TEREBRATULACEA FROM THE CRETACEOUS SHENLEY LIMESTONE

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ABSTRACT. The Lower Albian Shenley Limestone occurs very locally in Bedfordshire, England. The environment of deposition is discussed and it is shown that the rich brachiopod fauna is preserved as slightly disturbed life-assemblages. Terebratulacean hinge plates are shown to consist, in general, of two parts, here called 'primary' and 'secondary' hinge plates; hinge plate terminology is revised. A calcareous structure attached to the dorsal side of the brachidium is described for the first time and named the 'sub-loop skirt'. Systematic descriptions are given of four genera, six species, and two subspecies. Two genera are new: *Boubeithyris* and *Walkerithyris*. Four species and the two subspecies are new: *B. buzzardensis*, *W. mendax*, *Rectithyris shenleyensis*, *R. shenleyensis heathensis*, *Platythyris diversa*, and *P. diversa rubicunda*. The Shenley Limestone terebratulacean fauna is demonstrated to be in many respects transitional between the Aptian and Cenomanian faunas.

THE Lower Albian (Cretaceous) Shenley Limestone of Bedfordshire, England, contains a rich and diverse fauna of which brachiopods are a major part. The Terebratulacea are particularly important as they represent practically the entire known English Albian terebratulacean fauna. In other English Albian beds, the Gault and Upper Greensand, Terebratulacea are sparse, and although the Red Chalk contains a considerable number of brachiopods they represent few species.

The stratigraphical and evolutionary position of the Shenley Limestone Terebratulacea has caused some controversy in the past. Lamplugh and Walker (1903) described the then newly discovered Shenley Limestone fauna and compared it with the Belgian Tourtia fauna described by d'Archiac (1847). The superficial similarity between the two led Kitchin and Pringle (1920) to their 'overturn hypothesis' in which they attempted to show that the limestone bed was of Cenomanian age and that the succession at Shenley was inverted. Lamplugh (1922), however, showed that the bed was of Albian age and this has since been confirmed by ammonite evidence (Wright and Wright 1947). Since the brief description by Lamplugh and Walker (1903) the Terebratulacea of the Shenley Limestone have not been systematically described and there remains a gap in our knowledge of the English Cretaceous Terebratulacea between the work of Middlemiss (1959) on the Aptian fauna and the work of Sahni (1929) on the Chalk fauna. The absence of modern work on the Albian Terebratulacea is more noticeable because E. F. Owen has described other brachiopod groups (1959, 1962, 1963; Owen and Thurrell 1968).

The species described in this paper are all from the Shenley Limestone except *Platythyris capillata* (d'Archiac) from the Tourtia of Belgium and *P. diversa rubicunda* sp. nov. from the Red Chalk, which are included for completeness. In addition to the described species, others occur uncommonly in the Shenley Limestone, but the available material is considered insufficient for a systematic description. A few specimens of a species of *Sellithyris* have been found which is similar in external features to *S. sella* from the English Aptian and has similar internal structure.

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Lamplugh and Walker (1903) figured a biplicate terebratulid from the Shenley Limestone as *Terebratula biplicata* var. *dutempleana*. This probably represents an undescribed species of *Rectithyris*. They also referred some 'giant' terebratulids from the Shenley Limestone to *T. biplicata* Sowerby as the variety *gigantea*. The external and internal structures of these specimens suggest that they are in fact unusually large gerontic individuals of the Shenley species of *Rectithyris*.

The material studied is from the collections of the British Museum (Natural History) (BM) supplemented by the authors' own collecting. The collections at the Sedgwick Museum, Cambridge (SM), and the Institute of Geological Sciences, London (GSM), were also consulted, and material was obtained from the Natural History Museum in Brussels.

The techniques of serial grinding with a Croft grinder, supplemented by some dissection with mounted needles and a dental drill, were used to study the internal structures of the brachiopods. The serially ground surfaces of specimens were recorded on acetate peels which were then drawn and photographed with the aid of a Shadomaster projection apparatus. The internal structure of the brachiopods is represented by drawings of transverse serial sections, which usually represent only the brachial valve so that more details of hinge plate structure can be shown. All measurements given in the systematic descriptions are in millimetres (mm).

STRATIGRAPHICAL AND PALAEOECOLOGICAL BACKGROUND

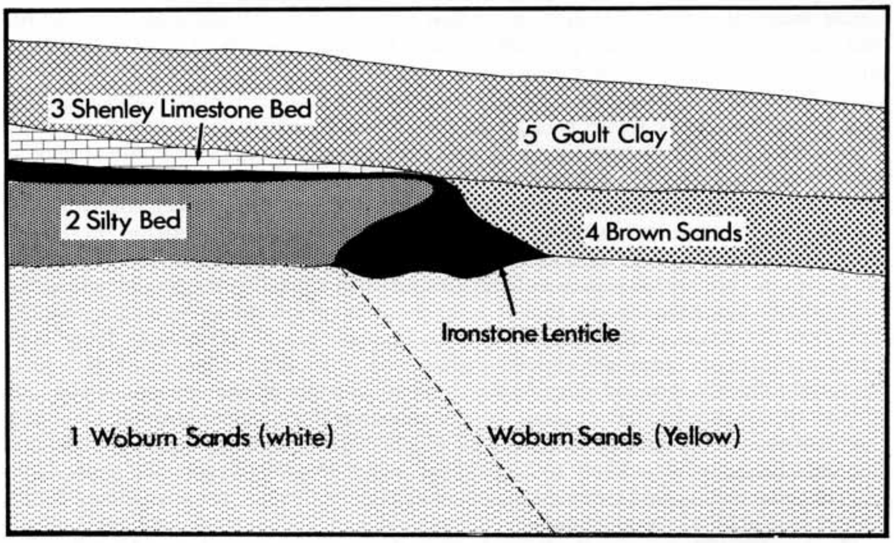
The Shenley Limestone occurs as part of a condensed bed of variable thickness, which lies at the base of the Gault, within the *regularis* Subzone of the *Leymeriella tardefurcata* Zone of the Lower Albian (Wright and Wright 1947). The bed is developed only in the region of Shenley Hill, approximately two miles (1·25 km) NW. of Leighton Buzzard, Bedfordshire. In this area the Woburn Sands (Aptian, at least in part) (Bed 1, text-fig. 1) are exploited for glass sands, and there are numerous pits which expose the base of the Gault. In the past the Shenley Limestone was more exposed than at present, and Lamplugh and Walker (1903) and Lamplugh (1922) described the exposures in some detail. Between 1963 and 1966 the limestone was exposed only in Mundays Hill pit (grid. ref. SP 940279) from which Cox made most of her observations and collections.

The stratigraphical relationship between the Shenley Limestone and other English Albian beds, especially its relationship with the nodule beds at the base of the Gault SE. of Shenley Hill, has been extensively investigated by several authors including Lamplugh and Walker (1903), Kitchin and Pringle (1920), Lamplugh (1922), Wright and Wright (1947), Casey (1961), and Bristow and Kirkaldy (1962). It is unnecessary here to enter into the stratigraphical argument and speculation that arose after the first description of these beds, but a brief description of the sediments of the Shenley Limestone bed and the mode of occurrence of the brachiopods therein may prove useful.

The bed (Bed 3, text-fig. 1) is composed mainly of iron-rich glauconitic sandstone in which the Shenley Limestone occurs as lenses and streaks of fine-grained, buff, or pink limestone and marl. At the base is a band of iron grit which rests non-conformably on laminated 'worm'-churned white sand and black clay (Bed 2, text-fig. 1, maximum thickness 4·5 m) which is unfossiliferous, although carbonaceous material is abundant. Lamplugh (1922) named this the 'Silty Bed' and interpreted it as representing estuarine conditions of deposition.

The top of the Shenley Limestone bed is brecciated, with a discontinuous development of secondary iron. A patchily developed band of red cirripede clay (Toombs 1935; Bristow and Kirkaldy 1962) overlies the limestone bed and passes up without a break, through a few centimetres of mottled green clays, into the overlying grey Lower Gault clays (Bed 5, text-fig. 1).

The Shenley Limestone is irregularly distributed throughout the sandstone bed (3) and is full of pebbles and grains of ironstone, quartz, and glauconite, all of which occur also as clastic components of the sandstone. The composition of the limestone approaches that of the sandstone as the percentage of clastic material increases.



TEXT-FIG. 1. Diagrammatic section to illustrate the stratigraphical position of the Shenley Limestone bed at Leighton Buzzard.

However, the junctions between sandstones and limestones are often sharp and marked by ribbons of ironstone which, by X-ray powder analysis, is shown to be probably goethite.

Most of the limestone is hard but parts are in the form of soft marl which is identical in appearance and composition to the harder rock. Lamplugh (1922) mentioned soft, marly material but interpreted it as recently weathered limestone in which the fossil shells were fragile and decomposed. The soft marl found during the course of this work has usually come from a position deep within a mass of newly excavated rock and is unlikely to have been subject to weathering. The brachiopod shells from this marl are well preserved and show a wide size range. It is easier to extract the smaller, more fragile shells from this soft material than from the hard limestone but they are probably of no more frequent occurrence in the former than in the latter. Part of the harder limestone contains abundant, randomly orientated burrows, which indicate that it was once a soft, churnable mud. It is likely that the whole of the limestone was formed as a soft marl which has become differentially cemented leaving patches of the original unaltered material.

A purplish grey calcareous mudstone, composed largely of clay minerals, occurs in small lenses, interbedded with the cream coloured limestone and the sandstone. It is sparsely fossiliferous and has yielded specimens of the belemnite *Neohibolites minimus* but no brachiopods.

Throughout the Shenley Limestone small scale channels, load structures, and erosion surfaces are evident. Periods of deposition of coarse sand alternated with the deposition of calcareous mud. Periods of time when large quantities of coarse clastic material entered the area alternated with quieter periods when sedimentation and current activity were probably slacker. Frequent periods of erosion probably separated periods of sedimentation.

It is difficult to envisage the conditions under which the calcareous mud could have been deposited. Packed with a large variety of fossils, brachiopods being the most numerous, it is in direct contrast to the sandstone which contains only an occasional poorly preserved shell. During deposition the currents must have been strong enough to bring quite coarse clastic material into the area and would have been too strong to prevent the fine mud from settling. Lamplugh believed that shelly patches on the sea floor consolidated quickly and remained cemented there as limestone lenticles, while the loose sand was winnowed away from around them. Certainly the present lenticular form of the limestone shows that it must have been eroded at intervals, but the continued existence of the soft marl which has never been cemented, shows that Lamplugh's theory does not entirely explain the formation or preservation of the limestone. The fine-grained porcellanous texture of some of the limestone gives it a similar appearance to that of some calcite mudstones of algal origin and, although there are none of the laminar structures usually associated with limestones of this type, this kind of sediment is likely to be of algal origin. Possibly vegetation could have played a part in trapping sediment and slowing currents, but as yet no evidence for its former existence has been found.

The brachiopods apparently thrived while the limestone was being deposited, or during quiet periods of inhibited sedimentation. Their excellent state of preservation is probably the result of being engulfed and protected by the soft plastic mud soon after death. If any of the shells were deposited in the coarse sand they were probably destroyed quickly by abrasion and solution.

