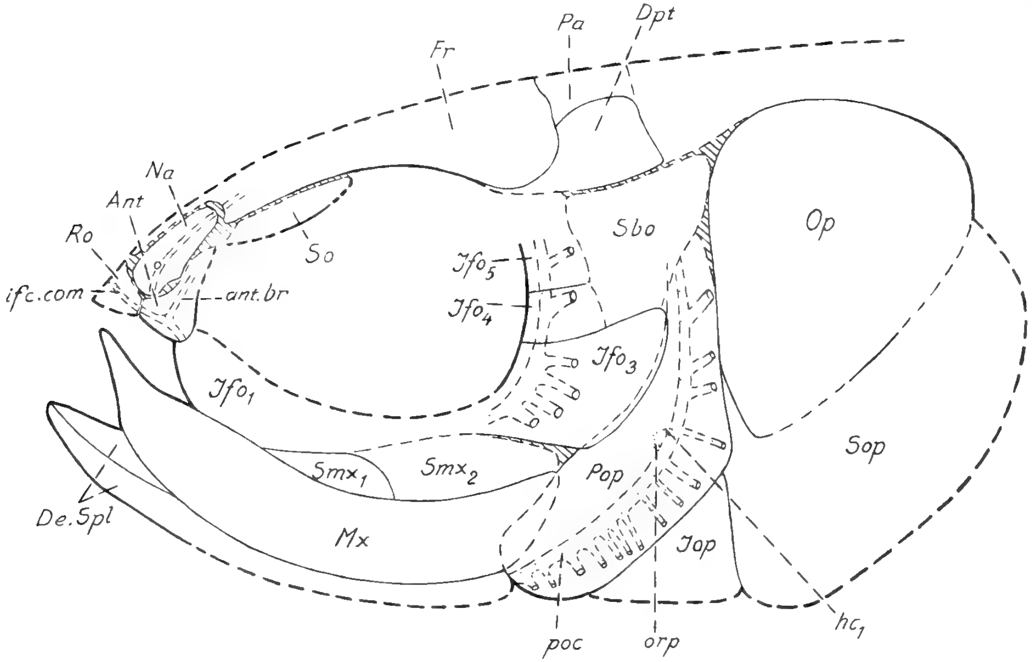

FIG. 14. *Pholidophoropsis maculata* sp. nov. Attempted restoration of head in lateral view. × 4·2.

Ant, antorbital; *De. Spl*, dentary; *Dpt*, dermopterotic; *Fr*, frontal; *Ifo*$_1$, *Ifo*$_3$–*Ifo*$_5$, infraorbitals 1 and 3–5; *Iop*, interoperculum; *Mx*, maxillary; *Na*, nasal; *Op*, operculum; *Pa*, parietal; *Pop*, preoperculum; *Ro*, rostral; *Sbo*, suborbital; *Sop*, suboperculum; *ant. br*, antorbital branch of infraorbital sensory canal; *hc*$_1$, anterior division of supramaxillary pit-line; *ifc*, infraorbital sensory canal; *ifc. com*, ethmoidal commissure; *orp*, post-maxillary pit-line; *poc*, preopercular sensory canal.

Dermal bones of cheek and opercular apparatus

The *maxillary* (*Mx*, Pl. 14, fig. 2; Text-fig. 14) is, in its anterior, mesially directed part rather delicate; its lateral, posteriorly directed part increases in height backwards. Its height cannot be measured exactly, but it seems to be about the same as in *Ph. caudalis*. The convexity of the anterior part of the dorsal margin of the maxillary exists, but it is not as pronounced as in *Pholidophoroides* species. The ventral margin of the maxillary is not exposed in the holotype and only for a short distance anteriorly in P.7582, but here traces of a delicate dentition are visible, indicating that probably the whole ventral margin is denticulate as in *Ph. caudalis*. The lateral surface of the posteriorly directed part of the maxillary is richly ornamented; in the holotype a few longitudinal striations parallel to the dorsal margin recall the striation in *Ph. crenulata*, but below them there are numerous short ganoin streaks and spots.

Only supramaxillary 1 of the *supramaxillaries* is preserved in the holotype, and it is defective (*Smx*$_1$, Pl. 14, fig. 2); in P.7582 both supramaxillaries are exposed.

Supramaxillary 1 seems to be relatively broader than in *Ph. crenulata*, its anterior tip being longer, and the striation on its lateral surface not as well marked as in that species, particularly not in P.7582, where only a few ganoin streaks are visible. Supramaxillary 2 (*Smx*2, Text-fig. 14), preserved in a defective state, has about the same shape as in *Ph. caudalis*, but its lateral surface practically lacks ornamentation. As in the *Pholidophoroides* species, the supramaxillaries do not overlap the dorsal margin of the maxillary.

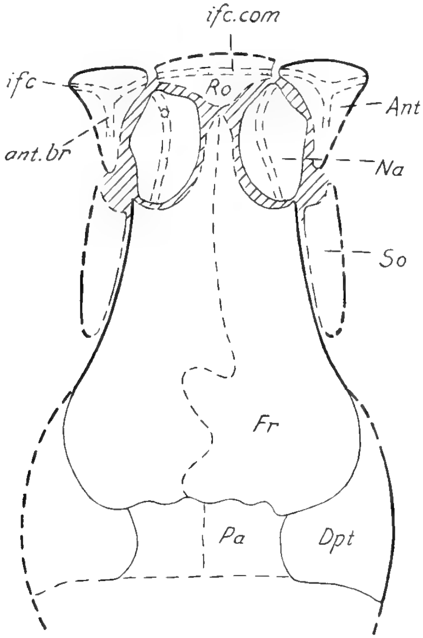

FIG. 15. *Pholidophoropsis maculata* sp. nov. Attempted restoration of head in dorsal view, the snout flattened. ×4·2. Lettering as in Fig. 14.

The bones of the infraorbital series are only partly preserved.

The *antorbital* (*Ant*, Pl. 14, fig. 2; Text-figs. 14, 15), only visible in the holotype, seems to have a broad triangular shape, not as elongate as in *Ph. crenulata*.

In both specimens *infraorbital* 1 (*lachrymal*) (Ifo_1, Pl. 14, fig. 2) is only preserved as fragments without traces of the sensory canal or of its tubules.

Infraorbital 2 is lacking.

Infraorbital 3 (Ifo_3, Pl. 14, fig. 2; Text-fig. 14) is, judging from the exposed part, almost semicircular in the holotype; in P.7582 its dorsal margin is defective, but also in this specimen infraorbital 3 is by no means as broad as in the *Pholidophoroides* species.

Dorsal to infraorbital 3 in the holotype there are two small bones which obviously represent *infraorbitals* 4 and 5 (Ifo_4, Ifo_5, Pl. 14, fig. 2; Text-fig. 14).

Posterior to infraorbitals 3–5 there are, in the holotype, some bony plates which may be fragments of a *suborbital* bone ; the lateral surface of these fragments is ornamented with ganoin spots. In P.7582 there are some bone fragments ventral to the dermopterotic ; they have also been interpreted as parts of a suborbital.

The *preoperculum* (*Pop*, Pl. 14, fig. 2 ; Text-fig. 14), best preserved in the holotype, is only slightly arched ; it is of almost the same height in the middle and in the ventral parts of the bone ; the dorsal limb seems to taper dorsally, but here the outline of the bone is difficult to follow. The middle and dorsal parts of the preoperculum have a surface ornamentation of lustrous ganoin spots ; such spots are lacking on the dorsal part of the ventral limb, probably indicating that this part of the bone is normally covered by the posterior end of the maxillary. In P.7582 the preoperculum is only partly preserved.

In the holotype the *operculum* (*Op*, Pl. 14, fig. 2) seems, at first sight, to be very low compared with the corresponding bone in *Ph. crenulata*, but its postero-ventral part is pressed in below the suboperculum and therefore its outline cannot be determined accurately. In P.7582 the operculum is partly crushed, but its ventral part is well exposed, showing that this bone has the same general shape as in the *Pholidophoroides* species. The lateral surface of the operculum is ornamented with ganoin spots.

The *suboperculum* (*Sop*, Pl. 14, fig. 2 ; Text-fig. 14), preserved only as fragments in both specimens, has the same general shape as in the *Pholidophoroides* species ; its antero-dorsal process is well developed. Like the operculum its lateral surface is ornamented with ganoin spots.

Only small fragments of the *interoperculum* (*Iop*, Text-fig. 14) are exposed in the holotype, in P.7582 its posterior part is exposed ; the lateral surface of this part shows a few ganoin spots.

Lower jaw

Only parts of the *dentary* (*De. Spl*, Pl. 14, fig. 2 ; Text-fig. 14) are exposed and they give little information regarding its shape. Anteriorly the dental part is, however, only gently ascending, its lateral surface is smooth and no teeth can be seen along its margin. The splenial part is separated from the dental by a well-marked ridge, ornamented with ganoin, and its lateral surface is, at least partly, provided with small ganoin spots and short streaks.

Sensory canal system of head

The sensory canal system of the head can be traced only in part.

The *supraorbital sensory canal* pierces the nasal as an arched canal from its antero-lateral corner to its posterior end. On the left nasal an elevated pore is visible near the anterior end of the canal, other pores or tubules cannot be seen. In the frontal the canal can only be traced imperfectly, but it seems to have the same course as in *Ph. crenulata* ; only a few short tubules from the mesial side of the canal are visible. The canal probably ends in the parietal, but its presence there cannot be established.

In the rostral there is an ethmoidal commissure (*ifc. com*, Pl. 14, fig. 2; Text-figs. 14, 15) joining the infraorbital sensory canals of both sides. This canal begins in the antorbital, in which it gives off posteriorly an antorbital branch. As the fragmentary infraorbital 1 (lachrymal) has no remains of the sensory canal and as infraorbital 2 is missing, nothing can be said regarding the part of the canal belonging to these bones. In infraorbital 3 of the holotype the canal is weakly arched and postero-ventrally gives off four diverging tubules with small ganoin spots on their surface; the anterior tubule is about half the length of the others. In specimen P.7582 the canal and its tubules are indistinct. In each of the infraorbitals 4 and 5 the canal gives off a single, posteriorly directed tubule. The further course of the infraorbital sensory canal is unknown.

Cephalic division of main lateral line

A deep arched groove on the parietal in the holotype may represent the middle pit-line (*mp*, Pl. 14, fig. 2).

On the lateral margin of the dermopterotic a single pore is visible in both specimens, indicating that the infraorbital sensory canal and the cephalic division of the main lateral line pierce this bone near its lateral margin. The further course of the main lateral line is not visible.

The *preopercular sensory canal* pierces the preoperculum in the middle of its length as in the *Pholidophoroides* species. From its morphologically posterior side it gives off 13 or 14 tubules in the holotype; the three anterior tubules are short and straight and are followed by four longer, straight tubules; posterior to the latter there are two long and slender tubules and posterior to them there can be traced four wider tubules, separated by wider interspaces; three of these tubules are situated dorsal to the posterior angle of the preoperculum. It cannot be stated with accuracy whether one more tubule exists in the dorsalmost part of the preoperculum. In the defective preoperculum of P.7582 only a few tubules are visible.

Little can be said about the *mandibular sensory canal* except that there is a series of short, backwardly directed tubules on the lateral surface of the splenial part of the dentary.

Exoskeletal shoulder girdle and squamation

The *suprascapula* and the *supracleithrum* cannot be identified. A rather strong *cleithrum* (*Cl*, Pl. 14, fig. 2) is partly exposed in P.7582 and the dorsal part of the same bone is visible in the holotype. Posterior to the dorsal part of the cleithrum parts of a rather large *postcleithrum* (*Pcl*, Pl. 14, fig. 2) with ganoin spots on its lateral surface are visible in both specimens.

The *squamation* is well preserved in the holotype. The scales are large and remarkably thin with a delicate concentric striation; their posterior margin is rounded and not serrated. The middle flank scales seem to be somewhat larger than the others. The axillary scales dorsal to the pectoral fin, also present in P.7582, are ornamented with ganoin spots. No lateral line scales can be distinguished.

Axial skeleton and paired and unpaired fins

The *axial skeleton* is entirely exposed in P.7582, but the separate ring-vertebrae are partly crushed and partly embedded in the rock and cannot be studied in any detail; their number cannot be stated with accuracy, but it seems to be about 48.

The *pectoral fin* is not entirely exposed in either of the two specimens available and consequently the number of lepidotrichia cannot be given. The first, strong lepidotrichium is fulcrated (*Fu*, Pl. 14, fig. 2).

The *ventral fin* can only partly be seen in the holotype, but in P.7582 both ventral fins are well exposed and in the right one 14 lepidotrichia can be counted, the two first ones comparatively short; the third is densely set with fulcra, also visible in the holotype. As already mentioned by Woodward (1895 : 466) the right basipterygium is preserved in P. 7582; the basipterygium can also be traced in the holotype.

All lepidotrichia in the *dorsal fin* are missing from the holotype, but parts of its anterior radials and some impressions indicate the position of the fin. In P.7582 the dorsal fin is rather well preserved with at least 13 lepidotrichia visible, the second one with a series of fulcra along its anterior margin; anterior to the first clearly visible lepidotrichium there are traces of one or two short lepidotrichia. The first radial is V-shaped and composed of two fused radials.

Of the *anal fin*, 9 clearly visible radials are preserved in the holotype. In P.7582 10 lepidotrichia and 5 radials can be seen, but as the anterior lepidotrichia are only exposed basally, it is impossible to say whether fulcra are present or not.

The *caudal fin* may be hemi-heterocercal as in the *Pholidophoroides* species, but as the fulcra on the dorsal margin are pressed down over the upper part of the caudal peduncle in the holotype and as the caudal fin is practically wanting in P.7582, nothing can be said regarding the true shape of this fin.

REMARKS. It is only with some hesitation that I have created a new species for the specimens 43055 and P.7582. In many respects they are very similar to *Ph. caudalis* (to which species Woodward referred specimen 43055), particularly in having thin scales of the same shape as in the holotype of *Ph. caudalis*. There are, however, many differences. In *Ph. maculata* the dorsal fin seems to be situated more posteriorly than in *Ph. caudalis*, the exoskeletal cranial bones are thicker in *Ph. maculata* than in *Ph. caudalis* and, moreover, richly ornamented with ganoin spots, infraorbital 3 and the preoperculum are differently shaped, and the number and position of the tubules belonging to the preopercular sensory canal are also different in the two species. All these facts seem to me to preclude the identification of 43055 and P.7582 as *Ph. caudalis*. It must, however, be remembered that our present knowledge regarding these species is rather defective, and a definitive solution to this question needs more and better preserved material. At present I find it most convenient to keep the two types apart as separate species.

HORIZON AND LOCALITY. Lower Lias; Lyme Regis, Dorset.

III. DISCUSSION

(*a*) *The taxonomic relationship between the genera and species within the family Pholidophoridae* s. str. *and a preliminary diagnosis of the family*

The description of the exoskeletal cranial bones in *Pholidophorus bechei* given above differs in some respects from that given by Miss Rayner (1948). The greatest difference concerns the shape of the antorbital and the course of the supraorbital and infraorbital sensory canals in the snout. The conditions described by Miss Rayner, already doubted by Griffith & Patterson (1963 : 32), can hardly be correct. Although I had no specimen with the exoskeletal bones of the snout preserved in their natural mutual position I think that my attempted reconstruction (Text-figs. 1, 2) comes nearer to the true conditions. This interpretation seems also to be corroborated by the arrangement of the corresponding structures in the well-preserved *Pholidophoroides crenulata*. Moreover, the material at my disposal clearly shows that the nasals do not meet in the median line but are separated by the anterior parts of the frontals. Apart from minor corrections regarding the shape of some bones such as the premaxillary, supraorbital 1, the dermosphenotic and the preoperculum, it has been possible to add some more details regarding the tubules of the sensory canal system.

Our present knowledge of *Pholidophorus bechei*, the type species of the genus *Pholidophorus*, is of course far from complete but it seems sufficient to serve as the basis for a discussion of taxonomic affinities, *i.e.* which other species may be referred to the genus *Pholidophorus* in a restricted sense and which species may be considered as belonging to other genera.

A species which, as far as could be made out, agrees with *Ph. bechei* in all features of generic value is *Ph. latiusculus* from the Upper Trias of Seefeld, Tyrol. Unfortunately the shape of the rostral and antorbital bones with their sensory canals are still unknown, but in other respects the agreement between the two species is so close that they must be considered congeneric. Consequently the diagnosis of the genus *Pholidophorus* s. str. given on p. 356 is based on these two species.

The species *Ph. caffii* from the Upper Trias of Viciarola, North Italy, considered by most authors as a synonym of *Ph. latiusculus*, is beyond doubt a distinct species. In many respects strikingly similar to *Ph. bechei* and *Ph. latiusculus*, it differs from both in some important respects, above all in the shape of the preoperculum and the preopercular sensory canal. The presence of only a single supramaxillary, if not merely an individual anomaly, is moreover a feature separating it from the two *Pholidophorus* species mentioned. Its reference to the same genus as those two species would widen the conception of the genus *Pholidophorus* rather excessively. On the other hand I find it at present inadvisable to create a new genus for a species founded on a single, defective specimen, in most respects similar to the true members of that genus, and therefore I have provisionally attributed it to *Pholidophorus*.

The specimen described above as *Ph.* cf. *pusillus* represents a species which, as far as can be judged from the partly incomplete material, seems to agree with *Ph. bechei* and *Ph. latiusculus* in all characters of generic value. Consequently it may be placed, at least provisionally, in the genus *Pholidophorus* s. str. Whether it really belongs to *Ph. pusillus* Agassiz is a question which at present must be left unanswered.

The rather numerous but unfortunately badly preserved specimens from the Lower Lias of Lyme Regis, Dorset, which I have described above under the species name *dorsetensis*, were referred to *Ph. caudalis* by Woodward (1895). They have, however, nothing to do with the true *Ph. caudalis* but show, as far as known, many similarities with *Ph. bechei* and *Ph. latiusculus*. The preoperculum, one of the most characteristic bones of those preserved, shows the same notch on its posterior margin as in the two species mentioned and the arrangement of the tubules belonging to the preopercular sensory canal is about the same as in those species, but the canal itself runs still nearer to the anterior margin of the bone, about as in *Leptolepis*. Further, the extension of the two supramaxillaries over almost the whole dorsal margin of the maxillary recalls a condition similar to that in *Leptolepis*, and the squamation consists of comparatively thin cycloid scales. The lower jaw is, however, only gently ascending anteriorly, not abruptly as in *Leptolepis*, and the nasals are comparatively large. In many respects these specimens are thus similar to the members of the genus *Pholidophorus* s. str., in others to *Leptolepis*, but they can, in my opinion, be placed neither in *Pholidophorus* nor in *Leptolepis*. Consequently I have proposed for the species *dorsetensis* a new genus, *Pholidolepis*, the preliminary diagnosis of which is given above (p. 387).

The genus *Pholidophoroides* was created by Woodward for the species *Pholidophorus crenulatus* and founded mainly on some scale characteristics and on the stoutness of the maxillary (see p. 393). Re-examination of the type species of the genus has revealed many other characteristics, especially a high number of infraorbitals (more than five), a rather broad preoperculum with the preopercular sensory canal running along the middle of the bone and with rather short and straight tubules in its ventral limb, and the presence of only a single supraorbital bone. Consequently, it seems to me that Woodward was quite correct in creating the genus *Pholidophoroides*. A further species showing, in general, the same characteristics is *Pholidophorus limbatus*, which therefore must be considered a second species of the genus.

Woodward thought that his *Ph. caudalis* probably belonged to his new genus *Pholidophoroides*. As far as the partly defective material makes comparison possible, it is quite obvious that *caudalis* is, in many respects, very similar to other members of that genus ; above all the preoperculum, the preopercular sensory canal and its tubules have the same characteristic shape in *caudalis* as in *Pholidophoroides*. There seems, moreover, to be only a single supraorbital. The exact number of infraorbitals is, unfortunately, indeterminable but nothing indicates that their number is more than five ; if this be so there is, in this respect, a difference of taxonomic importance between *caudalis* and the two *Pholidophoroides* species. The most striking difference between them is, however, that the squamation in *caudalis* consists of rather thin cycloid scales, in *Pholidophoroides* of thick ganoin scales. This difference in squamation prevents, in my opinion, *caudalis* being placed in the genus *Pholidophoroides* and because of this I have created for it the new genus *Pholidophoropsis*.

As a second *Pholidophoropsis* species I have, albeit with some hesitation, described two imperfect specimens under the new trivial name *maculata*. The reasons for the creation of this species are discussed on p. 422. In this connexion it must, however, be remembered that differences in the ganoin covering of the exoskeletal cranial bones may be dependent on ontogenetic age, as described for *Ph. bechei*, and that the *maculata* specimens may merely represent older individuals of *caudalis*. But as the largest *caudalis* specimen is 120 mm. in length, the smallest *maculata* 127 mm., the difference in respect of the absence or presence of ganoin spots should not be as pronounced as it actually is if the ganoin spots are a feature characterizing only the largest specimens.

The genera and species considered here are more or less closely related and constitute a family Pholidophoridae in a restricted sense ; a possible exception is the genus *Pholidolepis*, the systematic position of which cannot be determined until we have a better knowledge of the genus *Leptolepis*. This discussion must be deferred until a revision of that genus, now in preparation, is completed. It is of course very probable that many other species will be added to this family as soon as the members of the old genus *Pholidophorus* become better known.

Griffith & Patterson (1963) have in their valuable monograph on *Ichthyokentema purbeckensis* compared this genus with *Pholidophorus* as represented by *Ph. bechei* and *Ph. similis* Woodward. For this reason I must briefly mention the last named species although I have not yet had the opportunity of studying it myself. According to the description of *Ph. similis* given by de Saint-Seine (1949) there are so many dissimilarities between that species and the members of *Pholidophorus* s. str. described above, that it cannot be maintained in this genus. I need mention only the curious shape of the two postorbital infraorbitals (the dorsal one obviously corresponding both to infraorbitals 4 and 5 and to the dermosphenotic in *Pholidophorus*), the different shape of the maxillary, the suborbital, the preoperculum, the outline of the lower jaw and so on. All these features are atypical for the genus *Pholidophorus* as represented by *Ph. bechei* and *Ph. latiusculus* and most of them do not occur in the other pholidophorids described above. However, as I have no personal information regarding *Ph. similis* I shall confine myself to these comments.

Griffith & Patterson (1963) have convincingly shown that *Ichthyokentema purbeckensis* represents a family of its own, Ichthyokentemidae, and have given (p. 6) an exhaustive diagnosis of the new family. For the family Pholidophoridae as understood here no such diagnosis can be given at present because of our imperfect knowledge, particularly regarding the endocranium and many other details. The following diagnosis must therefore be considered a preliminary one.

Family **PHOLIDOPHORIDAE** s. str.

PRELIMINARY DIAGNOSIS. Fusiform Pholidophoriformes of small to medium size ; bones of head and scales with or without ganoin covering ; rostral toothless, not separating premaxillaries ; nasals not in contact in the mid-line ; dermosphenotic not elongated dorso-ventrally ; five to seven infraorbitals, infraorbital 3 the largest ; one to two supraorbitals ; two supramaxillaries (except in *Ph.* (?) *caffii*?) ; mandible gently ascending, with dentary (dentalo-splenial), articular and angular (angulo-supra-angular); dentition on premaxillary, maxillary and dentary, only weakly developed on two last named bones; single gular; preoperculum more or less angular; suture between operculum and suboperculum oblique; supraorbital sensory canal ending in parietal and having no anastomosis with infraorbital sensory canal; anterior and middle pit-lines on parietal, middle pit-line extending on to dermopterotic; preopercular sensory canal with moderate to rather long tubuli; preoperculum with anterior division of supramaxillary (horizontal) and postmaxillary (vertical) pit-lines, former sometimes with anterior portion on infraorbital 3; oral pit-line present on angular; vertebrae, as far as known, with annular centra; fulcra present on all fins (except in *Pholidolepis*); scales more or less rhomboid with smooth or pectinated hind edge, or cycloid with fine concentric striation; some longitudinal rows of deepened scales on the flank.

(*b*) *Some phylogenetic aspects of the genera and species within the family Pholidophoridae* s. str.

The genera and species of the family Pholidophoridae treated above are, as previously stated, more or less closely related. Their phylogenetic relationship is of course difficult to discuss on the basis of our present knowledge, but some comments may be appropriate.

The pholidophorids are generally considered to be advanced holosteans, probably the forerunners of the teleostean stage of development within the actinopterygians. One of the most striking differences between the holostean and teleostean stages is the transformation of the thick, ganoin-covered scales into thin cycloid scales. This trend of evolution is clearly demonstrated in the species now under consideration. The Upper Triassic species *Pholidophorus latiusculus*, *Ph.* cf. *pusillus* and *Ph.* (?) *caffii* as well as the Lower Liassic *Pholidophoroides limbata* have thick scales, in *Ph. crenulata* the anterior body scales are thinner and show, as stated by Woodward (1941), a concentric striation, and in *Pholidophorus bechei* the younger individuals show a weaker ganoin covering of the exoskeletal cranial bones and scales than do the adult specimens. In *Pholidophoropsis maculata* the ganoin covering on the exoskeletal cranial bones is confined to small scattered spots and streaks, whilst of the thin cycloid body scales, only some axillary scales carry a few ganoin spots; thicker ganoin scales exist only at the caudal fin base. In *Ph. caudalis* no ganoin spots are visible on the exoskeletal cranial bones or axillary scales; thicker scales occur only at the posterior end of the caudal peduncle as in *Ph. maculata*. In *Pholidolepis dorsetensis* a ganoin ornamentation is present at least on the maxillary, the supramaxillaries and the lower jaw, whereas the body scales are thin with a delicate concentric striation. This may indicate that these pholidophorids are at that phylogenetic stage at which the reduction of the ganoin covering of the scales is taking place, and further, that this reduction began in the anterior part of the body and that the posterior part of the caudal peduncle retained the ganoin scales longer.

These consecutive stages of scale reduction indicate, however, certainly not a straight phylogenetic series, which is evident from other facts.

The shape of the preoperculum together with the course of the preopercular sensory canal and the pattern of its tubules seem to be very useful indicators of the relationship between various taxonomic units. In the family Pholidophoridae s. str. the most primitive type is represented by the broad and little curved preoperculum in *Ph.* (?) *caffii* ; the preopercular sensory canal runs in the dorsal limb of the bone somewhat nearer to its posterior than to its anterior margin, in the ventral limb it runs in about the middle of its length. The tubules given off from the posterior side of the canal are comparatively few, wide and rather short. From this rather primitive preopercular type one can easily derive that of *Ph.* cf. *pusillus* ; the general shape of the preoperculum is about the same, but the preopercular sensory canal runs nearer to the middle of the bone and the tubules are more numerous in the ventral part of the bone and are, moreover, longer. A further stage is represented by *Ph. latiusculus*. Here, the preoperculum is more differentiated in that its dorsal and ventral parts are of a different shape and its posterior margin possesses a shallow notch ; the preopercular sensory canal runs a little nearer to the anterior than to the posterior margin of the bone and its tubules are more numerous; in the ventral part of the bone the tubules are rather long and slightly curved. The preoperculum of *Ph. bechei* has a fairly characteristic shape ; its anterior margin is slightly concave, its posterior margin is notched and its postero-ventral corner projects backwards. The number of tubules belonging to the preopercular sensory canal is even greater than in *Ph. latiusculus* and those in the ventral limb of the bone are still longer. The preoperculum of *Pholidolepis dorsetensis* recalls many of the characteristics of *Ph. bechei*, but the preopercular sensory canal runs nearer to its deeply concave anterior margin (obviously due to a reduction of the anterior part of the bone) and the tubuli are fewer and relatively shorter. In my opinion the preopercula in the three species, *Ph.* cf. *pusillus*, *Ph. latiusculus* and *Ph. bechei*, constitute a phylogenetic series which can be derived from the preoperculum in *Ph.* (?) *caffii* and from which series the preoperculum in *Pholidolepis* can also be derived.

In the genera *Pholidophoroides* and *Pholidophoropsis* the preoperculum has a somewhat different shape and the tubules of the preopercular sensory canal are straight and rather short, the longest being situated in the middle part of the bone, not in the ventral half. In all the species hitherto known the shape of the preoperculum is surprisingly uniform. It cannot be derived from *Ph.* (?) *caffii* as directly as can that of *Ph.* cf. *pusillus*, but probably from a still more primitive type. The genus *Pholidophoropsis* cannot, however, be directly derived from *Pholidophoroides* ; the members of the latter genus have a relatively high number of infraorbitals, seven against the general number of five ; in *Pholidophoropsis* the number of infraorbitals cannot be stated with accuracy, but there is nothing to indicate, at least not in *Ph. maculata*, that it exceeds five.

The structure of the preoperculum thus indicates that within the family Pholidophoridae in the restricted sense given above two diverging lines of evolution may be discerned, the one comprising the genus *Pholidophorus* s. str., probably giving rise to the genus *Pholidolepis*, perhaps leading on to the leptolepids, the other comprising the genera *Pholidophoroides* and *Pholidophoropsis*. In both these lines a reduction of the ganoin covering of the exoskeletal cranial bones and body scales has started independently (as probably in many other lines of evolution), in the *Pholidophorus* series from scales with a smooth posterior margin, in the *Pholidophoroides* series from scales with a pectinated or serrated hind margin.

The general phylogenetic evolution can of course be elucidated from other features also, but the material investigated is too fragmentary to illustrate this in great detail. Some indications may perhaps be worth noting.

The sensory pit-lines seem to show a tendency towards a successively more superficial position and consequently their markings on the underlying bones become successively less pronounced. The supramaxillary (horizontal) and postmaxillary

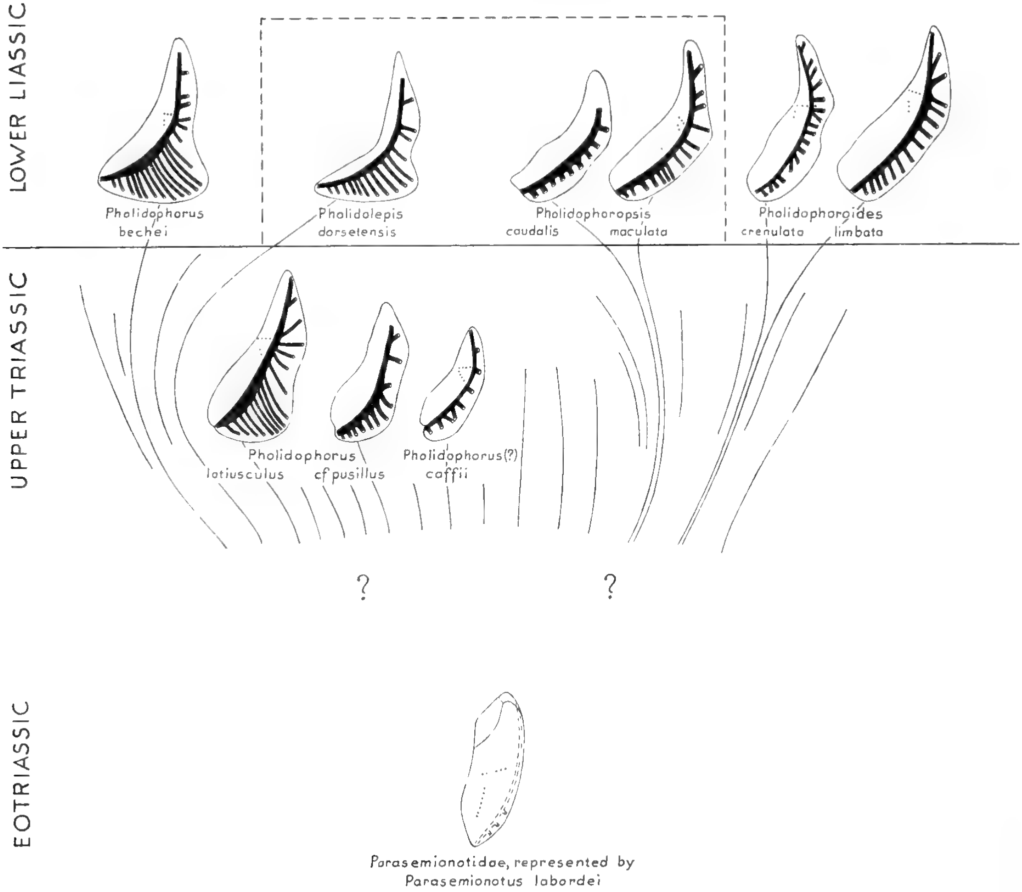

FIG. 16. Diagram illustrating the writer's opinion concerning phyletic relationships between certain genera and species of the family Pholidophoridae s. str., based on the condition of the preoperculum; within the rectangle are species with thin, cycloid scales. The possible derivation of the family from the parasemionotids is indicated by the preoperculum of *Parasemionotus labordei* (Lehman 1952, text-fig. 116). Further explanation in the text.

(vertical) pit-lines on the lateral surface of the preoperculum are rather well marked in *Ph.* (?) *caffii* and *Ph. latiusculus* (in *Ph.* cf. *pusillus* the lateral surface of the preoperculum is too damaged to enable any accurate statement in this respect), in *Ph. bechei* on the other hand they are very short and easily overlooked. In the *Pholidophoroides-Pholidophoropsis* series these pit-lines are rather well developed in *Ph. limbata,* much shorter in *Ph. maculata.*

The antorbital bone seems to undergo reduction in the holostean-teleostean evolutionary series ; in most teleosts it has lost its connection with the infraorbital sensory canal. Unfortunately this bone is unknown in *Ph.* cf. *pusillus,* in *Ph. latiusculus* and in *Pholidolepis* ; in *Ph.* (?) *caffii* it seems, however, to be relatively better developed than in *Ph. bechei.* In the *Pholidophoroides-Pholidophoropsis* series a successive reduction of the antorbital seems to occur ; in *Ph. limbata* and *Ph. crenulata* the antorbital has a rather great postero-dorsal extension and its sensory canal has a relatively long antorbital branch, in the *Pholidophoropsis* species the antorbital is more rounded and the antorbital branch is comparatively short.

My conception of the phylogenetic interrelationship in those members of the family Pholidophoridae s. str. studied by me and based on the shape of the preoperculum and the reduction of the ganoin covering of the cranial bones and scales is tentatively illustrated in Text-fig. 16 ; the rectangle encloses species with thin cycloid scales.

(*c*) *Some brief comments on the derivation of the family Pholidophoridae s. str.*

The question of the ancestry of the Pholidophoroidea has been treated by many authors. Quite recently Gardiner (1960) and Griffith & Patterson (1963) have taken up and discussed the question, also giving a summary of earlier ideas. Gardiner expressly states (p. 350) : " From all these facts it appears obvious that the Pholidophoridae have arisen directly from the Parasemionotidae ", whereas Griffith & Patterson are somewhat in doubt whether the Pholidophoroidea can be derived directly from that family.

It is not my intention to enter into this discussion ; according to Griffith & Patterson the two objections against a derivation of the Pholidophoroidea from the Parasemionotidae (the different course of the facial nerve and of the orbital artery) refer to the endocranium, which I have not studied. I only wish to put forward some remarks regarding certain exoskeletal cranial bones in the family Pholidophoridae s. str. ; above all, that our much widened knowledge of the species *Pholidophorus* (?) *caffii* seems to add new facts to this discussion.

As already mentioned above (p. 427) concerning the phylogenetic relationship of the members of the family Pholidophoridae s. str., I consider the preoperculum in *Ph.* (?) *caffii* to be the most primitive one, particularly because of the fact that the preopercular sensory canal lies somewhat nearer to the posterior than to the anterior margin of the bone, and that this canal possesses few tubules. In these respects it recalls to some extent the conditions in the Parasemionotidae. In the latter family the preoperculum is at an interesting stage of fragmentation into minor, separate bones, the variations of which have been clearly demonstrated by Lehman (1952). The antero-dorsal ones of these secondary bones, the so-called " anamestic bones ", apparently correspond to the suborbital bone or bones and to the posterior part of infraorbital 3 in more advanced groups (see above, p. 398). The persisting part of the pre-existent palaeoniscoid preoperculum, the preoperculum proper, is pierced by the preopercular sensory canal, which runs near the posterior margin of the bone; generally the canal itself is difficult to observe (at least this was the case in the specimens of *Parasemionotus labordei* (Priem) which I have had the opportunity to see in Paris and in Stockholm) and an opinion concerning its course can therefore be arrived at only on the basis of the position of its pores. That being so, it is naturally difficult to make out the direction in which the few and apparently very short tubules passed off from the preopercular sensory canal; Lehman (1952, text-fig. 116) depicts them as running in an antero-dorsal direction from the morphologically anterior side of the canal, whereas Gardiner (1960, text-fig. 67D) in his redrawing of Lehman's figure shows them as passing off in a postero-ventral direction from the posterior side of the canal. Which of these two interpretations is the correct one, cannot in my opinion be determined through direct observation, but since the tubules of the preopercular sensory canal, if present, are generally given off from the morphologically posterior side of the canal, the interpretation given by Gardiner seems to me to be the most likely one. If this be the case, the preoperculum in *Ph.* (?) *caffii* can easily be derived from that in *Parasemionotus* (or in some other parasemionotid) through a forward shift of the preopercular sensory canal in connection with a backward lengthening of the tubules given off from its posterior side.

