ENGLISH APTIAN TEREBRATULIDAE

by F. A. MIDDLEMISS

ABSTRACT. Terebratulidae from the English Aptian are systematically revised and their external and internal characters investigated, the latter chiefly by means of serial sections and dissections. Some new terms are introduced, notably for the hinge plates, and others redefined. Five new genera are proposed: *Rhombothyris* (type sp. *Terebratula extensa* Meyer), *Platythyris* (type sp. *P. comptonensis* nov.), *Sellithyris* (type sp. *Terebratula sella* J. de C. Sowerby), *Cyrtothyris* (type sp. *Terebratula depressa* var. *cyrta* Walker), and *Praelongithyris* (type sp. *P. praelongiforma* nov.). These genera show some uniformity in the absence of reversed plication and of convex hinge plates, the types of hinge plate present being the horizontal, concave, and virgate. The cardinal process throughout is relatively small and the loop relatively short.

Three main stratigraphical conclusions are drawn: (*a*) Aptian and Albian terebratulid faunas are clearly distinct; (*b*) Upper Aptian and Lower Aptian terebratulid faunas can be distinguished in England; (*c*) the Aptian fauna of England is very distinct from that of north-west Europe.

INTRODUCTION

THIS paper is based primarily on museum collections, especially those of London, Cambridge, and Paris, supplemented where possible by field collecting.

Terebratula sella J. de C. Sowerby (1823) was the first species from the English Aptian to be described. Sowerby (*in* Fitton 1836) also described *T. praelonga*. Little further was done in Britain until Davidson (1852–5; 1874; 1884) published his monograph, which still remains the standard work of reference. Other workers who contributed to the study of the group were Meyer (1864), Walker (1867; 1868; 1870), Keeping (1883), and Sahni (1929).

The techniques used have been based on those of Muir-Wood (1934; 1936; 1953), Buckman (1918), and Elliott (personal communication), and consist of serial sectioning, dissection with needles, grinding and dissection combined, and Buckman's burning method of exposing muscle impressions.

Measurements throughout the paper are given in millimetres. The transverse sections have been selected to illustrate, as far as possible, the diagnostic characters of the cardinal process, hinge plates, crura, and transverse lamella of the loop. Copies of all the complete series of sections have been deposited at the British Museum (Natural History). The sections are numbered to give the distance in millimetres from the ventral umbo.

Repositories of specimens are indicated as follows: BM, British Museum (Natural History); SM, Sedgwick Museum, Cambridge; GS, Geological Survey, London; CWW, C. W. Wright's collection, London.

Terminology. The terminology of Thomson (1927) and Muir-Wood (1934; 1936) is used with certain modifications. Definitions given refer only to terms which are new, or of which the connotation has been slightly altered, or which are thought to require further elucidation.

[Palaeontology, Vol. 2, Part 1, 1959, pp. 94–142, pls. 15–18.]

Terms relating to the general shell shape

Orientation. All directions are given with the antero-posterior axis vertical, the umbo uppermost.

Anterior and posterior length. The posterior length is that part of the line of maximum length which lies posterior of the line of maximum width; the anterior length is the corresponding part anterior of that line. The ratio posterior length/anterior length is the *P/A ratio.*

Cardinal and lateral slopes. The cardinal slopes are those parts of the ventral profile which lie between the umbo and the line of maximum width. The lateral slopes are those parts of the ventral profile which lie between the line of greatest width and the outer corners of the median plica. (*Arêtes cardinales* and *arêtes latérales* of d'Archiac 1846.)

Folding. When a shell is thrown into longitudinal ridges and furrows it is described as folded. In either valve of the shell the ridges are referred to as *folds* and the furrows as *sulci* (see plication).

Plication. When the anterior commissure of a shell is thrown into undulations it is said to be plicated. An undulation towards the ventral side is a *sinus*, one towards the dorsal side a *plica*. These do not necessarily imply the presence of folds and sulci on the valve.