The following observations on the mode of occurrence of the brachiopods suggest that they form a life assemblage which is not quite in the position of life, e.g. it has been moved and re-sorted within the area in which the animals lived:

1. The brachiopod shells are always randomly orientated within the limestone.
2. Most of the shells are entire.
3. The state of preservation of the shells is usually excellent; fine ornament, e.g. the capilliform ornament of *Platythyris diversa*, is usually undamaged.
4. There is no marked separation of different sizes or shapes of shell, species, or age groups. Several species may be mixed together in close proximity, and little evidence has been found for the concentration of particular species in individual limestone lenticles as stated by Lamplugh and Walker (1903). There are no nests of one species

comparable with the nests of *Sellithyris sella* in the Aptian of the Isle of Wight (Middlemiss 1962). Sometimes several individuals of one species may be found in close proximity, suggesting that they may have been part of a nest which was broken up after death. Gerontic individuals and juveniles of the same species are often found together in the same block. Young immature shells are common in the limestone, and juvenile shells of only 3 mm length can be separated from the softer marl. The stiff plastic clay probably saved these very small shells from being winnowed away by the currents.

5. Each species of brachiopod shows a wide range of variation in external morphology, which probably indicates a wide range of minor variation in habitat developed within the area at the time. In addition to the wide range in variation in normal external features, abnormal deformation of the shell is unusually common. Large deformities of shape are probably due to development in crowded conditions, but small bumps at the shell margin were probably formed as a result of reaction to attack by parasites. In the present study serial grinding of a specimen of *Rectithyris shenleyensis* revealed a boring in the wall of the pedicle valve close to the beak. A hole must have been bored through the shell wall by a parasite and an obstruction left inside the shell adjacent to the hole. The innermost layer of the shell wall was then laid down with a bulge, so that a small chamber was formed over the inner end of the bored hole. This is an example of a deformity formed on the inside of the shell wall but deformities of the external shell wall are probably more common.

TERMINOLOGY

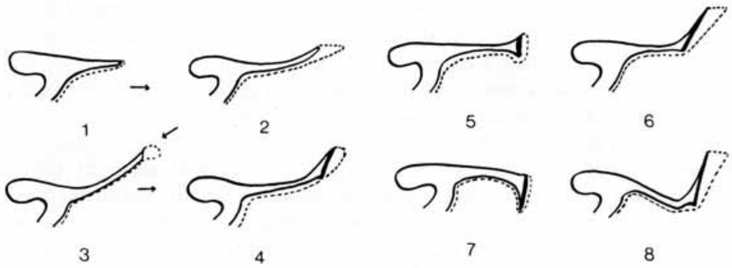
The terminology used in this paper follows the *Treatise on Invertebrate Paleontology, part H, Brachiopoda* (1965), and Middlemiss (1959). Certain terms, applying mainly to the hinge plates, are new or have been modified and are defined below.

Hinge plates

The hinge plates of the species investigated have a two-part structure. Each is composed of a 'primary' plate partially enclosed by a 'secondary' plate. The hinge plates are composed entirely of secondary layer material equivalent to the secondary layers of the shell wall (Williams 1956), and the terms used for the structure of the hinge plates are not equivalent to the terms 'primary' and 'secondary' as applied to the layers of the shell wall. Differences in the orientation of the calcite fibres of which they are composed probably enable the primary hinge plate to be distinguished from the secondary hinge plate in transverse section.

When the two part structure of hinge plates is taken into consideration, their classification involves the study of three important features (1–3 below) and terms describing variation in these features may be defined. The hinge plates of any species may be defined using a combination of these terms (text-fig. 2). Some of the terms used below are modified versions of terms introduced by Middlemiss (1959) and used in the *Treatise*.

1. *The width and concavity or convexity of the hinge plates.* In the living animal this was probably related to the size and shape of the attachment area of the dorsal adjustor muscle bases.



TEXT-FIG. 2. Explanation of terminology used to describe the structure of hinge plates in the Terebratulacea. Single hinge plates and inner socket ridges are shown in transverse section. The solid line represents the primary hinge plate and inner socket ridge; the broken line indicates the secondary hinge plate; the posterior extension of the crural base is shown in heavy black. 1, horizontal tapering; 2, concave, rounded, corniced; 3, concave, between rounded and cuneate, piped; 4, concave, cuneate, clubbed; 5, horizontal, cuneate, keeled; 6, horizontal, cuneate, clubbed; 7, convex, cuneate, keeled; 8, virgate, cuneate, clubbed.

Horizontal hinge plate. Not curved but flat; may be parallel to the commissural plane, or directed towards the floor of the brachial valve. Outline not greatly modified by secondary hinge plate development.

Concave hinge plate. Curved transversely, concave towards the pedicle valve. The curvature may be deep or shallow, and symmetrical or asymmetrical in transverse section.

Convex hinge plate. Curved transversely, convex towards the pedicle valve.

Virgate hinge plate. V-shaped in cross-section, concave towards the pedicle valve. This is an extreme case of a concave hinge plate.

2. *The form of the inner margin of the primary hinge plates.*

Tapering hinge plate. Tapers to a sharp edge running along its inner margin. The outline of this type of hinge plate is not usually modified by the secondary hinge plate which may be weakly developed.

Cuneate hinge plate. Thickens suddenly at its inner edge and ends abruptly with a flattened inner margin. The thick ends of the wedges of each pair of hinge plates are directed towards each other, while the thin ends pass outwards into the remainder of the hinge plates. The cuneate outline may be modified by the increased development of the secondary hinge plate. There are many variations of this type, involving changes in the proportion of the cuneate inner margin, but the construction remains basically the same. The increased downward extension of the cuneate inner margin produces a *keel*. The crural base usually extends posteriorly along the inner margin of a cuneate hinge plate between the primary and secondary portions of the hinge plate; its dorsal surface often enhances the keel.

In the living animal the cuneate type of hinge plate was probably associated with the need to provide a stronger 'anchorage' for the loop, and thus providing a greater support for the lophophore.

Rounded hinge plate. Has an inner margin which is gently rounded, i.e. it neither tapers to a sharp edge, nor is obviously cuneate.

3. *The degree of development of the secondary hinge plate.* This is always more strongly developed around the dorsal surface and inner edge of the hinge plate, away from the site of attachment of the dorsal adjustor bases. This development greatly modifies the outline of the hinge plates in transverse section. This is a source of possible confusion in the classification of the Terebratulacea, since much work has been based on the use of the *outline* of the hinge plates in transverse section as an important taxonomic character.

Clubbed hinge plate. The secondary hinge plate causes the outline to become thicker inwards, so that the inner margin is blunt or rounded. This is usually a modification of a cuneate primary hinge plate.

Piped hinge plate. A modification of a rounded or slightly cuneate hinge plate which becomes thinner inwards, but the inner margin is finished with a rounded thickened rim formed by the secondary hinge plate.

Corniced hinge plate. A modification of the rounded primary hinge plate in which the secondary hinge plate flares out into a cornice along the inner margin. Basically similar to the piped hinge plate.

The Terebratulacea appear to show a morphological progression from the tapering primary hinge plate, through the rounded to the cuneate form (text-fig. 2). In many species, e.g. *Rectithyris shenleyensis* (Walker) a progression from the rounded hinge plates in the extreme posterior umbo to the typical cuneate form developed anteriorly suggests that this morphological progression reflects a phylogenetic sequence which could have been repeated several times during the evolution of the Terebratulacea. Different species of the Terebratulacea, together possessing all types of hinge plate can be found in one bed of rock, e.g. the Shenley Limestone, showing that all types of hinge plates development occurred together at the same place and at the same point in geological time. The complete range of development of hinge plates of Terebratulacea since the early Mesozoic has not yet been worked out, but it seems that the form of the primary hinge plate may be of a considerable importance for the classification of the superfamily when used in conjunction with other morphological characters.

Ornament

The term 'ornament' is preferred to 'external sculpture'. 'Capillate ornament' is an ornament of capillae (fine radiating ribs more than 25 per 10 mm (Muir-Wood 1965) which are wavy and irregularly thickened along their lengths). It is characteristic of *Platythyris capillata* (d'Archiac).

GENERAL MORPHOLOGY OF THE SHENLEY LIMESTONE TEREBRATULACEA

All described species are biconvex when adult. The ventral profile varies, even within species, but transverse shells are rare. Depressed, compressed, and obese shells are all common, and younger individuals of a species may have depressed shells while the fully mature individuals of the same species may be compressed or obese. Very large size may be attained by fully mature or gerontic individuals of some species, e.g. *R. shenleyensis* (Walker). The beak angle varies between straight and incurved, although straight or incurved beaks are rare. Foramina may be telate, attrite, marginate, or labiate. They are usually mesothyrid, but may be permesothyrid. The foramen is usually large, but in a few individuals of all species it is tiny. The angle of truncation of the beak has a wide range of variation in most species. Variation in the beak angle produces a relative increase in the variation of the angle of truncation. The deltidial plates form a symphytium. In some species, e.g. *P. diversa* sp. nov. the apparent development of two separate deltidial plates is probably caused by a crack through the weakest point of the narrow-waisted symphytium. The anterior commisure is usually rectimarginate in juveniles and becomes uniplicate, sulciplicate, or episulcate. During ontogeny the sulciplicate stage may be derived from the rectimarginate stage without intervention of a uniplicate stage; this accords with the observations of Muir-Wood (1934) and Middlemiss (1959). Quadriplication and reversed plication are not found. Plication of the anterior commissure is not always accompanied by folding of the valves. When folding occurs it shows a wide range of development. In some species, e.g. *Boubeithyris boubei*, the brachial valve may be folded in reflection of the plication of the anterior commissure, while the pedicle valve remains unfolded.

The outer surface of the shells of most species is smooth. The species of *Platythyris* described here are exceptional in always having capillate ornament. Most species of Cretaceous terebratulids have fine striae visible in the inner layers of the shell wall.

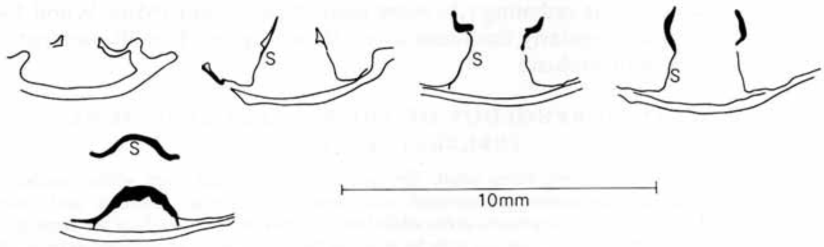
Examination of the microstructure of the shell wall shows that the primary layer (Williams 1956, 1966) is rarely visible in the Shenley Limestone Terebratulacea. The secondary fibrous and prismatic layers are well developed. In transverse section the fibres of the secondary layer show a saddle-and-keel structure similar to that described by Williams (1966) from recent Terebratulida.