The members of the family Pholidophoridae s. str. generally have two supramaxillaries, whereas the parasemionotids have only a single supramaxillary. In this respect *Ph.* (?) *caffii* resembles the parasemionotids, but since this species is represented by only a single specimen, one must keep in mind, as suggested in the description (p. 378), that this may be an individual anomaly. If, in future, further specimens of this species are discovered showing the presence of only a single supramaxillary, *Ph.* (?) *caffii* must be removed from the genus *Pholidophorus* s. str. and placed in a genus of its own, a genus which to some extent would be intermediate between the parasemionotids and the family Pholidophoridae s. str.

My opinion that the family Pholidophoridae s. str. (and probably many other pholidophoroids) may be derived from parasemionotid-like ancestors, perhaps still unknown, is demonstrated in Text-fig. 16, in which the preoperculum of *Parasemionotus labordei* is arbitrarily chosen as representing the parasemionotids.

As compared with *Ph.* (?) *caffii*, *Parasemionotus labordei* is a rather deep-bodied species (Lehman 1952, text-fig. 123). It is therefore perhaps worth noting that in the species *Helmolepis gracilis* Stensiö, obviously belonging to the Parasemionotidae, the size and the shape of the body is about the same as in *Ph.* (?) *caffii*. Unfortunately very little is known about the cranial bones of *Helmolepis*, the greater part of the head being missing, which makes a closer comparison between the two species impossible.

IV. ACKNOWLEDGEMENTS

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PLATE 1

Pholidophorus bechei Agassiz

Head, lateral view. B.M. 38107. ×4.

Ang, angular ; *De. Spl*, dentary ; *Dsph*, dermosphenotic ; *Ext*, extrascapular ; Ifo_2, Ifo_3, Ifo_4, Ifo_5, infraorbitals 2–5 ; *Iop*, interoperculum ; *Mx*, maxillary ; *Op*, operculum ; *Pmx*, premaxillary ; *Pop*, preoperculum ; *R. Br*, branchiostegal rays ; *Sbo*, suborbital ; Smx_1, Smx_2, anterior and posterior supramaxillaries ; *Sop*, suboperculum ; *Ssc*, suprascapula ; hc_1, anterior division of supramaxillary pit-line ; *l. l*, lateral line ; *orp*, postmaxillary pit-line.


Pmx
DeSpl
Mx
Smx1
Smx2
Ifo2
Ifo5
Ifo4
Ang
Ifo3
RBr
Dsph
prp
Sbo
hcl
Pop
Ext
Hop
Ssc
Op
Sop

PLATE 2

Pholidophorus bechei Agassiz

FIG. 1. Part of head. B.M. 39859. ×6.
FIG. 2. Cranial roof. B.M. P.3589*a*. ×5.
FIG. 3. Cranial roof. B.M. P.1052*d*. ×3·3.

Ang, angular; *Ant*, antorbital; *De. Spl*, dentary; *Dpt*, dermopterotic; *Dsph*, dermosphenotic; *Ext*, extrascapular; *Fr*, frontal; *Hm*, hyomandibular; Ifo_1, Ifo_3, Ifo_4, Ifo_5, infraorbitals 1 and 3–5; *Mx*, maxillary; *Na*, nasal; *Op*, operculum; *Pmx*, premaxillary; *Pop*, preoperculum; *Ro*, rostral; Smx_1, Smx_2, anterior and posterior supramaxillaries; So_1, So_2, supraorbitals 1 and 2; *Ssc*, suprascapula; *ap*, anterior pit-line; hc_1, anterior division of supramaxillary pit-line; *ifc. com*, ethmoidal commissure; *mp*, middle pit-line; *orp*, postmaxillary pit-line; orp_1, oral pit-line; *soc*, supraorbital sensory canal.


2
Pmx
Ro
So1
Pop
orp
hc1
So2
Dsph
Ext
Ssc
Na
Fr
Dsph
ap
mp
Dpt
Ext
De.Spl
Mx


1
Ssc
Dpt
Ob
Ifo3
So1
Na
Pmx
Ifo1
An
De.Spl
Mx
Smx
Smx2
Aqu
orp
Pop
hc

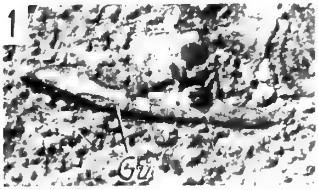

3
mp
Dpt
Smx2
So2
So1
Fr
Na
Ro
rc.com

PLATE 3

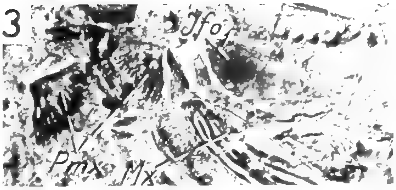
Pholidophorus bechei Agassiz

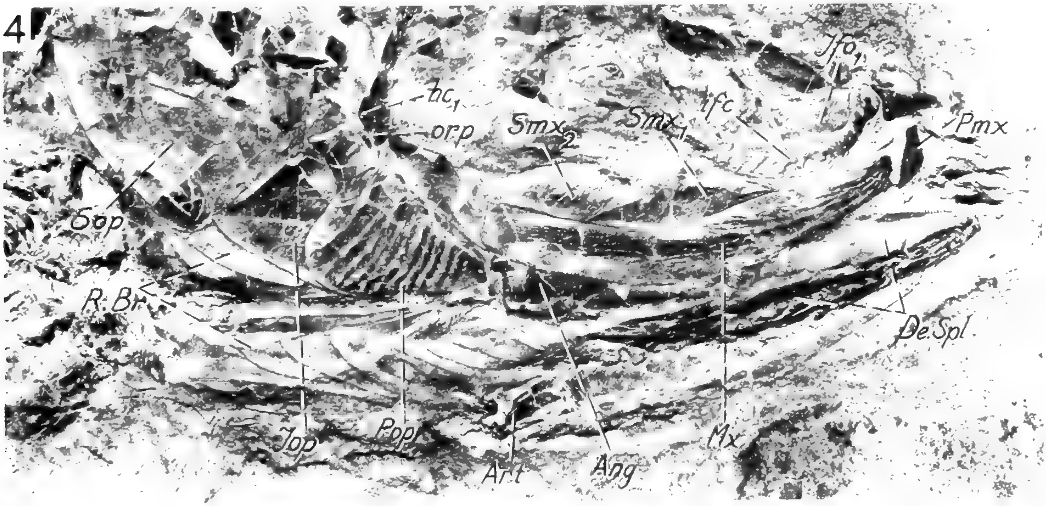
FIG. 1. Gular plate. B.M. P.3589*a*. ×6.
FIG. 2. Antorbital. B.M. 25276. ×3·75.
FIG. 3. Premaxillaries. B.M. P.154. ×6.
FIG. 4. Part of head. B.M. 38109. ×4.
FIG. 5. Part of head. B.M. P.1051. ×4.

Ang, angular ; *Ant*, antorbital ; *Art*, articular ; Ch_2, anterior part of ceratohyal ; *De. Spl*, dentary ; *Gu*, gular plate ; *Hh*, hypohyal ; Ifo_1, infraorbital 1 ; *Iop*, interoperculum ; *Mx*, maxillary ; *Pmx*, premaxillary ; *Pop*, preoperculum ; *Qu*, quadrate ; *R. Br*, branchiostegal rays ; Smx_1, Smx_2, anterior and posterior supramaxillaries ; hc_1, anterior division of supramaxillary pit-line ; *orp*, postmaxillary pit-line.


1
Gu


2
Ant


3
Ifo_1
Pmx
Mx


4
hc_1
or.p
Smx_2
Smx_1
ifc
Ifo_1
Pmx
Sop
R.Br
De.Spl
Iop
Pop
Art
Ang
Mx


5
Ifo_1
Ou
Ang
Smx_1
hc_1
Sop
Iop
Pop
De.Spl
Hh
R.Br
Ch_2

PLATE 4

Pholidophorus latiusculus Agassiz

Head of neotype. Geol. Paläontolog. Institut, Innsbruck. ×6.

De. Spl, dentary ; *Dpt*, dermopterotic ; *Fr*, frontal ; Ifo_3, Ifo_4, Ifo_5, infraorbitals 3–5 ; *Iop*, interoperculum ; *Mx*, maxillary ; *Na*, nasal ; *Op*, operculum ; *Pop*, preoperculum ; *Sbo*, suborbital ; *Scl*, supracleithrum ; Smx_1, Smx_2, anterior and posterior supramaxillaries ; So_1, supraorbital 1 ; *Sop*, suboperculum ; hc_1, anterior division of supramaxillary pit-line ; *ll*, lateral line.


De.Spl
Smx1
Smx2
Mx
Na
So1
Jfo3
Jfo5
Jfo4
ha1
Pop
ha
Jop
Fr
Dpt
Sbo
Op
Sop
Scl
ll
ll

PLATE 5

Pholidophorus latiusculus Agassiz

FIG. 1. Head. B.M. P.1063. ×6.
FIG. 2. Part of cranial roof of specimen Innsbruck Lit. F. ×6.
FIG. 3. Infraorbitals 3–5 and part of preoperculum of specimen Innsbruck Lit. F. ×6.

Figs. 2 and 3 show negative impressions lit from bottom right.

Cl, cleithrum ; *De. Spl*, dentary ; *Dpt*, dermopterotic ; *Dsph*, dermosphenotic ; *Ext*, extrascapular ; *Fr*, frontal ; *Ifo*$_2$, *Ifo*$_3$, *Ifo*$_4$, *Ifo*$_5$, infraorbitals 2–5 ; *Iop*, interoperculum ; *Mx*, maxillary ; *Na*, nasal ; *Op*, operculum ; *Pa*, parietal ; *Pop*, preoperculum ; *Sbo*, suborbital; *Scl*, supracleithrum ; *Smx*$_1$, *Smx*$_2$, anterior and posterior supramaxillaries ; *So*$_1$, *So*$_2$, supraorbitals 1 and 2 ; *Sop*, suboperculum ; *Vert*, ring-vertebrae ; *ap*, anterior pit-line ; *hc*$_1$, anterior division of supramaxillary pit-line ; *mp*, middle pit-line ; *orp*, postmaxillary pit-line ; *soc*, supraorbital sensory canal.

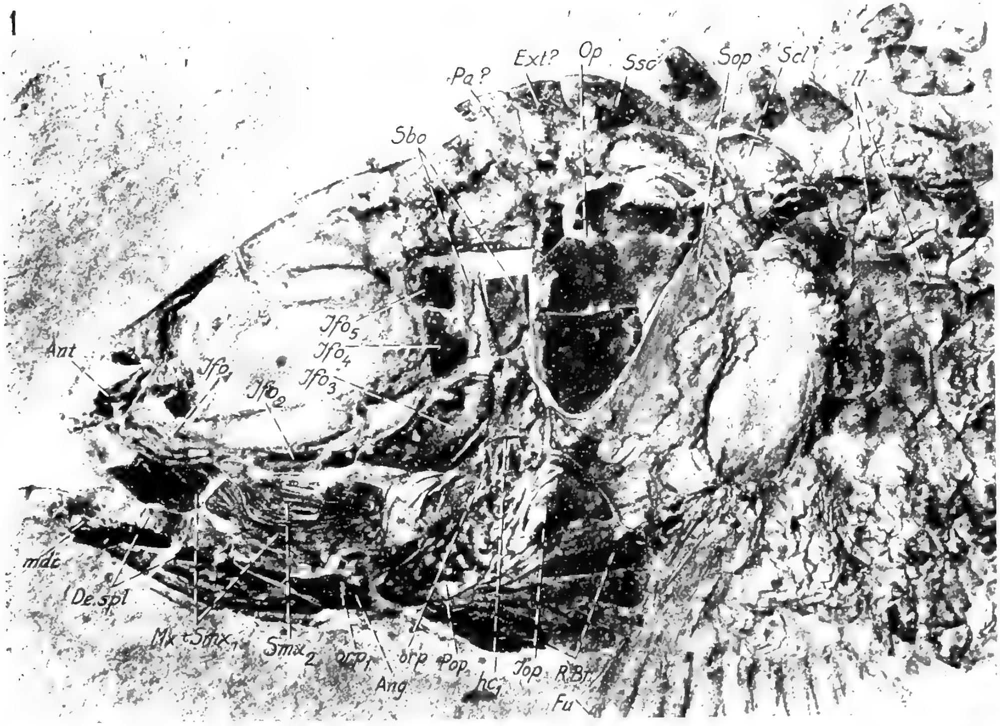

1
Na
So1
So2
Dsoh
soc
Ext
Pa
ap
mp
Fr
Dpt
Dsph
Sbo
Op
Scl
Jfo5
Jfo4
Jfo3
Jfo2
De.Spl
Mx
Smx1
Smx2
hc1
hc
orp
Pop
Jop
Sop
Cl
Vert
2
Fr
Dpt
soc
3
Pop
hc
orp
Jfo5
Jfo4
Jfo3

PLATE 6

FIG. 1. *Pholidophorus* (?) *caffii* Airaghi. Head of the holotype. ×10.
FIG. 2. *Pholidophorus* cf. *pusillus* Agassiz. Head. B.M. P.4418. ×7.5.

Ang, angular ; *Ant*, antorbital ; *Ant?*, probably antorbital ; *De. Spl*, dentary ; *Ext?*, probably extrascapular ; *Fu*, fulcra ; *Hm*, hyomandibular ; Ifo_1, Ifo_2, Ifo_3, Ifo_4, Ifo_5, infraorbitals 1–5 ; *Iop*, interoperculum ; *Mx*, maxillary ; $Mx + Smx_1$, maxillary and supramaxillary 1 ; *Op*, operculum ; *Pa?*, probably parietal ; *Pop*, preoperculum ; *R. Br.*, branchiostegal rays ; *Sbo*, suborbital ; *Sc*, scale ; *Scl*, supracleithrum ; Smx_1, Smx_2, anterior and posterior supramaxillaries ; *Sop*, suboperculum ; *Ssc*, suprascapula ; hc_1, anterior division of supramaxillary pit-line ; *l. l*, lateral line ; *mdc*, mandibular sensory canal ; *orp*, postmaxillary pit-line ; *orp?*, possibly postmaxillary pit-line ; orp_1, oral pit-line.

1


Pa?
Ext?
Op
Ssc
Sop
Scl
ll
Sbo
Ifo5
Ifo4
Ifo3
Ant
Ifo1
Ifo2
mdc
De.spl
Mx+Smx1
Smx2
orp1
Ang
orp
Pop
hc1
Iop
R.Br
Fu

2

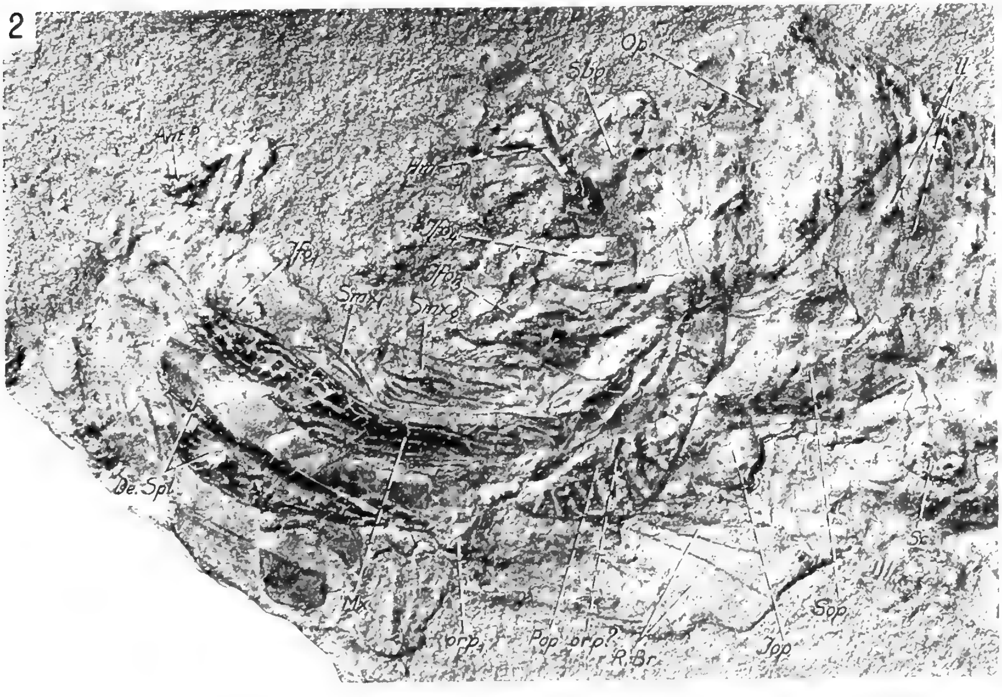

Op
Sbo
ll
Ant?
Hm
Ifo4
Ifo3
Ifo1
Smx1
Smx2
De.Spl
Mx
orp1
Pop
orp?
R.Br
Iop
Sop
Sc

PLATE 7

Pholidolepis dorsetensis gen. et sp. nov.

FIG. 1. Anterior part of head. B.M. 38536. ×5.
FIG. 2. Jaws. B.M. P.44708. ×5.
FIG. 3. Head of the holotype. B.M. 38164. ×5.

Ang, angular ; *De. Spl*, dentary ; *Dpt*, dermopterotic ; *Dsph*, dermosphenotic ; *Fr*, frontal ; *Hm*, hyomandibular ; *Mx*, maxillary ; *Na*, nasal ; *Pop*, preoperculum ; Smx_1, Smx_2, anterior and posterior supramaxillaries ; *So*, supraorbital ; *poc*, preopercular sensory canal ; *soc*, supraorbital sensory canal.

1


Soc
Hm
Mx
De.Spl
Mx
Pop

2


Smx₂
Smx₁
Ang
De.Spl
Mx

3


soc
Fr
Na
So
Dsph
De.spl
Mx
Dpt
Pop
poc

PLATE 8

Pholidophoroides crenulata (Egerton)

Head, lateral view. B.M. 38739*. ×5. (See also Pl. 15, fig. 4.)

Ang, angular; *Ant*, antorbital; *De. Spl*, dentary; *Dpt*, dermopterotic; *Dsph*, dermosphenotic; *Fr*, frontal; *Fu*, fulcra; Ifo_1, Ifo_3, infraorbitals 1 and 3; *Iop*, interoperculum; *Mx*, maxillary; *Na*, nasal; *Op*, operculum; *Pop*, preoperculum; *Sbo*, suborbital; Smx_1, Smx_2, anterior and posterior supramaxillaries; *So?*, fragment, perhaps of a supraorbital 2; *Sop*, suboperculum.

---

* Quoted as 38730 in error in Woodward 1895: 464.


Sop
Fu
Op
Jop
Dpt
Pop
Dsph
Sbo
Jfo3
So?
Fr
Jfo1
Ang
Sart e1
Smx1
Mx
Na
Ant
De Spl

PLATE 9

Pholidophoroides crenulata (Egerton)

Head in dorsal view. B.M. 38110. × 4·5. (See also Pl. 15, fig. 3.)

Ant, antorbital ; *Dpt*, dermopterotic ; *Dsph*, dermosphenotic ; *Ext*, extrascapular ; *Fr*, frontal ; Ifo_1, Ifo_3, Ifo_4, Ifo_5, Ifo_6, Ifo_7, infraorbitals 1 and 3–7 ; Ifo_8?, possibly an infraorbital 8 ; *Mx*, maxillary ; *Na*, nasal ; *Op*, operculum ; *Pop*, preoperculum ; *Ro*, rostral ; *Sbo*, suborbital ; " *Sbo* ", " accessory suborbitals " ; *Scl*, supracleithrum ; Smx_1, supramaxillary 1 ; *So*, supraorbital ; *Sop*, suboperculum ; *Ssc*, suprascapula ; *ifc*, infraorbital sensory canal ; *ifc. com*, ethmoidal commissure ; *soc*, supraorbital sensory canal.

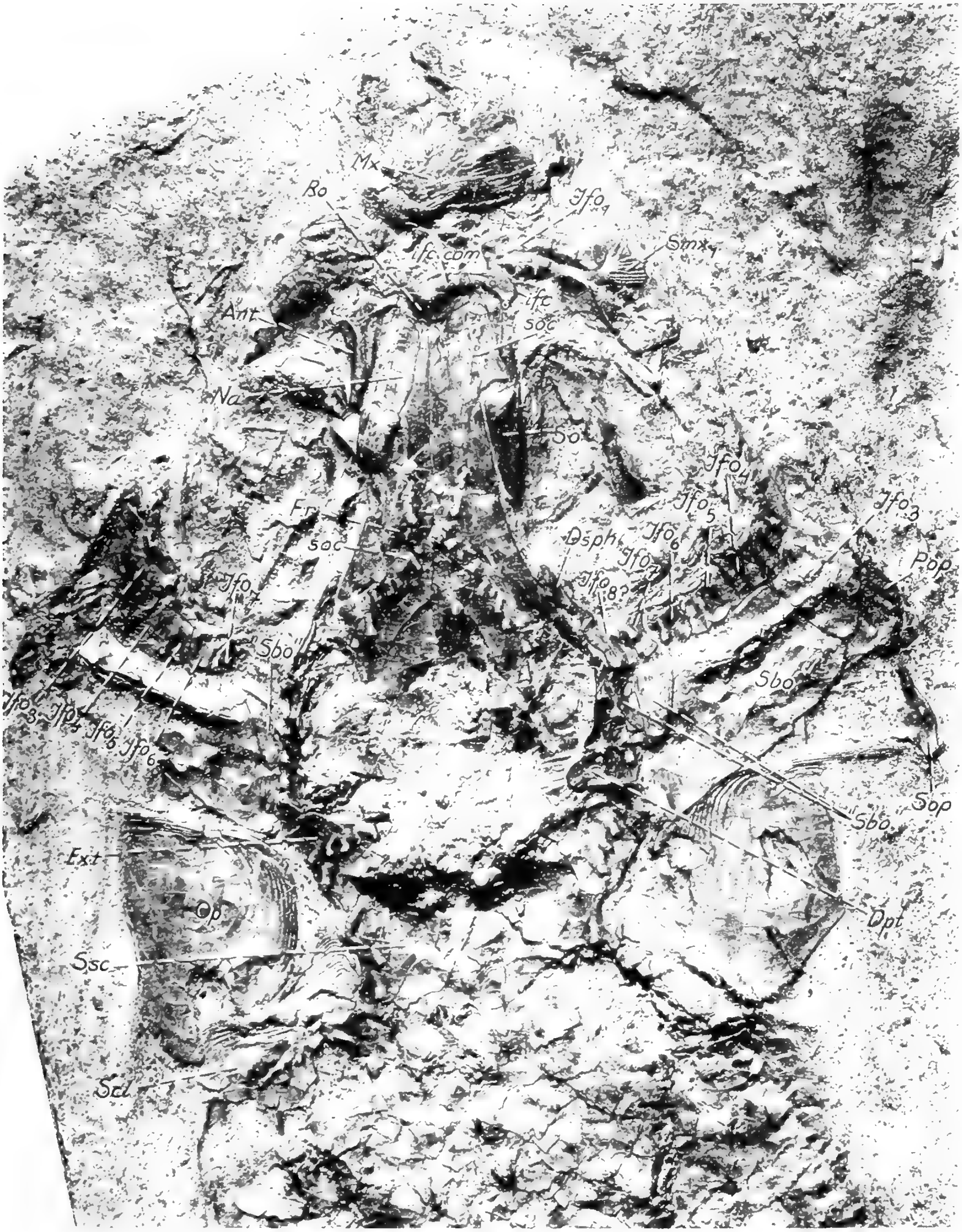

Mx
Ro
Ifo$_1$
ifc.com
Smx$_1$
Ant
ifc
soc
Na
So
Ifo$_4$
Ifo$_5$
Ifo$_3$
Fr
soc
Dsph
Ifo$_6$
Ifo$_7$
Ifo$_8$?
Pop
Ifo$_7$
Sbo
Sbo
Ifo$_3$
Ifo$_4$
Ifo$_5$
Ifo$_6$
Sbo
Sop
Ext
Op
Dpt
Ssc
Scl

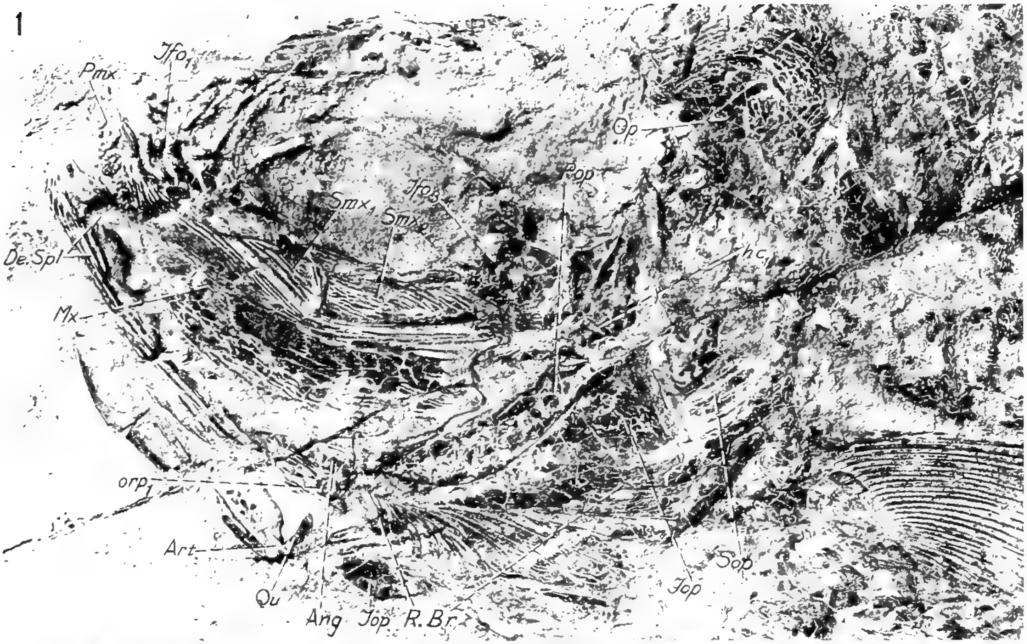
PLATE 10

Pholidophoroides crenulata (Egerton)

Fig. 1. Head. B.M. P.4415. (See also Pl. 15, fig. 8). ×4·5.
Fig. 2. Head. B.M. P.1046*b*. ×4·5.

Ang, angular ; *Ant*, antorbital ; *Art*, articular ; *De. Spl*, dentary ; *Dpt*, dermopterotic ; *Dsph*, dermosphenotic ; *Ext*, extrascapular ; *Fr*, frontal ; *Gu*, gular plate ; *Ifo*$_1$, *Ifo*$_3$, *Ifo*$_4$, *Ifo*$_5$, *Ifo*$_6$, infraorbitals 1 and 3–6 ; *Iop*, interoperculum ; *Mx*, maxillary ; *Op*, operculum ; *Pa*, parietal ; *Pmx*, premaxillary ; *Pop*, preoperculum ; *Qu*, quadrate ; *R. Br*, branchiostegal rays ; *Sbo*, suborbital ; *Smx*$_1$, *Smx*$_2$, anterior and posterior supramaxillaries ; *Sop*, suboperculum ; *Ssc*, suprascapula ; *hc*$_1$, anterior division of supramaxillary pit-line ; *orp*$_1$, oral pit-line.

1


Pmx
Jfo_1
De.Spl
Mx
Smx_1
Smx_2
Jfo_3
Pop
Op
hc_1
orp_1
Art
Qu
Ang
Jop
R.Br
Sop
Jop

2


Ssc
Ext
Sbo
Dpt
Pa
Dsph
Fr
Ant
Pmx
Op
Jfo_6
Jfo_5
Jfo_4
Jfo_3
Jfo_1
Smx_1
Smx_2
Gu
Sop
De.Spl
hc_1
Jop
Pop
Qu
Ang
Mx

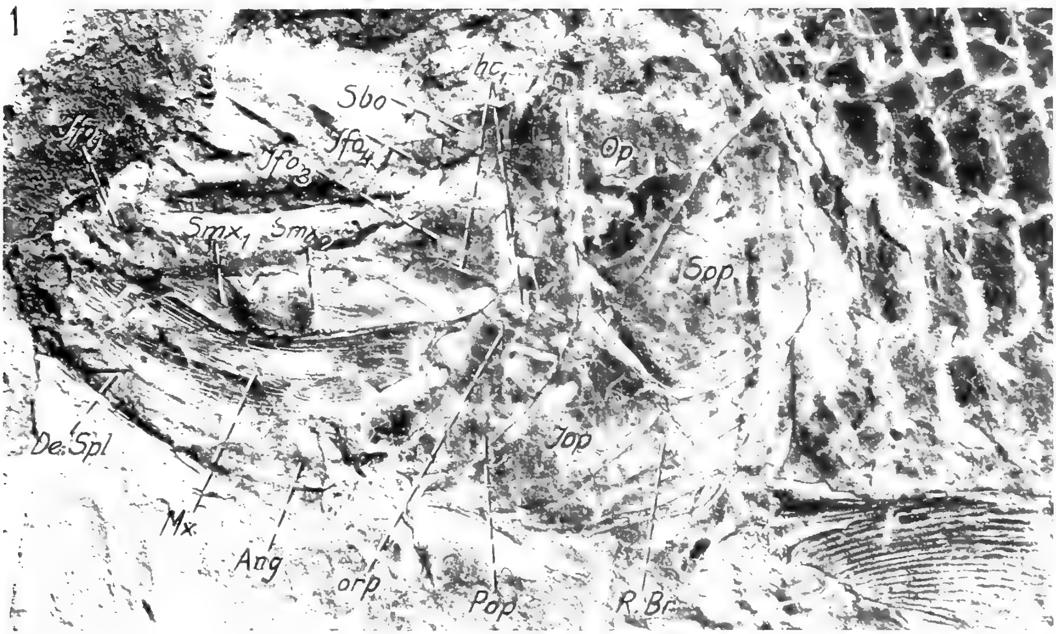
PLATE 11

Pholidophoroides limbata (Agassiz)

FIG. 1. Head of lectotype.. B.M. P.1047. Photo British Museum (Nat. Hist.). ×3.
FIG. 2. Head. B.M. 36472. ×2·2.

Ang, angular; *Ant*, antorbital; *Cl*, cleithrum; *De. Spl*, dentary; *Dpt*, dermopterotic; *Fr*, frontal; Ifo_1, Ifo_3, Ifo_4, Ifo_5, Ifo_6, infraorbitals 1 and 3–6; Ifo_7?, probably infraorbital 7; *Iop*, interoperculum; *Mx*, maxillary; Mx_s, maxillary of the left side; *Na*, nasal; *Op*, operculum; *Pop*, preoperculum; *R. Br*, branchiostegal rays; *Ro?*, probably rostral; *Sbo*, suborbital; " *Sbo* ", " accessory suborbital "; Smx_1, Smx_2, anterior and posterior supramaxillaries; *Sop*, suboperculum; hc_1, anterior division of supramaxillary pit-line; *mp*, middle pit-line; *orp*, postmaxillary pit-line; orp_1, oral pit-line.

1


Ifo$_1$
Sbo
hc$_1$
Ifo$_4$
Ifo$_3$
Op
Smx$_1$
Smx$_2$
Sop
De. Spl
Iop
Mx
Ang
orp
Pop
R. Br.

2


Dpt
mp
"Sbo"
Ifo$_7$?
Ifo$_6$
Fr
Na
Ant
Sbo
Op
Ro.?
Ifo$_5$
Ifo$_1$
Mx$_s$
Ifo$_4$
Ifo$_3$
hc$_1$
orp
Smx$_1$
Sop
Mx
Smx$_2$
Cl
Iop
Pop
orp$_1$
Ang

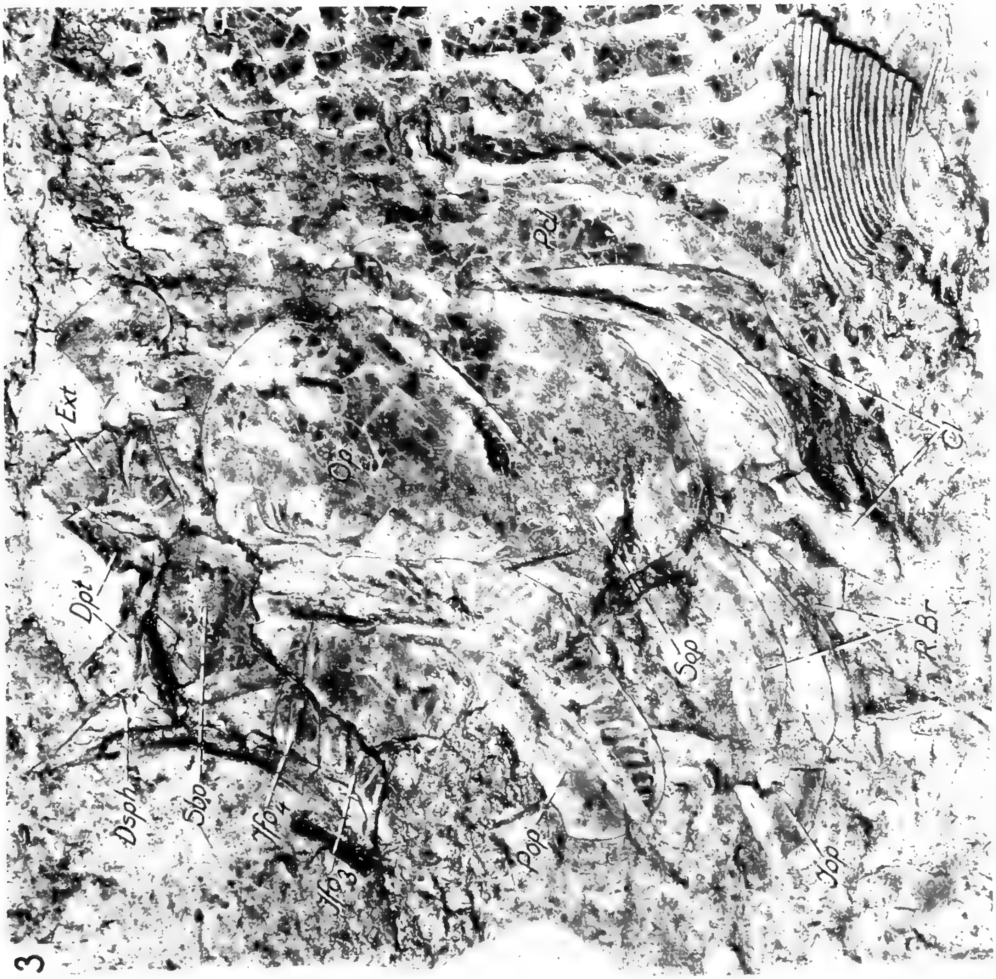
PLATE 12

Pholidophoroides limbata (Agassiz)

FIG. 1. Premaxillary and anterior part of maxillary of B.M. P.4422. ×10.
FIG. 2. Anterior part of head of B.M. P.4422. ×4.
FIG. 3. Posterior part of head of B.M. 38531. ×4.

Ant, antorbital; *Cl*, cleithrum; *De. Spl*, dentary; *Dpt*, dermopterotic; *Dsph*, dermosphenotic; *Ext*, extrascapular; *Ifo*$_1$, *Ifo*$_3$, *Ifo*$_4$, infraorbitals 1 and 3–4; *Iop*, interoperculum; *Mx*, maxillary; *Op*, operculum; *Pcl*, postcleithrum; *Pmx*, premaxillary; *Pop*, preoperculum; *R. Br*, branchiostegal rays; *Ro*, rostal; *Sbo*, suborbital; *So*, supraorbital; *Sop*, suboperculum; *ifc*, infraorbital sensory canal; *ifc. com*, ethmoidal commissure.

3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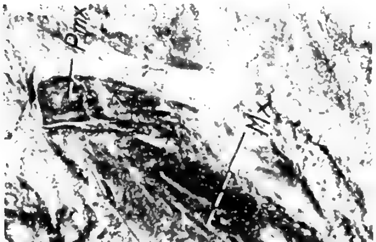
Sbo
Ifo4
Ifo3
Op
Pcl
Pop
Sop
Cl
R.Br
Iop

1


Pmx
Mx

2


So
Ifc.com
Rb
Pmx
Mx
De
Spl
Ant
Ifc
Ifo1

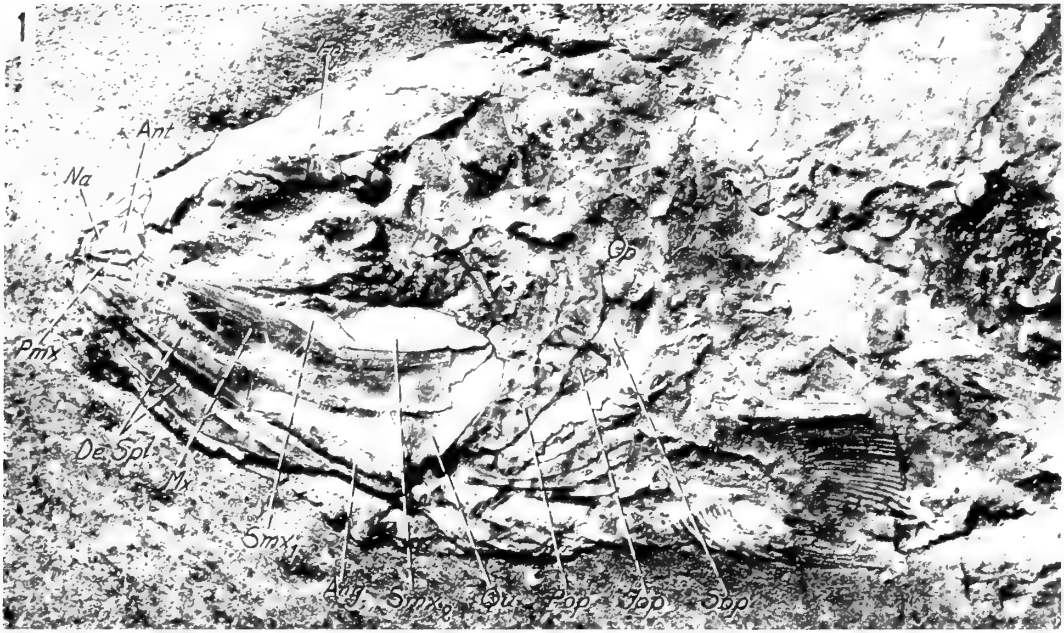
PLATE 13

Pholidophoropsis caudalis (Woodward)

FIG. 1. Head of paratype. B.M. P.3664*a*. Photo British Museum (Nat. Hist.). ×3·75.
FIG. 2. Head of holotype. B.M. P.3664. Photo British Museum (Nat. Hist.). ×3·75.