The terms used for combinations of sinuses and plicae are those of Buckman (1918) as restated by Thomson (1927) and Muir-Wood (1934; 1936), but some need further explanation when applied to Aptian forms:

Sulciplication, parasulcation, and episulcation. According to Buckman the sulciplicate stage consists of a sinus formed in the centre of a uniplica, the parasulcate stage of sinuses formed on either side of a uniplica and the episulcate stage of sinuses formed on either side and also in the centre of a uniplica. These definitions are easy to follow if the lateral commissure is plane but in most Aptian terebratulids it is strongly arched ventrally. In this case the terms parasulcate or episulcate have not been used unless there is a lateral sinus present which can be distinguished from the general arch of the lateral commissure.

Quadriplication. This term is used only where four plicae in the sense defined above can be counted.

Profile. The ventral profile is the outline of the shell in ventral view. The lateral profile is the outline of the shell when viewed from the side.

Terms relating to the beak

Beak. That part of the pedicle valve which lies posterior to the extreme posterior end of the brachial valve.

Beak angle. This has been measured by looking at the lateral profile of the shell, with the *commissural plane* vertical, this commissural plane being defined as the plane containing the dorsal umbo and those points on the anterior commissure which come midway between the summits of the highest plicae and the bases of the lowest sinuses. In this view the line bisecting the beak can be seen to make an external angle with the commissural plane, defined as the beak angle (text-fig. 1).

It has been customary to describe the beak as straight, erect, sub-erect, or incurved according to the beak angle, but these terms have been defined in different ways and used in almost opposite senses by different authors. In specific descriptions the terminology used here for the beak follows that of Thomson (1927) but the terms have been more rigidly defined, thus: *straight*, beak angle 0–20°; *nearly straight*, 20–30°; *sub-erect*, 30–70°; *erect*, 70–90°; *incurved*, more than 90°.

Produced. A produced beak is one that protrudes markedly beyond the posterior end of the brachial valve but is narrow and conical. 'Produced' is not synonymous with 'long', since a long beak may also be broad, but quite a short beak may be produced.

Umbo. The extreme posterior end of a valve. The true umbo is not usually visible in terebratulids, since that of the brachial valve is usually just hidden by the anterior border of the symphytium and that of the pedicle valve is, except in hypothyrid types, perforated by the foramen. It seems permissible, however, to refer to the most posterior visible part of the valve as the umbo.

Angle of Truncation. The angle made by the intersection of the plane containing the rim of the foramen with the lateral profile of the pedicle valve in the umbonal region.

Terms relating to the cardinalia

Hinge plates. The following terms are introduced to describe the types of hinge plates found: *concave*, hinge plate curved, concave towards the pedicle valve; *virgate*, hinge plate V-shaped in cross-

section, concave towards the pedicle valve; *horizontal*, hinge plate not curved but flat, more or less parallel to the commissural plane; *keeled*, part of the hinge plate is produced into a sharp edge, projecting dorsalwards; *tapering*, hinge plate becomes thinner inwards, its inner margin sharp; *clubbed*, hinge plate becomes thicker inwards, its inner margin in particular thickened and blunt or rounded; *piped*, hinge plate becomes thinner inwards but its inner margin is finished off with a narrow rounded thickened rim. A virgate hinge plate is divisible into two parts, the outer lamina from the socket ridge to the virgation and the inner lamina on the inner (median) side of the virgation. In text-fig. 1 these terms are illustrated diagrammatically as seen in transverse section.

Flange. In some species the inner lamina of the hinge plate passes anteriorly into the crural process while the outer lamina continues anteriorly along the outer side of the base of the crural process as a *flange*. This flange may not be attached to the base of the crus but slightly above it so that the crus extends below the flange as a *crural keel*. In some species the keel can be traced back into the carinalia, giving a keeled hinge plate, while in others it is developed only in the region of the crura (text-figs. 1 and 14).

GENERAL CHARACTERS OF ENGLISH APTIAN TEREBRATULIDAE

Shell-shape and plication. All species are biconvex in the adult stage, varying from elongated to transverse and from depressed to highly compressed. The shell is usually folded to some extent.