Prismatic layers are well developed, especially in *B. boubei*, *R. shenleyensis*, and *P. diversa*, and show maximum development in the posterior part of each valve towards the mid line, i.e. in the older parts of the shell. In the extreme posterior of each valve there are often several thin prismatic layers alternating with fibrous layers. These thin layers merge antero-laterally into one thick prismatic layer which lies to the inside of a fibrous layer, and thins away at the anterior and sides of the shell. The prismatic layers are often more sharply defined on their inner surfaces; the outer surfaces often show a less sharp transition from the fibrous layer to the prismatic layer. The prismatic secondary layer is not developed in the hinge plates and hinge teeth but is well developed in the parts of the shell formerly occupied by the muscle bases. Its development does not appear to be associated with growth lines. The development of secondary prismatic layers varies in the shells of different species and probably in shells from different localities.

The descending branches of the loop diverge to varying degree e.g. × 4 in *B. boubei* and × 5 in *P. diversa*. The descending branches are recurved into the high or low arched transverse band.

The inner socket ridges vary in width and thickness in different species. The teeth are fairly massive in some species but may be thin and blade-like in others. The angle of insertion of the teeth and the height of the hinge plates above the floor of the brachial valve vary with the external proportions of the shell. Compressed, more obese, shells have a higher angle of insertion of the teeth, and the hinge plates are raised higher above the floor of the brachial valve. Wider, more depressed shells have a lower angle of insertion of the teeth and the hinge plates are closer to the floor of the brachial valve.

During the course of this work, several specimens of different species have been found to have a thin sheet of calcite extending from the lower edge of the loop to the floor of the brachial valve (see text-fig. 3 and Pl. 41, fig. 7). The term '*sub-loop skirt*' is proposed for this structure, which is attached to the loop but is



TEXT-FIG. 3. Transverse sections through a young specimen of *Rectithyris shenleyensis* sp. nov., Shenley Limestone, Leighton Buzzard, to show a sub-loop skirt(s).

separated from the floor of the brachial valve by a low gap that connects the anterior and posterior cavities of that valve. This structure may represent the posterior body wall of the living animal which has become calcified during life. It may have developed as a result of a 'physiological accident', or it may have had a strengthening or protective function. The sub-loop skirt does not have a spicular structure but has a somewhat similar position in the shell to the spicule skeleton described by Steinich (1963) in a *Terebratulina* from the Chalk of Rügen in the Baltic. The sub-loop skirt has been found by dissection of two specimens of *P. diversa* from the Shenley Limestone and has also been seen in transverse sections of *R. shenleyensis* (Walker), *P. diversa rubicunda* subsp. nov., and a specimen of *Moutonithyris moutoniana* (d'Orbigny) from France.

SYSTEMATIC DESCRIPTIONS

Superfamily TEREBRATULACEA Gray, 1840
Family TEREBRATULIDAE Gray, 1840
Subfamily SELLITHYRIDINAE Muir-Wood, 1965
Genus BOUBEITHYRIS gen. nov.

Type species. Terebratula boubei d'Archaic, 1847.

Diagnosis. Ventral profile pentagonal or pentagonal-oval. Valves equiconvex. Beak fairly wide, short or moderately short, sub-erect. Foramen mesothyrid; attrite or marginate. Angle of truncation of beak 90–100°. Anterior commissure rectimarginate to sulciplicate to episulcate. Folding usually confined to anterior third of the shell.

Hinge plates thin, concave, rounded, usually corniced. Inner socket ridges narrow. Crural processes high, fairly straight, tips inwardly inclined. Transverse band fairly high arched.

Range. Albian to Cenomanian.

Remarks. The name of the genus is derived from the name of the type species. It has been described only from the Shenley Limestone and the Cenomanian 'Tourtias' of Belgium.

Boubeithyris is assigned to the Sellithyridinae because of its thin, concave hinge plates with very small crural bases, the three septum-like ridges in the floor of its brachial valve, the thin descending lamellae and high-arched transverse band. It differs from other genera of this subfamily mainly in having corniced hinge plates. It is distinguished externally by the regular oval shape, narrowing anteriorly.

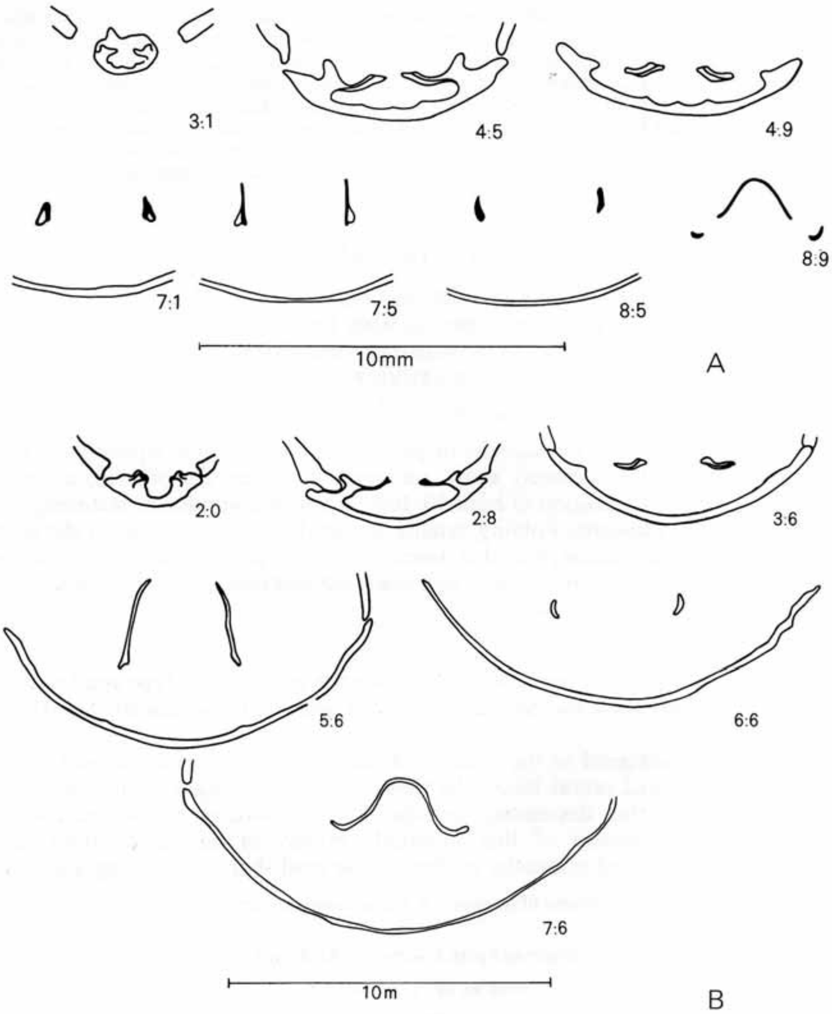
Species assigned. Boubeithyris boubei (d'Archiac); *B. buzzardensis* sp. nov.

Boubeithyris boubei (d'Archiac)

Plate 40, figs. 1–4; text-fig. 4

1847 *Terebratula boubei* d'Archiac, p. 320, pl. 19, fig. 11.
1903 *Terebratula boubei* d'Archiac; Lamplugh and Walker, p. 252, pl. 18, fig. 5.

Diagnosis. Boubeithyris of pentagonal oval ventral profile. P/A ratio 1 or slightly greater (rarely less than 1). Cardinal slopes straight. Beak sub-erect; beak ridges well defined, especially near the foramen which is large, circular, sometimes slightly telate or attrite, more commonly marginate. Anterior commissure rectimarginate to sulciplicate, rarely episulcate. Plication reflected by small folds and sulci at anterior end of brachial valve. Internal characters as diagnosed for the genus.



TEXT-FIG. 4. Transverse sections through two specimens of *Boubeithyris boubei* (d'Archiac). The concave, rounded, corniced hinge plates are seen in *a* at 4·5. The crural bases are attached to the extreme anterior ends of the hinge plates in *b* at 2·8. The high-arched transverse band is seen in *a* at 8·9 and in *b* at 7·6. *a*, BM BB76247, Shenley Limestone, Leighton Buzzard; *b*, BM BB76248, Tourtia (Cenomanian), Tournai.

Description. The ventral profile is usually pentagonal oval but some individuals, especially from the Shenley Limestone, may be more oval. More often, the anterior margin of the shell, although folded, has a 'squared off' appearance which enhances the pentagonal-oval outline.

Anterior commissure typically sulciplicate, but in a strongly folded shell may be slightly episulcate. At the other extreme some mature individuals are barely sulciplicate, retaining into maturity the rectimarginate condition of youth. No uniplicate individuals of this species have yet been found, and development appears to be straight from rectimarginate to sulciplicate. The plicae are close set and narrow, as are the folds at the anterior of the brachial valve, which are usually confined to the anterior third of the valve, or less. In extreme cases the folds may extend up to half the length of the valve. The pedicle valve may be gently folded at the tip or may show no folds at all. The shell usually shows no ornament, although fine radiating striae may be visible in the inner layers of some specimens.

The form of the hinge plates is fairly constant, but the corniced inner margins may be turned inwards from the vertical position so that in superficial appearance they approach the cuneate condition. Serial sections of one specimen showed short crural processes instead of the usual long pointed ones. It is possible that the long ends had been broken after death.

Neotype. The original specimens used by d'Archiac (1847) in his description of the species have been lost (Owen 1970, p. 55; confirmed by A. Dhont *in litt.*). A neotype resembling the specimen figured by d'Archiac 1847, pl. 20, fig. 1 is here chosen from the collections of the Institut Royal des Sciences Naturelles de Belgique in Brussels; registered number M.T.C. 10154 from the Tourtia of Tournai. Dimensions: length 31·0, width 17·0, thickness 12·0.

Remarks. In his original description d'Archiac (1847) described an ornament of radial lines on the outside of the shell. No true ornament has been observed during this work and d'Archiac was probably referring to the deep seated striae mentioned above.

Schloenbach (1867) believed '*T*.' *boubei* to be synonymous with '*T*.' *robertoni* d'Archiac, but his figure of a specimen of the latter from the Cenomanian Greensands of Quedlinburg (Harz) is rectimarginate and different in external form from the former. Some specimens of '*T*.' *robertoni* from the Tourtia of Tournai resemble some *B. boubei* in profile and beak characters, but the typical folding is absent. A specimen of *T. robertoni* from Tournai was sectioned and showed that the internal characters, especially the hinge plates, are fairly similar to those of *B. boubei*. The hinge plates of *T. robertoni* are concave with rounded inner margins but there are no secondary cornices as in *B. boubei*. The hinge plates of *T. ovata* Sowerby from the Warminster Greensand are similar to those of *T. robertoni* and all of these species may be related.

Meyer (1864) identified some single valves from the Lower Greensand pebble bed (Upper Aptian) of Godalming, Surrey, as this species. Davidson (1874) figured, after Meyer, a specimen as *T. boubei* from Godalming. This figure shows two deltidial plates, an anterior commissure which is slightly uniplicate, and a beak which is too long for *B. boubei*. The original specimen figured by Meyer is in the Sedgwick Museum in Cambridge and is a terebratellidine. Lamplugh and Walker (1903) figured specimens which they collected from the Shenley Limestone and recognized that they belonged to the d'Archiac species *T. boubei*.