Ang, angular ; *Ant*, antorbital ; *De. Spl*, dentary ; *Dpt*, dermopterotic ; *Ext*, extrascapular ; *Fr*, frontal ; Ifo_1, Ifo_3, Ifo_4, infraorbitals 1 and 3–4 ; *Iop*, interoperculum ; *Mx*, maxillary ; *Na*, nasal ; *Op*, operculum ; *Pmx*, premaxillary ; *Pop*, preoperculum ; *Qu*, quadrate ; *Sbo*, suborbital ; Smx_1, Smx_2, anterior and posterior supramaxillaries ; *So*, supraorbital ; *Sop*, suboperculum ; *Ssc*, suprascapula ; *soc*, supraorbital sensory canal.

1


Fr
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Pmx
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Spl
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Smx1
Ang
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Qu
Pop
Iop
Sop

2

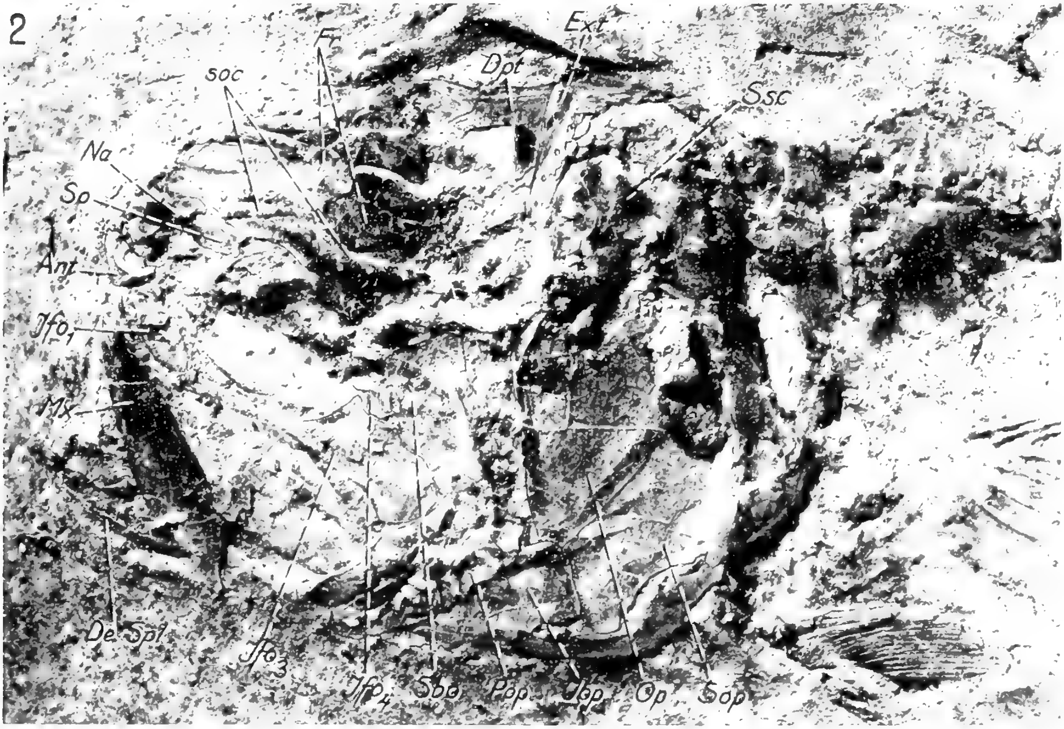

Ext
Fr
soc
Dpt
Ssc
Na
Sp
Ant
Ifo1
Mx
De
Spl
Ifo3
Ifo4
Sbo
Pop
Iop
Op
Sop

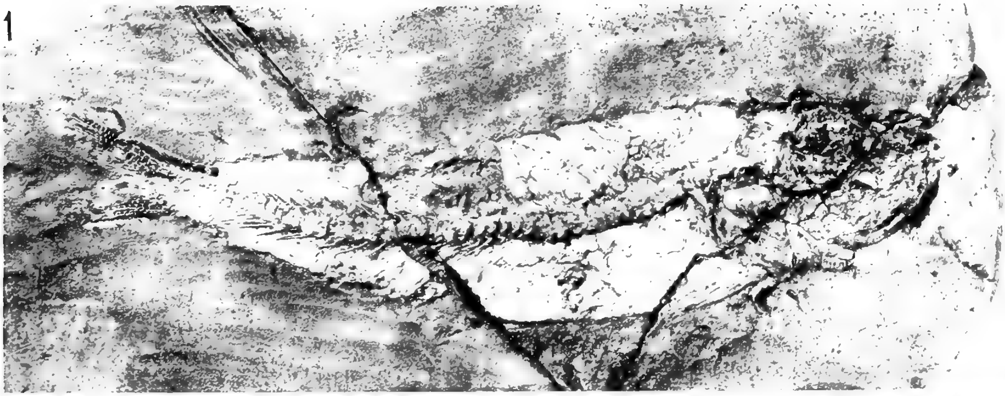
PLATE 14

Pholidophoropsis maculata sp. nov.

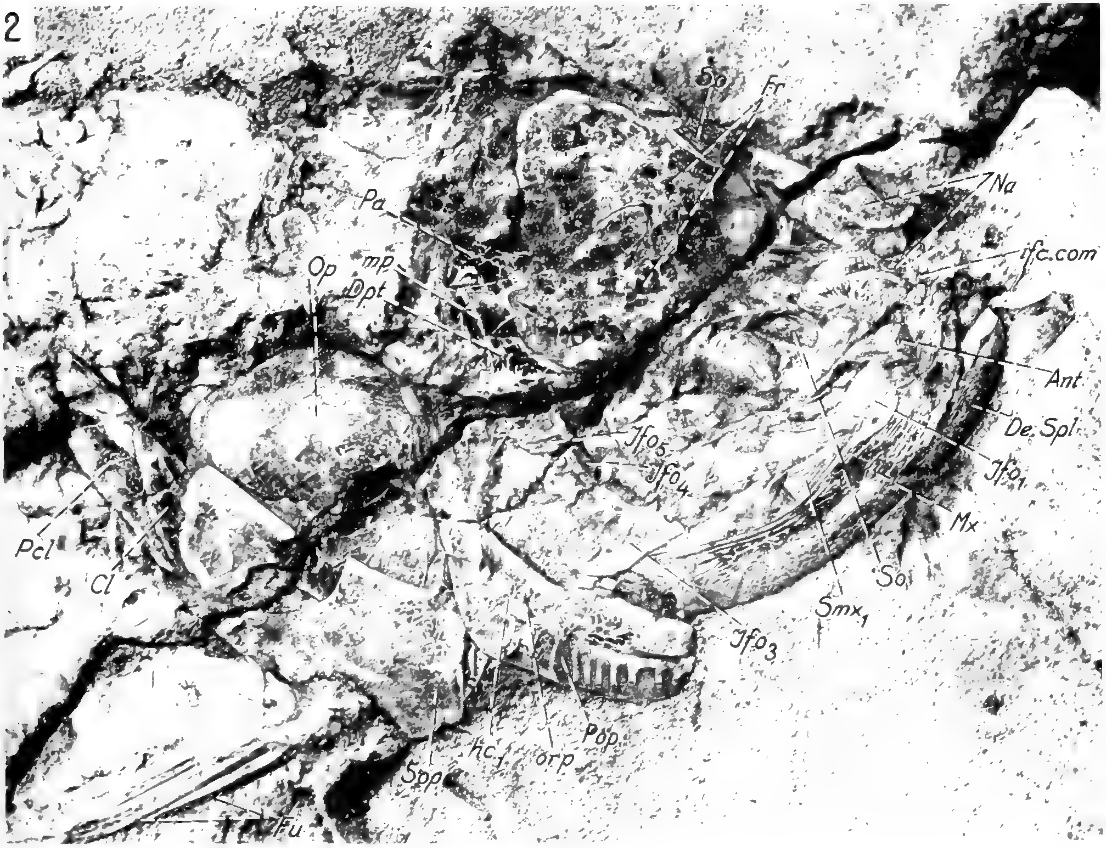
FIG. 1. Holotype, B.M. 43055. Nat. size.
FIG. 2. Head of same specimen. ×4.

Ant, antorbital ; *Cl*, cleithrum ; *De. Spl*, dentary ; *Dpt*, dermopterotic ; *Fr*, frontal ; *Fu*, fulcra ; Ifo_1, Ifo_3, Ifo_4, Ifo_5, infraorbitals 1 and 3–5 ; *Mx*, maxillary ; *Na*, nasal ; *Op*, operculum ; *Pa*, parietal ; *Pcl*, postcleithrum ; *Pop*, preoperculum ; Smx_1, supramaxillary 1 ; *So*, supraorbital ; *Sop*, suboperculum ; hc_1, anterior division of supramaxillary pit-line ; *ifc. com*, ethmoidal commissure ; *mp*, middle pit-line ; *orp*, postmaxillary pit-line.

1



2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Fr
Na
Pa
ifc.com
mp
Op
Dpt
Ant
De.Spl
Ifo$_5$
Ifo$_4$
Ifo$_1$
Mx
Pcl
Cl
So
Smx$_1$
Ifo$_3$
Pop
hc$_1$
orp
Spp
Fu

PLATE 15

Pholidophorus latiusculus Agassiz

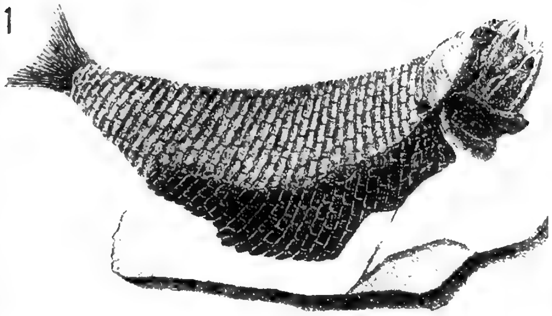
FIG. 1. Specimen figured by Kner (1866, pl. 3, fig. 3). Nat. size.
FIG. 2. Same specimen, now in Geol. Paläont. Institut, Innsbruck. Neotype. Nat. size.
FIG. 6. Lower jaw. Specimen Lit. F. Geol. Paläont. Institut, Innsbruck. ×6.
FIG. 7. Lower jaw and scale (perhaps *Ph.* cf. *pusillus*). B.M. P.11780. ×7·9.

Pholidophoroides crenulata (Egerton)

FIG. 3. Part of cranial roof (same specimen as in Pl. 9 but after preparation). B.M. 38110. ×5·7.
FIG. 4. Part of cranial roof (same specimen as in Pl. 8 but after preparation). B.M. 38730. ×5·7.
FIG. 5. Lower jaw. B.M. P.153. ×5·7.
FIG. 8. Posterior part of right lower jaw in mesial view (same specimen as in Pl. 10, fig. 1). B.M. P.4415. ×11·25.

Ang, angular; *Art*, articular; *De. Spl*, dentary; *Qu*, quadrate; *Sc*, scale; *ap*, anterior pit-line; *mp*, middle pit-line; *orp*, oral pit-line; *pp*, posterior pit-line; *pr. cor*, processus coronoideus of articular; *soc*, supraorbital sensory canal.

1



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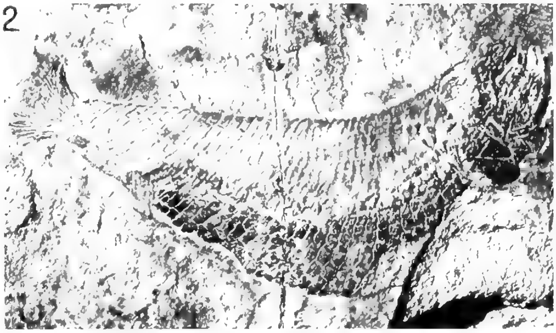
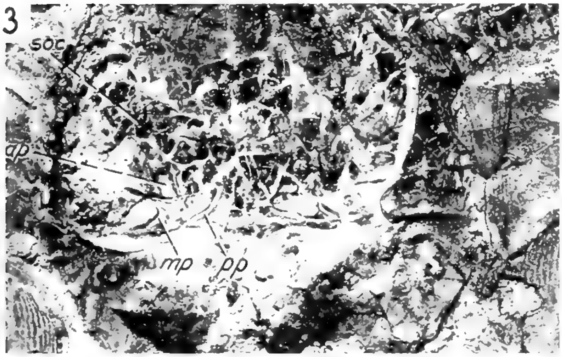
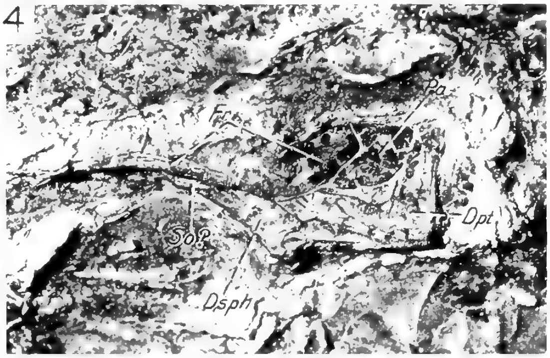


3


soc
ap
mp
pp

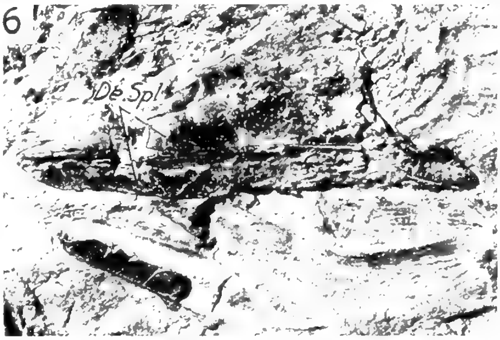
4


Pa
Fr
Dpt
So?
Dsph

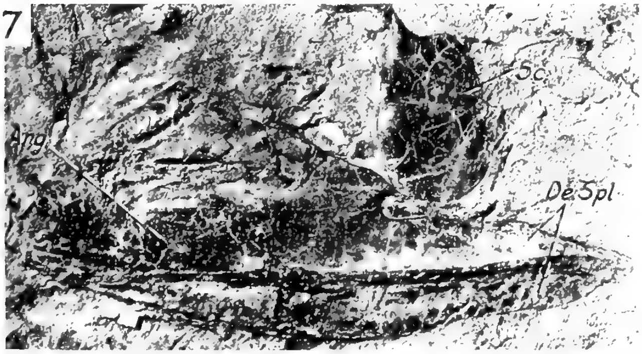
5


Qu
De.Spl
orp1
Ang

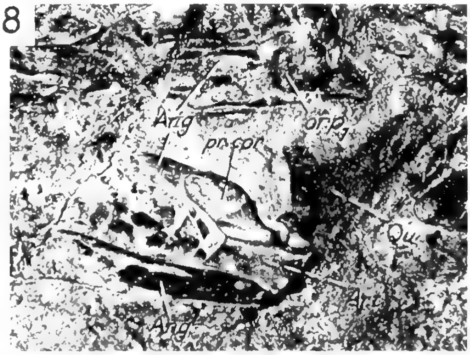
6


De.Spl

7


Sc
Ang
De.Spl

8


Ang
or.p1
pr.cor
Qu
Art
Ang

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SOME BRITISH JURASSIC AND CRETACEOUS OSTRACODA

F. W. ANDERSON
AND
D. BARKER

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 11 No. 9
LONDON : 1966

SOME BRITISH JURASSIC AND CRETACEOUS OSTRACODA

1. NEW GENERA OF PURBECK AND WEALDEN OSTRACODA

BY

FREDERICK WILLIAM ANDERSON, D.Sc.
(lately Chief Palaeontologist, Geological Survey of Great Britain)

2. OSTRACODS FROM THE PORTLAND BEDS OF DORSET

BY

DENNIS BARKER, Ph.D.
(Palaeoservices, Watford)

3. OSTRACODS FROM THE PORTLAND AND PURBECK BEDS OF THE AYLESBURY DISTRICT

BY

DENNIS BARKER, Ph.D.

Pp. 433–487 ; 9 *Plates* ; 32 *Text-figures*

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THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 11 No. 9
LONDON : 1966

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This paper is Vol. 11, *No.* 9 *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 28 *January,* 1966 *Price* £2 4*s.*

NEW GENERA OF PURBECK AND WEALDEN OSTRACODA

By F. W. ANDERSON*

SYNOPSIS

Three new genera are proposed for certain species of ostracoda from the Purbeck and Wealden strata hitherto referred to the Recent genera *Cypris*, *Candona*, *Cythere* and *Bythocypris*.

Candona mantelli Jones, *Candona phillipsiana* Jones and *Cypris purbeckensis* Forbes are assigned to a new genus *Mantelliana*, *Cypris pygmaea* Anderson and *Bythocypris ellipsoidea* Wolburg to *Damonella* gen. nov., *Cythere visceralis* Anderson to *Wolburgia* gen. nov.

Some additional species are described i.e. *Damonella buchaniana* sp. nov., *Wolburgia atherfieldensis* sp. nov., *W. tavola* sp. nov. and *W. polyphema* sp. nov.

All forms are believed to have lived in a marine or quasimarine environment.

INTRODUCTION

At many horizons in the Purbeck and Wealden succession certain ostracod species are extremely abundant. They may be large forms like *Mantelliana phillipsiana* (over 1·5 mm. long) or very small like *Damonella buchaniana* (less than 0·5 mm. in length) but in all cases they are rather featureless, thin-shelled forms in which the shell surface is smooth or at most very finely pustulate or punctate. Preservation is usually poor and it is unusual to find an undamaged specimen. It is not surprising that the classification of these forms has long caused difficulty. Forbes (1855) assigned his species *purbeckensis* to the genus *Cypris*, followed in this by Jones (1885) who placed his own new species *mantelli* and *phillipsiana* in *Candona* (1888), and Anderson (1940) who assigned a new species, *pygmaea*, to *Cypris*.

The resemblance of these shells to the Recent freshwater forms included in the subfamily Cypridinae is, however, largely superficial. Sylvester Bradley's (1941) study of the type species of *Cypris* and *Candona* and an increased knowledge of the Purbeck and Wealden forms assigned to these two genera make it quite clear that any genetic relationship between them is unlikely. In the writer's opinion no genus has been previously described to which these Purbeck and Wealden species can be assigned. There is, however, a general resemblance to some species of *Bythocypris* and Wolburg (1962) placed his new species *ellipsoidea* in that genus.

In association with the common forms here assigned to the new genera *Mantelliana* and *Damonella* are a number of species of rare occurrence. Anderson (1940) described one of these from the Purbeck beds of Swindon as *Cythere visceralis*. Since then more material has been found and a study of the hinge structure leaves no doubt that this species together with three other apparently related forms cannot be included in the genus *Cythere*. In these the hinge structure is not unlike that of *Campylocythere* but the carapace is quite different in shape and the type of ornamentation unique. Thus a new genus, *Wolburgia*, is proposed to receive them.

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SYSTEMATIC DESCRIPTIONS

Family **CYPRIDIDAE** Baird 1845

Genus ***MANTELLIANA*** nov.

DIAGNOSIS. Carapace thin, elongate to sub-ovate in lateral view, compressed, valves sub-equal.

Anterior and posterior margins carrying a very narrow flange which in turn may support a thin delicate fringe. Adductor muscle scars a close group of four to six scars with two others antero-ventrally. Hinge simple, adont ; margin of right valve with a marginal groove which receives the margin of the left valve.

Outer shell surface smooth or ornamented with extremely small close pustules arranged in longitudinal rows. Marked sexual dimorphism, female higher in posterior half of shell than male.

TYPE SPECIES. *Candona mantelli* Jones 1888.

Mantelliana mantelli (Jones)

(Text-figs. 1, 9)

1888 *Candona mantelli* Jones : 536, text-fig. *2a–b*.

DIAGNOSIS. Carapace delicate subreniform, higher in anterior half. Bearing narrow fringe on anterior and antero-ventral margins and on posterior and postero-ventral margins. Shell surface generally smooth, sometimes very finely and closely pustulate. Female more nearly reniform than male.

LECTOTYPE. GSM Mik(M)1004001. Left valve only. Male. Length 1·425 mm. (excluding fringe), height 0·760 mm., width of anterior fringe 0·030 mm., posterior fringe 0·020 mm.

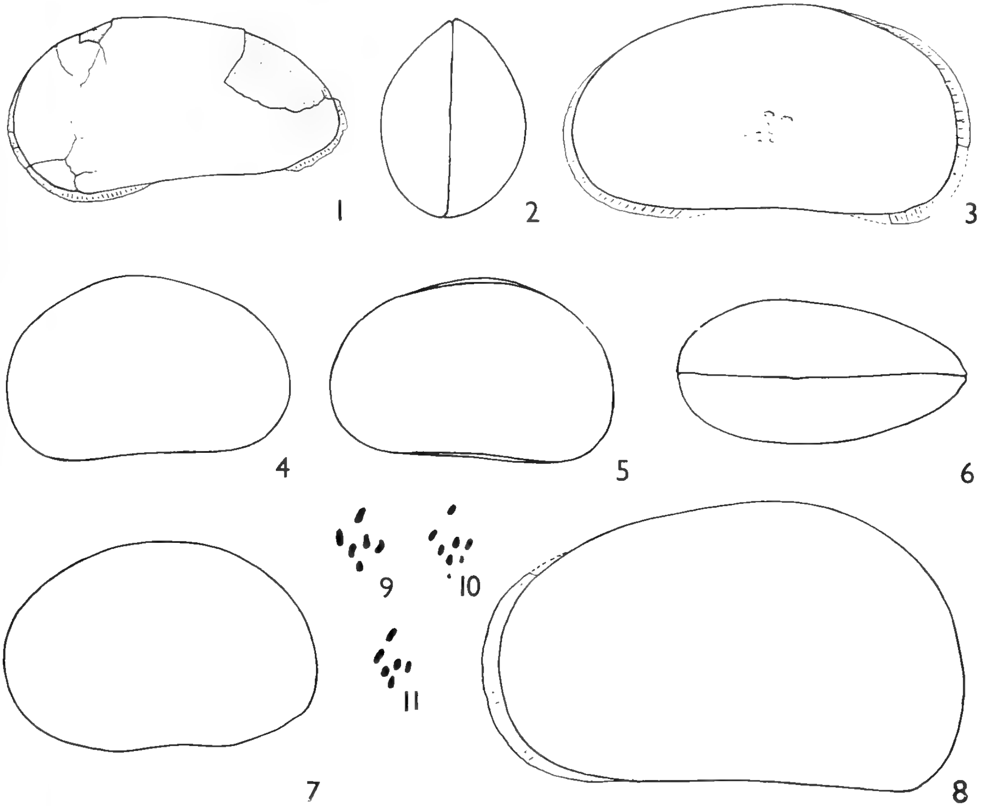
HORIZON AND LOCALITY. Weald Shales, Wealden (*Cypridea valdensis* Zone) ; between Shepherd's Chine and Atherfield Point, Isle of Wight.

DISCUSSION. Jones (1888) did not designate a holotype for this species and a lectotype has been selected from the rock fragment to which he refers (No. 3791, p. 535) which is probably the specimen figured by him in his text-fig. *2a*. In his description the anterior fringe is referred to but not figured. The posterior fringe is not mentioned. Juveniles are similar to the adult male in outline except in the earliest instars where the posterior half of the shell is less acute.

The pattern of the adductor muscle scars was not quite like that figured by Jones (1888, text-fig. *2a*) in any of the specimens seen, moreoever he regarded the narrow end of the shell as the anterior but the arrangement of the hinge so far as can be seen suggests that the shell is highest in the anterior half. The hinge is simple, apparently consisting of narrow flange-like teeth or thickenings of the shell margin joined by a narrow marginal groove. In the left valve are two elongate sockets joined by a straight marginal bar.

According to Jones the shell surface is very finely punctate, but the type material and the majority of other specimens examined appear to be quite smooth. Unusually well-preserved carapaces, however, have an outer shell surface closely covered with very minute pustules, a type of ornamentation which appears to be a characteristic of the genus.

Mantelliana mantelli appears to be confined to the Weald Clay of the Weald and the Weald Shales of the Isle of Wight. It is commonly found, sometimes in great abundance, in the marine and quasi-marine beds associated with forms such as *Theriosynoecum fittoni* (Mantell) and *Sternbergella cornigera* (Jones).



FIGS. 1–11. *Mantelliana mantelli* (Jones); *M. purbeckensis* (Forbes); *M. phillipsiana* (Jones). Fig. 1. *M. mantelli*. Lectotype. Left valve, male. Mik(M)1004001, ×30. Fig. 2. *M. purbeckensis*. Lectotype. Anterior, male. Mik(M)2090001, ×33. Fig. 3. *M. phillipsiana*. Topotype. Right valve, male. Oxford Mus.K.1010, ×36. Fig. 4. *M. purbeckensis*. Lectotype. Left valve, male. ×33. Fig. 5. *M. purbeckensis*. Lectotype. Right valve, male. ×33. Fig. 6. *M. purbeckensis*. Lectotype. Dorsum, male. ×33. Fig. 7. *M. purbeckensis*. Left valve, female. Mik(M)2682001, ×33. Fig. 8. *M. phillipsiana*. Holotype. Left valve, female. Oxford Mus.K.1003, ×36. Fig. 9. *M. mantelli*. Adductor muscle scars. Mik(M)1873001, ×40. Fig. 10. *M. phillipsiana*. Adductor muscle scars. Mik(M)1008016; ×40. Fig. 11. *M. purbeckensis*. Adductor muscle scars. BM(NH) I.1668, ×40.

Mantelliana phillipsiana (Jones)

(Text-figs. 3, 8, 10)

1878 *Candona phillipsiana* Jones : 108, pl. 3, fig. 3.

DIAGNOSIS. Carapace large, thin-shelled, subreniform in lateral view. Sexual dimorphism marked, male carapace tapering towards posterior with delicate anterior and posterior fringes, female higher in posterior half and only fringed anteriorly. External surface covered with minute, closely-set pustules.

HOLOTYPE. Oxford University Museum No. K1003. Internal mould of left valve. Length 1·620 mm., height (less fringe) 0·995 mm., fringe 0·045 mm. wide.

HORIZON AND LOCALITY. ? Wealden (Hastings Beds) ; Shotover Common, near Oxford.

DISCUSSION. Jones' original description of the species is quite clear and includes a reference to the very characteristic striated fringe. These delicate extensions of the shell are rarely found intact. In *M. phillipsiana* the fringes are more extensive than in *M. mantelli* ; in the male only the dorsal margin and a small part of the ventral margin are without them. Sexual dimorphism is more marked than in *M. mantelli* ; the male carapace in *M. phillipsiana* (Text-fig. 3) though not unlike *M. mantelli* is more regularly reniform and less tapering posteriorly, whilst the female is quite different in outline being high posteriorly and tapering towards the anterior.

Pre-maturation instars resemble the adult male in outline.

The species is often very abundant in the marine and quasi-marine beds of the Wadhurst Clay and Tunbridge Wells Sand in the Weald. It has not been found in the Weald Clay.

Mantelliana purbeckensis (Forbes)

(Text-figs. 2, 4–7, 11)

1855 *Cypris purbeckensis* Forbes *in* Lyell : 297, text-fig. 339*a*.
1865 *Cypris purbeckensis* Forbes ; Forbes *in* Lyell : 387, text-fig. 375*a*.
1865 *Cypris purbeckensis* Forbes ; Loriol & Jaccard, pl. 2, figs. 1–3.
1885 *Cypris purbeckensis* Forbes ; Jones : 347–348, pl. 9, figs. 1–6.
1886 *Cypris purbeckensis* Forbes ; Jones : 147, pl. 4, figs. 5*a–c*.
1963 " *Cypris* " *purbeckensis* Forbes ; Oertli : 18, pl. 5, figs. 28–32.

DIAGNOSIS. A large carapace. In side view subreniform, dorsally convex with greatest height anterior to centre of valve. Venter slightly concave. In dorsal view the shell is an elongate ovoid with greatest width posterior to centre. In end view bluntly ovoid with greatest width ventral to centre. The left valve little larger than the right overlapping it ventrally but with no appreciable overlap anteriorly and posteriorly. Outer shell surface generally smooth, sometimes faintly punctate near posterior end. Sexual dimorphism as for genus but not very marked.

LECTOTYPE. GSM Mik(M)2090001. A complete carapace. Length 1·050 mm., height 0·660 mm., width 0·540 mm.

HORIZON AND LOCALITY. Lower Purbeck ; Swanage.

Discussion. A fragment of hard limestone (GSM 4273) from the Lower Purbeck Beds in Durlston Bay, Swanage, Dorset, may be part of the material examined by Forbes (1855) and a lectotype for the species has been selected from it.

M. purbeckensis is a common species in the Lower Purbeck of England and a large number of specimens have been examined and utilized in this description. The muscle scar pattern is drawn from a specimen in the T. R. Jones Collection (BMNH., I.1668) and the internal details have been compiled from specimens in the Geological Survey Collections.

Jones' figures (1885, pl. 9, figs. 1–6) are fairly good except fig. 4, which incorrectly shows the shell gaping at both ends, and fig. 6 which appears to be of a monstrosity. A small percentage of the specimens examined, however, show similar outgrowths. All the Jones material came from the Lower Purbeck of the Vale of Wardour.

The largest specimen found measures 1·32 mm. in length but the majority of adult shells are between 1·05 and 1·23 mm. long. As Jones remarked (1885 : 348) the shape is somewhat variable. This is illustrated by the length/height ratios which vary from low forms with a L/H ratio of 1·79 to high forms with a L/H ratio of 1·47. Those thought to be females (Text-fig. 7) are high reniform variants with a L/H ratio between 1·47 and 1·64. Forms with a more acute posterior end and with a L/H ratio between 1·57 and 1·79 are believed to be the males.

The mean dimensions of the adult are, length 1·15 mm., height 0·69 mm. Prematuration growth stages generally resemble the male carapace in outline. Only two instars have been recognised, one with mean dimensions, length 0·85 mm., height 0·55 mm. and the other length 0·63 mm. and height 0·44 mm.

M. purbeckensis is the earliest species recorded from the Purbeck Beds appearing immediately above the Portland Stone. Later it is associated with *Fabanella boloniensis* (Jones) and *F. ansata* (Jones) and like them appears to have flourished in saline or hypersaline water. Frequently these three species are the only ones found in the gypsum-bearing strata of the Lower Purbeck. *M. purbeckensis* is not known to occur in strata higher than the lower part of the Middle Purbeck.

The species is a more robust than either *M. mantelli* or *M. phillipsiana* and appears to be the only species of *Mantelliana* without a fringe. There are, however, undescribed species of the genus in the Purbeck Beds in which the fringe is rarely seen and even when present is very narrow.

Family **ILYOCYPRIDIDAE** Kaufmann 1900

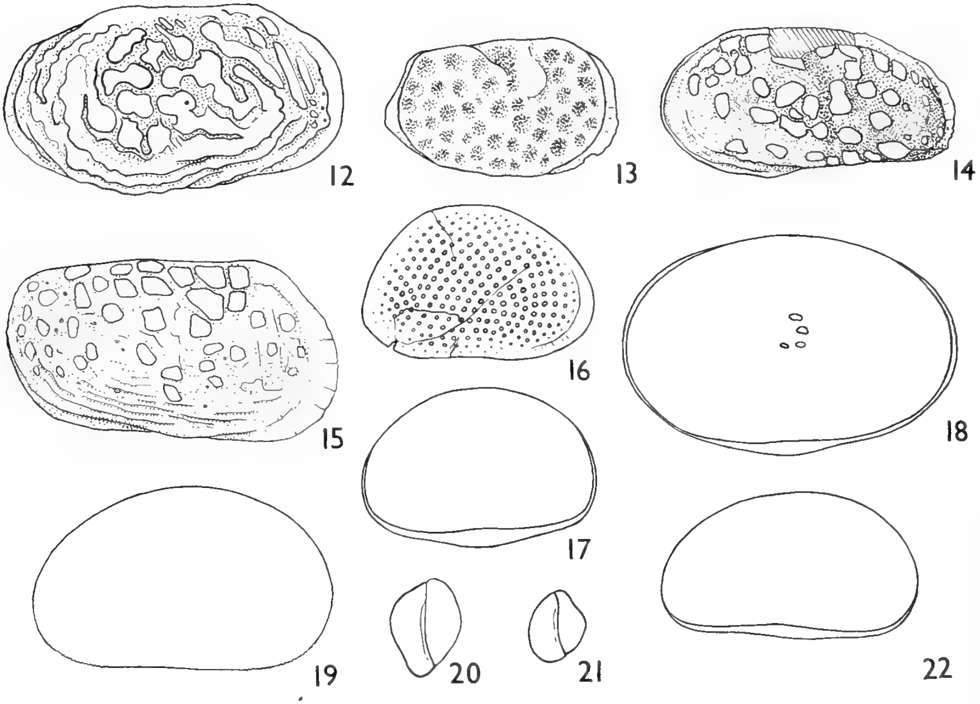
Subfamily **CYPRIDEINAE** Martin 1940

Genus ***DAMONELLA*** nov.

Diagnosis. Carapace small, ovoid in lateral view. Shell surface smooth or punctate. Adductor muscle scars as for *Scabriculocypris* and *Cypridea* i.e. a vertical arc, convex forward, of three scars, one behind and ventral and usually two small antennal scars anterior and ventral. Hinge simple ; in right valve a small flange-like tooth which may be denticulate, in front joined by a shallow groove to a smaller posterior adont flange-like tooth ; in left valve a groove receives the dorsal margin of right valve and a parallel bar fits into groove of right valve ventral to it ; shallow elongate sockets at each end of bar receive the flange-like teeth of right valve. Right valve smaller than left which extends downwards well beyond ventral contact margin.

Type species. *Cypris pygmaea* Anderson 1940.

Discussion. This genus has many of the characteristics of both *Cypridea* and *Scabriculocypris* i.e. hinge pattern, adductor muscle scar arrangement and strong ventral overlap of the valves. The right valve is slightly swollen dorsally and the



Figs. 12–22. *Wolburgia* and *Damonella* species. Fig. 12. *W. visceralis* (Anderson). Holotype. Right valve. Mik(M)722001, ×65. Fig. 13. *W. polyphema* sp. n. Holotype. Right valve. Mik(M)2488001. ×65. Fig. 14. *W. tavola* sp. n. Holotype. Left valve. Mik(M)2487001, ×92. Fig. 15. *W. atherfieldensis* sp. n. Holotype. Right valve. Mik(M)673001, ×145. Fig. 16. *D. punctatula* sp. n. Holotype. Right valve. Mik(M)2486001, ×65. Fig. 17. *D. buchaniana* sp. n. Holotype. Right valve. Mik(M) 2483001, ×65. Fig. 18. *D. ellipsoidea* (Wolburg). Right valve. Mik(M)2484001, ×65. Fig. 19. *D. denticulata* sp. n. Holotype. Right valve. Mik(M)2485001, ×65. Fig. 20. *D. ellipsoidea* (Wolburg). Posterior. Mik(M)2484001, ×30. Fig. 21. *D. buchaniana* sp. n. Holotype. Posterior. Mik(M)2483001, ×30. Fig. 22. *D. pygmaea* (Anderson). Topotype. Right valve. Mik(M)732001, ×65.

left considerably swollen ventrally producing an asymmetry in end view which is quite typical and is also seen in *Scabriculocypris* and in the Carboniferous genus *Carbonita*.

Damonella lacks the beak and notch of *Cypridea* and though apparently closely related to *Scabriculocypris* the outline is more oval than in that genus and the shell surface is smooth not punctate. There is a superficial resemblance to *Bythocypris* but the adductor muscle scars are quite different.

Damonella pygmaea (Anderson)

(Text-figs. 22, 30)

1941 *Cypris pygmaea* Anderson : 379, pl. 19, fig. 17.
1951 *Cytherella pygmaea* (Anderson) Anderson : 211.
1963 " *Cypris* " *pygmaea* Anderson ; Oertli : 19, pl. 5, figs. 34, 35.

DIAGNOSIS. Small bean-shaped carapace very little higher in front than behind ; narrow oval when seen from above. Left valve the larger. Shell surface smooth and glossy. Shell substance thin.

HOLOTYPE. GSM Mik(M)2482001. Complete carapace. Length 0·51 mm., height 0·30 mm., width 0·17 mm.

HORIZON AND LOCALITY. Upper Pebbly Beds, Lower Purbeck ; Town Gardens Quarry, Swindon, Wiltshire.

DISCUSSION. This is one of the most ubiquitous marine or quasi-marine species in the Purbeck and Wealden and ranges throughout. It is often very abundant, covering a bedding-plane almost to the exclusion of any other species. The shell is fragile and is is rare to find an undamaged specimen.