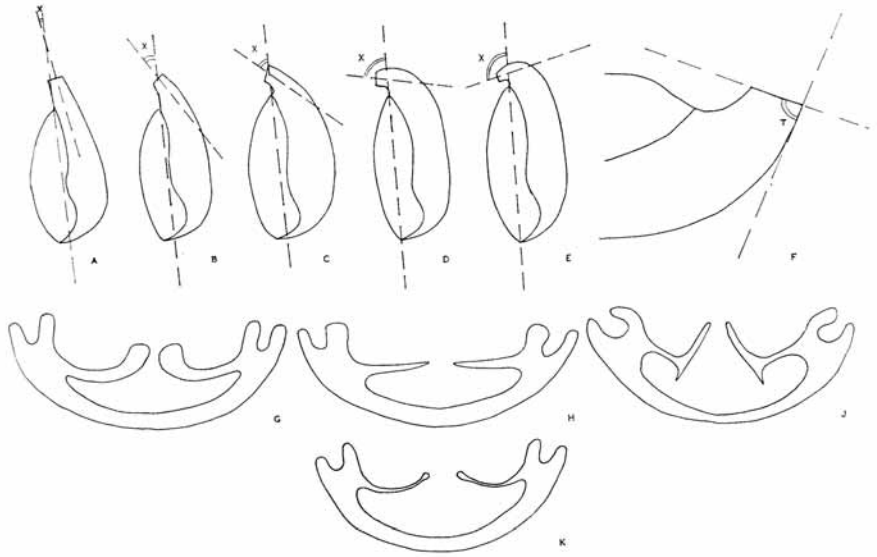
In the anterior commissure reversed plication of the intraplicate, paraplicate, or antiplicate types is never present in British species, although characteristic of a few European Lower Cretaceous species. The types of plication which may occur are the rectimarginate, sulcate, uniplicate, sulciplicate, parasulcate, episulcate, and quadriplicate stages (Thomson 1927, p. 58). The development of the commissure during ontogeny does not always follow the lines indicated by Buckman; for example, he regarded both the sulciplicate and the parasulcate stages as derived through a uniplicate phase but on different lines of development, of which the parasulcate can lead to the episulcate stage by the formation of a sinus in the median plica. In *Sellithyris sella*, however, both sulciplicate and parasulcate stages occur as variants of the one species and are both reached not through a uniplicate stage but directly from the rectimarginate. Muir-Wood (1936) notes a similar case in *Wattonithyris*. The sulciplicate stage is the commonest among the Aptian terebratulids but *Sellithyris* becomes episulcate through the addition of lateral sinuses to the sulciplicate stage. Quadriplication is found only in gerontic individuals of *Sellithyris upwarensis* and even there rarely; it is reached by adding external plicae to the lateral sinuses of the episulcate stage.

The shell is smooth, except for growth lines of variable prominence. Faint closely spaced radial striations are present, not visible on the outside of the shell and hence not to be confused with capillation, but often visible on specimens which have the outermost layer of shell worn away and upon calcite internal casts; these striae are not diagnostic of any particular species but are present in all Aptian species examined.

Beak and foramen. The beak angle lies between straight and erect, the former being rare. The foramen is in nearly all cases marginate but not labiate except in *Praelongithyris* and occasionally in *Cyrtothyris*. Forms with short beaks, such as *Rhombothyris*, have an attrite foramen.

The interior of the brachial valve. The cardinal process is always present but is typically small compared with that seen in some Upper Cretaceous genera. The hinge plates are continuous with the base of the cardinal process and are divided throughout.