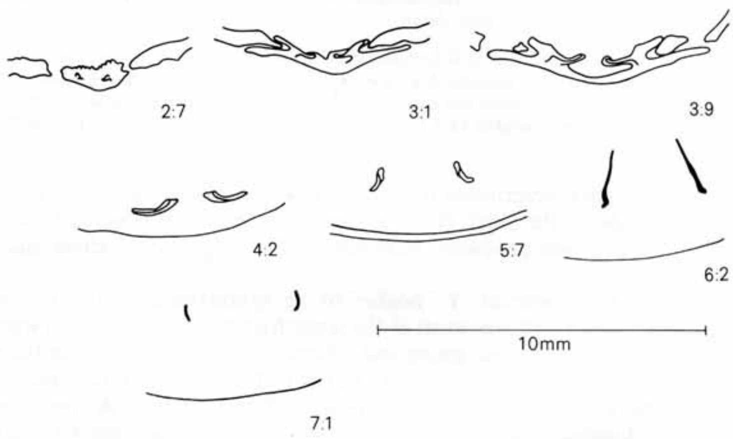
Although there may be some slight differences between some Shenley individuals of this species and some from the Tourtias, many individuals are identical. The hinge plates of some Tourtia individuals are thinner but present knowledge does not justify separation of Albian and Cenomanian members of this species.

Boubeithyris buzzardensis sp. nov.

Plate 40, figs. 5, 6; text-fig. 5

1903 *Terebratula ovata* Sowerby; Lamplugh and Walker, p. 252, pl. 17, fig. 6.

Diagnosis. Boubeithyris of pentagonal or pentagonal-oval ventral profile. P/A ratio 1–0·6. Foramen large, circular, attrite. Symphytium wide but short, well exposed. Beak ridges well defined. Cardinal slopes straight or slightly concave. Development of anterior commissure rectimarginate to sulciplicate to episulcate. Plication reflected by strong folds and sulci in anterior third of both valves. Internal structure as diagnosed for the genus.



TEXT-FIG. 5. Transverse sections through *Boubeithyris buzzardensis* sp. nov. The hinge plates within the cardinal process are markedly concave (2·7). At 3·9 and 4·2 the concave, rounded, corniced hinge plates are seen. BM BB76249, Shenley Limestone, Leighton Buzzard.

EXPLANATION OF PLATE 40

All figs. × 1·5.

Figs. 1–4. *Boubeithyris boubei* (d'Archiac). 1*a–c*, Neotype, M.T.C. 10154, Tourtia (Cenomanian), Tournai, Belgium. 2*a–c*, strongly biplicate specimen, BM BB76230, Tourtia, Tournai. 3*a–c*, pentagonal specimen, BM B26193, Shenley Limestone, Leighton Buzzard. 4*a–c*, an oval specimen, BM BB76231, Shenley Limestone.

Figs. 5, 6. *Boubeithyris buzzardensis* sp. nov., Shenley Limestone, Leighton Buzzard. 5*a–c*, BM B26199, Holotype. 6*a–c*, BM BB76233.

Figs. 7, 8. *Walkerithyris mendax* sp. nov., Shenley Limestone, Leighton Buzzard. 7*a–c*, BM BB76234, Holotype. 8*a–c*, a specimen with squarer uniplication, BM BB76235.

Fig. 9*a–c*. *Rectithyris shenleyensis* (Walker), Shenley Limestone, Leighton Buzzard. A typically triangular specimen, BM B26166.

COX and MIDDLEMISS, Cretaceous Terebratulacea

Description. The main characteristics of this species are the ventral profile, short beak, sulciplicate or episulcate anterior commissure, and well developed folds which affect the anterior of both valves equally. Variation depends on the differences in the ratio of length to width and small differences in the degree of folding. The shell is smooth except for some well-spaced growth lines that are quite prominent.

Holotype. BM B26199, from the Shenley Limestone. Figured on Pl. 40, fig. 5*a–c*. Dimensions: length 25·5, width 22·6, thickness 12·0.

Remarks. This species was identified by Walker (Lamplugh and Walker 1903) as *T. ovata* Sowerby, after he had compared specimens from the Shenley Limestone with *T. ovata* from the Warminster Greensand (Cenomanian). He believed that they did not differ any more than the species varied at Warminster. Re-examination of the materials shows that there are differences between the two species, although a few specimens of each tend to approach each other in external structure. The most important difference lies in the plication of the anterior commissure and the folding of the valves. The anterior commissure of *T. ovata* is sulcate or paraplicate, but that of *B. buzzardensis* is sulciplicate or episulcate. The long deep median sulcus on the brachial valve and the long median rib on the pedicle valve typical of *T. ovata* are absent from *B. buzzardensis*, which has evenly developed folds and sulci in the anterior third of each valve. The beak of *B. buzzardensis* is shorter, the P/A ratio lower, the valves more depressed, and the ventral profile more pentagonal. It has no ornament. The internal structure of these two species is similar but the secondary 'cornices' at the inner margins of the hinge plates are absent from *T. ovata*.

B. buzzardensis differs from *B. boubei* mainly in having a smaller beak, a lower P/A ratio, and folds which affect both valves equally. There is considerable difference in external form between extreme variations of one species and those of the other, but some less elongate and more pentagonal individuals of *B. boubei* closely resemble more oval, less strongly folded individuals of *B. buzzardensis*. However, the ratio of length to width of *B. buzzardensis* is usually lower and episulcate anterior commissures are more common.

Other species of English Albian Terebratulidae are distinct from *B. buzzardensis* in size, types of folding, beak characters, and internal structure. The species name is derived from the town of Leighton Buzzard in Bedfordshire.

Genus WALKERITHYRIS gen. nov.

Type species. Walkerithyris mendax sp. nov. (= *Terebratula moutoniana* d'Orbigny; Walker 1903).

Diagnosis. Ventral profile pentagonal. Brachial valve more obese than pedicle valve. Beak short, wide, suberect to nearly straight. Beak ridges fairly well defined, especially near the foramen. Symphytium short, wide. Foramen circular, mesothyrid; telate, attrite or slightly marginate, anterior commissure uniplicate. Hinge plates wide, thin, deeply concave, piped.

Known range. Albian.

Description. The lateral commissure is strongly convex towards the pedicle valve in the anterior part of the shell. The brachial valve is gently folded with a wide, median longitudinal fold that reflects the uniplicate anterior commissure and affects at least half the length of the valve. The pedicle valve is flattened and spatulate at the anterior end. The inner socket ridges are wide, with the upper surfaces convex towards the pedicle valve. None of the serial sections prepared so far has shown the loop, which is fragile and breaks easily.

Remarks. This genus is erected for the type species alone. It is distinguished from other English Albian genera by the form of the hinge plates and external features of the shell. The hinge plates are similar to those of the lower Cretaceous continental species *Loriolithyris russillensis* (de Loriol) and *Loriolithyris valdensis* (de Loriol). The wide piped hinge plates found in these species and described by Middlemiss (1968) are not commonly found in Cretaceous Terebratulidae and it might seem reasonable to include all species which possess them in the same genus. However, the external features of *Walkerithyris* are very different from those of the above mentioned species. *L. valdensis* and *L. russillensis* have massive beaks, strong plication and strongly folded valves. At present, without any more evidence to connect them, it is impossible to include these species and *W. mendax* in the same genus.

Walkerithyris mendax sp. nov.

Plate 40, figs. 7, 8; text-fig. 6

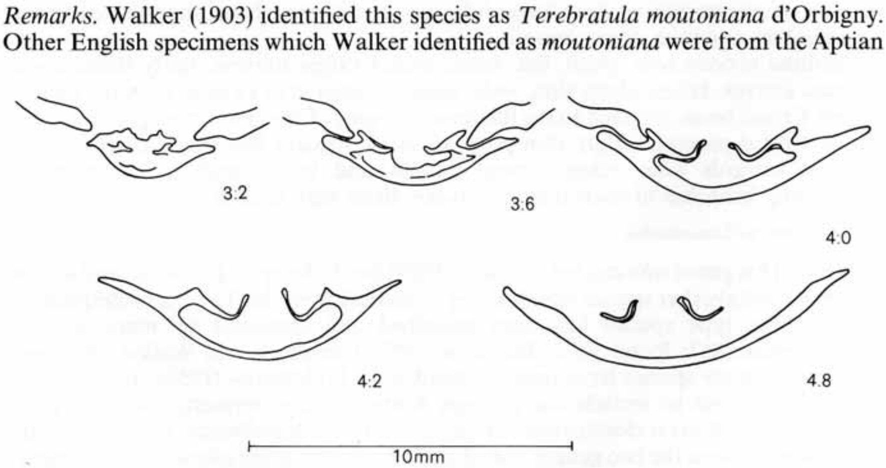
1903 *Terebratula moutoniana* d'Orbigny; Walker, p. 251, pl. 18, fig. 4*a*, *b* (non *Terebratula moutoniana* d'Orbigny 1849).

Diagnosis. External and internal structure as diagnosed for the genus. P/A ratio 1–0·5. Cardinal slopes straight or slightly convex. Angle of truncation of the beak about 90°.

Description. This species varies mainly in the ratio of width to length, the P/A ratio and the degree of uniplication of the anterior commissure. Some individuals are much longer than wide and have a more oval profile than others. The P/A ratio is normally about 1 but may be as low as 0·5. The uniplication may be very gentle or quite strong. Where the uniplication is strong the anterior end of the pedicle valve becomes increasingly flattened and spatulate.

Holotype. BM BB76234, from the Shenley Limestone. Dimensions: length 23·0, width 17·5, thickness 10·5.

Remarks. Walker (1903) identified this species as *Terebratula moutoniana* d'Orbigny. Other English specimens which Walker identified as *moutoniana* were from the Aptian



TEXT-FIG. 6. Transverse sections through *Walkerithyris mendax* sp. nov. The concave, piped hinge plates characteristically have a slightly sinuous outline, as at 4·0 and 4·8. BM BB76250, except for section 4·2, which is from BM BB76251; both from the Shenley Limestone, Leighton Buzzard.

of Brickhill and Upware, but these were later included by Middlemiss (1959) in a new genus, *Platythyris*.

Walkerithyris mendax differs from *Moutonithyris moutoniana* (d'Orbigny) primarily in its internal structure, but also differs externally. *M. moutoniana* as figured by d'Orbigny (1849) is more oval in shape, the ventral valve is more convex than the dorsal, the lateral commissure is straight for most of its length, the plication is more angular and the beak is longer and more erect. The typical adult *M. moutoniana* is much larger than *W. mendax*. The keeled, cuneate hinge plates of *M. moutoniana* (d'Orbigny) are in sharp contrast to the piped hinge plates of *W. mendax*. *W. mendax* resembles the Aptian species *Platythyris comptonensis* Middlemiss in its external features but the latter species is more oval, has a P/A ratio greater than 1, and has poorly defined beak ridges. The structure of the hinge plates of the two species is quite different; *P. comptonensis* has horizontal, tapering hinge plates while those of *W. mendax* are concave and piped. The form of the hinge plates and inner socket ridges distinguish this species from other English Albian species. The name of the species is derived from its deceptive external appearance which has caused it to be confused with other species in the past.

Subfamily RECTITHYRIDINAE Muir-Wood, 1965
Genus RECTITHYRIS Sahni, 1929

Type species. *Terebratula depressa* Lamarck, from the Cenomanian Tourtia, Belgium.