D. pygmaea is a flatter, larger shell than *D. buchaniana*, not so robust or regularly oval as *D. ellipsoidea*.

Damonella buchaniana sp. nov.

(Text-figs. 17, 21, 24)

DIAGNOSIS. Carapace sub-ovate in lateral view, oval from above and almost circular in end view. Shell surface smooth and glossy. Left valve the larger.

HOLOTYPE. GSM Mik(M)2483001. A complete carapace. Length 0·460 mm., height 0·300 mm., width 0·245 mm.

HORIZON AND LOCALITY. Upper Purbeck ; Portsdown No. 1. Borehole, Paulsgrove, Hampshire.

DISCUSSION. A very small shell with much the same stratigraphical range as *D. pygmaea* and often accompanying it. It is smaller, fatter and more robust than that species. *D. ellipsoidea* is larger, more regularly oval and proportionately lower.

Damonella ellipsoidea (Wolburg)

(Text-figs. 18, 20, 25, 26)

1940 *Cypria* sp.? Martin : 356, pl. 8, figs. 119–20.
1949 *Cypria L*61 Wolburg : 352, table 3, 5.
1951 ?*Cypria ovalis* Anderson, MS, ; 210.
1962 *Bythocypris ellipsoidea* Wolburg : 223, table 16, pl. 32*b*, fig. 20.

FIGURED SPECIMEN. GSM Mik(M)2484001. Complete carapace. Length 0·66 mm., height 0·4 mm., width 0·315 mm.

HORIZON AND LOCALITY. At a depth of 1438–40 ft., Lower Purbeck ; Henfield No. 1 Borehole, Sussex.

DISCUSSION. The carapace is regularly oval in both lateral and dorsal view. The outer shell surface is smooth. The left valve is the larger.

D. ellipsoidea ranges from the basal Purbeck to the base of the Weald Clay and is a common form in many of the marine or quasi-marine bands. It is distinguished from *D. pygmaea* by its more regular outline and by its more robust appearance. It is considerably larger than *D. buchaniana* and is relatively lower.

Damonella denticulata sp. nov.

(Text-figs. 19, 23)

DIAGNOSIS. A small delicate shell closely resembling *D. pygmaea* but with minute denticulations along the antero and postero-ventral margins. Shell surface smooth and glossy.

HOLOTYPE. GSM Mik(M)2485001. Right valve. Length 0·570 mm., height 0·340 mm.

HORIZON AND LOCALITY. Bed 12, Upper part of Weald Clay, Wealden ; Gillman's Brick Pit, Billingshurst, Sussex.

DISCUSSION. This species is externally distinguishable from *D. pygmaea* only by the denticulation of the margin. Internally the dentition is like that of the other species of the genus except that in two specimens, Mik(M)2485001 (Text-fig. 23) and Mik(M)613048, there is an indication that there may be four or five small denticles on the anterior flange-like tooth and that the shell margin just posterior to it may also be finely denticulate. These minute structures are difficult to see and only then when the preservation is perfect. The general organization of the hinge structures is, however, like that of the other species of the genus and it may be that these additional features will prove not to be confined to *D. denticulata* when better material becomes available.

Denticulation of the margins has not been seen in *D. pygmaea*, *D. ellipsoidea*, *D. buchaniana* or *D. punctatula*, even in *D. denticulata* it is not easily visible except in very well preserved material and it is probable that some of the specimens from the Weald Clay, identified as *D. pygmaea*, may in fact belong to the former species.

Damonella punctatula sp. nov.

(Text-fig. 16)

DIAGNOSIS. A small delicate carapace like *D. buchaniana* in shape but with more conspicuous anterior flange. Surface covered with circular punctations arranged in curved rows concentric near margins.

HOLOTYPE. GSM Mik(M)2486001. Right valve. Length 0·450 mm., height 0·310 mm.

HORIZON AND LOCALITY. At a depth of 33–34 ft., Wadhurst Clay, Wealden; Wadhurst No. 3 Borehole, Sussex.

DISCUSSION. This rare species can be easily distinguished from *D. buchaniana* by the punctate surface. The punctations are very regular and uniform in size in the centre of the valve becoming smaller towards the margin. The carapace is not so wide as *D. buchaniana*.

This species has only been found in the Wadhurst Clay of Sussex.

Family ? **CYTHERIDEIDAE** Sars 1925

Genus ***WOLBURGIA*** nov.

DIAGNOSIS. Carapace small, sub-oblong, flanged anteriorly and posteriorly. Dorsal margin straight, ventral margin reflexed. Adductor muscle scars in front of and lying obliquely to the upper scar of the row. Vestibule small. Normal pore canals large and widely spaced. Radial canals few and straight.

Dentition similar to that of *Campylocythere*. In right valve small flange-like teeth which may be denticulate, joined by narrow groove. Anterior and posterior sockets of left valve joined by bar which may be finely denticulate.

Valves ornamented with relatively large protuberances which may be rounded or flattened or with wide deep pits which leave raised ribs between in a reticulate pattern.

TYPE SPECIES. *Cythere visceralis* Anderson 1940.

Wolburgia visceralis (Anderson)

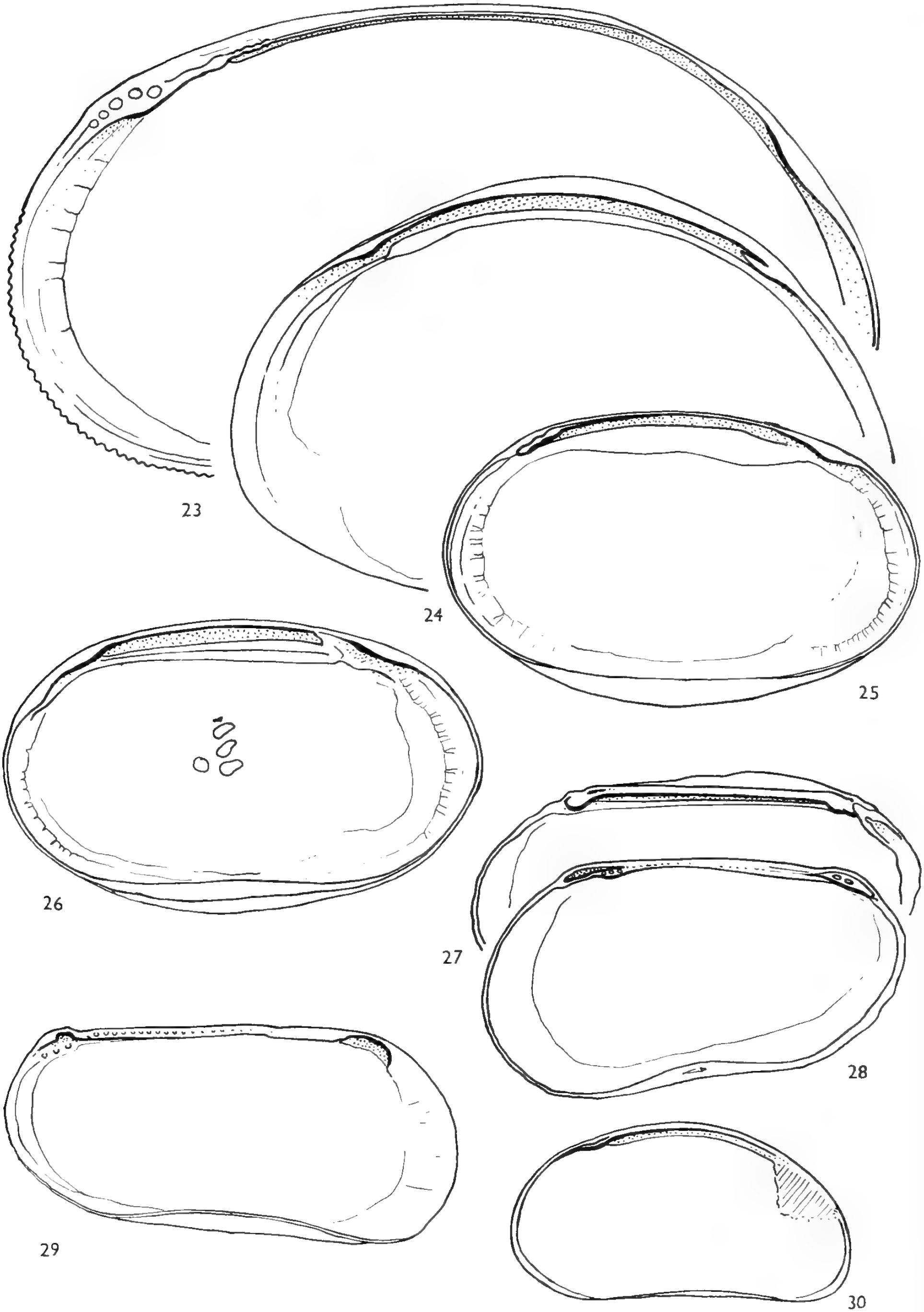
(Text-figs. 12, 27)

1941 *Cythere visceralis* Anderson : 374, pl. 9, fig. 11.

DIAGNOSIS. Surface ornamented with elongate rounded protuberances which may coalesce especially near shell margins to form periodically constricted ribs.

HOLOTYPE. GSM Mik(M)722001. Right valve. Length 0·670 mm., height 0·360 mm., width of single valve 0·190 mm.

HORIZON AND LOCALITY. Swindon Sands and Stone, Lower Purbeck; Town Gardens Quarry, Swindon, Wiltshire.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Discussion. The ornamentation distinguishes *W. visceralis* from the other members of the genus. It is a rare species known only from the Lower Purbeck. The form recorded by Klingler (1955, pl. 10, fig. 7) from the Kimmeridge as *Clithrocytheridea ? iuglandiformis* is not unlike *W. visceralis* but is a more elongate shell with a slightly different ornamentation.

Wolburgia atherfieldensis sp. nov.

(Text-figs. 15, 28, 29)

Diagnosis. Carapace very small, ornamented with relatively large, flat, rounded subangular protuberances, upper surface of protuberances apparently perforated by numerous small pores. Protuberances generally concentrated in dorsal half of shell, giving way to irregular, rounded ribs running parallel to ventral margin in ventral half of shell.

Holotype. GSM Mik(M)673001. Right valve. Length 0·290 mm., height 0·170 mm.

Horizon and locality. Weald Shales (Uppermost Wealden) ; Atherfield, Isle of Wight.

Discussion. This is the smallest species of the genus yet found. The ornamentation is similar to that of *W. tavola* but in the latter the flat domes cover most of the shell surface and the carapace is more acute posteriorly. *W. atherfieldensis* is known only from the Weald Shales of the Isle of Wight.

Wolburgia tavola sp. nov.

(Text-fig. 14)

Diagnosis. Carapace rather low, elongate and narrowing posteriorly. Shell surface finely reticulate and ornamented with large flattened domes over most of surface. Carapace crossed by shallow, vertical median sulcus.

Holotype. GSM Mik(M)2487001. Left valve. Length 0·410 mm., height 0·215 mm.

Horizon and locality. At a depth of 1777 ft., basal beds of the Upper Purbeck ; Winchester No. 1 Borehole, Hampshire.

Figs. 23–30. *Damonella* and *Wolburgia* species. Fig. 23. *D. denticulata* sp. n. Holotype. Interior of right valve. Mik(M)2485001, ×220. Fig. 24. *D. buchaniana* sp. n. Interior of right valve. Mik(M)2684001, ×220. Fig. 25. *D. ellipsoidea*. Interior of right valve. Mik(M)2680001, ×105. Fig. 26. *D. ellipsoidea*. Interior of left valve. Mik(M)268001, ×105. Fig. 27. *W. visceralis*. Holotype. Interior of right valve. Mik(M)722001, ×95. Fig. 28. *W. atherfieldensis* sp. n. Holotype. Interior of right valve. Mik(M) 673001, ×200. Fig. 29. *W. atherfieldensis* sp. n. Topotype. Interior of left valve. Mik(M)674001, ×200. Fig. 30. *D. pygmaea*. Interior of right valve. Mik(M)2683001, ×105.

DISCUSSION. A larger and more elongate carapace than *W. atherfieldensis* but with similar ornamentation. A median sulcus was not seen in *W. atherfieldensis*.

W. tavola is very rare, known only from the Upper Purbeck.

Wolburgia polyphema sp. nov.

(Text-fig. 13)

DIAGNOSIS. Carapace sub-oblong in lateral view. Anterior with wide smooth flange; posterior with narrower flange. Two sulci reach middle line of shell from dorsal margin separated by pear-shaped lobe. Surface covered by large, widely-spaced, shallow depressions which leave the shell coarsely reticulate. Postero-dorsal area almost at right angles to shell margin and bearing four rounded tubercles.

HOLOTYPE. GSM Mik(M)2488001. Right valve. Length 0·460 mm., height 0·270 mm.

HORIZON AND LOCALITY. Hard Cockle Beds, Lower Purbeck; Mountfield No. 4 Borehole, Sussex.

DISCUSSION. The ornamentation in this species differs considerably from that of the other members of the genus, but the shape of the carapace and the organization of the hinge link them together. This is a rare species known only from the Hard Cockle Beds of the Lower Purbeck.

REFERENCES

See p. 485.

OSTRACODS FROM THE PORTLAND BEDS OF DORSET

By DENNIS BARKER

Ostracods are described from the Portland Beds of four localities in Dorset. Twelve genera and nineteen species are recorded, of which three species are new. The stratigraphical distribution of the various species for each horizon are indicated on the diagram.

I INTRODUCTION AND ACKNOWLEDGEMENTS

HITHERTO, the only attempt to describe ostracods from the Portland Beds of England has been a short paper by Anderson (1941). This made incidental reference to a few species collected by Sylvester-Bradley from the top few feet of strata overlain by the " Swindon Series ", which formed the main subject of the paper. The present survey is, therefore, the first to attempt a comprehensive description, and even now (owing to paucity of exposures in the inland area of the outcrop) it is not as complete a survey as could have been hoped.

In a paper to the colloquium on the Jurassic System—1962, Sylvester-Bradley suggested that the Portland Beds of Dorset should be regarded as the standard section (" stratotype ") of the Portlandian stage. Although the lower boundary to this succession presents no problem, the upper boundary has become the subject of debate in the last few years. This is because the upper boundary of the Portland Beds has been found to vary from place to place, and also to interdigitate with the Lower Purbeck Beds. In fact the Swindon Roach is evidence of the last incursion of Portland facies from a sea lying to the South. (Sylvester-Bradley in press). The Lower Purbeck Beds therefore, are taken to be a facies of the uppermost Portlandian in England and consequently the question of the age of those beds above the Lower Purbeck deposits does not come within the scope of this paper.

Ostracods have been examined from Portland Beds at the following localities in Dorset ; Poxwell Quarry SY/743835, Hounstout Cliff, SY/952772, Friar Waddon from beside the track above Corton Farm SY/636855 and West Weare Cliff SY/681720. Samples from other localities were also examined but yielded no ostracods.

The samples from Poxwell Quarry were collected from about 45 ft. of beds ranging in age from the Cherty Series to the Lower Purbeck Beds. An interesting feature is the way in which the ostracod fauna illustrates the boundary between the Portland Stone and the Lower Purbeck Beds. The Roach and the beds below it contain a marine ostracod fauna whereas the laminated limestones and the beds above contain a brackish water fauna. *Cypridea dunkeri* occurs at the very top of the section.

Samples from beds 10 ft. below the Massive Bed to the Lower Parallel Band at Hounstout Cliff have yielded a characteristic marine ostracod fauna, as also have beds at West Weare Cliff from 10 ft. below the Black Nore Sandstone to the Basal Shell Bed. The ostracod fauna consists of the following species :

Macrodentina (*Macrodentina*) *transiens* (Jones)
Macrodentina (*Dictyocythere*) *retirugata* (Jones)
Macrodentina (*Polydentina*) *rudis* Malz
Galliaecytheridea wolburgi (Steghaus)
Galliaecytheridea postrotunda Oertli
Orthonotacythere rimosa Martin
Orthonotacythere elongata sp. nov.
Orthonotacythere levis sp. nov.
Cytherelloidea cf. paraweberi Oertli

The Portland Sand at Friar Waddon consists of about twenty-five feet of green cementstones with occasional *Exogyra* scattered through them. These beds mark the upper middle part of the Portland Sand and they have a fauna slightly different from those of Hounstout Cliff and West Weare Cliff. This is probably because the beds are more sandy. Samples of the sands beside the track at Coryates SY/630857, just west of Corton Farm, were also collected. These sands are below the cementstone mentioned above but do not contain ostracods.

From the following list and the one above it can be seen that this set of samples from Friar Waddon has a reduced fauna which shows similarities to both the Portland Stone and Portland Sand faunas. It would appear, therefore, that it is not yet possible to separate the Portland Sand and Stone by using ostracods alone.

The beds at Friar Waddon contain the following ostracods :

Macrodentina (*Dictyocythere*) *retirugata* (Jones)
Protocythere serpentina (Anderson)
Paraschuleridea eusarca (Anderson)
Cytherelloidea cf. paraweberi Oertli

See Table I for a comparison of the ostracod faunas from the Portland Beds of Dorset.

The author would like to record his sincere thanks to Prof. P. C. Sylvester-Bradley for his guidance throughout the work and for the use of the facilities of the Department of Geology at the University of Leicester. Thanks are also due to Dr. R. H. Bate of the British Museum (Natural History) and to Dr. F. W. Anderson of the Geological Survey and Museum for many helpful discussions and access to the ostracod collections under their care. The award of a University of Leicester Research Scholarship is gratefully acknowledged.

All the figured material forming the basis of the present paper has been deposited in the collections of the British Museum (Natural History).

Reference numbers prefixed by P.Q., H., W.W. and F.W. are the collection numbers of the author.

TABLE I. A comparison of the Ostracod faunas from the Portlandian Beds of Dorset

PORTLAND SAND	PORTLAND STONE	LOWER PURBECK BEDS	
..	..	×	*Cypridea dunkeri*
..	..	×	*Theriosynoecum forbesii*
..	..	×	*Fabanella boloniensis*
..	..	×	*Fabanella ansata*
..	..	×	*Mantelliana purbeckensis*
..	×	..	*Paracypris* sp. ?
..	×	..	*Procytheropteron bicosta*
..	×	..	*Macrodentina* (*Macrodentina*) *rugulata*
×	×	..	*Macrodentina* (*Macrodentina*) *transiens*
×	×	..	*Macrodentina* (*Dictyocythere*) *retirugata*
×	×	..	*Paraschuleridea eusarca*
×	×	..	*Protocythere serpentina*
×	×	..	*Orthonotacythere rimosa*
×	×	..	*Orthonotacythere levis*
×	..	..	*Orthonotacythere elongata*
×	..	..	*Macrodentina* (*Polydentina*) *rudis*
×	..	..	*Galliaecytheridea wolburgi*
×	..	..	*Galliaecytheridea postrotunda*
×	..	..	*Cytherelloidea paraweberi*

II SYSTEMATIC DESCRIPTIONS

Superfamily **CYPRIDACEA** Baird 1845

Family **PARACYPRIDIDAE** Sars 1923

Genus ***PARACYPRIS*** Sars 1866

Paracypris? sp.

(Pl. 3, figs. 10–13)

1955 *Paracypris*? sp. B, Schmidt : 52, pl. 1, figs. 3–4.
1957 *Paracypris*? sp. B, Schmidt ; Oertli : 653, pl. 1, figs. 19–22.

MATERIAL. One carapace and one valve from Bed P.Q. 7 and eight valves from Bed P.Q. 12 at Poxwell Quarry.

DESCRIPTION. Carapace elongate, tapering to a pointed posterior. Dorsal margin convex and smoothly curved, while ventral margin is very slightly concave. Greatest height is to anterior of the centre and anterior margin smoothly rounded. Carapace is narrowly pyriform in dorsal view, greatest inflation being at the position of greatest height and narrowing to posterior.

	Dimensions in mm.			Proportions			
	L	H	I	L	H	I	Specimen Number
Carapace . .	0·79	0·31	0·23	1·00	0·39	0·29	Io. 2168
Left valve . .	0·77	0·31	—	1·00	0·40	—	Io. 2170
Left valve juvenile .	0·64	0·25	—	1·00	0·39	—	Io. 2169

REMARKS. The few specimens (9 valves and fragments and 1 carapace) of this species do not show any internal details and were found only in the Portland Stone of Poxwell Quarry.

Superfamily **CYTHERACEA** Baird 1850
Family **CYTHERIDEIDAE** Sars 1925
Subfamily **CYTHERIDEINAE** Sars 1925
Genus ***GALLIAECYTHERIDEA*** Oertli 1957

Galliaecytheridea wolburgi (Steghaus)

(Pl. 2, figs. 1–8)

1951 *Cyprideis wolburgi* Steghaus : 213, pl. 14, figs. 24, 25 ; pl. 15, fig. 26.
1955 *Cyprideis wolburgi wolburgi* (Steghaus) ; Schmidt : 58, pl. 2, figs. 25, 26.
1955 *Cyprideis wolburgi minuta* Schmidt : 58, pl. 2, figs. 27–30.
1957 *Galliaecytheridea wolburgi* (Steghaus) Oertli : 657, pl. 2, figs. 56–60, pl. 3, figs. 61–68.

MATERIAL. Numerous valves and carapaces from various beds at Hounstout Cliff. Sixty-two valves and sixteen carapaces from various beds at West Weare Cliff.

	Dimensions in mm.			Proportions			
	L	H	I	L	H	I	Specimen Number
Carapace	0·83	0·50	0·39	1·00	0·60	0·47	Io. 2158
Right valve	0·83	0·45	—	1·00	0·54	—	. .
Left valve	0·97	0·54	—	1·00	0·56	—	Io. 2155
Right valve	0·96	0·49	—	1·00	0·51	—	Io. 2157
Carapace	1·12	0·60	0·49	1·00	0·54	0·44	Io. 2156

REMARKS. This is the first time *Galliaecytheridea wolburgi* has been recorded from the Portland Beds of England. These numerous specimens are characteristic of the species in shape and hinge but are much larger than the French material, x ± 2s for 24 males = 1·00 mm. ± 0·12 mm., x ± 2s for 52 females = 0·83 mm. ± 0·06 mm.

Galliaecytheridea postrotunda Oertli

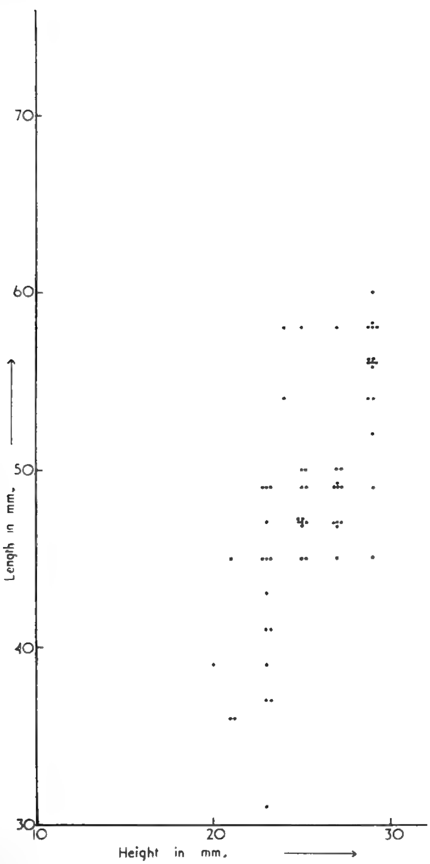
(Pl. 3, figs. 1–6)

1957 *Galliaecytheridea postrotunda* Oertli : 656, pl. 2, figs. 45–55.

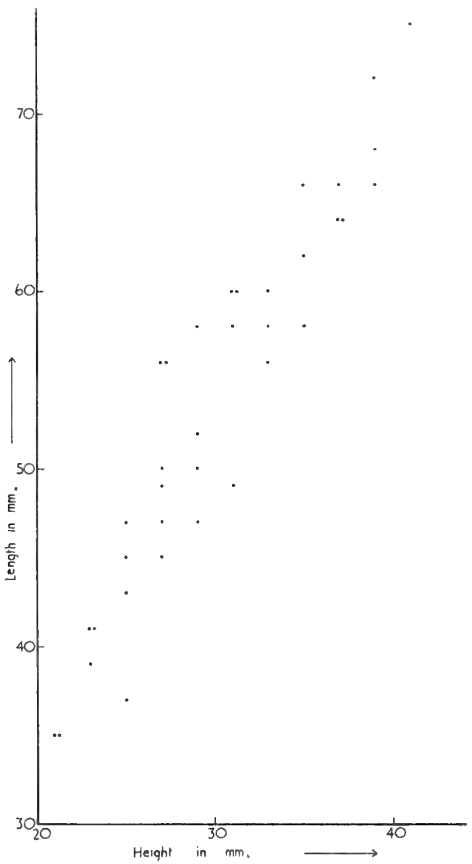
MATERIAL. Numerous specimens from various beds at Hounstout Cliff.

FIG. 31. Diagrams to show the size distribution of *Galliaecytheridea postrotunda* from Bed H.8, *Orthonotacythere elongata* and *Orthonacythere rimosa* from Bed H.7, and *Macrodentina* (*Macrodentina*) *rugulata* from Bed PQ. 8.

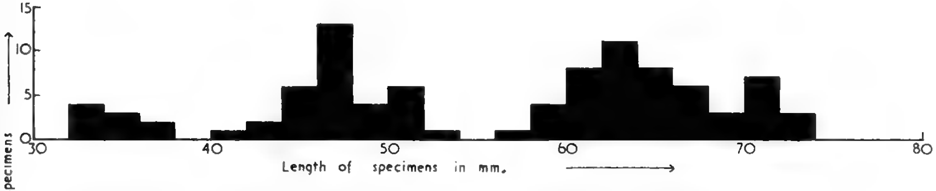
L/H ratio for *Orthonotacythere elongata*



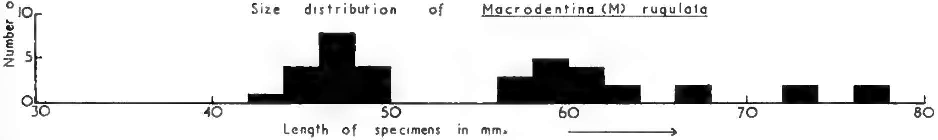
L/H ratio for *Orthonotacythere rimosa*



Size distribution of *Galliaecytheridea postrotunda*



Size distribution of *Macrodentina (M) rugulata*



	Dimensions in mm.			Proportions			
	L	H	I	L	H	I	Specimen Number
Left valve . .	0·73	0·41	—	1·00	0·56	—	Io. 2166
Carapace . .	0·66	0·39	0·29	1·00	0·59	0·44	Io. 2164
Carapace . .	0·50	0·29	0·21	1·00	0·58	0·42	Io. 2165

REMARKS. These specimens correspond to the holotype, the size distribution as indicated in Text-figure 31, showing a slight difference in length between males and females.

Family **BRACHYCYTHERIDAE** Puri 1954

Genus ***MACRODENTINA*** Martin 1940

Subgenus ***MACRODENTINA*** Martin 1940

Macrodentina (Macrodentina) rugulata (Jones)

(Pl. 2, figs. 9–12)

1885 *Cythere retirugata* var. *rugulata* Jones : 350, pl. 9, figs. 17–20.
1941 *Cythere retirugata* Jones var. *rugulata* Jones ; Anderson : 373, pl. 18, fig. 1.
1956 *Dictyocythere* (*Rhysocythere*) *rugulata* (Jones) Sylvester-Bradley : 18, pl. 4, figs. 1, 2, 5–10, 12–15.
1958 *Macrodentina* (*Macrodentina*) *rugulata* (Jones) Malz : 18, pl. 6, figs. 83–86.

MATERIAL. Thirty-six valves from Bed P.Q. 12 at Poxwell Quarry.

	Dimensions in mm.		Proportions		
	L	H	L	H	Specimen Number
Right valve . .	0·71	0·45	1·00	0·63	Io. 2160
Left valve . .	0·71	0·47	1·00	0·66	Io. 2159
Right valve (juv.) .	0·60	0·35	1·00	0·58	Io. 2161
Right valve . .	0·47	0·27	1·00	0·57	Io. 2162

REMARKS. Specimens of *Macrodentina* (*M.*) *rugulata* are only found in the Roach of Poxwell Quarry. These specimens (see Text-fig. 1) are much smaller than those described from the Aylesbury district and Portesham Quarry (Barker 1964*a*, *b*). The largest forms have a paramphidont hinge and are therefore thought to be adult. The reasons for this reduction in size must be left unexplained until more specimens have been obtained from the Portland Stone of other localities.

Macrodentina (Macrodentina) transiens (Jones)

(Pl. 2, figs. 13–15)

1885 *Cythere transiens* Jones : 349, pl. 9, figs. 13–16.
1956 *Dictyocythere* (*Rhysocythere*) *transiens* (Jones) Sylvester-Bradley : 19, pl. 3, figs. 11–13.
1958 *Macrodentina* (*Macrodentina*) *transiens* (Jones) ; Malz : 17, pl. 6, figs. 81, 82.

MATERIAL. Fourteen valves and sixty-seven carapaces from various beds on West Weare Cliff. One hundred and seventeen valves from various beds at Poxwell Quarry.

A carapace from Bed P.Q. 12 has the following dimensions: length 0·58 mm., height 0·35 mm., inflation 0·33 mm.

These specimens correspond in all details to those described by Sylvester-Bradley 1956.

Subgenus ***DICTYOCYTHERE*** Sylvester-Bradley 1956

Macrodentina (Dictyocythere) retirugata (Jones)

(Pl. 1, figs. 1–8)

1885 *Cythere retirugata* Jones : 350, pl. 9, figs. 21, 23.
1885 *Cythere retirugata* var. *textilis* Jones : 350, pl. 19, fig. 24.
1941 *Cythere retirugata* var. *textilis* Jones ; Anderson : 374, pl. 18, fig. 3.
1941 *Cythere retirugata* var. *decorata* Anderson : 374, pl. 18, fig. 4.
1956 *Dictyocythere* (*Dictyocythere*) *retirugata* (Jones) Sylvester-Bradley : 15, pl. 3, figs. 7–10, pl. 4, figs. 3, 4, 11, 16, 17.
1956 *Dictyocythere* (*Dictyocythere*) *decorata* (Anderson) Sylvester-Bradley : 17, pl. 3, fig. 1.
1958 *Macrodentina* (*Dictyocythere*) *decorata* (Anderson) Malz ; 25, pl. 6, figs. 87, 88.
1958 *Macrodentina* (*Dictyocythere*) *textilis* (Jones) Malz : 26, pl. 6, figs. 80–91.

MATERIAL. Five valves from Bed P.Q. 12 at Poxwell Quarry. Sixty-one valves and three carapaces from various beds at Hounstout Cliff. One hundred and fifty-eight valves and ten carapaces from various beds at Friar Waddon. Thirty-eight valves and four carapaces from Bed W.W. 9 at West Weare Cliff.

	Dimensions in mm.			Proportions			
	L	H	I	L	H	I	Specimen Number
Right valve	0·70	0·45	—	1·00	0·64	—	Io. 2153
Left valve	0·70	0·52	—	1·00	0·74	—	—
Carapace	0·73	0·49	0·45	1·00	0·67	0·62	Io. 2152
Carapace	0·81	0·47	0·41	1·00	0·58	0·51	Io. 2154

REMARKS. These specimens are similar to those from the Aylesbury district except that they are smaller. They are presumably adult since they have the adult hinge.

Subgenus ***POLYDENTINA*** Malz 1958

Macrodentina (Polydentina) rudis Malz

(Pl. 6, figs. 1–8)

1958 *Macrodentina* (*Polydentina*) *rudis* Malz : 31, pl. 4, figs. 57–64.

MATERIAL. Three carapaces and thirty-seven valves from Bed H.7, three carapaces from Bed H.8 at Hounstout Cliff and four valves from Bed W.W.9 at West Weare Cliff.

DESCRIPTION. Carapace somewhat triangular in lateral outline with a more or less straight dorsal margin which slopes down towards the posterior. Ventral margin very slightly convex. Anterior smoothly curved, meeting the dorsal margin at a slight angle where there is a slight swelling formed by the anterior hinge teeth and socket. Posterior is narrower than the anterior and is bluntly rounded. The valves are inturned slightly on the dorsal margin. Ventral margin concave to form a concave ventral surface. Greatest inflation to posterior. In dorsal view the sides are rather flat and the ends are slightly pointed. Left valve larger than right and overreaching it all round, most strongly to anterior and posterior. Males are longer than the females.

The lateral surfaces are reticulate, the dominant pattern being concentric round the margins and more or less vertical in the central region. Normal pore canals irregularly spaced over the carapace. Radial pore canals not observed. Muscle scars not seen. Hinge paramphidont. There are slight anterior and postero-ventral vestibules. The line of concrescence parallels the outer margin.

REMARKS. This is the first recorded occurrence of *Macrodentina* (*Polydentina*) *rudis* in England.

Family **CYTHERURIDAE** Müller 1894

Genus ***ORTHONOTACYTHERE*** Alexander 1933

Orthonotacythere rimosa Martin

(Pl. 5, figs. 7, 8, 11, 12)

1940 *Orthonotacythere rimosa* Martin : 335, pl. 6, figs. 84–86
1961 *Orthonotocythere* cf. *rimosa* Martin ; Martin : 117, pl. 14, fig. 21*a–c*.

MATERIAL. Three valves from Bed P.Q. 7 and two carapaces and twenty valves from Bed P.Q. 12 at Poxwell Quarry. Twelve carapaces and fifty-eight valves from various beds on Hounstout Cliff.

Measurements of two specimens are :

	Dimensions in mm.			Proportions			
	L	H	I	L	H	I	Specimen Number
Carapace . .	0·50	0·27	0·29	1·00	0·54	0·58	Io. 2754
Right valve fragment	0·54	0·33	—	1·00	0·61	—	Io. 2753

REMARKS. These specimens correspond in all details to those described from the Aylesbury district but the valves are badly encrusted.

Orthonotacythere levis sp. nov.

(Pl. 5, figs. 10, 13, 14)

DIAGNOSIS. *Orthonotacythere* with rounded caudal region and well rounded, smooth lateral surfaces.

HOLOTYPE. Io. 2755. Left valve, from Poxwell Quarry. Length 0·45 mm. height 0·25 mm.

Paratype. Io. 2756, from Poxwell Quarry.

Other material. Three right and two left valves from Bed P.Q.12 at Poxwell Quarry. Two right and four left valves from Bed H.7 at Hounstout Cliff.

Description. Lateral outline subtrapezoidal with dorsal and ventral margins subparallel. Anterior margin smoothly and evenly rounded, with the posterior margin obliquely rounded, sharpest towards the dorsal margin. Greatest height and inflation just posterior of centre.

Lateral surface covered by many small, faint puncta. Valves swollen towards the ventral margins, particularly near the postero ventral margin. Radial and normal pore canals and muscle scars are not seen. Hinge antimerodont. Inner margin and line of concrescence coincide.

Remarks. This species is distinguished from others of the genus *Orthonotacythere* by its more rounded outline and smooth lateral surfaces.

Orthonotacythere elongata sp. nov.

(Pl. 6, figs. 9–11)

Diagnosis. *Orthonotacythere* with ventral margin sloping upwards to posterior dorsal corner in lateral view. Adults with reticulate ornamentation, juveniles also with spines.

Holotype. Io. 2760. Left valve from Poxwell Quarry Bed P.Q. 12. Length 0·45 mm., height 0·25 mm.

Other material. One hundred and eight valves and twenty-five carapaces, adults and juveniles, from various beds at Hounstout Cliff.

Description. Carapace somewhat triangular in outline, the dorsal margin being long and straight. Ventral margin slightly irregularly convex and closing with the dorsal margin forming a blunt point. The anterior margin is smoothly rounded but forms a slight angle with the dorsal margin. The greatest inflation is centrally since the dorsal outline is sub rectangular and the greatest height is near the anterior.

The lateral surfaces are reticulate with a major ridge running parallel to the dorsal margin just ventral of the centre of the valve and ending before reaching the anterior and posterior borders. Towards the posterior this ridge becomes stronger to form a slight ala and may be at the position of greatest inflation. There is a central deep narrow sulcus from the dorsal margin almost to the venter of each valve.

The internals of the valves are not seen but the hinge consists of notched terminal teeth with straight connecting crenulate socket. The line of concrescence appears to be parallel to the inner margin.

Remarks. This species differs from others of *Orthonotacythere* by its characteristic shape, see Pl. 6. Proportions of adults and juveniles are given in the Text-figure on p. 451.

Genus ***PROCYTHEROPTERON*** Ljubimova 1955

Procytheropteron bicosta sp. nov.

(Pl. 5, figs. 1–6, 9)

Diagnosis. A *Procytheropteron* with sharp ventro-lateral angle, smooth lateral surfaces, and a slight longitudinal ridge running just below middle height.

Holotype. A right valve from Poxwell Quarry Bed P.Q. 7. Length 0·54 mm., height 0·29 mm. Io. 2752.

Paratypes. Io. 2750–51, from Poxwell Quarry.

Other material. Twenty-one left valves and twelve right valves from various beds at Poxwell Quarry.

Description. Lateral outline subelliptical. Both the dorsal and ventral margins are smoothly and strongly convex. The anterior is slightly pointed and the posterior is slightly drawn out to a point, particularly in the left valve. The right valve is longer but less high than the left.

Both valves are strongly swollen near the ventral margins to form a sharp angle or ridge and a ventral surface which is flat and slopes inwards. The inner ventral margin of the valves is almost straight. On the lateral surface there is a slight sigmoidal shaped ridge a short distance above the antero ventral margin. The lateral surfaces are smooth. Muscle scars are in a vertical row of four to the anterior of the centre at the position of greatest height. The normal and radial pore canals are not seen. The hinge is entomodont and the line of concrescence coincides with the inner margin.