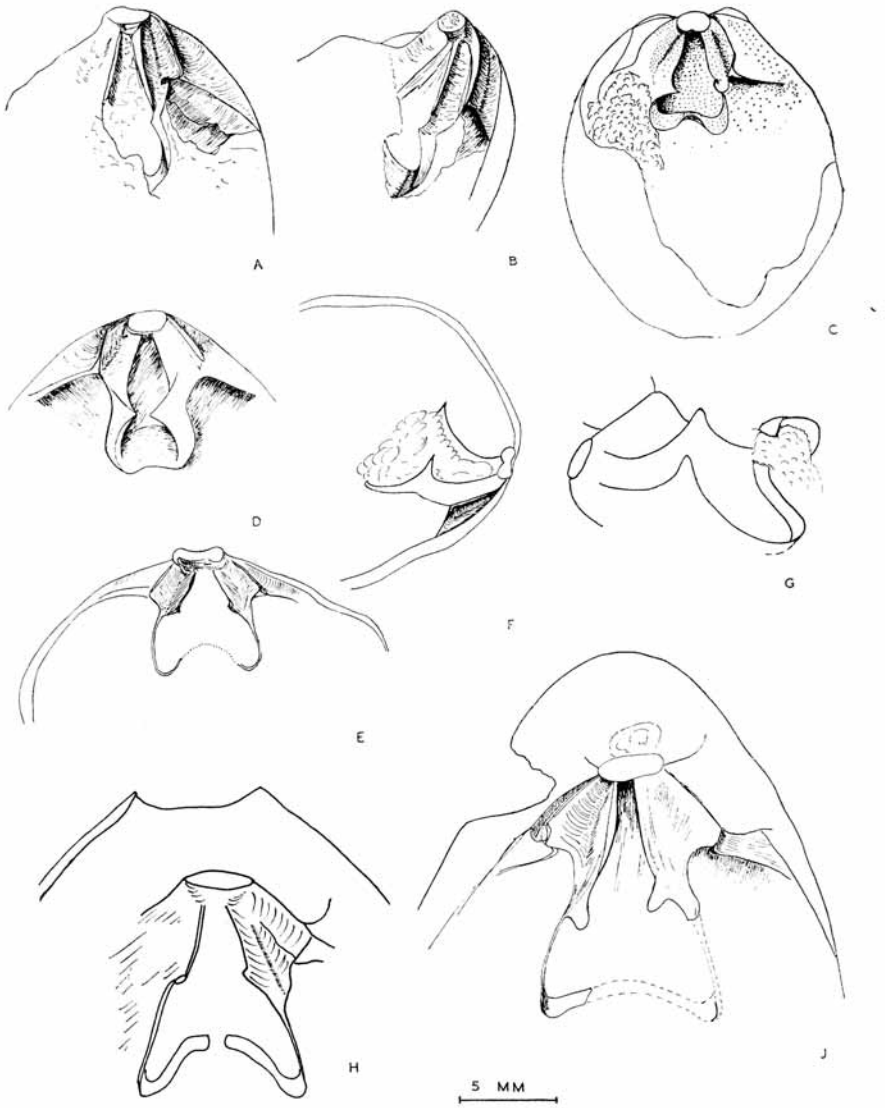
Callus is usually deposited at the junction of the cardinal process with the hinge plates and enables the originally small cardinal process to keep pace in growth with the growth of the shell. The callus is punctate, its outward growth taking place in an irregular manner so that the outer boundary of the callus frequently presents an indefinite, furry appearance in section. The cardinal process is thus enlarged by callus deposition so that



TEXT-FIG. 1. A–E, The Beak Angle (X). A, Straight beak; B, nearly straight; C, sub-erect; D, erect; E, incurved. F, The Angle of Truncation (T). G–K, Terms relating to the hinge plates. Diagrammatic representations of transverse sections through terebratulids with G, concave clubbed; H, horizontal tapering; J, virgate keeled; K, concave piped hinge plates.

it comes to enclose the posterior ends of the hinge plates, but since the callus is less dense than the primary shell material the incipient hinge plates and sockets may sometimes be distinguished, enclosed by callus, in the transverse sections (text-figs. 7, 20).