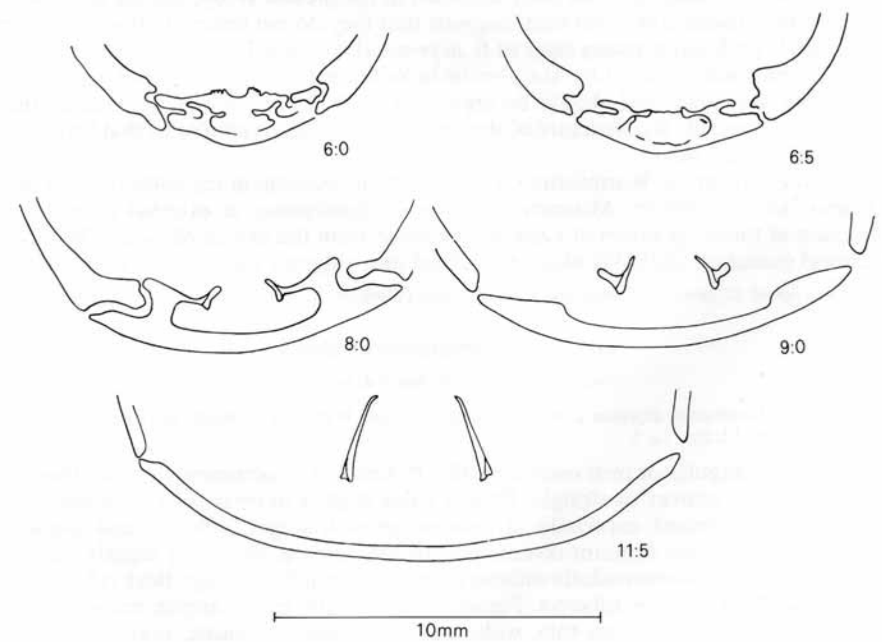
Emended diagnosis. Ventral profile variable. Beak straight to erect. Foramen telate, attrite, marginate, or sometimes labiate. Symphytium large, often well exposed. Anterior commissure rectimarginate to uniplicate, or rectimarginate to sulciplicate without uniplicate intermediate stage; fully mature adults with rectimarginate anterior commissures common. Shell smooth.

Cardinal process low, small, flat. Inner socket ridges narrow, fairly thick, upper surfaces convex. Hinge plates thin, wide, slightly concave to virgate; cuneate, may be keeled. Crural bases attached to the flat inner margins of the anterior ends of the hinge plates. Crural processes high, thin pointed; fairly straight but bases and tips often concave towards each other. Crural flanges and keels small or rudimentary. Descending branches of loop thin; transverse band high arched.

Range. Albian to Cenomanian.

Remarks. This genus was erected by Sahni (1929) for *T. depressa* Lamarck, and he also included several other species described by d'Archiac from the Tourtia of Belgium. In the past the type species has been described and discussed by many authors (Schloenbach 1867; Pictet 1872; Davidson 1852; Lamplugh and Walker 1903) and many Cretaceous species have been included in it. Middlemiss (1959) erected a new genus *Cyrtothyris* to include the English Aptian species formerly included in *T. depressa*. *Cyrtothyris* is closely related to *Rectithyris* and Middlemiss, in discussing the differences between the two genera, stated that 'the nature of the relationship is obscure in the present (1959) state of knowledge of the Albian terebratulids'. These Albian species which are described below and which were included in *T. depressa* Lamarck by Lamplugh and Walker (1903) thus hold an important position between the two genera.

In comparing the Albian species with those of the Aptian and Cenomanian, past authors have used different methods of recording their internal structures. The Albian species described here have been studied by the use of acetate peels to record the serially ground transverse sections of the shell. This method, which allowed more details of shell structure to be shown, has proved more successful than former methods. For example, the use of peels shows the structural relationships between different types of hinge plates which is of particular importance in the study of the phylogeny and classification of these Cretaceous genera. Middlemiss (1959) used the form of the hinge plates and crural processes to differentiate *Cyrtothyris* from *Rectithyris*. He described the hinge plates of *Cyrtothyris* as clubbed and virgate, with the inner lamina the same length as the outer in transverse section; crural flanges and keels were well developed. In the same publication Middlemiss described *Rectithyris* as having virgate hinge plates, with the inner lamina shorter than the outer in transverse section. The hinge plates were keeled, but there were no true crural flanges or crural keels. Acetate peels show that *R. depressa* has slightly concave, cuneate hinge plates, but otherwise the internal structure is much as described by Middlemiss. The crural bases are attached to the inner margins of the hinge plates, so accentuating the keel; crural flanges and crural keels are indeed rudimentary. The Albian species of *Rectithyris* described below have



TEXT-FIG. 7. Transverse sections through *Rectithyris depressa* (Lamarck). The hinge plates are initially horizontal, cuneate (6·0 and 6·5) and become cuneate, keeled (8·0). The crura are flanged and slightly keeled (9·0 and 11·5). BM duplicate specimen, Tourtia (Cenomanian), Tournai.

concave to slightly convex cuneate hinge plates which have crural bases attached to their anterior inner edges. The keels, if developed at all, are very rudimentary; small crural flanges and keels are frequently, but not always, developed. The extreme posterior ends of the hinge plates are sometimes covered with sufficient secondary material to appear 'clubbed'. The internal characteristics of the Albian species suggest that they should be included in the genus *Rectithyris* but that they probably represent an intermediate position between *Cyrtothyris* and *Rectithyris*.

In external features the Albian species often closely resemble the Aptian species. Slightly labiate foramina described by Middlemiss in *Cyrtothyris* are well developed in the Albian *R. shenleyensis*. Various degrees of inflation, compression and plication of the shell, which Middlemiss described as common in fully mature and gerontic individuals of *Cyrtothyris*, are also commonly found in *Rectithyris*.

The divided inner hinge plates described by Sahni (1929) as characteristic of this genus, have not been seen in any of the numerous Albian and Cenomanian specimens examined in this study.

In his original description Sahni included the d'Archiac species *T. robertoni*, *T. viquesneli*, *T. tornacensis*, *T. roemeri*, *T. bouei*, and *T. crassa* in this genus because of the characters of beak and foramen, quoting d'Archiac's figures and descriptions. '*R.*' *roemeri* and '*R.*' *bouei* have not been sectioned in the present study, but the small size and strongly biplicate external form suggests that they do not belong to this genus. *R. viquesneli* is probably a young stage of *R. depressa* (Davidson 1855; Middlemiss 1959). *R. tornacensis* was included by Middlemiss in *Sellithyris*. '*R.*' *robertoni* and '*R.*' *crassa* have been sectioned, and should be separated from *Rectithyris* by features of the cardinalia, especially the structure of the hinge plates which is similar to that found in *Boubeithyris* gen. nov.

Specimens from the Warminster Greensand (Cenomanian) in the collections of the Geneva Natural History Museum resemble *R. shenleyensis* in external form. The structure of the hinge plates of a similar specimen from the British Museum (Natural History) collection (B25239) which was sliced also suggests reference to *Rectithyris*.

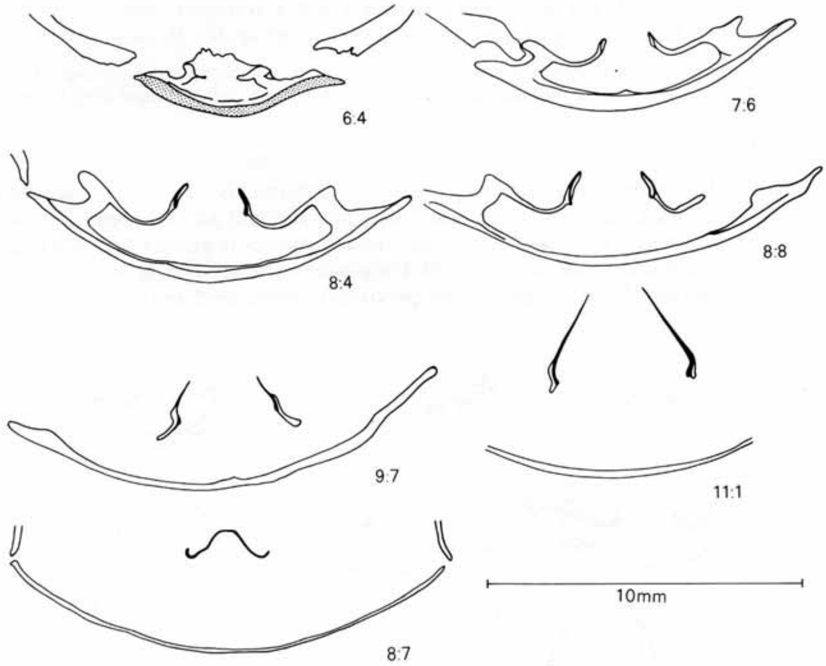
Species assigned. R. depressa (Lamarck); *R. shenleyensis* (Walker); *R. shenleyensis heathensis* subsp. nov.

Rectithyris shenleyensis (Walker)

Plate 40, fig. 9; Plate 41, figs. 1–4; text-fig. 8

1903 *Terebratula depressa* Lamarck var. *shenleyensis* Walker; Lamplugh and Walker, p. 251, pl. 17, figs. 1*a*, *b*.

Diagnosis. Triangular or oval ventral profile. P/A ratio 1 or commonly greater than 1. Cardinal slopes convex or straight. Pedicle valve slightly more convex than brachial valve. Shell depressed, especially in younger growth stages, inflated, and slightly compressed with age. Anterior commissure rectimarginate, becoming slightly sulciplicate in some fully mature adults without intervening uniplicate stage. Beak ridges well developed. Beak erect or suberect. Foramen mesothyrid, telate, attrite, marginate or slightly labiate. Hinge plates thin, wide, strongly concave, cuneate, may be slightly keeled. Crural bases attached to anterior inner margin of hinge plates. Crural processes high, pointed, inwardly inclined, fairly straight except for curved base. Small crural flange and keel usually present.



TEXT-FIG. 8. Transverse sections through *Rectithyris shenleyensis* (Walker). The hinge plates are initially horizontal (6·4), becoming concave, cuneate, keeled (7·6–8·8). BM B26236, except for section 8·7, which is from BM BB76252; both from the Shenley Limestone, Leighton Buzzard.

Description. The triangular ventral profile of the adult of this species is very characteristic. Adult individuals may be more oval when the P/A ratio approaches 1. Young individuals are depressed, have an oval ventral profile and an almost flat brachial valve, a rectimarginate anterior and an erect or suberect beak, often with a small circular foramen. In the adult, sulciplication of the anterior commissure may occur with or without increased inflation of the shell, but occurs only in fully mature or gerontic individuals. A slightly labiate foramen is common; the combination of such a foramen with the telate condition produces the characteristic 'keyhole' shape seen in many specimens.

Lectotype (here chosen). GSM 51262, figured by Lamplugh and Walker 1903, pl. 17, figs. 2*a*, *b*; from the Shenley Limestone.

Rectithyris shenleyensis heathensis subsp. nov.