Remarks. This species can be easily recognised by its characteristic shape, particularly in end view.

Family **PROGONOCYTHERIDAE** Sylvester-Bradley 1948

Subfamily **PROTOCYTHERINAE** Lyubimova 1955

Genus ***PROTOCYTHERE*** Triebel 1938

Protocythere serpentina (Anderson)

(Pl. 4, figs. 1, 3–7)

1941 *Cythereis serpentina* Anderson : 375, pl. 19, fig. 12.
1951 *Protocythere sigmoidea* Steghaus : 219, pl. 15, figs. 42–45.
1958 *Protocythere bireticulata* Malz : 39, pl. 11, fig. 69.
1960 *Protocythere sigmoidea* Steghaus ; Fernet : 21, Pl. 1, figs. 11–13.
1963 *Protocythere serpentina* (Anderson) Oertli : 22, pl. 7, fig. 57.

Material. Seventy-five valves and seven carapaces from various beds at Poxwell Quarry. Two valves from Bed W.W.9 and two carapaces from Bed W.W.13 at West Weare Cliff. Eleven valves and two carapaces from various beds at Friar Waddon.

	Dimensions in mm.		Proportions		
	L	H	L	H	Specimen Number
Left valve	0·79	0·41	1·00	0·52	Io. 2747
Right valve (juvenile)	0·54	0·25	1·00	0·46	Io. 2745
Left valve (juvenile)	0·62	0·33	1·00	0·53	Io. 2171
Right valve	0·83	0·43	1·00	0·52	Io. 2746

REMARKS. These specimens show the same wide variation in ornamentation as in specimens from the Aylesbury district.

Genus *PARASCHULERIDEA* Swartz & Swain 1946

Paraschuleridea ? eusarca (Anderson)

(Pl. 4, figs. 2, 8–10)

1941 *Cytheridea ? eusarca* Anderson : 376, pl. 19, fig. 15.

MATERIAL. Over two hundred valves and carapaces from various beds at Poxwell Quarry, two carapaces and five valves from Bed F.W.7 and three valves from Bed F.W.11 at Friar Waddon.

DESCRIPTION. Lateral outline subelliptical with a convex dorsal margin. Anterior more broadly rounded than the posterior. Ventral margin antero-marginally concave. Outline in dorsal view elliptical with the left valve overreaching the right.

Shell surface is smooth with some irregularly spaced normal pore canals. Approximately 18 straight, irregularly spaced, radial pore canals anteriorly and up to 10 posteriorly. Hinge hemimerodont. Line of concrescence and inner margin coincide. Muscle scars in a vertical row of four just anterior of the valve centre, with one large frontal scar opposite the top two adductors.

REMARKS. This species has been placed in the genus *Paraschuleridea* rather than *Eocytheridea* Bate (1963 : 35) although further research into *P. eusarca* may extend the range of *Eocytheridea* and necessitate the discarding of *Paraschuleridea* for this species.

Family **CYTHERELLIDAE** Sars 1866

Genus *CYTHERELLOIDEA* Alexander 1933

Cytherelloidea paraweberi Oertli

(Pl. 3, figs. 7–9)

1957 *Cytherelloidea paraweberi* Oertli : 651, pl. 1, figs. 12–15.

MATERIAL. One carapace from Bed W.W.9 at West Weare Cliff and three valves and one carapace from Bed F.W.4 at Friar Waddon. The carapace from Bed W.W.9 measures : length 0·68 mm., height 0·39 mm., inflation 0·25 mm.

REMARKS. Very few specimens have been found but they correspond closely with the type specimen.

REFERENCES

See p. 485.

OSTRACODS FROM THE PORTLAND AND PURBECK BEDS OF THE AYLESBURY DISTRICT

By DENNIS BARKER

SYNOPSIS

The transition from Portland to Purbeck conditions in the Aylesbury district is discussed with the aid of three sections which are described and their ostracod faunas compared. A series of facies marking the transition can be recognized by means of the lithology, macrofauna and ostracods. No evidence of Middle or Upper Purbeck ostracods has been found. Seventeen genera and twenty-two species are described, of which three species are new.

INTRODUCTION AND ACKNOWLEDGEMENTS

THE Portland and Purbeck Beds of the Aylesbury District have been the subject of study by geologists since the middle of last century. At that time Morris (1856) was able to demonstrate, with the aid of the lithology and macrofaunas of the beds exposed in the Bugle Pit, Hartwell, a change from marine Portland conditions through estuarine to freshwater Purbeck conditions. Jones (1885) described the ostracods from the Lower Purbeck Beds of this area and thought that the mingling of the marine with freshwater ostracods would repay careful study. Jukes-Browne (*in* Woodward 1895), Chapman (1899), Merrett (1924) and Sylvester-Bradley (1941) have each noted a transition from marine Portland to freshwater Purbeck based on the study of the ostracods. Some geologists such as Jones (1885), Chapman (1899) and Merrett (1924) have suggested that Middle and even Upper Purbeck ostracods may be present in places. This has not been confirmed in the present investigation, though Casey & Bristow (1963, 1964) believe sands (previously regarded as Cretaceous) containing Middle Purbeck lamellibranchs, in the Whitchurch and Stewkley area, can be interpreted as the transgressive margin of the Cinder Bed.

The present paper attempts to investigate the nature of the transition from Portlandian to Purbeckian conditions in the Aylesbury district by means of a study of the ostracod fauna. The work is based mainly on the fieldwork and collections made by Prof. P. C. Sylvester-Bradley in the Thame Valley during the summer of 1939. Samples were examined from exposures at the following localities :

1. AY Aylesbury. A pit about half a mile south west of Walton Court Farm—on the footpath that leads from Bishopstone to Ceely Road, Southcourt Estate, 42/806112.
2. BP Bugle Pit, Hartwell near Aylesbury, 42/794121.
3. CH Coneyhill. Field pit near the lodge to Eyethorpe, 42/759151.
4. CL Creslow. Small overgrown pit near cottages, 42/811219.

5. CP Cuddesden Palace. Field pit north east of Cuddesden Palace, 41/602032.
6. CW Long Crendon. CWA, B—auger borings by the site of the old windmill, 41/693093. CWC, D, E were small pits by the side of the road, 41/689093.
7. GN Garsington village, Clinkards Farm. Excavations to the north side of the village on the west side of the ridge, GNA-G, 41/586028.
8. HD Haddenham. Pit one mile east of Haddenham on the lower Aylesbury Road, HDA, B 41/763096.
9. HG Hurdlesgrove Farm. Field pit a little south of Hurdlesgrove Farm about one mile north of Whitchurch on the Buckingham Road, 42/804228.
10. NW Excavations one mile north of Whitchurch on the Buckingham Road, NWA-F, 42/805225.
11. OV Oving. A pit south of the North Marston Road, 42/793212.
12. TW Towersey, half a mile north of the village on the eastern side of the Kingsey Road, 41/735059.
13. WH Warren House Farm near Stewkley, pit south of the farm, 42/851242.

The sections then extant are now filled in or overgrown but the three most complete sections are described below.

The author is indebted to Prof. P. C. Sylvester-Bradley, who suggested the work, for his help and encouragement and for the use of the facilities of the Department of Geology, University of Leicester. Thanks are also due to Dr. R. H. Bate of the British Museum (Natural History) and to Dr. F. W. Anderson of the Geological Survey and Museum for many helpful discussions and access to the ostracod collections under their care. This work was carried out partly during the tenure of a University of Leicester Research Scholarship.

All the figured material forming the basis of the present paper has been deposited in the collections of the British Museum (Natural History).

FACIES

Davies (1899) stated that he used the term Purbeck as a facies name and not as a time name. This use of the term is followed here and five successive facies are distinguished in the Portland and Purbeck Beds of the Aylesbury district. These facies are listed in ascending order as follows :

A. At the base are massive cream coloured limestones of the Portlandian containing ammonites such as *Titanites giganteus* (J. Sowerby), *Titanites pseudogigas* (Blake), which were described from this area. Woodward (1895) noted large lamellibranchs which he identified as *Perna bouchardi*, *Cardium dissimile*, *Pecten lamellosus*, *Trigonia gibbosa* var. *manselli*. Marine ostracods are also present. This is referred to as the Portland facies.

B. Laminated marls and limestones with, according to Woodward (1895), *Trigonia gibbosa* var. *manselli* and *Ostrea expansa*, together with fish remains and a mixture of marine and euryhaline ostracods. This is referred to as the marine Purbeck facies.

C. Laminated marls and limestones containing gastropods which Davies (1899) tentatively identified as species of *Paludina*. Fitton (1836) reported *Cyclas parva*, modiolae, *Planorbis* and mytili from these beds. Fish remains and euryhaline ostracods are also to be found. This is the brackish Purbeck facies.

D. Marls and limestones becoming sandy upwards with *Paludina* and small modiolae and a *Cyclas*? reported by Fitton (1836). Freshwater beds of similar age at Swindon have yielded (Sylvester-Bradley 1941) *Physa bristovii* (Forbes MS) Phillips, *Valvata helicoides* (Forbes MS) de Loriol, *Viviparus inflatus* (Sandberger), *Clavator reidi* Groves and *Clavator grovesi* Harris. This is the oligohaline Purbeck facies.

E. Sands and sandstones of the Whitchurch region containing marine lamellibranchs. Casey has recently identified some specimens first collected by Bristow as Middle Purbeck in age. (Casey & Bristow 1963). No ostracods have been obtained from these beds.

These five facies demonstrate a gradual change from marine Portland to more or less freshwater beds of the Lower Purbeck and back again to the marine sands of the Middle Purbeck.

The beds classed as Middle or Upper Purbeck in age by Jones, Chapman and Merrett were of facies D, i.e. oligohaline. The occurrence of Middle Purbeck ostracods is based on two figures of *Cypridea granulosa* var. *paucigranulata* Jones (1885). The specimen on which his figures are based comes from a locality called Whitchurch, the existence and position of which is very doubtful, (see Sylvester-Bradley 1949). I have not found any specimens of *Cypridea granulosa* or its varieties in the Aylesbury district.

In many descriptions of the Purbeck Beds, the terms freshwater, marine, estuarine and brackish have been used without discussion. The writer considers the Purbeck ostracods to be either oligohaline, euryhaline or marine, partly on account of relationships to living representatives of known habitat, partly according to their association with other fossils, and partly on account of the lithological conditions of the beds enclosing them. Those ostracods found in both oligohaline and marine conditions are considered to be euryhaline, i.e. capable of existing under widely varying conditions of salinity. When euryhaline forms are found in the absence of marine or oligohaline ostracods it would appear that conditions of salinity variation were at their maximum. In the beds under discussion the marine ostracod fauna is characterized by :

Macrodentina (*Macrodentina*) *rugulata* (Jones)
Macrodentina (*Macrodentina*) *transiens* (Jones)
Macrodentina (*Dictyocythere*) *retirugata* (Jones)
Protocythere serpentina (Anderson)
" *Macrocypris* "? sp. Anderson
Paraschuleridea buglensis sp. nov.
Orthonotacythere rimosa Martin
Procytheropteron brodiei (Jones)
Wolburgia visceralis (Anderson)

TABLE I

	1	2	3	4	5	6a	6b	6c	7	8	9	10	11a	11b	11c	12	13	14	15	16	17	18	19	20
Macrodentina (*Macrodentina*) *rugulata*	..	..	..	..	..	33	99	51	45	288	4	86	..	..	..	..	..	..	..	..	..	..	..	..
Macrodentina (*Macrodentina*) *transiens*	16	1	17	303	49	91	..	6	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Macrodentina (*Dictyocythere*) *retirugata*	..	..	..	..	..	50	190	90	31	166	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Protocythere serpentina	26	3	82	98	12	68	1	39	3	111	1	..	..	..	..	..	11	..	..	..	..	..	..	..
" *Macrocypris* "? sp.	..	..	..	..	..	2	..	1	1	9	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Paraschuleridea buglensis	22	3	36	4	24	68	10	11	11	68	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Orthonotacythere rimosa	..	..	1	14	..	..	..	38	6	17	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Procytheropteron brodiei	..	..	7	..	..	..	6	64	54	104	..	..	..	..	..	..	..	..	..	13	..	..	1	..
Wolburgia visceralis	54	..	19	1	..	..	..	..	..	..	..	..	..	..	..	..	2	..	..	..	..	..	..	..
Fabanella boloniensis	..	1	..	..	..	8	..	..	2	57	51	6	14	4	55	100	..	..	24	36	2	6	107	33
Fabanella ansata	..	..	..	..	2	5	..	..	1	85	65	50	20	15	33	623	..	..	..	..	..	..	45	11
Mantelliana purbeckensis	..	..	..	..	..	..	..	..	..	..	..	..	..	8	100	21	..	1	..	7	1	..	77	24
Cypridea tumescens praecursor	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4	15	8	2	..	10	6
Cypridea dunkeri	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	4	1
Klieana alata	..	..	..	..	..	..	..	..	..	..	..	10	..	..	..	..	..	243	63	23	5	..	150	98
Darwinula leguminella	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2	..	..	..	..
Ilyocypris (*Rhinocypris*) *jurassica*	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	6	..	..	..	..
Dicrorygma fragilis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	6	..	..	..	..
Dicrorygma decipiens	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	3	..	..	..	..

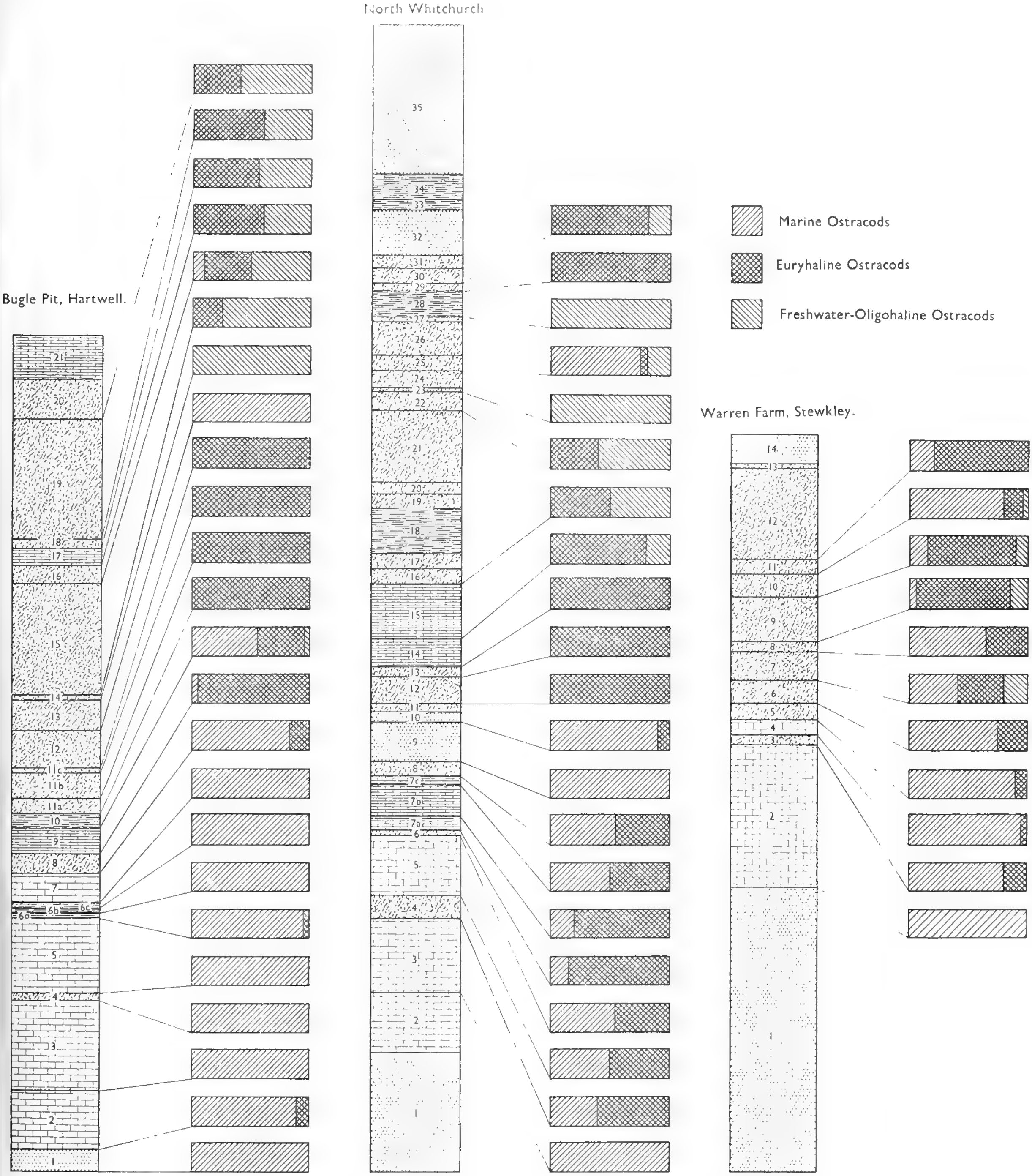


FIG. 32. Lithological variation and proportion of marine, euryhaline and oligohaline ostracods present in the sections at Hartwell, Whitchurch and Stewkley. Numbers on the columns refer to those given in the text description of each section.

The euryhaline fauna is characterized by :

Fabanella bolonensis (Jones)
Fabanella ansata (Jones)
Mantelliana purbeckensis (Forbes)

The oligohaline fauna is characterized by :

Cypridea tumescens (Anderson) *praecursor* Oertli
Cypridea dunkeri
Klieana alata Martin
Scabriculocypris trapezoides Anderson
Darwinula leguminella (Forbes)
Rhinocypris jurassica jurassica (Martin)
Dicrorygma fragilis Martin
Dicrorygma decipiens (Anderson)

The ostracod faunas for the sections described below are given in Tables I–III, which show the number of valves found in the beds which contain ostracods.

THE BUGLE PIT, HARTWELL

The Bugle Pit seems to have been mentioned first in the literature by Morris (1856). Since then it has been described repeatedly. A comparison of the sections obtained by Woodward (1895), Merrett (1924) and Sylvester-Bradley (1939) is shown below.

In 1939 Professor Sylvester-Bradley examined the exposure and collected carefully from all the beds present. The material was subjected to a preliminary examination in the production of his papers of 1940 and 1941. This section is important in that it exposed the thickest continuous section in the Portland and Purbeck Beds in this area. The section has now almost disappeared under tip ; only about three feet of the upper beds could be seen at the south east of the quarry in 1962.

The ostracods obtained from the Bugle Pit have been plotted as shown in Table I. The sections at the three localities are drawn to scale and the relative percentages of the three faunas indicated for each bed in which ostracods are found. Four of the five facies indicated above are well developed in the Bugle Pit ; facies E and the upper part of the facies D are absent.

The Bugle Pit, Hartwell

		ft.	in.
BP 22	Very coarse grit (infilling what is apparently a solution pipe in the beds below)		
BP 21	Fine grained limestone, with occasional disseminated shells seen to	1	6
BP 20	Soft grey marl	1	4
BP 19	Grey pebbly marl up to . . . . This bed cuts down and across an extremely uneven and eroded surface of the beds below.	4	0

				ft.	in.
W 11	M 10	*BP 18	Marly subsoil seen to		4
	M 9	*BP 17	Thin bedded broken shelly limestone		7
	M 8	*BP 16	Soft grey marl		7
	M 8	BP 15	Rubbly white chalky marl	3	9
	M 7	BP 14	Clayey brown marl		1½
	M 7	BP 13	Hard gritty marlstone	1	0
	M 6	BP 12	Marly shale with alternating layers of marlstone, ostracods at the base	1	3
	M 5	BP 11c	Ostracod marl with fishes		2
	M 4	BP 11b	Laminated shales with fishes		10
	M 3	BP 11a	Ostracod marl with shells and fishes		6
	M 2	BP 10	Soft black or brown shale		6
W 10	M 1	BP 9	Laminated blue hearted cementstone with plant and insect remains along partings		9–10
W 9		BP 8	Tough highly bituminous shaley marl with large oysters and other lamellibranch casts		8
W 8		BP 7	Hard fine grained limestone with a band of *Trigonia* casts seen near the base	1	0
W 7		BP 6c	Marly shale		2–3
		BP 6b	Black shales		2–3
		BP 6a	Marly shale with a layer of lamellibranchs at the top		2
W 6		BP 5	Blue hearted marly limestone with large Portland lamellibranchs	2	6
		BP 4	Brown clay with serpulae		3
		BP 3	Blue hearted rather soft marly limestone, *Trigonia* etc.	3	0
W 5		BP 2	Hard blue hearted limestone with oysters, bottom 3 in. fossil casts	2	0
W 4		BP 1	Yellow brown sand seen to		9

W = H. B. Woodward's section 1895
M = Merrett's section 1924
BP = Sylvester-Bradley's collection 1939

NORTH WHITCHURCH

In 1939 Sylvester-Bradley opened up trenches by the roadside north of Whitchurch. The accompanying section is a composite one made up from the sections exposed in the trenches and at a pit in the field south of Hurdlesgrove Farm. Text-figure 32 shows the section and the proportions and ranges of the three ostracod faunas. Facies A, B, C and D can be recognized in this section and facies E is reported to be present near Whitchurch itself (Casey & Bristow 1964).

TABLE II

	3	4	5	6	7a	7b	7c	8	9	10	12	13	14	15	16	22	23	24	25	26	28	29	30	31
Macrodentina (*Macrodentina*) *rugulata*	..	40	44	85	5	6	40	51	12	14	..	..	..	..	..	..	..	..	6	..	..	..	..	..
Macrodentina (*Macrodentina*) *transiens*	..	..	51	28	5	2	14	13	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Macrodentina (*Dictyocythere*) *retirugata*	51	169	6	37	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Protocythere serpentina	9	..	7	..	..	..	2	10	52	..	..	..	..	..	..	..	..	..	6	..	..	..	..	..
Paraschuleridea buglensis	5	1	2	10	..	..	16	9	126	42	..	..	..	..	..	..	..	..	43	..	..	..	..	..
Procytheropteron brodiei	2	62	8	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Cythere sp.	..	..	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Fabanella boloniensis	..	94	50	41	56	14	43	46	..	2	..	..	3	17	11	1	..	..	..	..	..	2	..	..
Fabanella ansata	..	318	38	71	19	12	32	18	..	2	1	..	9	7	1	..	..	..	2	..	..	..	..	..
Mantelliana purbeckensis	..	..	32	14	4	14	..	..	..	..	1	48	57	32	17	2	..	..	..	1	..	5	98	1
Cypridea tumescens praecursor	..	..	..	..	..	..	..	..	..	..	..	..	..	2	1	1	..	..	..	..	..	..	..	..
Cypridea dunkeri	..	..	..	..	..	..	4	6	1	..	..	..	..	9	30	..	..	..	..	..	2	..	..	..
Scabriculocypris trapezoides	..	..	..	..	..	..	..	..	..	1	..	1	..	2	1	1	..	..	..	..	1	..	..	..

The samples were collected from excavations one mile north of Whitchurch on the Buckingham road, also from a field pit a little south of Hurdlesgrove Farm, about one mile north of Whitchurch on the western side of the Buckingham road.

North Whitchurch

		ft.	in.
NWD.	Trench dug into bank beside road.		
35	Sand and slipped material about	5	0
34	Yellow sandy clay		10
33	Tough grey sandy clay		4
32	Yellow sand about	1	6
31	Tough sandy clay		5
30	Soft white marl		6
29	Grey clay		3
28	Yellow sand and clay		10
27	Black clay		1–2
26	Crumbly white marl and clay	1	2
25	Grey marlstone seen to		6
	Possible gap in section		
NWE.	Pit dug in grass verge		
24	Crumbly white marl		9
23	Marlstone		1
22	Marly and sand clay		8
21	Marlstone and soft marl	2	4
20	Grey sand and clay		5
19	Crumbly hard marlstone, top a mass of gastropod casts		6
NWF.	Pit dug in grass verge a little to the north of NWE.		
18	Thinly laminated grey sand and clay in alternate layers	1	6
17	Black clay		6
16	Mottled red and green clay and marl with oysters		6
15	Brittle marlstone	1	10
14	Hard fine grained limestone or calcite mudstone		11
13	Laminated marl and clay		4
12	Hard brittle marlstone, greenstained down joints		11
11	Soft grey clayey marl	3	0
10	Sandstone		4
9	Loose sand, highly bituminous smell	1	4
8	Shelly clay with boulders and pebbles of limestone		6
7c	Shelly oolite with large lamellibranchs		3
7b	Hard laminated Pendle	1	0
7a	Soft Pendle, alternating layers of marlstone and ostracods (ooliths?)		6
6	Shelly clay		2

HG.	Old quarry in field south of Hurdlesgrove Farm	*ft.*	*in.*
5	Roach, *Trigonia* casts etc.	2	0
4	Soft shaley marl with perished shells and large oysters		9
3	Rubbly limestone full of lamellibranch casts	2	6
2	As above but with finer grain and fewer fossils	2	0
1	Sand, seen to	4	0

WARREN HOUSE FARM, STEWKLEY

The old pit to the south of this farm forms the most northerly outcrop of the Portland and Purbeck Beds in England. It is a very small outlier and is probably preserved due to being downfaulted at some time. The section exposed in 1939 is shown below. The quarry is now overgrown and only about three feet of the topmost beds can be seen. It was first described by Fitton (1836) and in 1962 C. R. Bristow and M. J. Hughes were able to expose beds containing large Portland lamellibranchs by means of excavation (Bristow personal communication), i.e. beds 2 and 3 of the section below. Text-fig. 1 shows that marine influence is strong all through the section. The marine ostracod fauna is present throughout but is soon joined first by the euryhaline and then by the oligohaline ostracod faunas.

The earliest appearance of oligohaline ostracods is notable since they are to be found in a bed (WH 7) containing *Trigonia* and *Protocardia* sp. (Nos. 11928–31 in Leicester University Coll). This is the only bed containing a few *Cypridea* sp., the fauna being mainly euryhaline with some marine ostracods. It would appear that some form of mixing had occurred or that seasonal variation in salinity and fauna was possible so that *Cypridea* could live in the same place as the marine ostracods. A surprising feature of the bed WH 7 is its similarity to the Swindon Roach, the difference being in the ostracod faunas. This is the bed referred to by Jones (1885 : 328) as containing *Trigonia* and as being underlain by a cypridiferous marl.

The oligohaline faunas in the rest of the beds do not contain *Cypridea* and form about twenty per cent or less of the whole fauna.

Bed WH 8 is a shelly marl containing *Ostrea expansa* (11926–27 in Leicester University Coll.) and other lamellibranchs together with a dominantly marine ostracod fauna. This is a typical marine deposit.

Beds WH 8, 10, 11 have a dominantly marine ostracod fauna with both euryhaline and oligohaline ostracod species present, whereas Bed WH 9 has a dominantly euryhaline ostracod fauna with a small percentage of marine and oligohaline ostracods. In both cases some form of mixing or seasonal variation in salinity and faunas could have occurred.

The conclusions to be made are as follows :

1. Conditions of deposition were rapidly changing ;
2. The limestones of beds WH 1, 2, 3 can be easily correlated with similar beds at the Bugle Pit and at North Whitchurch. This is facies A. The rest of the

beds can be classed as facies B, but representing a more changeable region possibly a shallow embayment with a river emptying into it. Facies C and D are missing but facies E comes in at the top in the form of bed WH 14.

3. A likely explanation for the mixing of the faunas is the erosion and redeposition of oligohaline and euryhaline ostracods into deposits of marine ostracods.

Table III

	1	2	3	4	5	6	7	8	9	10	11	12
Macrodentina (Macrodentina) rugulata	..	2	23	10	25	17	116	89	10	133	190	49
Macrodentina (Macrodentina) transiens		20	..	..	..	16	1	20	3	7	3	20
Macrodentina (Dictocythere) retirugata	..	..	21	..	21	6	..	..	..	6	10	2
Protocythere serpentina	..	..	..	..	..	..	..	9	..	..	2	3
"*Macrocypris*" ? sp.	..	..	..	14	8	5	..	..	..	..	..	1
Paraschuleridea buglensis	..	4	..	..	2	8	..	28	..	..	1	11
Orthonotacythere rimosa	..	..	..	..	..	3	..	..	..	..	1	..
Procytheropteron brodiei	..	..	..	2	..	3	..	..	..	..	..	..
Wolburgia visceralis	..	..	..	..	..	1	..	..	..	..	..	..
Fabanella boloniensis	..	..	3	1	3	6	35	6	48	41	20	199
Fabanella ansata	..	..	8	1	4	13	79	18	49	79	19	166
Mantelliana purbeckensis	..	..	..	..	..	..	..	52	65	100	..	..
Cypridea tumescens praecursor	..	..	..	..	..	..	10	..	..	..	..	..
Klieana alata	..	..	..	..	..	..	..	..	6	4	12	4
Scabriculocypris trapezoides	..	..	..	..	..	..	44	..	25	28	..	..

Warren House Farm, Stewkley

WH.	Quarry to the south of the farm house	ft.	in.
14	Red subsoil	1	0
13	Grey marl		2
12	Crumbly white and grey marl	3	0
11	Shaley marl with layers of ostracods		6
10	Grey marl		9
9	White laminated marl with ostracods and disseminated vegetation specks	1	6
8	Crumbly shelly marl, *Ostrea expansa* and medium sized lamellibranchs		4
7	Marlstone with *Trigonia* and *Protocardia*	1	0
6	Grey marl, ostracods abundant		9
5	Shaley shelly marl with large oysters		7
4	Shelly limestone with *Trigonia* etc.		5–7
3	Shaley shelly marl with large oysters		4
2	Rubbly limestone with *Trigonia*, *Protocardia*, *Pecten*, *Exogyra* spp., etc.	4	9
1	Sand, seen to	9	6

SUMMARY OF RESULTS

The major marker horizon in all three sections is the Crendon Sand at the base. Above this are the Creamy Limestones with large lamellibranchs and ammonites, some of which Buckman (1923 : 24, 26), had described from localities nearby. The ammonites from the topmost beds in the Long Crendon area were considered by Buckman to be younger than any from the Dorset coast. This marine facies is followed by facies B, C and D as indicated earlier, especially in the Bugle Pit and at North Whitchurch. At Warren House Farm conditions have changed; facies C and D are missing and facies B modified to take their place.

An examination of the ostracods shown in the Text-figure indicates that the euryhaline forms *Fabanella boloniensis* and *Fabanella ansata* are present in facies B, C and D. On the Dorset coast *Fabanella boloniensis* and *Mantelliana purbeckensis* are to be found in supersaline conditions (Anderson 1958).

Since the ostracods *Fabanella ansata* and *Mantelliana purbeckensis* are characteristic of the Lower Purbeck Beds of Dorset and as they appear in the upper part of the Creamy Limestones of the Aylesbury district, it would appear that Lower Purbeck conditions had set in before the end of Portland times in the Aylesbury district (cf. Casey & Bristow 1963 : 4).

No evidence has been found of Middle or Upper Purbeck ostracods in these sections but Middle Purbeck lamellibranchs have been obtained from the so-called Wealden Beds above the Purbecks of this region, (Casey & Bristow 1963, 1964).

In conclusion it can be stated that the transition from Portland to Purbeck conditions is marked by a series of facies which can be recognized by means of lithology, macrofauna and ostracods.

SYSTEMATIC DESCRIPTIONS

Suborder PODOCOPINA Sars 1866

Superfamily **CYPRIDACEA**

Family **CYPRIDIDAE**

Subfamily **CYPRIDINAE** Baird 1845

Genus ***MANTELLIANA*** Anderson

Mantelliana purbeckensis (Forbes)

(Pl. 7, fig. 5)

For complete synonymy see Anderson p. 438.

MATERIAL. Two hundred and thirty-nine valves and carapaces from the Bugle Pit (see Table I). Three hundred and twenty-six valves and carapaces from North Whitchurch (see Table II). Two hundred and seventeen valves and carapaces from Warren House Farm, Stewkley (see Table III). Other specimens were also obtained from similar horizons at Haddenham and Towersey.

REMARKS. This species is believed to be euryhaline in the Aylesbury district. It is seldom well preserved but muscle scars have been seen and cross-sections through the shell have indicated the size and shape of the duplicature and vestibule (see Barker in press).

Subfamily **ILYOCYPRIDINAE** Kaufman 1960

Genus ***RHINOCYPRIS*** Anderson 1941

Rhinocypris jurassica (Martin)

(Pl. 7, figs. 17, 18)

1940 *Ilyocypris jurassica jurassica* Martin : 312, pl. 4, figs. 51–54.
1941 *Rhinocypris scabra* var. *hamata* Anderson : 378, pl. 19, fig. 19.
1963 *Rhinocypris jurassica jurassica* (Martin) Oertli : 18, pl. 5, figs. 25–27.

MATERIAL. Six valves from Bed 16 at the Bugle Pit.

DESCRIPTION. Carapace thin shelled with a sub-elliptical lateral outline. The anterior margin is slightly larger than the posterior and both are evenly and smoothly curved. Dorsal margin slightly convex, ventral margin slightly concave. Greatest height midway between centre and anterior. The left valve overreaches the right valve around the free margin but not along the dorsal margin.

Shell surface covered by many small pustules closely arranged and of uniform size. Three major spines or hollow tubercles are present near the dorsal margin, separated by two transverse grooves, one medially from the dorsal margin to the centre of the valve and another smaller groove to anterior of this. There are about six to eight smaller spines of more or less equal size situated mainly posterior to the large anterior spine. Those nearer the posterior dorsal margin are curved to the rear. Hinge adont. The line of concrescence is parallel to and a short distance from the outer margin, a slight vestibule around the anterior border and at the posterior ventral corner being formed.

Muscles scars seen internally on a central node but not distinguishable. Normal and radial pore canals not clearly seen.

REMARKS. Mandelstam (1956) has described what appears to be the same genus under the name *Origoilyocypris*. The specimen figured by Oertli (1963) as *Rhinocypris jurassica jurassica* is much smoother and not so spinose as the specimens described here.

Subfamily **CYPRIDEINAE**

Genus ***CYPRIDEA*** Bosquet 1952

Cypridea dunkeri Jones

(Pl. 7, figs. 1, 2)

1885 *Cypridea dunkeri* Jones: 339, pl. 8, figs. 9, 10, 17.
1941 *Ulwellia papulata* Anderson : 381, pl. 18, fig. 8.
1963 *Cypridea dunkeri* Jones ; Oertli : 15, pl. 1, fig. 6.

MATERIAL. Six valves and carapaces from the Bugle Pit (see Table I). Five valves and carapaces from North Whitchurch (see Table II). One carapace from Haddenham.

REMARKS. *Cypridea dunkeri* is characteristic of the oligohaline facies but few specimens are usually found.

Cypridea tumescens (Anderson) ***praecursor*** Oertli

(Pl. 7, fig. 4)

1940 *Cypridea valdensis* (Fitton); Martin: 288, pl. 1, figs. 1–4.
1939 *Cyamocypris tumescens* Anderson: 306, pl. 13, figs. 4, 7.
1963 *Cypridea valdensis praecursor* Oertli: 16, pl. 3, figs. 13–19, pl. 4, fig. 20.

MATERIAL. Forty-five valves and carapaces from the Bugle Pit (see Table I). Forty-one valves and carapaces from North Whitchurch (see Table II). Ten valves and carapaces from Bed 7 at Warren House Farm, Stewkley. Eighty-three valves and carapaces from similar beds at Haddenham, and thirty-four specimens at Towesey.

	Dimensions in mm.			Proportions			
	L	H	I	L	H	I	Specimen Number
Carapace . .	1·17	0·71	0·51	1·00	0·61	0·44	Io. 1223
Left valve . .	1·17	0·73	—	1·00	0·62	—	Io. 1224
Right valve . .	1·02	0·61	—	1·00	0·60	—	Io. 1225

REMARKS. This species is characteristic of the oligohaline facies. Specimens are few and some are broken. There is variation in lateral outline as suggested by Oertli (1963). Specimens from other horizons in the Purbeck Beds show a wide variation in shape (cf. those figured by Anderson) but all the specimens probably belong to the same group.

Family **PARACYPRIDIDAE** Sars 1923

Genus ***PARACYPRIS*** Sars

Paracypris? sp.

(Pl. 9, figs. 9, 10)

MATERIAL. Four carapaces from Bed NW 5 at North Whitchurch (see Table II). Two hundred and sixty-eight carapaces from various beds at Haddenham of similar age to the North Whitchurch material.

DESCRIPTION. Characteristic elongate shape with the greatest height just anterior of the centre. The dorsal margin is short and straight or obliquely convex. The ventral margin is longer and concave. Anterior margin is obliquely curved, sharpest towards the venter. Carapace smooth on external surface.

The internal details have not been seen but in some specimens there are faint indications of elongate muscle scars in a vertical row of four at the position of greatest height.

REMARKS. This form shows many similarities in shape to *Paracypris* although not definitely identified as such at the present time.

Superfamily **DARWINULACEA** Brady & Norman 1889

Family **DARWINULIDAE** Brady & Norman 1889

Genus ***DARWINULA*** Brady & Robertson 1885

Darwinula leguminella (Forbes)

(Pl. 7, fig. 9)

1855 *Cypris leguminella* Forbes *in* Lyell : 294, text-fig. 334*c*.
1885 *Darwinula leguminella* (Forbes) Jones : 346, pl. 8, figs. 80, 31.
1885 *Cyprione Bristovii* Jones : 344, pl. 8, figs. 27–29, 32.