The divided hinge plates are in no cases convex and are horizontal in very few species, most forms possessing concave or virgate hinge plates. The crural processes are direct continuations of the hinge plates and are blade-shaped structures, commonly bending inwards and anteriorly towards their pointed distal ends. The loop has the same general shape in all species, directly continuing the crural bases which distally become concave inwards and at their distal extremities become recurved to form the transverse lamella in such a way that the inner surface of the descending lamella is continuous with the outer surface of the transverse lamella, no ascending lamella being present. The loop is short—in all species less than half the length of the shell—the ratio between total length of shell and the distance from the dorsal umbo to distal end of loop varying from 2·09 in *Praelongithyris praelongiforma* to 3·17 in *Sellithyris coxwellensis*. The ratio between the total



TEXT-FIG. 2. Camera lucida drawings of dissections of Aptian terebratulids. A, B, *Rhombothyris extensa* (Meyer), showing cardinalia and part of the loop; B, seen obliquely. SM B.80770, Brickhill, Bucks. C, D, *Platythyris comptonensis* nov., showing cardinalia and loop. C, SM B.80768, Brickhill; D, SM B.80766, Upware. E, F, *Sellithyris sella* (J. de C. Sowerby), showing cardinalia and loop (loop partly restored; F, seen obliquely. BM BB.16206, Ferruginous Sands, Atherfield, Isle of Wight. G, H, *Cyrtothyris cyrta* (Walker), showing hinge plates, crura and loop (incomplete), BM BB. 16242, Upware, Cambs. G, seen obliquely. J, *Praelongithyris praelongiforma* nov., showing cardinalia and loop (incomplete). SM B.80779, Upware.

width of shell and the maximum width of loop varies from 2·60 in *Rhombothyris extensa* and *Cyrtothyris dallasi* to 4·66 in *Platythyris comptonensis*.

The inner socket ridges are continuous at their posterior ends with the cardinal process and tend to be large and massive, especially in *Rhombothyris*. The teeth and sockets are never crenulate; denticula and accessory sockets are sometimes present but are developed to varying degrees within one species. The angle of insertion of the teeth varies within one species according to the proportions of the shell, thicker and more compressed variants having teeth at a greater angle to the commissural plane than thinner, more depressed forms. The median dorsal septum or 'euseptoidum' (Muir-Wood 1934, p. 529) is constantly well developed only in *Platythyris*; where present in other genera it is usually most marked between the widest parts of the dorsal muscle scars. The muscle scars are seldom very clearly visible, especially those in the pedicle valve; the impressions are not deeply incised into the floor of the valve except in *Rhombothyris*, and in nearly every case it is very difficult to distinguish the posterior adductors, as Buckman (1918) remarks apropos of Cretaceous terebratulids.

SYSTEMATIC DESCRIPTIONS

Introductory. Genera. The chief characters used in dividing the Aptian Terebratulidae into genera are internal. The English species are divisible into genera based primarily on the form of the hinge plates, crura and loop and the shape and relationships of the dorsal muscle scars. These characters can in most cases be correlated with external characters such as the form of the beak and the ontogeny of the shell shape, especially of the plication.

The generic classification adopted here was foreshadowed to some extent by Keeping (1883, p. 23) in a table based entirely on external appearance of the species. The grouping shown in his table, which was not intended to be phylogenetic, has been broadly confirmed by study of the internal characters except that Keeping regarded the *microtrema-extensa-meyeri* series (*Rhombothyris*) as closely related to '*Terebratula praelonga*' (*Praelongithyris*).

Species. Specific diagnosis is based mainly upon external form, including in particular: characters of the beak, such as length, angle, and degree of production; sharpness of the beak ridges; size, shape, and distinctness of the symphytium; size of the foramen, its position relative to the beak ridges and the angle of truncation; P/A ratio; course of the lateral commissure; development of plication; degree of folding of the shell; type of shell ornamentation.