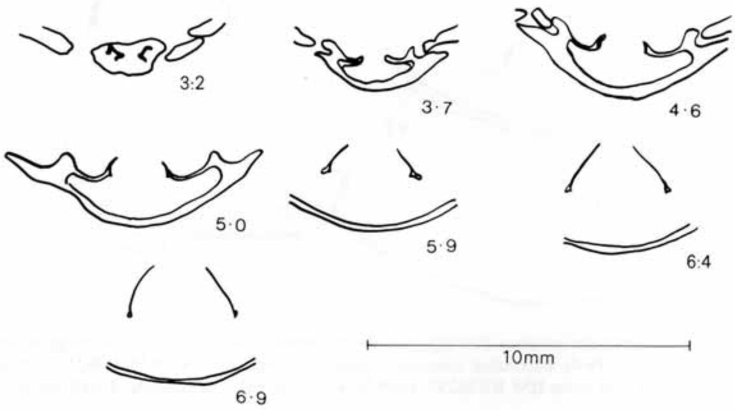
Plate 41, fig. 5; text-fig. 9

Diagnosis. R. shenleyensis of pentangular-oval or rhomboidal ventral profile, valves often equally convex. P/A ratio 1 or slightly more. Beak short, wide, sub-erect to nearly straight. Foramen mesothyrid, large, circular. Symphytium well exposed, beak ridges well defined. Anterior commissure gently uniplicate from an early age. Lateral commissure gently arched. Gentle fold in anterior half of brachial valve; anterior half of pedicle valve somewhat spatulate. Internal characters as for *R. shenleyensis*.

Description. The ventral profile, which is pentangular-oval to subcircular, with some individuals developing a pentagonal or rhomboidal outline, and the uniplication are the main distinguishing features of this subspecies.

Holotype. BM BB76241, from the Shenley Limestone. Dimensions: length 31·0, width 26·5, thickness 14·5.

Remarks. *R. shenleyensis heathensis* resembles *C. uniplicata* (Walker) from the English Aptian, but the beak ridges of the former are more distinct and the beak is usually wider and less conical. The P/A ratio of the Aptian species is greater and the pedicle valve has a slight sulcus in the anterior half. Uniplicate varieties of *R. depressa* from the Tourtias are larger, have longer, more produced beaks and may develop slight



TEXT-FIG. 9. Transverse sections through *Rectithyris shenleyensis heathensis* subsp. nov. The initially horizontal hinge plates are seen within the cardinal process at 3·2; they become concave, cuneate, and slightly keeled at 4·6 and 5·0. The crura are flanged and slightly keeled at 5·9–6·9. BM B26176, Shenley Limestone, Leighton Buzzard.

EXPLANATION OF PLATE 41

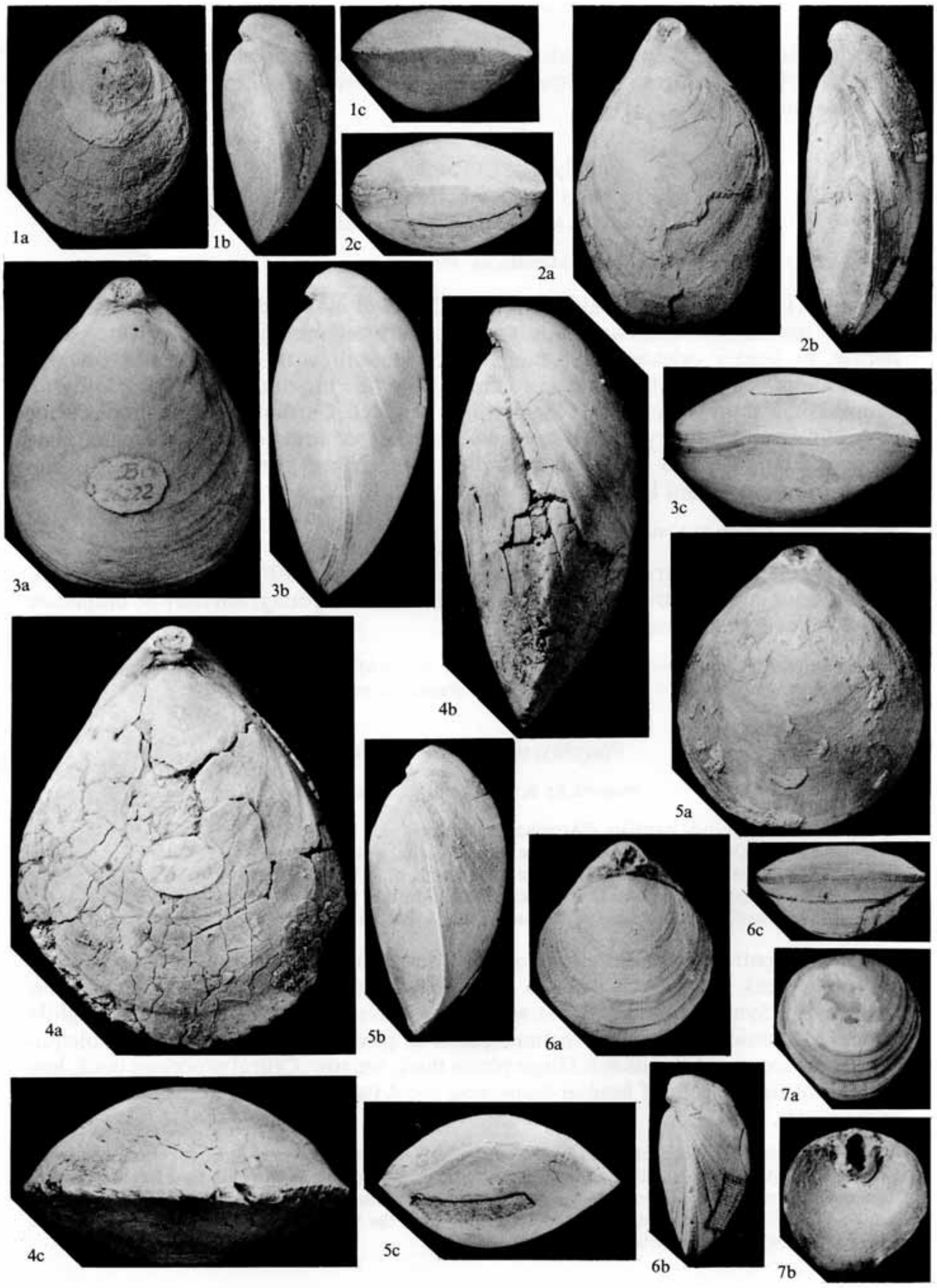
All figs. × 1·5.

Figs. 1–4. *Rectithyris shenleyensis* (Walker), Shenley Limestone, Leighton Buzzard. 1*a–c*, young, gently uniplicate specimen, BM BB76239. 2*a–c*, an elongate specimen, BM BB76240. 3*a–c*, a slightly biplicate specimen, BM BB76236. 4*a–c*, a gerontic specimen, BM BB76238.

Fig. 5*a–c*. *Rectithyris shenleyensis heathensis* subsp. nov., Shenley Limestone, Leighton Buzzard. Holotype, BM BB76241.

Fig. 6*a–c*. *Platythyris capillata* (d'Archiac), Tourtia (Cenomanian), Tournai, Belgium. A young, rectimarginate specimen, BM B35421.

Fig. 7*a*, *b*. *Platythyris diversa* sp. nov., Shenley Limestone, Leighton Buzzard. A brachial valve dissected to show the sub-loop skirt. The loop was broken during dissection and is incomplete above the anterior part of the skirt.



COX and MIDDLEMISS, Cretaceous Terebratulacea

sulciplication which is never developed in *R. shenleyensis heathensis*. The name of the subspecies is derived from the name of Heath and Reach, a village near Shenley Hill, Bedfordshire.

Family PYGOPIDAE Link, 1830
Subfamily PLATYTHYRIDINAE Dieni and Middlemiss, 1975
Genus PLATYTHYRIS Middlemiss, 1959

Type species. Platythyris comptonensis Middlemiss, 1959.

Diagnosis (after Dieni and Middlemiss, 1975). Shell elongate, oval or pear-shaped. Lateral commissure arched; anterior commissure rectimarginate, uniplicate, sulciplicate, or gently sulcate. Shell capillate, or smooth with more or less obvious longitudinal striae. Umbo suberect to erect. Foramen mesothyrid to permesothyrid. Symphytium short or very short. Beak ridges rounded. Cardinal process small. Hinge plates horizontal to very slightly concave, tapering, or with rounded inner margins; becoming cuneate and keeled in gerontic stage. Crural processes incurved. Loop short; transverse band low-arched.

Range. Upper Aptian to Cenomanian.

Remarks. The angle of truncation has a wide range, between 90° and 100°, in this genus. The anterior commissure is always rectimarginate in the young, but may be uniplicate to sulciplicate or sulcate in adults.

Species assigned. P. comptonensis Middlemiss, 1959; *P. minor* Middlemiss, 1959; *T. capillata* d'Archiac, 1847; *P. floresana* Dieni and Middlemiss, 1975; *P. diversa* sp. nov.

Platythyris capillata (d'Archiac)

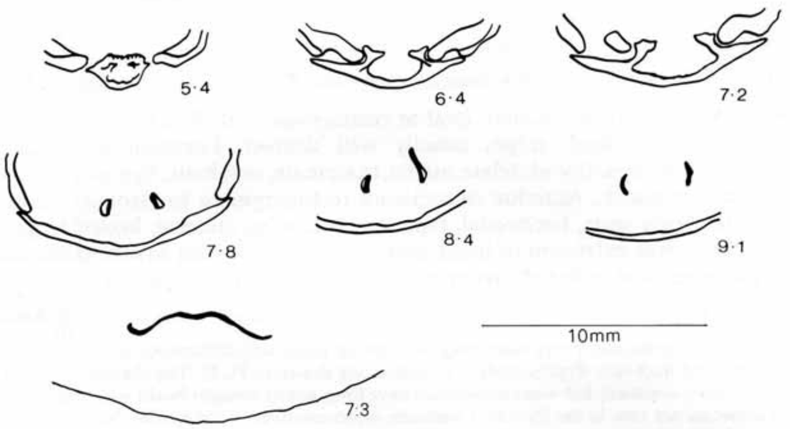
Plate 41, fig. 6; Plate 42, figs. 1, 2; text-fig. 10

1847 *Terebratula capillata* d'Archiac, pl. 20, figs. 1–3.
1867 *Terebratula capillata* d'Archiac; Schloenbach, p. 454.
1871 *Terebratula capillata* d'Archiac; Quenstedt, p. 385, pl. 17, figs. 75–76.
1972 *Platythyris capillata* (d'Archiac); Popiel-Barczyk, p. 142, pl. 2, fig. 8, pl. 4, fig. 1.
1974 *Capillithyris capillata* (d'Archiac); Katz, p. 258, pl. 84, fig. 12*a–c*.

Diagnosis. Ventral profile circular to oval. Valves equiconvex. P/A ratio 1 or less. Beak sub-erect, beak ridges well defined. Foramen large, circular, attrite or marginate, mesothyrid. Symphytium short but well exposed. Cardinal slopes straight or slightly concave. Anterior commissure rectimarginate to gently uniplicate to slightly sulciplicate, sometimes slightly sulcate. Hinge plates thick, narrow. Crural processes thick, low with blunt tips. Width of loop at transverse band twice its width at anterior ends of hinge plates.