REMARKS. A rare species in the Aylesbury district.

Superfamily **CYTHERACEA** Baird 1850

Family **CYTHERIDAE** Baird 1850

Genus ***FABANELLA*** Martin 1961

Fabanella boloniensis (Jones)[1]

(Pl. 7, fig. 7)

1882 *Cythere boloniensis* Jones: 615–616, text-figs. A, B.
1883 *Cythere ? boloniensis* Jones; Jones: 58, text-figs. 1–9.
1885 *Candona boloniensis* (Jones) Jones: 348, pl. 9, figs. 7, 8.
1940 *Cyprideis polita* Martin : 352, pl. 7, figs. 110–113, pl. 9, figs. 149–151.
1961*a* *Fabanella polita* (Martin) Martin : 186, 190–192, pl. 1, figs. 1–4, 10–12.
1961*b* *Fabanella polita polita* (Martin) ; Martin : 113, pl. 14, fig. 9.
1963 *Fabanella polita polita* (Martin) ; Oertli : 21, pl. 7, figs. 46–52.

MATERIAL. Five hundred and six valves and carapaces from various beds at the Bugle Pit (see Table I). Three hundred and eighty valves and carapaces from various beds at North Whitchurch, (see Table II). Three hundred and sixty-two valves and carapaces from various beds at Warren House Farm, Stewkley, (see Table III). Beds of similar age have yielded three hundred and eighty-eight valves and carapaces at Haddenham, ninety-nine valves and carapaces at Towesey and seven valves and carapaces at Coneyhill.

REMARKS. In the Aylesbury district *Fabanella boloniensis* has been shown to be a euryhaline ostracod capable of existing in various environments (Barker 1963). It is smallest in the oligohaline facies and largest in the marine facies.

Fabanella ansata (Jones)

(Pl. 7, fig. 8)

1885 *Candona ansata* Jones : 349, pl. 9, figs. 9–12.
1947 *Candona ansata* Jones ; Anderson *in* Arkell : 129, text-fig. 28 (9).
1963 *Fabanella ansata* (Jones) Oertli : 22, pl. 16, figs. 43–45.

MATERIAL. Nine hundred and fifty-five valves and carapaces from various beds at the Bugle Pit (see Table I). Five hundred and thirty valves and carapaces from

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[1] Anderson & Barker consider *Fabanella polita* (Martin) to be a synonym of *Fabonella boloniensis* (Jones). They propose a fuller discussion of this species elsewhere.

various beds at North Whitchurch, (see Table II). Four hundred and thirty-six valves and carapaces from various beds at Warren House Farm, Stewkley, (see Table III). Beds of similar age have yielded five hundred and ten valves and carapaces at Haddenham, one hundred and eighty valves and carapaces at Towersey and seven at Coneyhill.

DESCRIPTION. The lateral outline is subreniform with the greatest height towards the posterior and the greatest inflation central. Anterior and posterior margins obliquely curved, slightly sharper towards the venter. Ventral margin concave and slightly inturned. Dorsal margin slightly inturned and more or less straight. In dorsal view carapace is acutely elliptical. Left valve is larger than and overreaches the right valve. External surface smooth with a few normal pore canals irregularly spaced. Radial pore canals numerous, fine straight and closely spaced around the anterior, posterior and ventral borders. Adductor muscle scars in a vertical row of four just anterior of centre. Frontal scars situated to anterior of adductors opposite the top and bottom scars. In some specimens a small fifth scar can be seen above and in line with the four adductors ; this may be the " fulcral point " (Van Morkhoven 1962 : 48) rather than a muscle scar. Hinge lophodont. A small anterior vestibule widest antero-ventrally and a narrow posterior vestibule parallel to the outer margin.

	Dimensions in mm.			Proportions			
	L	H	I	L	H	I	Specimen Number
Carapace . .	1·17	0·73	0·59	1·00	0·63	0·50	..
Left valve . .	1·00	0·73	—	1·00	0·73	—	..
Right valve . .	0·95	0·56	—	1·00	0·59	—	..
Carapace . .	0·96	0·62	0·50	1·00	0·65	0·52	In. 48669

REMARKS. This species is characteristic of euryhaline conditions in the Aylesbury district and varies in size according to the salinity. It is smallest in the oligohaline facies and largest in the marine facies (Barker 1963).

Family **CYTHERIDEIDAE** Sars 1925

Subfamily **CYTHERIDEINAE** Sars 1925

Genus ***GALLIAECYTHERIDEA*** Oertli 1957

Galliaecytheridea crendonensis sp. nov.

(Pl. 8, figs. 7–11)

HOLOTYPE. Io. 1257, carapace from Bed CWE 2, Long Crendon. Length 0·68 mm., height 0·39 mm., inflation 0·31 mm.

PARATYPES. Io. 1258–59 from Bed CWE 2, Long Crendon.

Diagnosis. *Galliaecyatheridea* with pronounced caudal process.

Material. Six valves from Bed CWE 2 and one valve from Bed CWE 3 at Long Crendon. Also six valves from Bed CH 8 and one valve from Bed CH 7 at Coneyhill.

Description. Carapace asymmetrically subelliptical in lateral outline. Right valve with a pronounced caudal process. Dorsal of the right valve more or less straight, converging posteriorly with the ventral margin. Anterior margin obliquely curved, sharper towards the venter. Left valve has a more rounded outline with a very much reduced and rounded caudal process. Dorsal margin more or less straight, converging towards the posterior. Ventral margin convex. Anterior margin smoothly and obliquely curved, slightly sharper towards the venter. Greatest height at the centre. In dorsal view the outline is elliptical with the greatest inflation in the centre. The left valve is greater in height than the right, but the right valve is greater in length due to the caudal process.

The outer surface is ornamented by irregularly spaced and sized pits, the larger usually being near the centre. In both valves there is a slight furrow just behind the anterior margin. Line of concrescence and inner margin coincide throughout. The selvage forms the outer margin all round except anteriorly in the right valve where it runs a short distance inside the outer margin. Pore canals not seen. Hinge hemimerodont, consisting of two terminal teeth subdivided into six or seven toothlets and connected by a smooth narrow groove in the right valve. The left valve has complementary elements and also an accommodation groove behind the median ridge. There are four adductor muscle scars in a vertical row slightly concave to the anterior. A frontal scar is situated opposite the top adductor and a rather large mandible scar, possibly made up of two scars, somewhat below and anterior to the bottom adductor.

Remarks. Sexual dimorphism has not been observed in this species. The shape of the posterior is characteristic of the species. So far it has only been found at Long Crendon and Coneyhill.

Family **BRACHYCYTHERIDAE** Puri 1954

Genus ***MACRODENTINA*** Martin 1940

Remarks. Sylvester-Bradley (1956) considered the genus *Dictyocythere* (Jones) to consist of two subgenera, *Dictyocythere* and *Rhysocythere*, differentiated on the basis of hinge structure. However, Malz (1958) showed that *Rhysocythere* is a junior synonym of Martin's genus *Macrodentina*, and subdivided this genus into three subgenera on the basis of hinge structure, *Macrodentina* ss. *Macrodentina* (*Dictyocythere*) and *Macrodentina* (*Polydentina*). The differences between the three subgenera of Malz were considered to be strong enough to raise them to full generic level in Volume Q of the *Treatise on Invertebrate Palaeontology*. In the present work the differences between the subgenera are thought to be insufficient to give them full generic status and the classification of Malz is followed.

Subgenus ***MACRODENTINA*** Martin 1940

Macrodentina (Macrodentina) rugulata (Jones)

(Pl. 8, figs. 16, 17)

1885 *Cythere retirugata* var. *rugulata* Jones : 350, pl. 9, figs. 17–20.
1940 *Cythere retirugata* Jones var. *rugulata* Jones ; Anderson : 373, pl. 18, fig. 1.
1956 *Dictyocythere* (*Rhysocythere*) *rugulata* (Jones) Sylvester-Bradley : 18, pl. 4, figs. 1, 2, 5–15.
1958 *Macrodentina* (*Macrodentina*) *rugulata* (Jones) Malz : 18, pl. 6, figs. 83–86.

MATERIAL. Six hundred and six valves and carapaces from various beds at the Bugle Pit (see Table I). Two hundred and ninety-seven valves and carapaces from various beds at North Whitchurch (see Table II). Five hundred and sixty-four valves and carapaces from various beds at Warren House Farm, Stewkley (see Table III). Beds of similar age have yielded one hundred and thirteen valves and carapaces at Haddenham, ten valves at Towesey and twenty valves and carapaces at Coneyhill.

DESCRIPTION. Carapace subtrapezoidal in lateral outline with greatest height to the anterior of centre. Dorsal view inflated elliptical with the greatest inflation medially and towards the venter. Ventral surface has about eight subparallel longitudinal ridges. The dorsal and ventral margins are convex outwards. Anterior and posterior margins obliquely rounded, sharper towards the venter. The left valve is larger than the right.

Lateral surfaces smooth except near the ventral margins where there are three long ridges similar to those on the ventral surface but decreasing in length towards the centre of the valve. Normal pore canals regularly spaced over the carapace. Radial pore canals straight, about twenty being irregularly spaced around the anterior border and very few on the posterior border. Four adductor muscle scars in a vertical row of four just anterior of the valve centre. Hinge paramphidont. Line of concrescence parallel to the outer margin except at the anterior ventral corner where it forms a slight vestibule.

	Dimensions in mm.			Proportions			
	L	H	I	L	H	I	Specimen Number
Carapace ♀ .	. 0·83	0·54	0·49	1·00	0·65	0·59	Io. 1236
Left valve ♂ .	. 0·95	0·56	—	1·00	0·59	—	. .
Left valve ♀ .	. 0·88	0·56	—	1·00	0·64	—	Io. 1237
Right valve ♀	. 0·83	0·54	—	1·00	0·65	—	Io. 1238
Right valve ♂	. 0·90	0·51	—	1·00	0·57	—	. .
Carapace ♂ .	. 0·96	0·58	0·54	1·00	0·60	0·56	I. 1655
Left valve ♂ .	. 0·88	0·58	—	1·00	0·66	—	I. 1670
Carapace ♀ .	. 0·78	0·48	0·45	1·00	0·62	0·58	GSM, No. 70338

REMARKS. A common easily recognized species in the Aylesbury district.

Macrodentina (Macrodentina) transiens (Jones)

(Pl. 8, figs. 1–6)

1885 *Cythere transiens* Jones : 349, pl. 9, figs. 13–16.
1956 *Dictyocythere* (*Rhysocythere*) *transiens* (Jones) Sylvester-Bradley : 19, pl. 3, figs. 11–13.
1958 *Macrodentina* (*Macrodentina*) *transiens* (Jones) Malz : 17, pl. 6, figs. 81, 82.

DIAGNOSIS. Small reticulate *Macrodentina* tapering strongly to the posterior in lateral view. No sexual dimorphism.

MATERIAL. Four hundred and eighty three valves and carapaces from various beds at the Bugle Pit (see Table I). One hundred and fourteen valves and carapaces from various beds at North Whitchurch (see Table II). Ninety valves and carapaces from various beds at Warren House Farm, Stewkley (see Table III). Beds of similar age have yielded forty two valves and carapaces at Towersey, three hundred and fifty-seven valves and carapaces at Long Crendon and two hundred and twenty valves and carapaces at Coneyhill.

DESCRIPTION. Broadly ovate asymmetrical lateral outline, greatest height being anterior of the centre. In dorsal view the sides are subparallel and the ends rounded, the posterior being more pointed. Dorsal margin straight or very slightly convex and slopes down towards the posterior. Ventral margin slightly convex, the ventral surface being slightly ridged longitudinally. The anterior margin is more broadly rounded than the posterior.

Shell surface strongly pitted. The pits arranged in rows near the margins but more irregularly situated towards the centre. On the left valve there is a small posteriorly directed spine at the posterior ventral corner. Normal pore canals are situated in a pit. Radial pore canals are present not difficult to distinguish. Four adductor muscle scars are situated in a vertical row about the centre of the valves. Hinge paramphidont.

	Dimensions in mm.			Proportions			
	L	H	I	L	H	I	Specimen Number
Carapace	0·61	0·37	0·32	1·00	0·61	0·52	..
Carapace	0·59	0·37	0·32	1·00	0·63	0·49	Io. 1239
Right valve	0·61	0·32	—	1·00	0·52	—	Io. 1241
Left valve	0·59	0·37	—	1·00	0·63	—	Io. 1240

REMARKS. This species is smaller than and easily distinguished from the other species of *Macrodentina* by means of its shape.

Subgenus ***DICTYOCYTHERE*** Sylvester-Bradley 1956

Macrodentina (Dictyocythere) retirugata (Jones)

(Pl. 8, figs. 18–22)

1885 *Cythere retirugata* Jones : 350, pl. 9, figs. 21–23.
1885 *Cythere retirugata* var. *textilis* Jones : 350, pl. 9, fig. 24.
1941 *Cythere retirugata* Jones var. *textilis* Jones ; Anderson : 374, pl. 18. fig. 3.
1941 *Cythere retirugata* Jones var. *decorata* Anderson : 374, pl. 18, fig. 4.

1956 *Dictyocythere* (*Dictyocythere*) *retirugata* (Jones) Sylvester-Bradley : 15, pl. 3, figs. 7–10, pl. 4, figs. 3, 4, 11, 16, 17.
1956 *Dictyocythere* (*Dictyocythere*) *decorata* (Anderson) Sylvester-Bradley : pl. 17, pl. 3, fig. 1.
1958 *Macrodentina* (*Dictyocythere*) *retirugata* (Jones) Malz : 25, pl. 6, figs. 87, 88.
1958 *Macrodentina* (*Dictyocythere*) *textilis* (Jones) Malz : 26, pl. 6, figs. 89–91.

MATERIAL. Five hundred and twenty-seven valves and carapaces from various beds at the Bugle Pit (see Table I). Two hundred and sixty-three valves and carapaces from various beds at North Whitchurch (see Table II). Sixty-six valves and carapaces from various beds at Warren House Farm, Stewkley (see Table III). Beds of similar age have yielded six valves at Coneyhill.

DESCRIPTION. Lateral outline subtrapezoidal with greatest height to anterior of centre. Pyriform in dorsal view with greatest inflation towards the posterior. The dorsal margin is straight and the ventral margin is sinuous, slightly concave medially. Anterior margin smoothly and obliquely rounded, sharper towards the venter. Posterior margin smaller and almost straight forming a posterior dorsal slope. The inflation is greatest towards the venter so that the ventral surface is almost flat with about six rows of elongate reticulae more or less parallel to its length.

The surface is strongly reticulate, the reticulation arranged in rows parallel to the margins near the venter, posterior and anterior but irregularly elsewhere. Normal pore canals large, situated in each cell of the reticulum. Inside these polygonal areas fine " second order " reticulations can often be seen. In some specimens the reticulation has been smoothed out to form circular rather than polygonal pits, leaving faint indications for the fine reticulations in some places. The radial pore canals are sparse and straight, with about twelve to the anterior border and eight to the posterior. Four adductor muscle scars are in a vertical row just posterior of the position of greatest height. A single frontal scar is situated in line with the second dorsal adductor. Hinge holamphidont. Line of concrescence not clear but there are vestibules around the anterior and at the posterior ventral corner. The right valve overlaps the left around the anterior half of the carapace and the left valve overlaps the right around the posterior half of the carapace.

REMARKS. The variation in ornamentation of this species is so continuous when a large number of specimens are examined that it is impossible to separate the three morphological types shown in Pl. 8.

Family **CYTHERURIDAE** Müller 1894

Genus ***PROCYTHEROPTERON*** Ljubimova 1955

Procytheropteron brodiei (Jones)

(Pl. 8, figs. 23–26, Pl. 9, fig. 8)

1894 *Cytheropteron brodiei* Jones : 167, pl. 9, fig. 12.
1964 *Procytheropteron brodiei* (Jones) Anderson: 154, pl. 11, figs. 41, 42.

MATERIAL. Two hundred and thirty-five valves and carapaces from various beds at the Bugle Pit (see Table I). Seventy-two valves and carapaces from various beds at North Whitchurch (see Table II). Five valves from beds four and six at Warren House Farm, Stewkley (see Table III). Beds of similar age have yielded ten valves and carapaces at Haddenham, and two valves at Long Grendon.

DESCRIPTION. Carapace smooth and glossy with a sub-circular lateral outline drawn out slightly to posterior, and with the greatest height to the anterior. Swollen in dorsal view with the greatest inflation centrally situated. Anterior margin is obliquely curved, sharpest towards the venter. Posterior margin is drawn out in a projection. Both valves are swollen near the ventral margins and form an angle with the concave ventral surface which is ornamented with three or four longitudinal subparallel ridges to each valve.

Ornamentation consists of faint longitudinal reticulations on the lateral surfaces. Normal pore canals are regularly distributed. Anterior border has about seven straight radial pore canals.

Line of concrescence and inner margin coincide. Hinge hemimerodont. Four poorly distinguished adductor muscle scars are in a vertical row just anterior of the centre. Outer margin forms a lip centrally on the ventral margin. Posterior projection is slightly hollow so forms a slight tube with the opposite valve.

	Dimensions in mm.			Proportions		
	L	H	I	L	H	I
Carapace . . .	0·48	0·29	0·29	1.00	0·60	0·60
Left valve . .	0·47	0·29	—	1.00	0·62	—

REMARKS. This species differs from those of *Cytheropteron* by having a smooth median portion to the hinge and a more rounded lateral outline.

Genus ***ORTHONOTACYTHERE*** Alexander 1933

Orthonotacythere rimosa Martin

(Pl. 8, figs. 12, 13)

1940 *Orthonotacythere rimosa* Martin : 335, pl. 6, figs. 84–86.
1961 *Orthonotacythere rimosa* Martin ; Martin : 117, pl. 14, fig. 21*a–c*.

MATERIAL. Seventy-eight valves and carapaces from various beds at the Bugle Pit (see Table I). Four valves from beds 6 and 11 at Warren House Farm, Stewkley (see Table III).

DESCRIPTION. Subtrapezoidal in lateral outline with the dorsal and ventral margins subparallel. Greatest height and greatest inflation are posterior of centre. Anterior margin is obliquely rounded sharper to venter ; posterior margin subtriangular forming a caudal process to the posterior corner. Ventral margin slightly convex ; dorsal margin long and straight.

The ornamentation consists of an irregular reticulate rib pattern with a few strong ridges radiating from the ventral margin just posterior of the centre where the inflation is greatest. The major ridge is inside but more or less parallel to the anterior, ventral and posterior margins. A few short radial pore canals are to be seen at the anterior and posterior margins. The muscle scars are not clear. Inner margin and line of concrescence coincide.

	Dimensions in mm.			Proportions			
	L	H	I	L	H	I	Specimen Number
Carapace . .	0·59	0·39	0·32	1·00	0·58	0·54	Io. 1242
Right valve . .	0·73	0·39	—	1·00	0·53	—	Io. 1244
Left valve . .	0·66	0·37	—	1·00	0·56	—	Io. 1243

REMARKS. The rib pattern appears to be slightly stronger than the figured specimens of Martin (1940), but since the specimens described here are larger they may represent a later instar.

O. rimosa differs from *O. diglypta* Triebel by having weaker ornamentation and a straight dorsal margin. The sulcus is not so deep in *O. rimosa* as it is in *O. interrupta*.

Family **LIMNOCYTHERIDAE** Klie 1938

Genus ***DICRORYGMA*** Poag 1962

Dicrorygma fragilis (Martin)

(Pl. 7, figs. 19, 20)

1940 *Limnocythere fragilis* Martin : 348, pl. 7, figs. 105–109, pl. 9, fig. 152.

MATERIAL. Six valves from Bed BP 16 at the Bugle Pit, (see Table I).

DESCRIPTION. Valves thin and fragile, subreniform in lateral outline. Dorsal margin straight, ventral margin longer but sinuous. Anterior and posterior obliquely rounded, the posterior being the larger, and both are slightly compressed near the margins. Shell surface smooth. A subcentral sulcus occurs near the venter just posterior of the centre and another vey faint one near to the dorsal margin just above the muscle scars. Normal pore canals few in number, sieve type and irregularly distributed. There are about ten radial pore canals to the posterior margin and fewer to the anterior. They are fairly straight and irregularly spaced. Hinge is weakly developed lophodont. Four adductor muscle scars are arranged in a slight curve concave to the anterior just in front of the centre. A frontal scar occurs opposite to the top adductor with possibly a fulcral point just below it. Two mandibular scars are arranged antero ventrally to the adductors. The line of concrescence runs parallel to the outer margin and a short distance inside it forming a vestibule to the anterior and posterior ventral borders.

REMARKS. Very few specimens are to be found in this region.

Dicrorygma decipiens (Anderson)

(Pl. 7, figs. 15, 16)

1941 *Cytherella* ? *decipiens* Anderson : 380, pl. 19, figs. 20, 21.

MATERIAL. Three valves from Bed 16 at the Bugle Pit (see Table I).

Description. Thin fragile valves are subreniform in lateral outline. The dorsal margin and the ventral longer and concave medially. Posterior is larger and more obliquely rounded than the anterior and both are slightly flattened round the margins. Surfaces of the valves are covered by numerous discontinuous ridges more or less parallel to the outer margins. There is a slight subcentral sulcus just posterior of the centre and a much fainter one near the dorsal margin just above the muscle scars. A few normal pore canals of the sieve type are distributed irregularly. About ten fairly straight and irregularly spaced radial pore canals are in the posterior margin and fewer in the anterior. Hinge is lophodont. Four adductor muscle scars are in slight curve, concave to the anterior, and situated just anterior of the valve centre. There is also a frontal scar and two mandibular scars though they are difficult to see because of the ornament. The line of concrescence runs parallel to the outer margin and a short distance inside it forming a vestibule to the anterior and posterior ventral borders.

Remarks. *Dicrorygma decipiens* is easily distinguished from *D. fragilis* by means of its lateral outline and its distinctive ornamentation. This species is very rare.

Genus ***THERIOSYNOECUM*** Branson 1933

Theriosynoecum forbesii (Jones)

(Pl. 7, fig. 6, Pl. 9, figs. 11, 12)

1885 *Metacypris forbesii* Jones : 344, pl. 8, figs. 11–16.
1940 *Metacypris forbesii* Jones ; Martin : 336, pl. 6, figs. 89–94.
1957 *Gomphocythere forbesii forbesii* (Jones) Wicher : 270.
1962 *Bisulcocypris forbesii* (Jones) Pinto & Sanguinetti : 39, pl. 3, figs. 1–4, pl. 12, figs. 1*a–d*.

Material. Five carapaces and six valves from Bed TW 2 at Towersey. Twenty-seven carapaces and thirty-one valves from Bed HDB la at Haddenham.

Remarks. According to Pinto & Sanguinetti (1962) *Theriosynoecum* differs from *Bisulcocypris* in having a less well-defined hinge, accommodation groove and velate ridges. The species considered here has no accommodation groove but otherwise corresponds to *Theriosynoecum.* Plate 9, figs. 11, 12, show the wide variation in ornamentation of *Theriosynoecum forbesii* which approaches that of *Bisulcocypris verrucosa* (Jones) described by Pinto & Sanguinetti. (See discussion by Sohn & Anderson 1964).

Family **PROGONOCYTHERIDAE** Sylvester-Bradley 1948

Subfamily **PROTOCYTHERINAE** Ljubimova 1955

Genus ***KLIEANA*** Martin 1940

Klieana alata Martin

(Pl. 7, figs. 10–14)

1940 *Klieana alata* Martin : 322, pl. 5, figs. 64–73 ; pl. 11, figs. 158–161.
1963 *Klieana alata* Martin ; Oertli : 22, pl. 7. figs. 53–56.

Diagnosis. A *Klieana* with almost reticulate pitting and distinct sexual dimorphism.

HOLOTYPE. Senckenberg Museum Nr. X/E 319, female carapace.

MATERIAL. Five hundred and ninety-two valves and carapaces from various beds at the Bugle Pit (see Table I). Seventy valves and carapaces from various beds at North Whitchurch (see Table II). Twenty-six valves and carapaces from various beds at Warren Farm, Stewkley (see Table III). Beds of similar age have yielded three hundred and thirty valves and carapaces at Haddenham and two hundred and sixty-five valves and carapaces at Towersey.

DESCRIPTION. *Females:* lateral outline subdeltoidal with the greatest height anterior of the centre. Dorsal outline similar to a broad arrow head with the greatest inflation to the posterior of centre. Anterior margin slightly swollen, smooth and obliquely rounded, sharpest to venter. The posterior margin is similar but not so swollen. A strongly developed posteriorly directed winglike process near the ventral margin is smooth and shiny showing only faint relics of pitting. Ventral surface flat with four subparallel longitudinal ridges to each valve. The dorsal margin is slightly convex. Left valve larger than right. *Males:* Dorsal outline irregularly elliptical with the greatest inflation to the posterior of the centre. Both anterior and posterior margins are slightly swollen, smooth and obliquely curved, sharpest to the venter. The flat ventral surface has four subparallel longitudinal ridges to each valve. Dorsal margin is slightly concave and the left valve is larger than the right.

Both the males and females have the lateral surfaces covered by small pits, almost reticulate in pattern in the case of the female but much finer in the male. There are about six straight evenly spaced radial pore canals to the anterior border and three similarly to the posterior. Four muscle scars are placed centrally in a vertical row slightly concave to the anterior. Hinge hemimerodont. Line of concrescence follows the inner margin all round and the selvage forms the principle ridge round the contact margin, forming a strong lip medially on the female venter and just posteriorly on the male venter.

	Dimensions in mm.			Proportions			
	L	H	I	L	H	I	Specimen Number
Carapace ♀ . .	0·56	0·39	0·37	1·00	0·70	0·66	Io. 1245
Carapace ♂ . .	0·71	0·39	0·34	1·00	0·55	0·48	Io. 1248
Right valve ♀ .	0·59	0·37	—	1·00	0·63	—	Io. 1247
Left valve ♀ . .	0·59	0·41	—	1·00	0·69	—	Io. 1246
Right valve ♂ .	0·76	0·39	—	1·00	0·51	—	Io. 1250
Left valve ♂ . .	0·69	0·37	—	1·00	0·54	—	Io. 1249

REMARKS. These specimens show the characteristic features of *Klieana alata*, but occasionally there is some variation in ornamentation. In some specimens the posteriorly directed wing-like process is reduced so that the valve becomes almost smoothly rounded. There may also be some reduction in the strength of the pitting which is often reduced or lost completely near the margins of the specimens.

Genus *PROTOCYTHERE* Triebel 1938

Protocythere serpentina (Anderson)

(Pl. 9, figs. 13–18)

1941 *Cythereis serpentina* Anderson : 375, pl. 19, fig. 12.
1951 *Protocythere sigmoidea* Steghaus : 219, pl. 15, figs. 42–45.
1958 *Protocythere bireticulata* Malz : 39, pl. 11, fig. 69.
1960 *Protocythere sigmoidea* Steghaus ; Fernet : 21, pl. 11, figs. 11–13.
1963 *Protocythere serpentina* (Anderson) Oertli : 22, pl. 7, fig. 57.

MATERIAL. Four hundred and fifty-five valves and carapaces from various beds at the Bugle Pit (see Table I). Eighty valves and carapaces from various beds at North Whitchurch (see Table II). Fourteen valves and carapaces from various beds at Warren House Farm, Stewkley (see Table III). Beds of similar age have yielded twenty-three valves and carapaces at Haddenham, seventy-eight valves and carapaces at Towersey, three hundred and thirty-eight valves and carapaces at Coneyhill.

DESCRIPTION. Carapace subrectangular in outline with dorsal and ventral margins almost parallel. Anterior margin broadly rounded and denticulate on the inner edge. Posterior margin angular with the ventral part denticulate. The ventral margin is more or less straight whereas the dorsal margin is straight with a dorsal bulge forming a prominent anterior hinge ear or eye tubercle. Left valve is larger than right.

Major ornamentation consists of two ribs, one parallel to the dorsal margin, the other parallel to the ventral margin. A third rib runs from the posterior dorsal corner to the anterior ventral corner just before which it usually swells to form a node. The ribs make a continuous Z shape on the lateral surface and are usually roughly rounded and increase in size from dorsal to ventral. Anterior margin well rounded and inflated. Shell surface is usually covered by fine reticulations. There are occasional small tubercles in various positions. The strength and variation in shape and ornamentation is shown in Pl. 9. The normal pore canals are not seen. There are about thirteen radial pore canals around the anterior border associated with the denticles and also about fifteen radial pore canals on the posterior ventral margin associated with denticles. Adductor scars in a vertical row of four situated on the posterior side of a pit in the anterior part of the shell. Hinge hemimerodont. Line of concrescence follows the inner margin all round.

REMARKS. *Protocythere serpentina* has been described by Oertli (1963) from Middle Kimmeridge to Lower Purbeck Beds in Villemoyenne 2. *P. bireticulata* was described from twelve metres below Purbeck ostracods in the Ile d'Oleron by Malz (1958). *P. sigmoidea* was described from the Kimmeridge 3*a* of Fuhrberg by Steghaus (1951). In England *P. serpentina* has so far only been described from the uppermost Portland beds.

A single population of the present species exhibits all the variations described for the species mentioned above (see Pl. 9, fig. 13). As a consequence all are considered to be conspecific.

Genus *PARASCHULERIDEA* Swartz & Swain 1946

Paraschuleridea buglensis sp. nov.

(Pl. 9, figs. 5–7)

1941 *Cytheridea politula* Jones & Sherborn ; Anderson : 375, pl. 19, fig. 14.

DIAGNOSIS. Elliptical in dorsal outline with subreniform lateral outline. Hinge antimerodont. Outer surface smooth with left valve larger than and overreaching the right all round.

HOLOTYPE. GSM Mik (M) 724001. Figured Anderson (1941, pl. 19, fig. 14).

PARATYPES. Il. 1227–29, from bed BP 6*a*, Bugle Pit, Hartwell.

MATERIAL. Two hundred and fifty-seven valves and carapaces from various beds at the bugle Pit (see Table I). Two hundred and fifty-four valves and carapaces from various beds at North Whitchurch (see Table II). Fifty-four valves and carapaces from various beds at Warren House Farm, Stewkley (see Table III). Beds of similar age have yielded fifty-six valves and carapaces at Haddenham, fifty-five valves and carapaces at Towersey, one hundred and fifty-six valves and carapaces at Long Crendon and eighty-nine valves and carapaces at Coneyhill.

REMARKS. A robust carapace, reniform in lateral outline and characteristic of the marine faies in the Aylesbury district. It is placed in the genus *Paraschuleridea* because of the similarity in the hinge and muscle scar pattern to the type species. However, the shape is even more smoothly rounded especially in dorsal view. No sexual dimorphism has been observed. The only other comparable genus is *Galliaecytheridea*, but it differs in lateral outline and is therefore not considered to be related.

Family uncertain

Genus *WOLBURGIA* Anderson 1965

Wolburgia visceralis (Anderson)

(Pl. 8, figs. 14, 15)

1940 *Cythere visceralis* Anderson : 374, pl. 19, fig. 11.
1966 *Wolburgia visceralis* (Anderson) Anderson : 443, text-figs. 12, 27

MATERIAL. Seventy-six valves and carapaces from various beds at the Bugle Pit (see Table I). One valve from Bed WH 6 at Warren House Farm, Stewkley (see Table III). Beds of similar age have yielded seventy-seven valves and carapaces at Long Crendon and one hundred and three valves and carapaces at Coneyhill.

DESCRIPTION. Lateral outline subtrapezoidal with the greatest height at the centre. Anterior margin is obliquely rounded, sharpest towards the venter. Posterior margin also oblique forming a rounded angle with the dorsal margin. The left valve is slightly larger than the right valve. Carapace is subelliptical in dorsal view with the greatest inflation at the centre.

Ornamentation of rounded ridges constricted irregularly and arranged concentrically around the margins. The anterior margin is the thicker and is separated from the lateral surfaces by a furrow. There are many normal canals arranged irregularly over the surface. About nine radial pore canals are evenly spaced around the anterior margin with five around the posterior margin. Hinge adont and is a long straight groove about 2/3 the length and narrowing to the posterior in the right valve. In the left valve there is a ridge narrowing to the posterior and possibly slightly serrate in the posterior third. Inner margin and line of concrescence are coincident.

	Dimensions in mm.			Proportions		
	L	H	I	L	H	I
Carapace	0·56	0·34	0·34	1·00	0·61	0·61
Right valve	0·69	0·37	—	1·00	0·54	—
Left valve	0·64	0·34	—	1·00	0·53	—

REMARKS. This species is characteristic of the marine horizons in the Aylesbury district.

Genus ***SCABRICULOCYPRIS*** Anderson 1941

Scabriculocypris trapezoides Anderson

(Pl. 7, fig. 3)

1941 *Scabriculocypris trapezoides* Anderson : 377, pl. 18, fig. 5.
1963 *Scabriculocypris trapezoides* Anderson ; Oertli : 20, pl. 6, figs. 37–39.

MATERIAL. Ninety-seven valves and carapaces from various beds at Warren House Farm, Stewkley (see Table III).

REMARKS. Specimens have characteristic fine reticulate ornamentation and asymmetrical view from anterior and posterior. Inflation is less than indicated by Oertli (1963, pl. 6, fig. 39*b*).

INCERTAE SEDIS

? " ***Macrocypris*** " sp.

(Pl. 9, figs. 3, 4)

1940 *Macrocypris horatiana* Jones & Sherborn ; Anderson : 380, pl. 19, fig. 16.

MATERIAL. Thirteen valves and carapaces from various beds at the Bugle Pit, Hartwell. Twenty-eight valves and carapaces from various beds at Warren House Farm, Stewkley.

REMARKS. These specimens correspond closely to those of Anderson but the hinge and muscle scars were not seen.

Suborder PLATYCOPINA Sars 1866

Family **CYTHERELLIDAE** Sars 1866

Genus ***CYTHERELLOIDEA*** Alexander 1933

Cytherelloidea cf. ***paraweberi*** Oertli

(Pl. 9, figs. 1, 2)

1957 *Cytherelloidea paraweberi* Oertli : 651, pl. 1, figs. 12–15.

MATERIAL. Six valves from Bed CWE 2 and one valve from Bed CWE 3 at Long Crendon.

DESCRIPTION. A species of *Cytherelloidea* showing external and internal features characteristic of that genus but being more rectangular in outline and having a straight ventral margin. The ornament consists of a continuous ridge just anterior of and parallel to the outer margin and tending to be most prominent towards the posterior and venter. There is a slight depression situated centrally in each valve. In the females each valve also has two shallow posterior cavities internally, one postero-ventral and one postero-dorsal. The right valve has a slight groove internally round the margin of the valve which is deeper towards the dorsal and ventral.

Length of right valve from Bed CWE 2*b* Long Crendon 0·64 mm., and height 0·37 mm.

REMARKS. This species is very similar in shape and of similar age to *C. paraweberi* Oertli but differs in being not quite so long and having a slightly more arched dorsal margin and a straighter venter.

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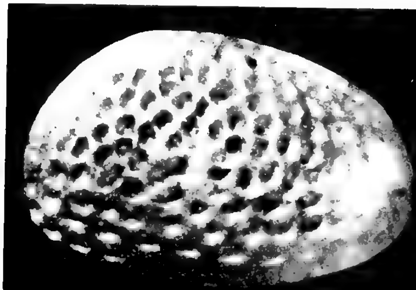
PLATE 1

Macrodentina (Dictyocythere) retirugata (Jones) p. 453

All specimens fron Houstout Cliff Bed. 6.

FIGS. 1, 3, 4. Left, right and dorsal views of female carapace, Io. 2152, length 0·79 mm.
FIGS. 2, 8. Internal and external views of female right valve, Io. 2153, length 0·70 mm.
FIGS. 5–7. Right, dorsal and left views of male carapace, Io. 2154, length 0·83 mm.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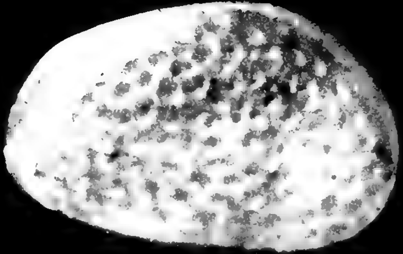
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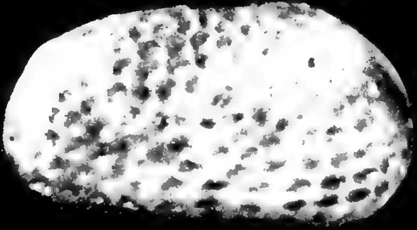
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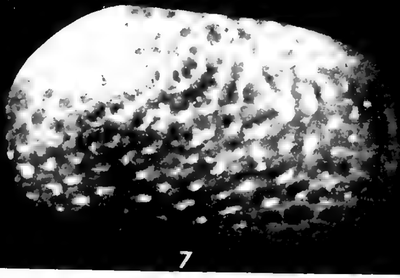
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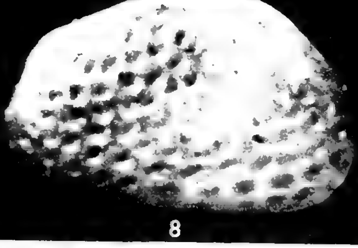
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PLATE 2

Galliaecytheridea wolburgi (Steghaus) p. 450

All specimens from Hounstout Cliff, Bed 7.