Neotype. The original specimens used by d'Archiac (1847) are lost (Owen 1970, p. 55; confirmed by A. Dhont *in litt.*). A neotype resembling the specimen figured by d'Archiac 1847, pl. 20, fig. 1 has been chosen from the collections of the 'Institut Royal des Sciences Naturelles de Belgique' in Brussels, and is figured here on Pl. 42, fig. 1. Registered number M.T.C. 10156 from the Tourtia of Tournai. Dimensions: length 34·0, width 32·0, thickness 18·0.

Remarks. D'Archiac (1847) recognized different varieties of this species but did not indicate the considerable intermediate variation which occurs between his chosen varieties. Many specimens closely resemble d'Archiac pl. 20, fig. 1 and have circular ventral profiles, fairly small, somewhat produced beaks, large circular foramina, slightly concave cardinal slopes and rectimarginate or slightly sulciplicate anterior commissures. Specimens which resemble d'Archiac var. a, pl. 20, fig. 2 have oval, ventral profiles, are often obese, have slightly sulciplicate or sulcate anterior commissures, and fairly large wide beaks. The specimens resembling d'Archiac var. b, pl. 20, fig. 3, are smaller, fairly depressed and have rectimarginate anterior commissures; these are certainly juveniles of the other varieties.



TEXT-FIG. 10. Transverse sections through *Platythyris capillata* (d'Archiac). The horizontal, tapering hinge plates are seen at 5·4–7·2, the subrectangular free bases of the crura at 7·8, and the low-arched transverse band at 7·3. BM 3412, except for section 7·3, which is from BM 35422; both from Tourtia (Cenomanian), Tournai.

Three specimens from Tournai were sectioned to show the internal structure. One was a young specimen but the other two corresponded in external appearance to d'Archiac pl. 20, figs. 1, 2.

The young specimen and the d'Archiac var. a. were shown to have the horizontal, tapering hinge plates typical of the genus (text-fig. 10). The other specimen, similar to d'Archiac's fig. 1 in external appearance was found to have thick, horizontal hinge plates which did not taper, but the inner margins were deflected sharply downwards at right angles to the rest of the plate; the crural base was extended along the inner margin of the hinge plate for much of its length. This type of construction was not found in any other specimens of the species and appears to be a gerontic modification of the normal type of hinge plate structure; it occurs also in *P. diversa.* D'Archiac figured specimens with disjunct deltidial plates and this condition has been observed in many specimens examined by the authors, but has proved to be the result of fracturing through the narrow 'waist' of the symphytium.

Schloenbach (1867) mentioned that '*T.*' *capillata* occurred in the Cenomanian of Germany but without figuring a specimen. He believed that it occurred rarely in the Tourtia of Essen, but was found commonly in the Tourtia of Dresden.

Quenstedt (1871) described the German '*T.*' *capillata* d'Archiac as usually small, with a short beak and hardly any folding. He figured a specimen which was small, with a small erect beak, small foramen, depressed shell, and gently uniplicate anterior commissure. The ornament is capillate. No German specimens have been available for sectioning, and although the external morphology would appear different from most Belgian specimens, it is thought wise to retain these specimens within *P. capillata* (d'Archiac) for the present.

Platythyris diversa sp. nov.

Plate 42, figs. 3–6; text-figs. 11, 13*a–c*

1903 *Terebratula capillata* d'Archiac; Lamplugh and Walker, p. 249, pl. 16, figs. 1*a*, *b*.

Diagnosis. Ventral profile circular, oval or pentagonal-oval. P/A ratio about 1. Beak sub-erect or erect; beak ridges usually well defined. Foramen large, circular, mesothyrid, or permesothyrid; telate, attrite, marginate, or labiate. Symphytium, short, wide, 'narrow-waisted'. Anterior commissure rectimarginate to strongly uniplicate. Hinge plates fairly wide, horizontal, tapering; becoming cuneate, keeled in gerontic stage. Anterior free extension of hinge plates very narrow with square cross-section. Crural processes low, pointed, strongly curved inwards. Loop narrow.

Holotype. BM BB76242, from the Shenley Limestone. Dimensions: length 23·5, width 22·0, thickness 10·5.

Description. This species has a very wide range of external form, with differences in the proportions of length, width, and thickness. Representative variations are shown in Pl. 42. The characters of beak and foramen are fairly constant, but some individuals have long, nearly straight beaks with small foramina. Labiate foramina are rare in the Shenley Limestone representatives of the species, but are common in those of the Red Rock, which appear sufficiently distinctive to form a separate subspecies, described below. An extreme variety from the Shenley Limestone has a pentagonal ventral profile (Pl. 42, fig. 4), the brachial valve more obese than the pedicle valve, and the anterior commissure strongly uniplicate. These individuals bear a strong resemblance to *Walkerithyris mendax*, but the distinctive capillate ornament and tapering, horizontal hinge plates revealed by sectioning show the true taxonomic position of these individuals.

Juveniles all have depressed shells and rectimarginate anterior commissures. Slight uniplication may develop at an early stage.

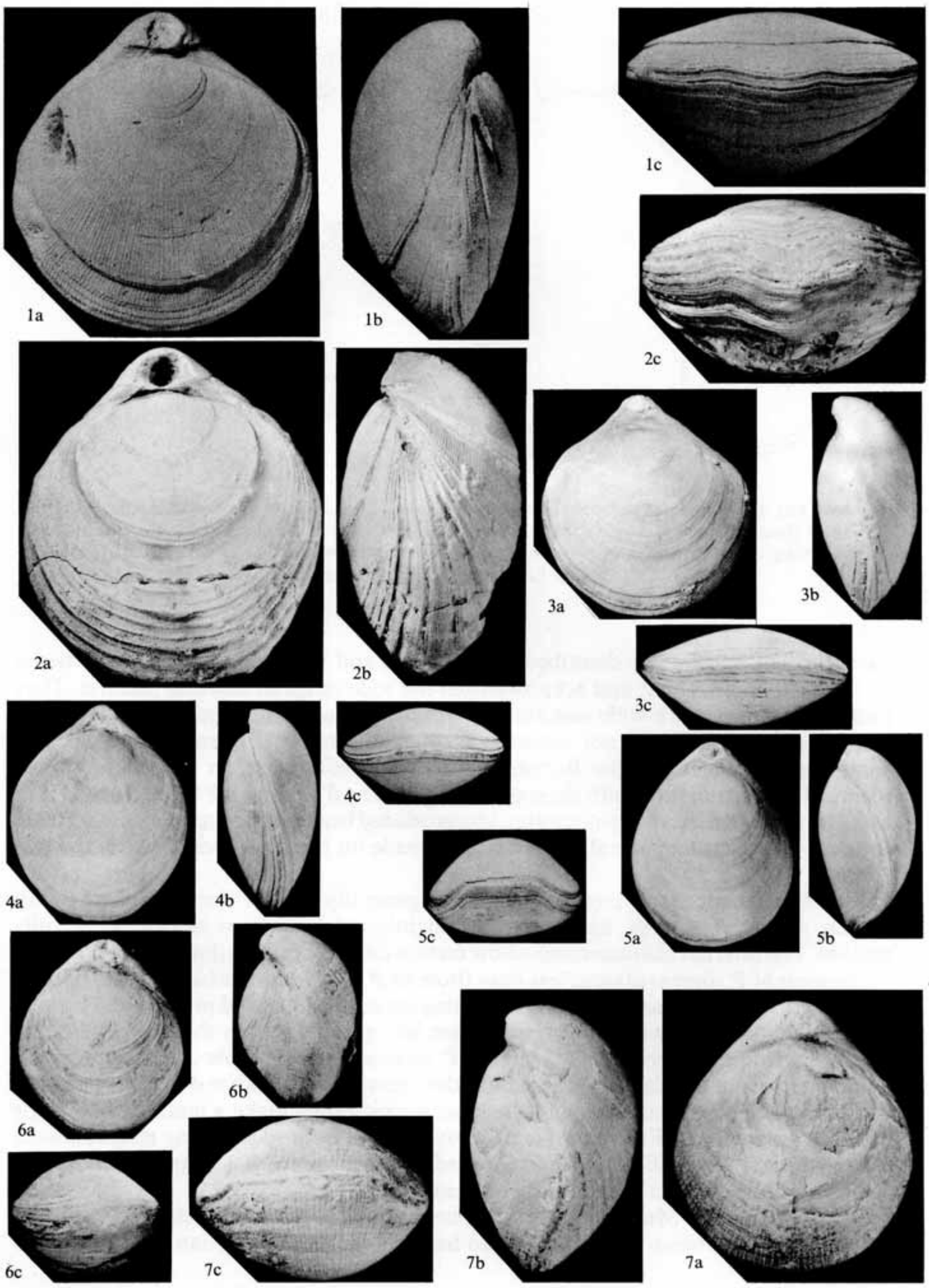
EXPLANATION OF PLATE 42

All figs. × 1·5.

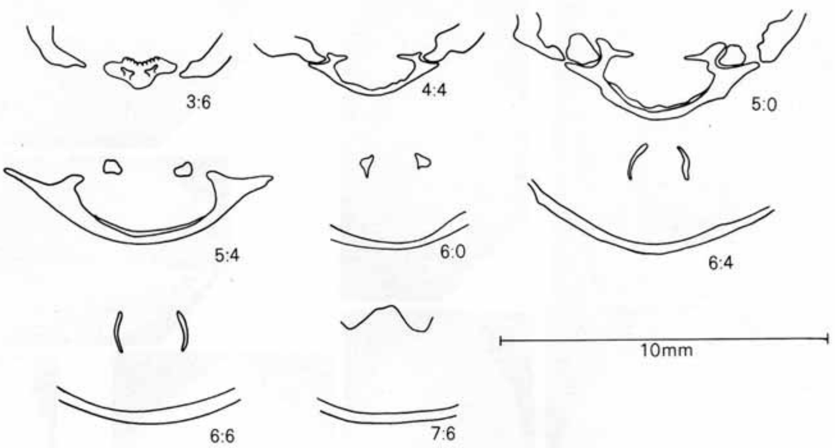
Figs. 1, 2. *Platythyris capillata* (d'Archiac), Tourtia (Cenomanian), Tournai, Belgium. 1*a–c*, Neotype, M.T.C. 10156. 2*a–c*, a gerontic specimen, BM B46351.

Figs. 3–6. *Platythyris diversa* sp. nov., Shenley Limestone, Leighton Buzzard. 3*a–c*, Holotype, BM BB76242. 4*a–c*, a small oval, very gently uniplicate specimen, BM 20061. 5*a–c*, a uniplicate specimen similar in external form to *Walkerithyris mendax*, BM 8539. 6*a–c*, a small, obese specimen approaching *P. diversa rubicunda*, BM BB76243.

Fig. 7*a–c*. *Platythyris diversa rubicunda* subsp. nov., Red Rock (Upper Albian), Hunstanton, Norfolk. Holotype, BM BB4191.



COX and MIDDLEMISS, Cretaceous Terebratulacea



TEXT-FIG. 11. Transverse sections through *Platythyris diversa* sp. nov. The horizontal, tapering hinge plates are seen at 3·6–5·0, the subrectangular free bases of the crura at 6·0, the close-set, incurving crural processes at 6·4, and the low-arched transverse band at 7·6. BM BB76253, Shenley Limestone, Leighton Buzzard.

Remarks. This species was described by Lamplugh and Walker (1903) who identified it as *T. capillata* d'Archiac, and acknowledged the wide range of external features. They had at their disposal a wide selection of Tourtia material for comparison with that from Shenley, but could not separate them taxonomically. Many of the Shenley Limestone specimens in the British Museum collections are, in the main, almost identical in external form with the specimen figured by d'Archiac (1847, pl. 20, fig. 1) but are always smaller, have slightly wider, less produced beaks, and remain rectimarginate to uniplicate. Certain generalizations can be made on the difference between the two species.

The Tourtia species *P. capillata* reaches a generally greater size than the English Albian species *P. diversa*, and it may be slightly sulciplicate or sulcate when fully mature. The internal characteristics show certain differences. The descending branches of the loop of *P. diversa* diverge less than those of *P. capillata*. The hinge plates of both species are horizontal and tapering, becoming cuneate and keeled in old age. Those of *P. capillata* are narrower, thicker, and taper less gradually than those of *P. diversa*.

The horizontal, tapering hinge plates of *P. diversa* resemble those of *P. comptonensis* Middlemiss from the English Aptian but other internal features are different. The loop in *P. comptonensis* is narrower and the inner socket ridges make a much deeper angle with the hinge plates. Externally, some individuals of both species may resemble each other but they have different ornament, and *P. comptonensis* has sharper beak ridges and a lower angle of truncation of the beak.

In the Sedgwick Museum there are two specimens with the external form and ornament of *P. diversa*. These are said to have come from the Aptian of Upware and were collected by Keeping. The Aptian deposits of Upware are no longer exposed and there is some doubt about the exact limits of their age, but if these specimens are in fact from the Aptian the range of the species could be at least that old.

The name of this species refers to the diversity of the external form.

Platythyris diversa rubicunda subsp. nov.

Plate 42, fig. 7; text-figs. 12, 13*d*–*f*

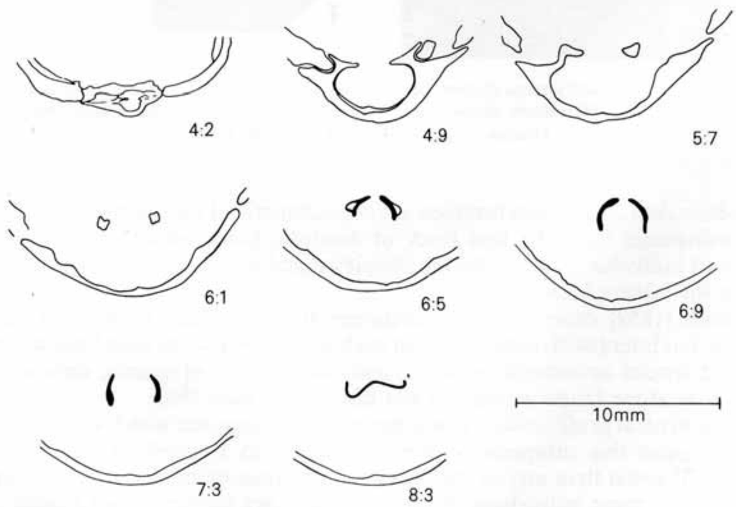
1852 *Terebratula capillata* d'Archiac; Davidson, p. 46, pl. 5, fig. 12.
1874 *Terebratula capillata* d'Archiac; Davidson, p. 33, pl. 17, fig. 2.

Diagnosis. *Platythyris diversa* of oval or pentagonal ventral profile, obese as adult; beak short, thick; foramen commonly labiate; anterior commissure rectimarginate or uniplicate.

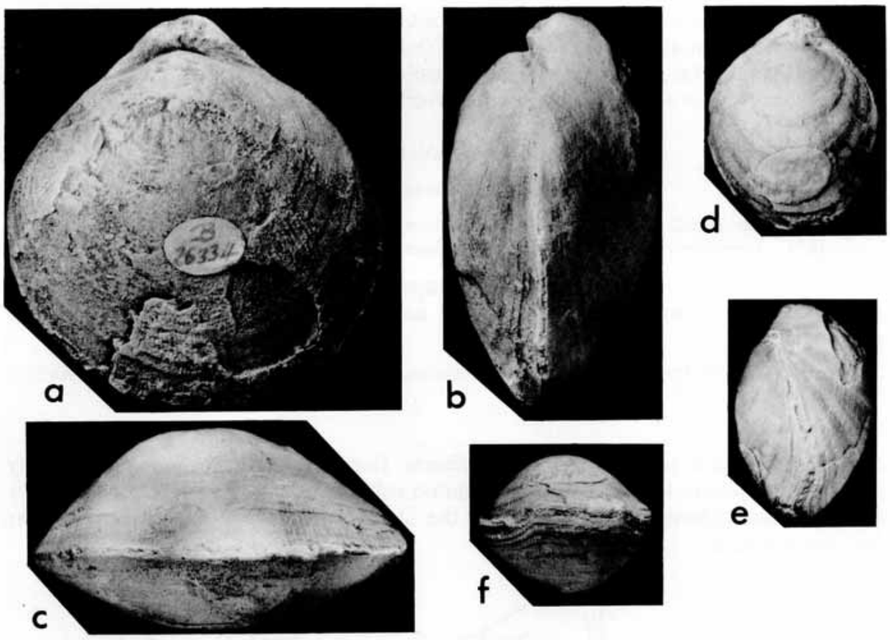
Holotype. BM BB4191 from the Red Rock of Hunstanton, Norfolk. Dimensions: length 28·5, width 25·0, thickness 18·0.

Range. Albian.

Remarks. The external features of *P. diversa* from the Red Rock are sufficiently distinctive to justify the erection of a separate subspecies, which is described here for completeness, although specimens from the Shenley Limestone which show similar features are rare.



TEXT-FIG. 12. Transverse sections through *Platythyris diversa rubicunda* subsp. nov. The horizontal, tapering hinge plates are seen at 4·2 and 4·9, the subrectangular free bases of the crura at 6·1, the close-set incurving crural processes at 6·9, and the low-arched transverse band at 8·3. BM BB76254, Red Rock (Upper Albian), Speeton, Yorkshire, except for section 4·2, which is from BM BB76255, Red Rock (Upper Albian), Hunstanton, Norfolk.



TEXT-FIG. 13. *a–c*, *Platythyris diversa* sp. nov., Shenley Limestone, Leighton Buzzard. A gerontic specimen. BM B26334. × 1·5. *d–f*. *Platythyris diversa rubicunda* subsp. nov. Red Chalk (Upper Albian), North Grimston, Yorkshire. BM BB76244. × 1·5.

The obese shell and labiate foramen are characteristic of the majority of individuals of this subspecies from the Red Rock of Norfolk, Lincolnshire, and Yorkshire. A minority of individuals, more like the Shenley members of the species, are less obese and lack the labiate foramen.

Davidson (1852) described this subspecies from the Red Rock as *T. capillata* d'Archiac, but later (1874) suggested that perhaps the specimens may have constituted a different species or subspecies of *T. capillata*. He was, of course, unaware of the Shenley Limestone fauna which was not discovered until 1903.

The oval ventral profile, obesity, and the relatively large size which some individuals may attain, give this subspecies a closer similarity to *P. capillata* var. a. from the Tourtia of Tournai than any of the Shenley Limestone members of this species. The hinge plates of some individuals of the subspecies are narrower and thicker than is typical for *P. diversa*, and approach the form of those of juvenile *P. capillata*. The name of the subspecies refers to the red colour of the shell, derived from the Red Rock matrix (Albian) of Hunstanton, Norfolk, and to the obese shape of the typical form.

CONCLUSIONS

The stratigraphical and geographical isolation of the Cretaceous brachiopod-bearing beds makes stratigraphical conclusions difficult to draw from the study of the Terebratulacea. Nevertheless, it is possible to make some comparisons between the Shenley Limestone fauna and that of other Cretaceous horizons. Middlemiss (1959) considered the Aptian and Albian terebratulacean faunas as distinct, but the present work on the Shenley Limestone fauna indicates that the distinction is not absolute. Owen (1960) came to a similar conclusion when considering the Cretaceous rhynchonellid genus *Cyclothyris*, although the English Cretaceous rhynchonellids have a wider distribution than the terebratulaceans. When the English Aptian and Albian are compared, it is evident that some Aptian genera are absent from the Albian. *Cyrtothyris* and *Praelongithyris* are absent from the Shenley Limestone, although *Rectithyris shenleyensis* is probably related to the former genus. *Rhombothyris* is not found in the Shenley Limestone and seems to have disappeared at the end of the Aptian. Rare individuals of *Sellithyris* cf. *sella*, a typical Aptian species, occur in the Shenley Limestone. Specimens labelled *T. capillata* in the Keeping Collection from the Upper Aptian, Upware, Cambridgeshire, now in the Sedgwick Museum, Cambridge (SM B2543-40), suggest the possible occurrence of *P. diversa* in the Aptian. Poorly preserved specimens similar to *Boubeithyris boubei* are in the British Museum and Sedgwick Museum collections from the Upper Aptian of Seend, Wiltshire (BM 88829; SM B28131-2). This is probably the first appearance of an Albian-like brachiopod fauna in the Aptian. *W. mendax* does not appear in the English Aptian but this has already been discussed as a peculiarly isolated species that appears to be confined to the Shenley Limestone. The base of the Gault near Leighton Buzzard, at Billington Crossing and Chamberlain Barn pits, contains a fauna of phosphatized Terebratulacea similar to the Shenley Limestone fauna, including *B. boubei*, *W. mendax*, and *P. diversa*.

Other English Albian beds contain a somewhat different terebratulid fauna; for example the commonest biplicate species in the Red Chalk, Upper Greensand, and Gault *Moutonithyris dutempleana* (d'Orbigny), does not occur in the Shenley Limestone. Neither does another biplicate species, the small '*T.*' *biplicata* Sowerby, which is known from the Warminster Greensand (Cenomanian) and occasionally the Upper Greensand. *W. mendax*, *B. boubei*, and *B. buzzardensis*, on the other hand, all occur in the Shenley Limestone but not in the remainder of the English Albian. These differences are probably a reflection of differences in environment and the numbers of fossils preserved at different horizons. A point of similarity between the Red Chalk and the Shenley Limestone is the presence of *P. diversa*, although the Red Chalk has a different subspecies. *Rectithyris* cf. *shenleyensis* occurs in the Warminster Greensand (Cenomanian). *T. ovata* of the Warminster Greensand is closely related to *B. boubei* of Shenley.

The similarity between the Belgian Tourtia (Cenomanian) terebratulacean fauna and that of the Shenley Limestone is not as great as Lamplugh and Walker (1903) supposed. They have only one species, *B. boubei*, in common. *R. depressa*, *P. capillata*, *T. robertoni*, *T. crassa*, *T. tornacensis* and other species illustrated by d'Archiac (1847) are absent from the Shenley Limestone. Typical Shenley Limestone species which are absent from the Tourtias are *R. shenleyensis*, *P. diversa*, *B. buzzardensis*, and *W. mendax*. The faunas are related at the generic level but the superficial similarity of the species is probably the result of the similar environments suggested by the lithological similarity of the matrices. In conclusion, the evidence suggests that the Shenley Limestone (Lower Albian) terebratulacean fauna is transitional between Aptian and Cenomanian faunas.

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