FIGS. 1, 2. Internal and external views of male left valve, Io. 2155, length 1·02 mm.
FIG. 3. Dorsal view of male carapace, Io. 2156, length 1·12 mm.
FIGS. 4, 5. Internal and external views of male right valve, Io. 2157, length 0·98 mm.
FIGS. 6–8. Left, right and dorsal views of female carapace, Io. 2158, length 0·85 mm.

Macrodentina (Macrodentina) rugulata (Jones) p. 452

All specimens from Hounstout Cliff Bed 6.

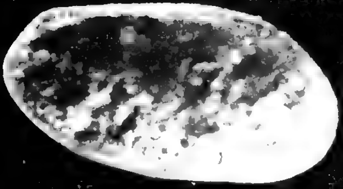
External views.

FIG. 9. Left valve, Io. 2159, length 0·72 mm.
FIG. 10. Right valve, Io. 2160, length 0·73 mm.
FIG. 11. Juvenile right valve, Io. 2161, length 0·62 mm.
FIG. 12. Juvenile right valve, Io. 2162, length 0·46 mm.

Macrodentina (Macrodentina) transiens (Jones) p. 452

Specimen from Poxwell Quarry, Bed 12.

FIGS. 13–15. Right, left and dorsal views of carapace, Io. 2163, length 0·79 mm.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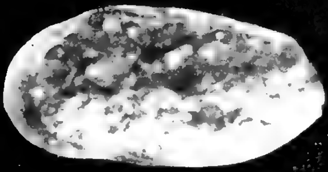
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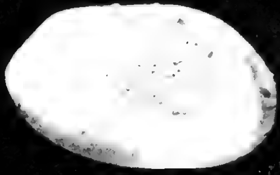
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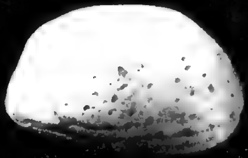
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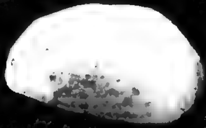
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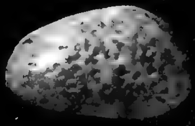
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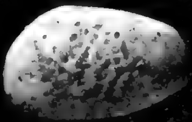
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PLATE 3

Galliaecytheridea postrotunda Oertli p. 450

All specimens from Hounstout Cliff, Bed 8.

FIGS. 1–4. Right and left views of carapace, Io.2164, length 0·66 mm.
FIGS. 2, 3, 5. Right, left and dorsal views of juvenile carapace, Io. 2165, length 0·50 mm.
FIG. 6. External view of left valve, Io. 2166, length 0·73 mm.

Cytherelloidea paraweberi Oertli p. 457

Specimen from Friar Waddon, Bed 4.

FIGS. 7–9. Right, dorsal and left views of carapace, Io.2167, length 0·68 mm.

Paracypris ? sp. p. 471

All specimens from Poxwell Quarry.

FIGS. 10, 11. Right and left views of carapace, Io. 2168, length 0·79 mm.
FIG. 12. External view of juvenile left valve, Io. 2169, length 0·64 mm.
FIG. 13. External view of left valve, Io. 2170, length 0·75 mm.


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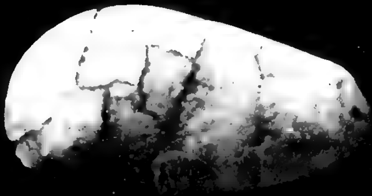
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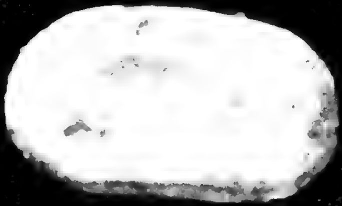
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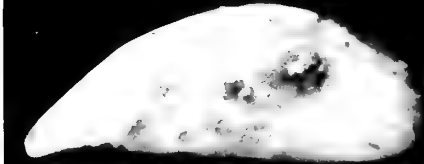
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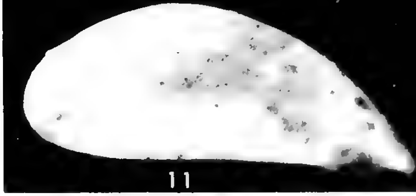
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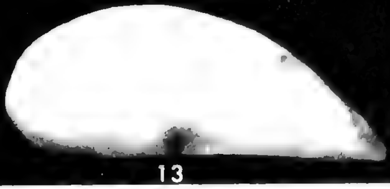
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PLATE 4

All specimens are from Poxwell Quarry, Bed 12.

Protocythere serpentina (Anderson) p. 456

FIG. 1. External view of juvenile left valve, Io. 2171, length 0·62 mm.
FIG. 3. External view of juvenile right valve, Io. 2745, length 0·50 mm.
FIGS. 4, 5. External and internal views of right valve, Io. 2746, length 0·79 mm.
FIGS. 6, 7. External and internal views of left valve, Io. 2747, length 0·83 mm.

Paraschuleridea ? eusarca (Anderson) p. 457

FIGS, 2, 8. External and internal views of left valve, Io, 2748, length 0·68 mm.
FIGS. 9, 10. External and internal views of juvenile right valve, Io. 2749, length 0·56 mm.


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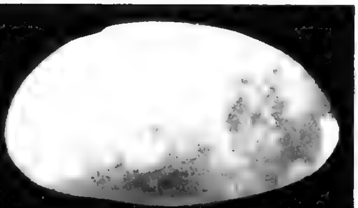
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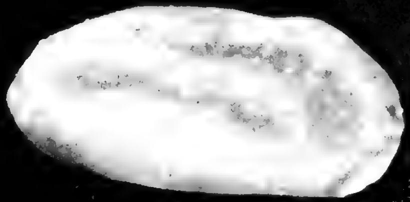
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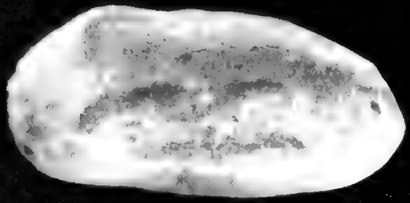
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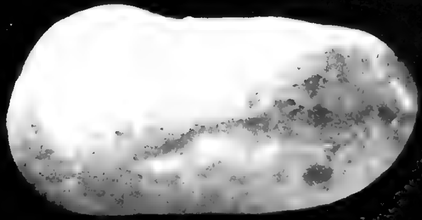
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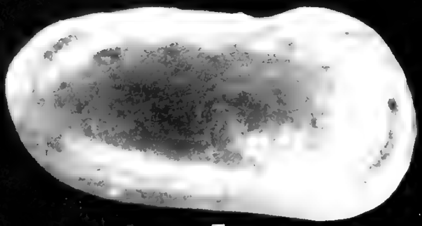
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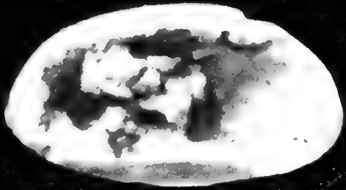
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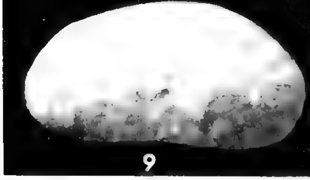
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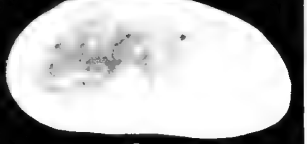
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PLATE 5

All specimens from Poxwell Quarry, Bed 12.

Procytheropteron bicosta sp. nov. p. 456

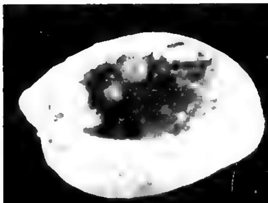
FIGS. 1, 2, 4. Internal, external and dorsal views of left valve, Io. 2750, length 0·48 mm.
FIG. 3. External view of left valve, Io. 2751, length 0·43 mm.
FIGS. 5, 6, 9. External, ventral and dorsal views of right valve, Io. 2752, length 0·54 mm.

Orthonotacythere rimosa Martin p. 454

FIG. 7. External view of right valve, Io. 2753, length 0·52 mm.
FIGS. 8, 11, 12. Right, left and dorsal views of juvenile carapace, Io. 2754, length 0·50 mm.

Orthonotacythere levis sp. nov. p. 454

FIGS. 10, 13. Internal and eternal views of left valve, Io. 2756, length 0·45 mm.
FIG. 14. External view of left valve, Io. 2755, length 0·45 mm.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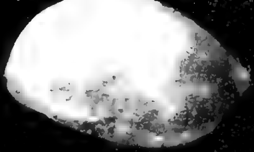
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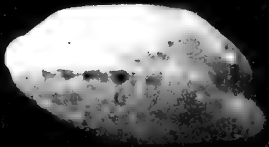
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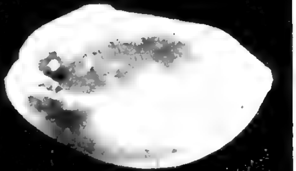
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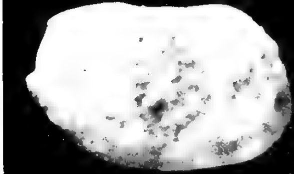
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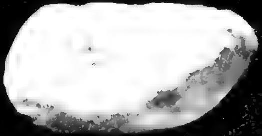
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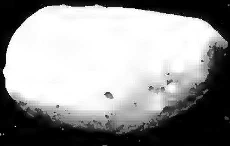
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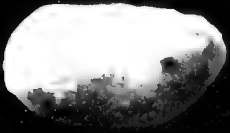
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PLATE 6

All specimens are from Hounstout Cliff, Bed 7.

Macrodentina (Polydentina) rudis Malz p. 453

FIGS. 1, 2, 5. Left, right and dorsal views of male carapace, Io. 2757, length 0·73 mm.
FIGS. 3, 4, 8. Left, right and dorsal view of female carapace, Io. 2758, length 0·66 mm.
FIGS. 6, 7. External and internal views of female left valve, Io. 2759, length 0·64 mm.

Orthonotacythere elongata sp. nov. p. 455

FIGS. 9–11. Left, dorsal and right views of carapace, Io. 2760, length 0·52 mm.


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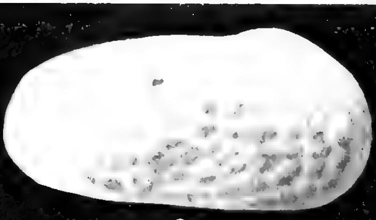
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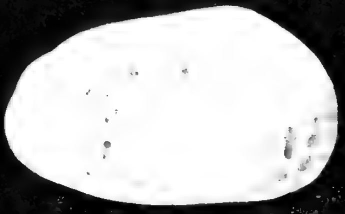
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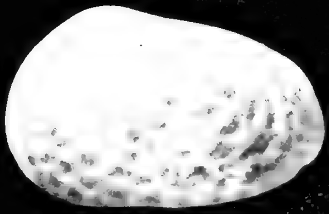
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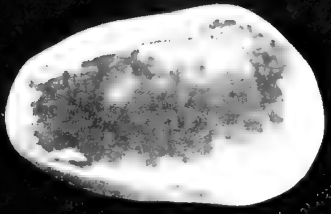
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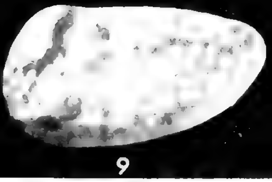
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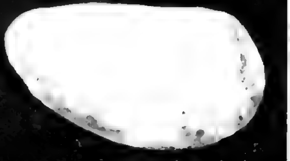
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FIGS. 1, 2. ***Cypridea dunkeri,*** carapace from Bed NWF 15, Io. 1220; length 0·97 mm. 470

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FIG. 12. External view of female right valve from Bed BP 3, Io. 2807; length 0·58 mm.

FIG. 13. Dorsal view of female carapace from Bed BP 3, Io. 1245; length 0·64 mm.

FIG. 14. Dorsal view of female carapace from Bed BP 3, Io. 2808; length 0·56 mm.

FIGS. 15, 16. ***Dicrorygma decipiens,*** left valve internal and external views from Bed BP 6, Io. 1265; length 0·41 mm. 479

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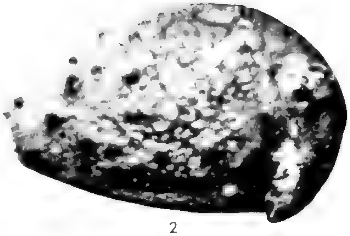
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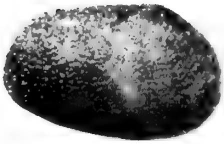
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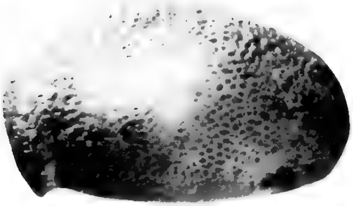
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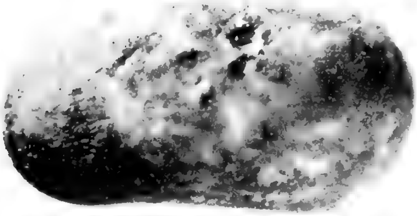
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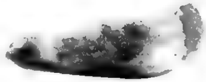
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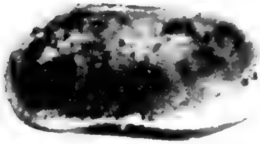
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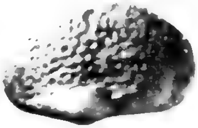
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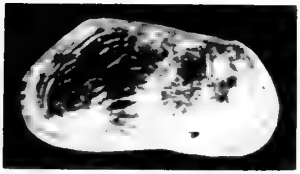
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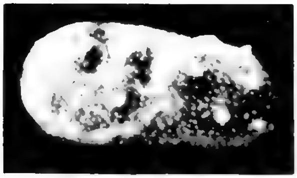
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PLATE 8

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FIGS. 1, 2, 5, 6. ***Macrodentina (Macrodentina) transiens,*** carapace, right, left, dorsal and ventral views, from Bed BP 4, Io. 1239 ; length 0·60 mm. 476

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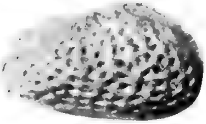
FIGS. 25, 26. Internal and external views of right valve from Bed BP 14, Io. 2230 ; length 0·45 mm.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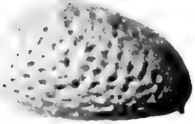
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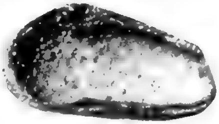
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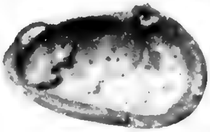
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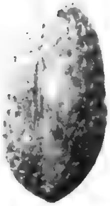
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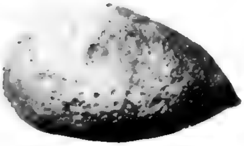
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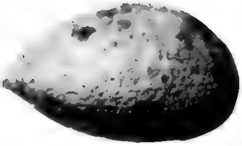
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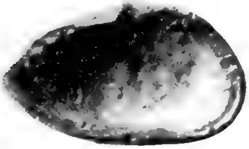
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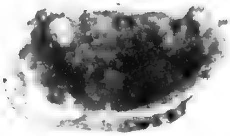
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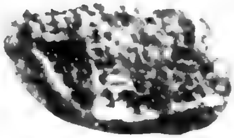
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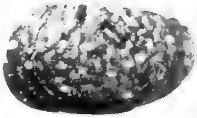
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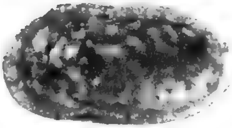
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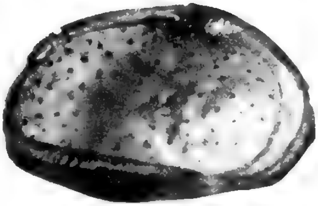
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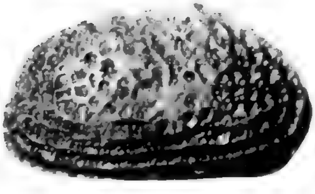
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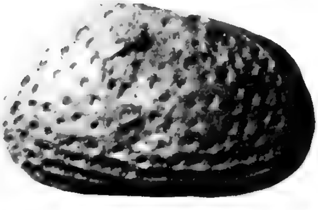
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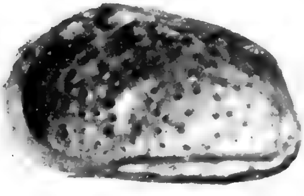
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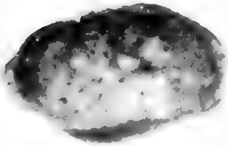
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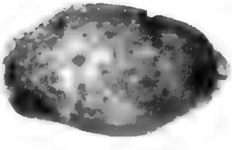
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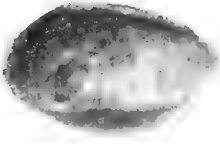
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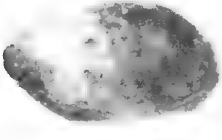
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FIGS. 1, 2. ***Cytherelloides* cf. *paraweberi*,** external and internal views, right valve from Bed CWE 2, Io. 1255; length 0·62 mm. 485

FIGS. 3, 4. **" *Macrocypris* "** ? carapace, right and dorsal views, from Bed WH 4, Io. 2232; length 0·85 mm. 484

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FIG. 7. Dorsal view of carapace from Bed BP 6*a*, Io. 1227; length 0·68 mm.

FIG. 8. ***Procytheropteron brodiei*** dorsal view of carapace from Bed BP 8, Io. 2231; length 0·47 mm. 477

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FIG. 16. Internal view of left valve Io. 1253, by transmitted light.

FIGS. 17, 18. Dorsal and ventral views of carapace from Bed BP 6*c*, Io. 1251; length 0·74 mm.

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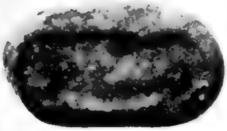
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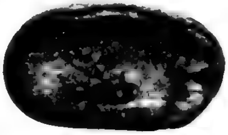
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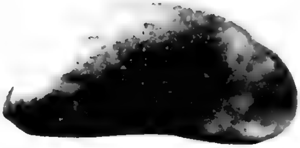
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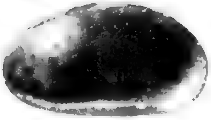
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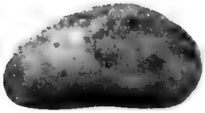
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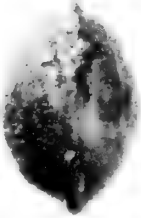
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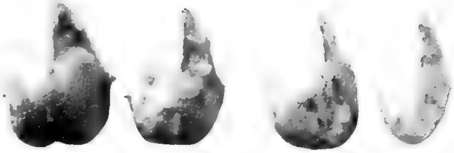
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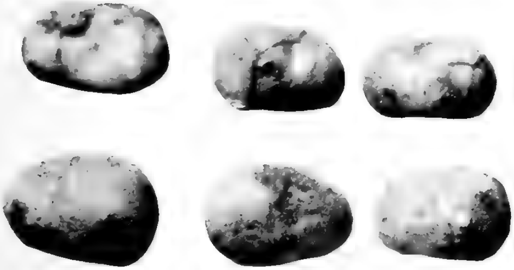
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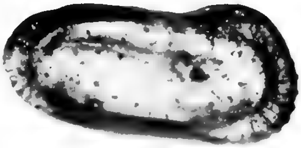
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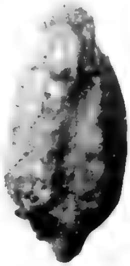
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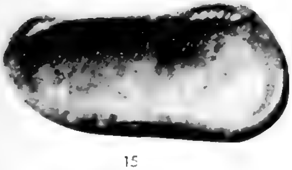
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TRILOBITES OF THE HENLLAN ASH, ARENIG SERIES, MERIONETH

H. B. WHITTINGTON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 11 No. 10
LONDON: 1966

TRILOBITES OF THE HENLLAN ASH, ARENIG SERIES, MERIONETH

BY

H. B. WHITTINGTON D.Sc.

Professor of Geology, Harvard University, Cambridge, Massachusetts, U.S.A.

Pp. 489–505 ; 5 *Plates*

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THE BRITISH MUSEUM (NATURAL HISTORY)
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TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

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TRILOBITES OF THE HENLLAN ASH, ARENIG SERIES, MERIONETH

By HARRY BLACKMORE WHITTINGTON

CONTENTS

SYNOPSIS

New collections have been made from the only beds in the type area of the Arenig Series that yield a shelly fauna. These beds are termed the Henllan (rather than *Calymene*) Ash, and the Erwent (rather than *Ogygia*) Limestone is considered to be an upper member of this Ash. The five species include two identical with, and three similar to, species recently described from *extensus* Zone beds of the Mytton Flags of West Shropshire. This fauna may be widespread in Wales, and is like faunas of similar age in southern Europe but unlike those of Sweden. One new species, *Myttonia fearnsidesi*, is described.

I INTRODUCTION AND ACKNOWLEDGMENTS

IN describing the geology of Arenig Fawr and Moel Llyfnant, Fearnsides (1905) introduced the terms Henllan or *Calymene*-Ashes and Erwent or *Ogygia*-Limestone for beds which contain the only shelly fauna known from the type area of the Arenig Series. The fossils were first listed by Salter (1853 : 57 ; *in* Ramsay 1866 : 255–257) and the most recent list is that of Fearnsides (1905 : 620), only the calymenid having been re-described in recent years.

Fearnsides gave no estimates of thickness in his stratigraphical column (1905 : 609), but from his map the combined thickness of the Henllan and Erwent beds is 200 feet at the minimum. It is clear from his account (cf. also his text-figs. 1, 2) that he regarded the Erwent Limestone as an uppermost, more calcareous part of the ashy beds, and he gives the thickness of this " highly fossiliferous band " as " not more than 10 or 12 feet" (Fearnsides 1905 : 621). It is here proposed that the Erwent Limestone be regarded as a member of the Henllan Ash, and geographical names are preferred, in conformity with recommendations of the American Commission on Stratigraphic Nomenclature (1961). The present work is on fossils collected in place, and at one locality from scree material, coming from beds which lie within the Henllan Ash outcrop as mapped by Fearnsides, and close to, if not exactly on, the outcrop of the Erwent member. On the east side of Moel Llyfnant the trilobites *Ogygiocaris?* cf. *selwyni* and *Neseuretus parvifrons*, with a species of the brachiopod *Orthis*, are abundant through about 50 feet of beds, a far greater thickness than Fearnsides gives for the Erwent Limestone. Reference of the fossils to the broader stratigraphical unit, the Henllan Ash, is thus preferred.

This investigation was carried out in connection with that of the adjacent Bala area, and some localities were visited in company with Professor Alwyn Williams and Dr. D. A. Bassett. I am indebted to my wife for her help in collecting at all the localities. Professor W. F. Whittard has kindly discussed the trilobites with me, and Mr. A. G. Brighton loaned material from the Sedgwick Museum. Miss Marjorie K. Whallon has printed the photographs from my negatives and aided in preparing the plates from them. Collections were made in 1957 during the tenure of a Guggenheim Memorial Fellowship. In 1964, funds provided by National Science Foundation grant GB–1807 enabled me to make further collections and aided in the preparation of this account.

II LOCALITIES

All lie within the area of Fearnsides' map (1905, pl. 41), on the west slopes of Arenig Fawr and the east slopes of Moel Llyfnant.

1. Sixty paces upstream from north-east to south-west trending wall, 400 yards south-south-east of Hafotty Ffilltirgerig, National Grid reference 818387. Much of the material preserved in the Sedgwick Museum is labeled as coming from this locality.
2. At and above the south end of highest wall on north-east flank of Moel Llyfnant, National Grid reference 812357. The fresh rock exposed in crags is extremely difficult to break, collecting being possible only from weathered rock and scree.
3. Weathered outcrop about 1,000 feet south of locality 2.
4. Weathered outcrop, west side of Llechwedd Erwent, National Grid reference 820346.
5. Weathered outcrop, east side of Llechwedd Erwent, short distance north of south-east trending fence, National Grid reference 826344.

III AGE AND RELATIONS OF THE TRILOBITE FAUNA

The asaphid and *Neseuretus parvifrons* are abundant at all the localities investigated, *Ampyx* aff. *salteri* occurring (quite abundantly) only at locality 1, and *Myttonia fearnsidesi* sp. nov. rarely only at locality 3. The species of *Orthis* is common, and less frequent are inarticulate brachiopods. One pelecypod valve has been found, but no cephalopods, a group stated to be abundant by Fearnsides (1905 : 620). The ash rests on beds that have yielded *Didymograptus extensus*, and is overlain by shale containing *D. hirundo* (Fearnsides 1905 : 619–622).

Whittard's (1955–64) monograph of trilobites from West Shropshire describes the following species from the Mytton Flags :

Ampyx salteri Hicks
Myttonia confusa Whittard
Neseuretus parvifrons (Salter)
Neseuretus brevisulcus Whittard
Neseuretus complanatus Whittard
Neseuretus murchisoni (Salter)
Cyclopygid
Ogygiocaris selwyni (Salter)

From the data given by Whittard it appears that most, if not all, of these species occur together at particular localities in the lower one-third of the Mytton Flags. The generic assemblage is that of the Henllan Ash, and the species are closely related or identical. Whittard (1955 : 16–17 ; 1960 : 144 ; 1964 : 236) regards the Shropshire strata as of *extensus* Zone age, and it thus appears that the Henllan Ash also belongs within this zone, an assumption also made by Whittard (1960 : 145). The occurrence in the Arenig Series of a species of *Myttonia?* in *extensus* Zone beds in Caernarvonshire (Whittard 1955 : 31), *Ampyx* in Pembrokeshire (Whittard 1955 : 17), of species of *Neseuretus* in Anglesey (*extensus* Zone, Shirley 1936 : 401–402) and Pembrokeshire (Whittard 1960 : 138–139, pl. 21, figs. 1, 2), and *Ogygiocaris? selwyni* in the Lleyn Peninsula and Ramsey Island (Whittard 1964 : 236), suggests that this fauna may be widespread in Britain.

Stubblefield (1939 : 52–53), in reviewing Arenig trilobite faunas of the Anglo-Welsh area, emphasized the absence of Scandinavian forms. In outlining faunal provinces of late Arenig time (Whittington 1963 : 18–20, text-fig. 2), I have suggested that the British faunas are like those of central and southern Europe, and that *Ampyx* is one genus common to several provinces at this time, including Britain and Scandinavia. This appears to be true of early Arenig time, for the trinucleid and *Neseuretus* represent groups unknown in Sweden (Tjernvik 1956), but present in the Montagne Noire district of southern France, according to Dr. W. T. Dean (personal communication). The affinities of the asaphid species *selwyni* are less certain (see below). To place it in *Ogygiocaris* suggests Scandinavian relations, while *Megalaspidella* is an Arenig Argentine genus which may be related to *Plesiomegalaspis* Thoral 1946, from the Montagne Noire (cf. Jaanusson *in* Moore 1959 : O347).

The relationship between Anglo-Welsh and central and southern European trilobite faunas continues through Llanvirn and Llandeilo time (Whittington 1963 : 20–21) but is modified at the beginning of the Upper Ordovician (*Nemagraptus gracilis* Zone) by the entry of Baltic elements (Whittington & Williams 1955). These elements continue to be important in younger rocks (Whittington 1962 : 12–13, 18, 21).

IV SYSTEMATIC DESCRIPTIONS

Family **TRINUCLEIDAE** Hawle & Corda 1847

Genus ***MYTTONIA*** Whittard 1955

Myttonia fearnsidesi sp. nov.

(Pl. 1, figs. 1–6)

Diagnosis. Anteriorly pits in radial rows lying between radial ridges, laterally only outer two pits in such radial sulci, inner pits irregularly arranged ; weak girder developed laterally, not anteriorly.

Description. Cephalon of width (tr.) at posterior margin about 9 mm., length (sag.) approximately 2·5 mm. Convex glabella pyriform, occipital ring not preserved in holotype, anteriorly glabella (Pl. 1, fig. 1) appears to overhang the fringe slightly. No glabellar furrows visible. Axial furrow broad beside basal part of glabella, narrowing forward. Cheek convex, no eye tubercle or reticulation preserved on external surface. Posterior border and border furrow broken on holotype. Fringe slopes gently outward and downward, exterior marginal rim broad and strongly convex, as is the posterior rim ; at genal angle these rims merge into the base of the genal spine, which is curved, has a median groove, and extends back far beyond the pygidium (Pl. 1, fig. 4). Anteriorly the upper lamella of fringe (Pl. 1, fig. 3) has pits in radial grooves between raised ridges, anterolaterally and laterally only the the outer two pits are in such grooves. This arrangement allows radii to be distinguished (as indicated in the figure) but the irregular arrangement of the pits in the inner part of the fringe anterolaterally and laterally makes the writing of a fringe-formula (Whittard 1955 : 27–29, text-fig. 3) impractical. The lower lamella is more completely preserved in the holotype (Pl. 1, figs. 5, 6) and shows the convex marginal rim, and that the pits anteriorly are situated in grooves between low radial ridges. Laterally such grooves and ridges are not evident, but a broad, smooth, gently convex area about which the fringe is flexed is suggestive of a weakly developed girder. On the upper lamella (Pl. 1, fig. 3) the pits appear to be arranged as follows. Outer row appears to bifurcate at radii 5–8, the two rows being particularly distinct in radii 8–15, while in radii 16, 19, 20, 22, 23, the outer row appears to have again doubled by bifurcation. The second row of pits from the outer margin becomes irregularly arranged after radius 7, and is conspicuous in containing very large pits laterally which lie inside the " girder " in the region of radii 15–20. The third row from the outer margin is absent in radii 0 and 1, bifurcates at radii 7–9, and beyond here consists of irregularly placed tiny pits close to the margin of the cheek lobe. The arrangement of the pits on the right side can be studied in the external mould of the lower lamella (Pl. 1, fig. 6) and radii distinguished as shown. The outermost row bifurcates at radius 5 (there appears to be an inter-radial pit between radii 5 and 6), and at radii 16, 20–22 the outermost row is seen to bifurcate again. The second row from the outer margin is developed as on the left side, the third row is clearly present in radii 1–8, being tiny and irregular beyond here, with a suggestion of bifurcation, but the preservation is poor. The arrangement of pits thus appears to be symmetrical about the midline, and in the two other known but poorly preserved cephala it seems to be similar.

Thorax of six segments, which become narrower (tr.) posteriorly, have a strongly convex axial ring and the pleurae extending out horizontally, flexed down at the margin. The pleural furrow is broad and shallow, occupying the region between the narrow marginal ridges. The pygidium has the axis rapidly tapering but reaching to the raised marginal rim, the broad border descending vertically. Three or four axial rings may be distinguished, on the pleural regions a first, and a faint second, interpleural ridge is visible.

HOLOTYPE. Counterpart moulds of entire skeleton, incomplete on right side, B.M., It. 303 (Pl. 1, figs. 1–6), locality 3.

OTHER MATERIAL. Two poorly preserved and incomplete cephala from same locality and horizon as holotype.

DISCUSSION. The strong external marginal rim on the fringe, combined with the absence of a well-developed girder and the irregular arrangement of the pits, suggest that this species belongs in *Myttonia*. In the type species (Whittard 1955 : 29–31, pl. 3, figs. 5–7) the arrangement of pits is irregular in the entire fringe, and there is no suggestion of radial ridges and sulci anteriorly or laterally. However, Professor Whittard (personal communication) informs me that he has a second species of *Myttonia*, from early Arenig beds of Shropshire, in which the outer rows of pits are arranged in radial sulci, yet there is no girder. Presumably the present species is like this undescribed form from Shropshire, and may also resemble that mentioned by Whittard (1955 : 31) from Dwyrhos Quarry, Caernarvonshire, which also occurs in early Arenig strata.

Family **RAPHIOPHORIDAE** Angelin 1854

Genus ***AMPYX*** Dalman 1827

Ampyx aff. ***salteri*** Hicks

(Pl. 2, figs. 1–6)

1905. *Ampyx Salteri* (?) or *domatus* Linn.; Fearnsides : 620.

DESCRIPTION. Cephalon triangular in outline, length (sagittal, excluding frontal spine) greater than half the width (tr.). In front of occipital furrow glabella expands forward progressively to maximum width at margin of cephalon, in front of here narrowing rapidly so that glabella projects only a short distance in front of anterior border. Frontal spine relatively short and upwardly curving, rounded in section. Impressed in the flank of the glabella are two subcircular areas (Pl. 2, figs. 1, 5), muscle areas 1p and 2p, the anterior slightly the larger. These areas are situated a short distance inward from the margin of the glabella, and the region between them and the axial furrow is not inflated. Axial furrow shallow, cheek convex with posterior border sloping steeply downward to broad border furrow, which latter narrows distally and dies out inside the genal angle. Narrow, outward-sloping border at vertical margin of anterolateral part of cheek (Pl. 2, figs. 2, 3), this border apparently becoming narrower and disappearing beneath the glabella. At genal angle borders are extended by long, backwardly-directed and slightly curving spine which reaches back far beyond the posterior margin of the pygidium. Suture normal for genus, curving over outer part of cheek and running along the margin of border (Pl. 2, fig. 3, as shown by the slight displacement of the free cheek).

Thorax of six segments, typical in form with pleural furrow deepening distally. Pygidium of length (sag.) slightly greater than half width (tr.), outline of posterolateral margins rounded, outer parts of pleural regions bent steeply down to form broad border. Axis extremely faintly defined, inner part of pleural region horizontal, first pleural furrow present, deepest distally.

MATERIAL. All from locality 1: B.M., It. 304, enrolled exoskeleton (Pl. 2, figs. 4, 5), was recovered in the present investigation, the remainder are in the W. G. Fearnsides and T. McKenny Hughes collection, SM A 41041–41054, twelve partly preserved exoskeletons and two cranidia (41049, 41053); 10344–10347, three partly complete exoskeletons and one thorax and pygidium.

DISCUSSION. The Arenig species is quite like the type, *Ampyx nasutus* (Whittington 1950: 554–556, pl. 74, figs. 3–9, text-fig. 6), particularly in the presence of the depressed muscle areas 1p and 2p in the flanks of the glabella, presence of the anterolateral border of the cheek, and outline of the pygidium. The glabella does not display an elongate, narrow (tr.), gently convex region between the axial furrow and the outer edges of the first two muscle areas. Such a region is present in the younger species *A. linleyensis* Whittard (1955: 18–21, pl. 2, figs. 1–8), *"A." costatus* Boeck (Størmer 1940: 132, pl. 2, figs. 13–18), and *A. virginiensis* (Whittington 1959: 465–473, pl. 29; pl. 30, figs. 1–14, 16, 17, 20–30; pl. 31; text-fig. 7). This area was regarded by Whittard as the ala, but as discussed earlier (Whittington 1959: 460–461) it seems more likely to be part of the true glabella.

The Arenig material is compressed and distorted, but shows a general resemblance to type material of *A. salteri* Hicks (Whittard 1940, pl. 5, fig. 8; 1955, pl. 1, fig. 15) and to material from Shropshire referred to this species by Whittard (1955: 15–18, pl. 1, figs. 16–21). It appears to differ in not displaying the gently convex anterior lateral glabellar lobe, and in that the pygidial axis is so weakly defined. Pending the description of more material from South Wales, the Arenig material is considered to be congeneric with Hicks' species, but possibly not conspecific.

Family **ASAPHIDAE** Burmeister 1843

Genus ***OGYGIOCARIS*** Angelin 1854

Ogygiocaris ? cf. ***selwyni*** (Salter)

(Pl. 2, figs. 7–12; Pl. 3; Pl. 4, fig. 16)

1905. *Ogygia Selwynii* Salter; Fearnsides: 620.

DESCRIPTION. Complete holaspides (Pl. 3, fig. 9) show the association of the parts of the exoskeleton, and the specimens range in length (sag.) from one centimetre

(Pl. 2, fig. 9) to approximately twelve centimetres. The gently convex glabella is outlined by shallow axial and preglabellar furrows, tapering forward slightly from the posterior margin to a minimum width between the eye lobes, in front of here expanding slightly. Internal moulds (Pl. 2, fig. 10) show a shallow furrow running along the posterior margin which ends in the axial furrow in a deep pit, the mould of the articulating boss. In external moulds this furrow is exceedingly faint. Approximately in line (tr.) with the anterior margin of the posterior border furrow is a small median tubercle. Faint glabellar furrows have been observed in one specimen (Pl. 3, fig. 9). Furrows 1p and 2p are lenticular depressions, equidistant from each other and the posterior margin, 2p being in line (tr.) with the posterior margin of the eye lobe. Furrow 3p is a larger depression, extending closer to the axial furrow, and in line with the anterior part of the eye lobe. Preglabellar furrow separates the glabella from a moderately wide (sag. and exs.), gently convex anterior border, which is continued around the cheek by the anterolateral and lateral border into the base of the fixigenal spine. Shallow anterior pit at intersection of axial and preglabellar furrows, border furrow on cranidium deeper than preglabellar furrow (Pl. 3, fig. 6). Eye lobe of length (exs.) approximately one-third that of cephalon; eye surface bearing many tiny facets (Pl. 2, fig. 8). The two branches of the facial suture diverge in front of the eyes at an angle exceeding 90°, and meet at the anterior margin at a very oblique angle, producing a blunt anterior point to the cranidium (Pl. 2, fig. 10). Posterior branch of suture runs outward in sigmoidal curve to cross the posterior margin at more than half the width; broad, shallow posterior border furrow dies out before reaching lateral border. Hypostome (Pl. 2, fig. 7; Pl. 3, figs. 1, 2) having gently curved anterior margin, no anterior border; lateral border with projecting shoulder, posterolaterally broader where it curves around to join the posterior border which is narrowest medially. Margin of posterior border with a sharply folded edge, the median part of which is extended dorsally in a blunt point. Anterior wing large, triangular, dorsally directed. Middle body subdivided by middle furrow into large anterior body and small, crescentic posterior body, the tips of which are inflated. The curved sutural margin of the hypostome fits into an embayment in the anterior part of the doublure (Pl. 3, fig. 2; Pl. 4, fig. 16), and the tip of the anterior wing is directed up toward the boss formed by the anterior pit. Doublure of free cheek of similar width to the border, apparently no vincular furrow or panderian opening.

Thorax (Pl. 3, figs. 9–11) of eight segments, pleural furrow broad and shallow, doublure of pleurae poorly preserved but panderian openings not observed. Pygidium (Pl. 3, figs. 3–5, 7–11) with convex axis clearly outlined by broad, shallow axial furrows, the tip prominent. The articulating furrow is distinct, and some specimens show five or six additional ring furrows but in others such ring furrows cannot be seen. The border of the pleural region is of constant width, concave upward, and the broad, shallow first pleural furrow runs out to the inner margin. Three or four additional pleural furrows, exceedingly shallow, can be made out on some specimens, on others they are not visible. The paradoublural line is strong in many specimens (perhaps as a result of compression), the doublure of the same width as the border, concave distally but becoming convex upward near the inner edge.

This edge is parallel to the margin of the pygidium, and passes around the tip of the axis. As measured along the line of the third pleural furrow, the width of the border is less than half that of the pleural region.

Terrace lines are present on the frontal glabellar lobe, the anterior cephalic border, the hypostome, the pygidium, and the doublure. These lines are in the form of raised ridges, one side of the ridge steeper than the other.

The original of Pl. 2, fig. 9 is a meraspid of degree 6, which has well marked furrows on the pygidium, six axial rings and seven pleural furrows being visible. A small cranidium (Pl. 2, figs. 11, 12) is probably a meraspid of a similar degree, and has the frontal glabellar lobe more inflated than in larger examples.

MATERIAL. Common at localities 1–5. Specimens B.M., It. 305–315. SM A 10348, internal mould of thorax and pygidium, A 10350, internal mould of cranidium, A 10351, internal mould of cranidium, A 10352–53, internal moulds of pygidia, Llechwedd Erwent; A 45293, 45294 (45296 counterpart), 45295, 45297–99, all moulds of parts of thorax and pygidium, Llechwedd Erwent; A 45317, internal mould of hypostome, Llechwedd Erwent; A 45318 (counterpart 45330), mould of entire exoskeleton, Hafotty Ffilltirgerig; 45319, counterpart moulds of exoskeleton showing hypostome, Hafotty Ffilltirgerig.

DISCUSSION. Whittard (1964 : 236) referred material in the Sedgwick Museum from Hafotty Ffilltirgerig (locality 1) to *Ogygiocaris selwyni*, and material from Llechwedd Erwent (localities 4, 5) to *O. murchisoniae*. I have examined these specimens, together with the much larger amount of material obtained from localities 2, 3 and 5, and conclude that they represent a single species. This species is like that described from the lower Arenig Series of West Shropshire by Whittard (1964 : 232–238, pl. 34, figs. 7–13; pl. 35; pl. 36, figs. 1–7; pl. 37, figs. 2–11) as *O. selwyni*. There are, however, slight differences between the two groups of specimens, for the pygidium of the Welsh material, as seen both in casts from external moulds and in internal moulds, is less furrowed than examples from West Shropshire, and has a relatively narrower doublure (compare Pl. 3, figs. 4, 5, 7, 9, 10, with Whittard 1964, pl. 37, figs. 2–11). Whittard was able to distinguish between two groups of pygidia in his material, one relatively longer than the other, but such groups cannot be distinguished in the Arenig material.

The holotype of the species *selwyni* (Whittard 1964 : 236–237, pl. 37, fig. 1) is a poorly preserved pygidium from ashes near Hengwrt uchaf, a locality about eight miles south-south-west of Llechwedd Erwent, and in early Arenig strata (Wells 1925). This pygidium is like some of those here described, but shows stronger pleural furrows, possibly as the result of distortion. A second Arenig species, from South Wales, is *murchisoniae*, the holotype being a distorted, incomplete exoskeleton (Whittard 1964 : 238–239, pl. 38, figs. 5, 6). As Whittard remarked, this is an unsatisfactorily defined species and the topotype pygidium he figures (pl. 38, fig. 7) is distorted and shows relatively strong axial and pleural furrows. Additional topotype material of both these species is required to define them more satisfactorily, and pending the collection of such material the present specimens are compared to *selwyni*. I accept Whittard's (1964 : 232) view that the earliest definition of this species is by Salter (*in* Murchison 1859).

The differences between cf. *selwyni* from Arenig, and material from West Shropshire placed in this species by Whittard, appear to be minor, and Whittard places this species in *Ogygiocaris*. If the specimens from the Henllan Ash are compared with those of the type species of *Ogygiocaris*, *O. dilatata* (Henningsmoen 1960 : 213–221, pl. 1, figs. 1–7 ; pl. 2, figs. 1–6 ; text-fig. 4), it may be seen that they differ principally in not exhibiting the deep outer part of the occipital furrow and subdivision of the occipital ring, in showing in only one specimen the glabellar furrows, and in having the pygidium far less furrowed, with a narrower doublure which does not have the inner edge scalloped. These differences appear to me to preclude the placing of cf. *selwyni* in *Ogygiocaris*., if weight is given to the pygidial characters, as Henningsmoen does. However, Whittard does not consider pygidial characters, and specifically the nature of the inner edge of the doublure, to be of such weight, and hence places *selwyni* in *Ogygiocaris*.

In considering other genera in which cf. *selwyni* might be placed I compared the Welsh species to *Megalaspidella kayseri* Kobayashi 1937, the type species of the genus, which has recently been redescribed (Harrington & Leanza 1957 : 161–164, text-figs. 74, 75). The Argentine species has the glabella tapering slightly but evenly forward, shows no glabellar furrows, and has the anterior branch of the suture running almost straight forward. In other features of the exoskeleton, including the relatively narrow doublure, the lack of furrows on the pygidium, and the shape of the hypostome it is quite like the Welsh species. If weight is given to the course of the anterior branch of the suture (as Whittard does), cf. *selwyni* cannot be placed in *Megalaspidella* (nor in *Plesiomegalaspis* Thoral, 1946, type species from the Arenig of southern France, which Jaanusson, *in* Moore 1959, considers probably congeneric with *Megalaspidella*). I have adopted the compromise of placing cf. *selwyni* in *Ogygiocaris*? The present case illustrates well the problems of asaphid systematics, and the wide differences of opinion that exist (cf. Whittard 1964 : 231–232, 245, 255).

Family **CALYMENIDAE** Edwards 1840

Genus ***NESEURETUS*** Hicks 1873

Discussion. The argument by Whittard (1960 : 138–139) for the use of this name rather than *Synhomalonotus* is here accepted. New evidence from the present specimens supports the view expressed by Whittard (1960 : 140–141) that *Neseuretus* is a calymenid and not a homalonotid. The cephalic border of *Neseuretus* (Pl. 5, figs. 5, 6, 8, 10) is rolled under so that the inner edge is close to the dorsal exoskeleton, as in *Flexicalymene* (Evitt & Whittington 1953, pl. 9, figs. 1–6), and the rostral, connective and hypostomal sutures are so situated that the rostral plate in *Neseuretus* is extremely like that of *Flexicalymene*. The hypostome is unlike those known of such other calymenids as *Flexicalymene* (Evitt & Whittington 1953, pl. 9, figs. 8–10) or *Platycalymene* (Whittard 1960, pl. 21, fig. 9) in possessing the trapezoidal extension of the anterior border. However, the anterior wing, middle body, lateral and posterior borders are quite like those of known calymenids, except that the posterior border is not notched. Apart from the unique anterior extension of the border, the hypostome of *Neseuretus* is also like that of *Bavarilla hofensis* (Sdzuy 1955, pl. 6, figs. 50, 51), a genus which Sdzuy placed in Calymenidae, but later (1957) removed to the Homalonotidae. At this early stage in their evolution, it is difficult to decide whether particular genera are calymenids or homalonotids, and it would seem best to regard them as belonging to one family, here considered to be Calymenidae. The thorax and pygidium of *Neseuretus* (Pl. 5, figs. 1–4) are like those of younger calymenids such as *Pharostoma* (Whittard 1960, pl. 18, figs. 2–4, 8), *Platycalymene* (Shirley 1931, pl. 1, figs. 8, 10) and *Flexicalymene* (Shirley 1931, pl. 1, fig. 15 ; Whittington 1965, pl. 16, figs. 14–17 ; pl. 18, figs. 1–5) in the convexity of the axial ring (the distal inflation well seen on the inner surface but not apparent on the external surface), the broad, deep pleural furrow, the convex posterior band and the sharp downturn of the pleurae at the fulcrum. Just inside the fulcrum there is an oblique angulation in the outline of the posterior margin of the pleurae. Interpleural furrows are present distally on the pygidium (Pl. 4, figs. 9–13), the doublure narrow and curled under. These features of thorax and pygidium are not like those of Ordovician homalonotids (Whittard 1961, pl. 22, figs. 8–19 ; Dean 1961, pl. 54, fig. 3 ; pl. 55, figs. 1, 3–5, 7–10, 12–14). Considering the evidence reviewed by Whittard (1960 : 140–141), and that added here, I conclude that *Neseuretus* is best regarded as a calymenid possessing an unusual hypostome, the relatively long (sag. and exs.) preglabellar area being associated with the unusual forward extension of the anterior hypostomal border.

In the Tremadoc and Arenig are the genera *Bavarilla, Neseuretus, Pharostoma, Pharostomina,* and *Bathycheilus,* and it appears to be from this group of genera that evolutionary lines lead to later calymenids and homalonotids. Among younger calymenids *Neseuretus* is distinguished from *Platycalymene* (Llanvirn-Caradoc) by the relatively shorter glabella, much weaker 3p glabellar furrows, and the longer preglabellar area. The forked hypostome of *Platycalymene,* with the convex macula is also distinctive. *Flexicalymene* (Llandeilo-Ashgill) differs from *Neseuretus* in lacking the extended anterior border of the hypostome, the posterior border of which is forked, in the rounded outline of the 2p and 3p glabellar lobes which are separated from the median lobes by shallow furrows, the relatively shorter preglabellar area, and the relatively narrower pygidium.

Neseuretus parvifrons (M'Coy)

(Pl. 4, figs. 1–13 ; Pl. 5, figs. 1–10)

1851. *Calymene parvifrons* M'Coy : 167, pl. 1F, figs. 7, 7*a*.
1852. *Calymene parvifrons* M'Coy ; Salter : iii, pl. 1F, figs. 7, 7*a*.
1905. *Calymene parvifrons* M'Coy ; Fearnsides : 620.
1931. *Synhomalonotus parvifrons* (M'Coy) Shirley : 10–14, pl. 1, figs. 1–4.
1960. *Neseuretus parvifrons* (M'Coy) Whittard : 142–146, pl. 19, figs. 1–6.

DESCRIPTION. A much more complete synonomy is given by Whittard, but I differ from him and other authors in attributing the species to M'Coy. His description, in Sedgwick & M'Coy (1851–1855), was published in 1851 in the first fascicule. Although M'Coy attributed the species to Salter, Salter's description was not published until 1852, in the appendix to the second fascicule. This procedure in dealing with those species first described in Fascicule I by M'Coy, and later by Salter in Appendix A, follows that adopted by Dean (1961 : 324, 346).

The following notes are in amplification of Whittard's description. Entire exoskeletons have been collected, and the largest cephalon is approximately 35 mm. in breadth (tr.). Faint glabellar furrows 3p are present on casts from external moulds (Pl. 4, figs. 1, 3, 7) and are " perched ", i.e. they commence a short distance in from the axial furrow. The preglabellar area (anterior area of Whittard) is convex transversely, most strongly so near the anterior margin, where it is widest. Longitudinally the profile may be almost horizontal (Pl. 4, fig. 6) or downward curving (Pl. 4, fig. 4), and in some specimens it appears to curve very slightly upward. Many specimens show a faint change in slope near to the anterior margin, but there is no distinct anterior border or border furrow. The openings of relatively large canals through the exoskeleton are visible along the anterior margin (Pl. 4, fig. 8). The paraglabellar area has not been observed in casts from external moulds, but is faintly visible in some internal moulds as a semi-circular area, set off by a slight change in slope from the inner posterior corner of the cheek. The cephalic border (Pl. 4, fig. 3) becomes defined laterally by a shallow border furrow, and is wider and more distinct on the anterior part of the cheek. On the cranidium the border furrow curves inward and backward (the " anterior furrow " of Whittard), becoming shallower as it approaches the junction of the axial and preglabellar furrows, to which it is connected by a broad, shallow depression. The area between these furrows, here called the preglabellar area (" anterior area " of Whittard), thus appears to be composed in large part by the anterior border. Ventral views (Pl. 5, figs. 5, 6, 10) show the curled-under doublure, which is flattened on the ventral-facing and inward facing slopes. The inner edge of the doublure lies close beneath the border furrow in the dorsal exoskeleton. The rostral suture runs along the outer edge of the margin, the connective sutures run inward at an oblique angle to each other across the ventral-facing part of the doublure, on the inward-facing part they curve and diverge slightly. The rostral plate is thus axe-shaped in outline, and divided by a sharp flexure into two parts. It is extremely like the rostral plate of *Flexicalymene* (Evitt & Whittington 1953, pl. 9, figs. 1–6). Hypostome (Pl. 5, figs. 5, 8) with middle body oval in outline, surrounded by narrow lateral and posterior borders. Anterior border extended laterally into the anterior wings, and anteriorly as a flat plate, subtrapezoidal in outline, that extends beneath the posterior part of the preglabellar area, the curved anterior margin (hypostomal suture) lying against the margin of the rostral plate (Pl. 5, figs. 6, 10). The anterior wing is rectangular in ventral aspect, and extends beneath the boss formed by the anterior (hypostomal) pit. The middle body is of length (sag.) slightly greater than width, divided by a deep middle furrow which runs a short distance backward and slightly inward, and is situated opposite the shoulder. The anterior lobe is thus smaller than the posterior, both lobes being gently inflated. Lateral border furrow shallow beside and behind shoulder, deepening posteriorly and forming a smooth curve with the posterior border furrow. Posterolateral margin of borders obliquely angulate.

Thorax of thirteen segments, axis approximately one-third total width. Articulating furrow deepens distally, this deepening helping to give the distal part of the axial ring a lobate, inflated appearance in the internal mould (Pl. 5, fig. 2). On the external surface this appearance is much less conspicuous (Pl. 5, fig. 3). Pleural furrow deep, narrow, running slightly diagonally backward to beyond the fulcrum, the posterior band convex, the outer part of the pleura broadly facetted, the tip broad and rounded. About half way across the inner part of the pleura there is a distinct angulation in the posterior margin, so that outside here the margin of the pleura runs more strongly outward and backward to the curved, backwardly directed tip (Pl. 5, figs. 3, 4). Four or five axial rings are clearly outlined on the pygidium, beyond the fifth ring the axis is slightly distended, then the most posterior portion is narrower, and parallel-sided where it runs down the steep posterior slope (Pl. 4, figs. 9–11). Pleural regions divided by six pleural furrows, interpleural furrows are present distally on the first three pleurae, but extend from the axial furrow to the margin on succeeding pleurae. Doublure is narrow and curled under (Pl. 4, figs. 12, 13). During enrollment the outermost parts of the pleural regions of the pygidium, and the tip of the axis, lay against the vertical, inward-facing part of the cephalic doublure (Pl. 5, fig. 6). The concave face of the posterior part of the rostral plate forms a recess, which received the convex tip of the pygidial axis (Pl. 4, figs. 9, 11).

HOLOTYPE. SM A 9570, internal mould of incomplete cranidium (Whittard 1960 : 145, pl. 19, figs. 1, 2), from Taihirion, north-west of Arenig Fawr, National Grid Reference 811397. Salter (1853 : 57) describes this locality as " under the trap and volcanic ash beds of Arenig bach ", implying that it lay within the band of Henllan Ash shown running north of Taihirion on Fearnsides' map (1905, pl. 41). No new collections have been made hereabouts, but there seems no doubt that the material described above is conspecific with the holotype.

OTHER MATERIAL. Common at localities 1–5. Figured specimens B.M., It. 316–324. SM A 9571 (Shirley 1931, pl. 1, fig. 3 ; Whittard 1960, pl. 19, fig. 3), 45684 (Whittard 1960, pl. 19, fig. 4), 9572–75, 45337–38, 45679–83, from Hafotty Ffilltirgerig ; 45635–45643, from Llechwedd Erwent.

DISCUSSION. Smaller than any cranidia of *Neseuretus* described by Whittard are two from locality 2 and one from locality 3. The original of Pl. 5, fig. 7, is a partial and disarticulated exoskeleton, but ten thoracic segments may be seen, so that cranidia of this size may be late meraspides. The cranidium appears relatively more convex than larger ones (compare Pl. 5, figs. 7, 9, with Pl. 4, figs. 1, 3, 7) and the axial, preglabellar, and anterior furrows thus relatively deeper. A granulation is present on the external surface, and the palpebral lobe is relatively large—the anterior margin almost in line with the anterior margin of the glabella, the posterior margin opposite the outer end of lateral glabellar furrow 1p.

Whittard (1960 : 145) distinguished four species of *Neseuretus* coming from the same beds in the Mytton Flags. His main criterion for *N. parvifrons* is that there is no border furrow in the preglabellar area, rather that it slopes evenly downward to the margin. As indicated in the above description, an extremely faint border furrow, or slight change in slope, is present in some specimens in the present collection. In *N. brevisulcus* Whittard (1960 : 146–147, pl. 19, figs. 7–14) such a border furrow and border are present, but the distinctness of these features varies (cf. Whittard's figures 7 and 13). The distortion of the Arenig material militates against making slight distinctions between specimens, but none in my collection appears to be as flat in profile as the holotype of Whittard's *N. complanatus* (compare Pl. 4, figs. 6, 7, with Whittard 1960, pl. 20, figs. 4, 5). *N. murchisoni* (Whittard 1960 : 148–150, pl. 20, figs. 6–15 ; pl. 21, figs. 1, 2) has the border clearly defined and also upturned, and rare specimens in the present collections appear to be of this type and are described below. Thus two of the species recognized by Whittard are also present in the Arenig area.

Shirley's (1936 : 401–402, pl. 29, figs. 1–4) species *N. monensis* is from the early Arenig of Anglesey, and is distinguished by having the palpebral lobes situated in line with glabellar lobes 2p. This position is apparently more posterior than that in *N. parvifrons*, but this distinction is slight in view of the distortion of the material and the few fragmentary specimens of *N. monensis* known.

Neseuretus murchisoni (Salter)

(Pl. 4, figs. 14, 15, 17–19)

1865. *Calymene parvifrons* var. *Murchisoni* Salter : 102, pl. 9, figs. 26–28.

Description. Only the cranidium has been recognized, and it agrees well with those described by Whittard (1960 : 148–150, pl. 20, figs. 6–15 ; pl. 21, figs. 1, 2) from the lower Arenig of West Shropshire. The glabella has the frontal lobe relatively wider and more inflated than in *N. parvifrons*, giving a less forwardly tapering appearance. The preglabellar area is markedly inflated, separated by the border furrow from the inflated, inner anterior corner of the cheek, and the anterior part of the area is abruptly flexed to form an upwardly and forwardly projecting border. At the margin of this border the exoskeleton curves over and extends backward and downward to the rostral suture—this suture being situated a short distance down the ventral side of the border (Pl. 4, fig. 14). This contrasts with the condition in *N. parvifrons* (Pl. 4, fig. 3), in which the rostral suture runs along the margin of the preglabellar area. The palpebral lobe is relatively high, rising higher than the mid-part of the glabella, and on the inner side slopes steeply down to the axial furrow. In *N. parvifrons* the palpebral lobe is relatively farther out from the axial furrow, is not so high and the slope into the axial furrow less steep.

Material. From locality 2 forty-seven cranidia are of *parvifrons* type, only one being referrable to *murchisoni* ; at locality 3 the corresponding figures are 8 and 1 ; one cranidium has been recovered from locality 4, and one from locality 5. This appears, therefore, to be a relatively rare but widespread species.

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EXPLANATION OF PLATES

A light coating of ammonium chloride was applied to the specimens before taking the photographs. Numbers of specimens in the British Museum (Natural History), London, are prefixed by the letters B.M., It., those in the Sedgwick Museum, Cambridge, with the letters SM A.

PLATE 1

Myttonia fearnsidesi sp. nov.

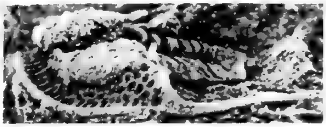
Counterpart moulds of exoskeleton, locality 3. Holotype. B.M., It. 303.

FIGS. 1–4. Latex cast from external mould, left lateral, anterior views, × 6; oblique view, × 12; dorsal view, × 6.

FIG. 5. Latex cast of external mould of ventral surface, exterior view, × 6.

FIG. 6. Mould of ventral surface (including lower lamella of fringe) of exoskeleton, exterior view, × 12.

Radial rows of pits are numbered from the sagittal line (0) outward.



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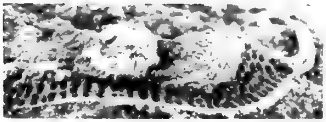

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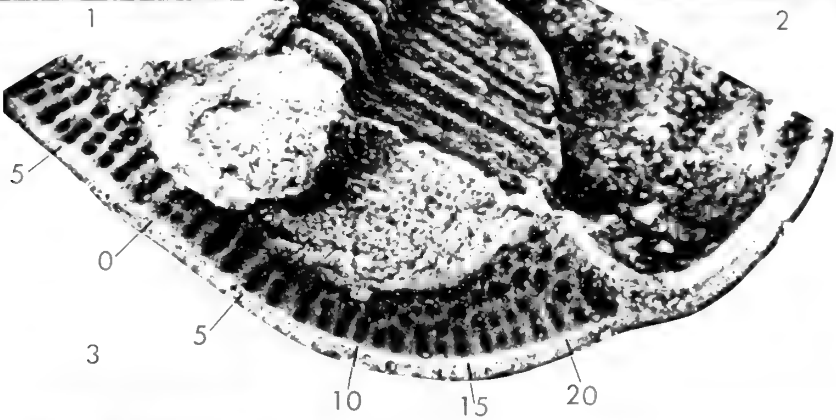

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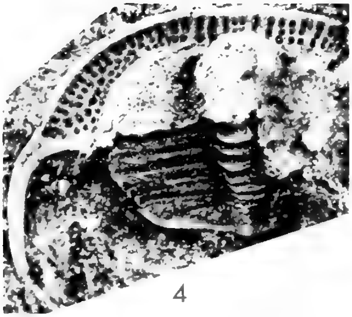

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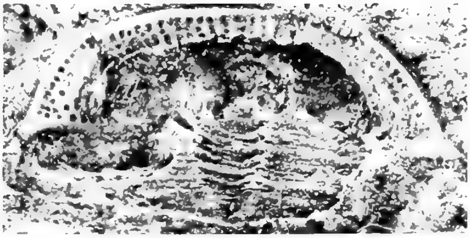

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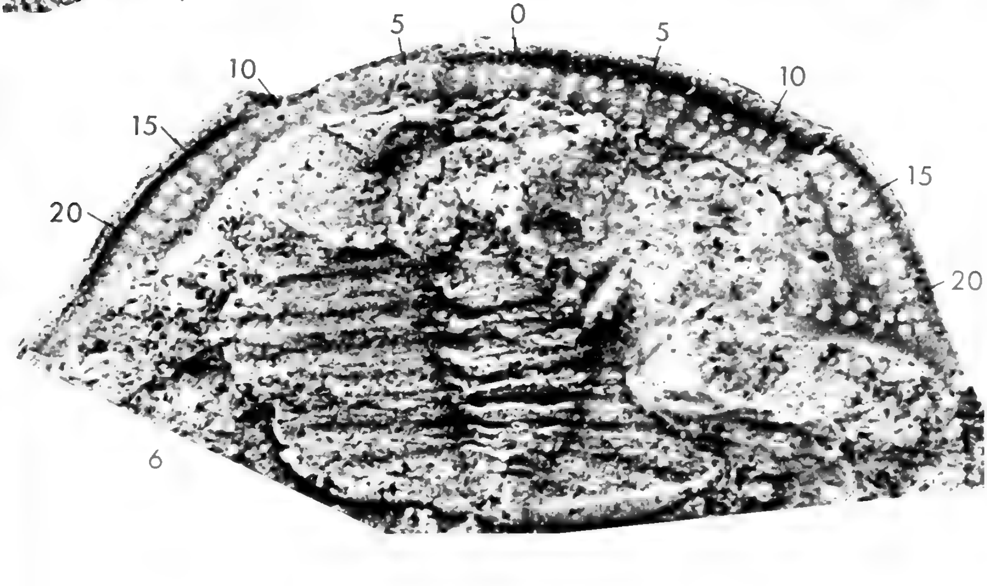

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PLATE 2

Ampyx aff. ***salteri*** Hicks

FIGS. 1–3. Cast of external mould of partial exoskeleton, dorsal, anterior, left lateral views, ×3. SM A 41050. Locality 1.

FIGS. 4, 5. Internal mould of exoskeleton, probably enrolled, showing frontal glabellar and right genal spines, right lateral, dorsal views, ×3. B.M., It. 304. Locality 1.

FIG. 6. Internal mould of extended exoskeleton, dorsal view, ×3. SM A 41044. Locality 1.

Ogygiocaris ? cf. ***selwyni*** (Salter)

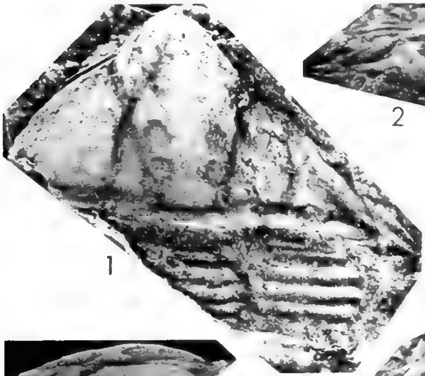
FIG. 7. Latex cast of external mould of hypostome, exterior view, ×4·5. Locality 4. B.M., It. 305.

FIG. 8. Internal mould of surface of eye lobe, exterior view, showing facets, ×9. B.M., It. 306. Locality 3.

FIG. 9. External mould of meraspid degree 6 exoskeleton, exterior view, ×6. B.M., It. 307. Locality 2.

FIG. 10. Incomplete internal mould of cranidium, dorsal view, ×1·7. B.M., It. 308. Locality 3.

FIGS. 11, 12. Internal mould of small (probably meraspid) cranidium, showing inflated frontal lobe of glabella, dorsal, anterior views, ×3. B.M., It. 309. Locality 2.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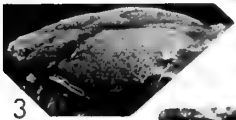
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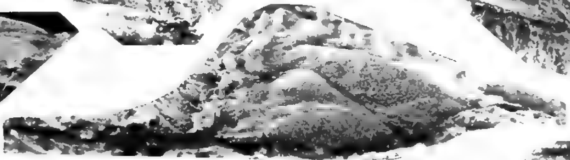
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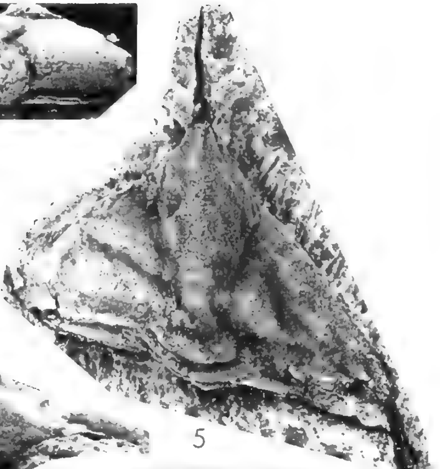
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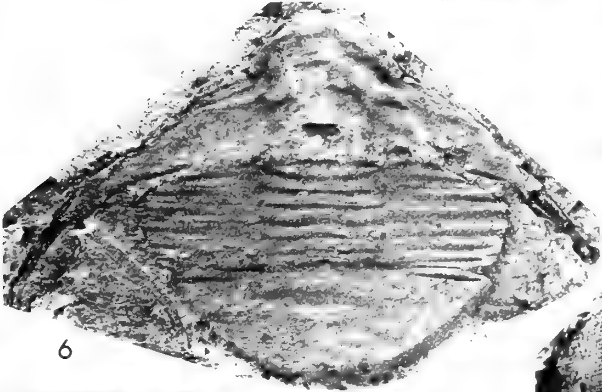
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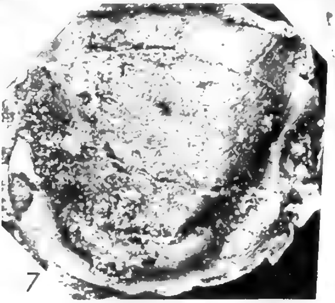
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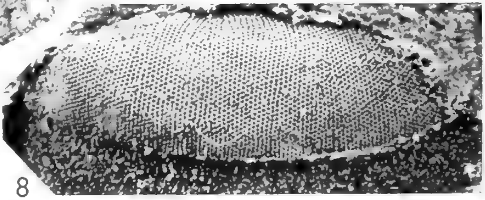
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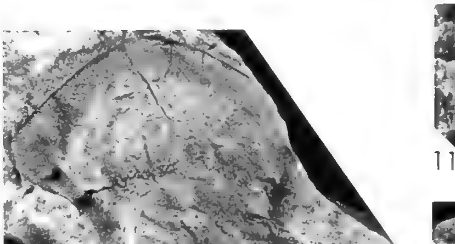
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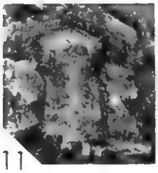
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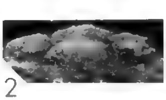
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PLATE 3

Ogygiocaris ? cf. ***selwyni*** (Salter)

FIG. 1. Internal mould of hypostome, exterior view, ×4·5. B.M., It. 310. Locality 5.

FIG. 2. Internal mould of hypostome and adjacent parts of free cheeks, exterior view, ×4·5. B.M., It. 311. Locality 4.

FIGS. 3, 5. Internal mould of pygidium showing ventral surface of doublure, right lateral, dorsal views, ×3. B.M., It. 312. Locality 2.

FIG. 4. Latex cast of external mould of incomplete pygidium, showing grooves in external surface, dorsal view, ×3. B.M., It. 313. Locality 2.

FIG. 6. Latex cast of external mould of frontal lobe of glabella and adjacent part of cranidium, dorsal view, showing lines on external surface and anterior pit, ×4·5. B.M., It. 314. Locality 2.

FIGS. 7, 8. Latex cast of external mould of two thoracic segments and pygidium, dorsal, right lateral views, ×1·7. SM A 45296. Llechwedd Erwent.

FIG. 9. Internal mould of entire exoskeleton, dorsal view, showing glabellar furrows, ×1·7. SM A 45318. Locality 1.

FIGS. 10, 11. Internal mould of thorax and pygidium, dorsal, right lateral views, ×2. SM A 45293. Llechwedd Erwent.


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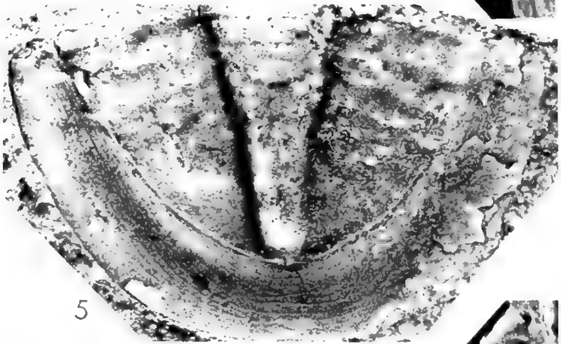
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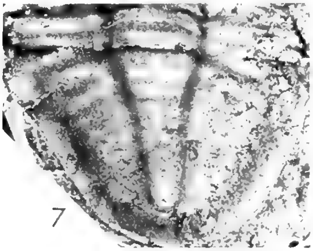
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PLATE 4

Neseuretus parvifrons (M'Coy)

FIGS. 1, 2, 4, 8. Latex cast of external mould of incomplete cranidium, dorsal, anterior, right lateral views, ×3; anterior view of margin of preglabellar area showing canals, ×9. B.M., It. 316. Locality 2.

FIG. 3. Latex cast of external mould of incomplete cephalon, dorsal view, showing course of facial and rostral sutures along which the exoskeletal parts are slightly displaced, ×3. B.M., It. 317. Locality 2. The median depression in the anterior margin of the preglabellar area of the cranidium is an accidental feature of the cast.

FIGS. 5, 6, 7. Latex cast of external mould of incomplete cranidium, anterior, right lateral, dorsal views, showing flattened profile and almost horizontally extending preglabellar area, ×3. B.M., It. 318. Locality 2.

FIGS. 9–11. Latex cast of external mould of pygidium, dorsal, posterior, right lateral views, ×4·5. B.M., It. 319. Locality 3.

FIGS. 12, 13. Internal mould of posterior thoracic segments and pygidium, right lateral, posterior views, showing narrow, curled doublure, ×3. B.M., It. 320. Locality 2.

Neseuretus murchisoni (Salter)

FIGS. 14, 19. Latex cast of external mould of incomplete and distorted cranidium, anterior, dorsal views, ×3. B.M., It. 326. Locality 5. Anterior view shows that rostral suture crosses downward-facing surface of border, a short distance from the margin.

FIGS. 15, 17, 18. Latex cast of external mould of incomplete and distorted cranidium, right lateral, oblique, dorsal views, ×4·5. B.M., It. 325. Locality 2.

Ogygiocaris ? cf. *selwyni* (Salter)

FIG. 16. Latex cast of external mould of ventral surface of free cheek, ventral view, showing doublure, emargination along hypostomal suture, and median suture, ×3. B.M., It. 315. Locality 2.


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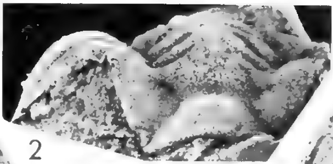
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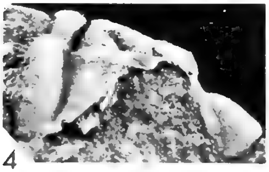
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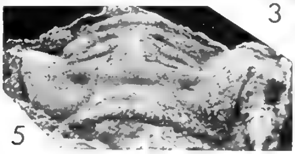
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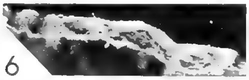
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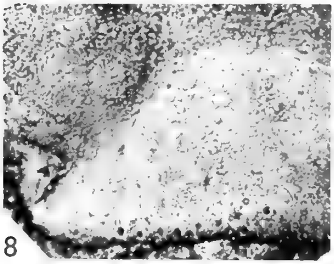
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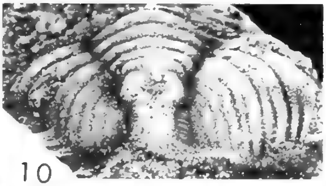
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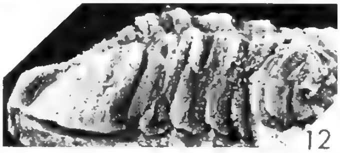
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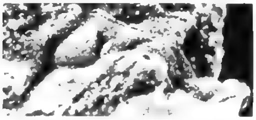
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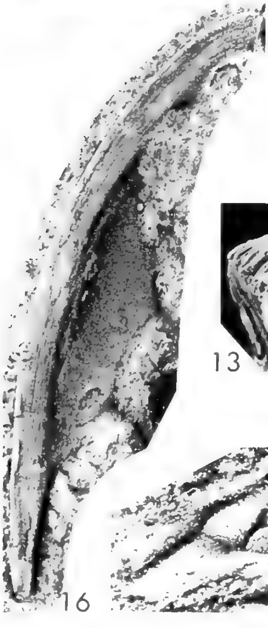
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PLATE 5

Neseuretus parvifrons (M'Coy)

FIGS. 1–4. Counterpart moulds of partial exoskeleton; 1, 2, internal mould, left lateral, dorsal views; 3, 4, latex cast of external mould, dorsal, oblique views, ×3. B.M., It. 321. Locality 5.

FIGS. 5, 6, 8, 10. Latex casts from moulds of ventral surface of exoskeleton, including that of doublure and hypostome; 6, 10, ventral and oblique views before the hypostome was entirely excavated; 5, 8, ventral and oblique views after excavation of the hypostome, ×4·5. B.M., It. 322. Locality 2.

FIG. 7. Latex cast of disarticulated exoskeleton of meraspid, dorsal view, ×6. B.M., It. 323. Locality 2.

FIG. 9. Internal mould of cranidium of small, probably meraspid, cranidium, dorsal view, ×6. B.M., It. 324. Locality 2.


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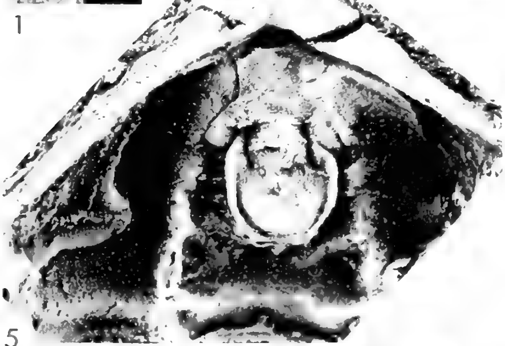
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