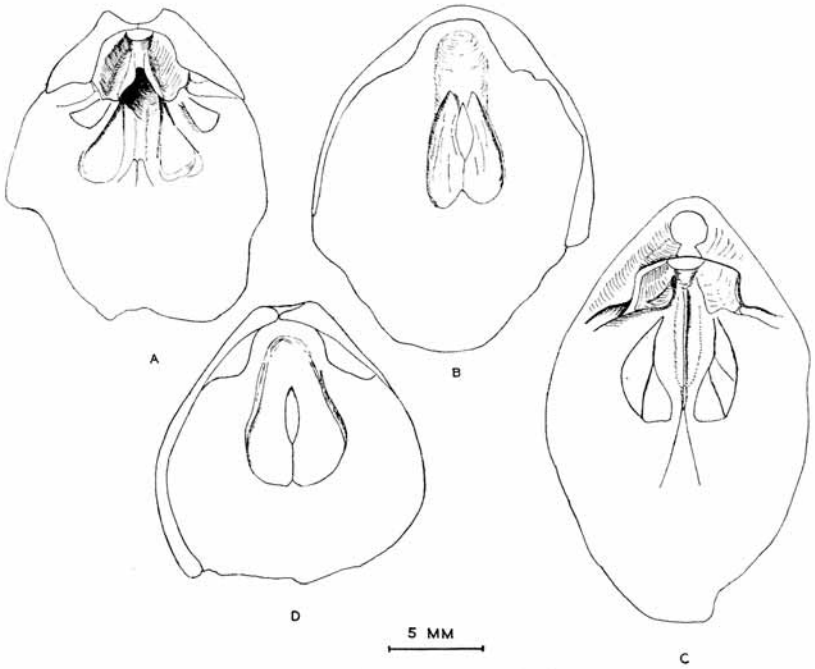
Internal characters may assist in specific classification, for example the proportions of the hinge plates relative to the size of the shell, the relations of the crural flange and keel to the crura and hinge plates, and the degree of incision of the dorsal muscle scars.

Genus RHOMBOTHYRIS gen. nov.

Type species *Terebratula extensa* Meyer 1864

Diagnosis. Beak very short, nearly straight to sub-erect. Beak ridges poorly defined except immediately adjacent to the foramen. Foramen mesothyrid, attrite, somewhat

marginate; angle of truncation 105–110°. Symphytium very short. Shell elongate-oval. Development of anterior commissure rectimarginate to sulcate or rectimarginate to uniplicate, thence to sulciplicate.



TEXT-FIG. 3. Camera lucida drawings of muscle impressions in Aptian terebratulids. A, *Rhombothyris extensa* (Meyer), interior of brachial valve with hinge plates *in situ* but crura and loop removed. The posterior and anterior adductor scars are separate. BM BB.16236, CWW Coll., Bargate Beds, Compton, Surrey. B, *Rhombothyris extensa* (Meyer), interior of pedicle valve, showing adductor, diductor and ventral pedicle adjustor scars. BM BB.16237, CWW Coll., Bargate Beds, Compton, Surrey. C, *Platythyris comptonensis* nov., last stage of dissection showing interior of brachial valve and part of pedicle valve, crura and loop removed and hinge plates incomplete. The strong euseptoidum shows well; the posterior and anterior adductor scars are closely adjoined. BM BB.16238, CWW Coll., Bargate Beds, Compton, Surrey. D, *Platythyris comptonensis* nov., interior of pedicle valve, showing adductor and diductor scars, the latter continuous with the ventral pedicle adjustor scar. SM B.80769, Brickhill.

Hinge teeth inserted at 40–70° to commissural plane; accessory articulation may be well developed. Hinge plates concave, clubbed. Inner socket ridges rather massive. Anterior adductor muscle impressions in brachial valve well incised; elongated pear-shaped. Posterior adductor impressions on postero-lateral sides of anterior adductors but very difficult to see. Euseptoidum absent or weakly developed.

Remarks. The name refers to the rhombic shape of the rim of the foramen in its usual

attrite condition, the telate condition being very faintly indicated only in some very young individuals. No species from outside England have been seen which could be referred to this genus.

Rhombothyris extensa (Meyer)

Plate 15, figs. 1, 2; text-figs. 2–4

Terebratula extensa Meyer 1864, p. 252, pl. 12, figs. 1–4.
Terebratula extensa Meyer; Walker 1868, p. 404, pl. 18, figs. 5–5*a*.
Terebratula extensa Meyer; Davidson 1874, p. 43, pl. 5, figs. 22–24.

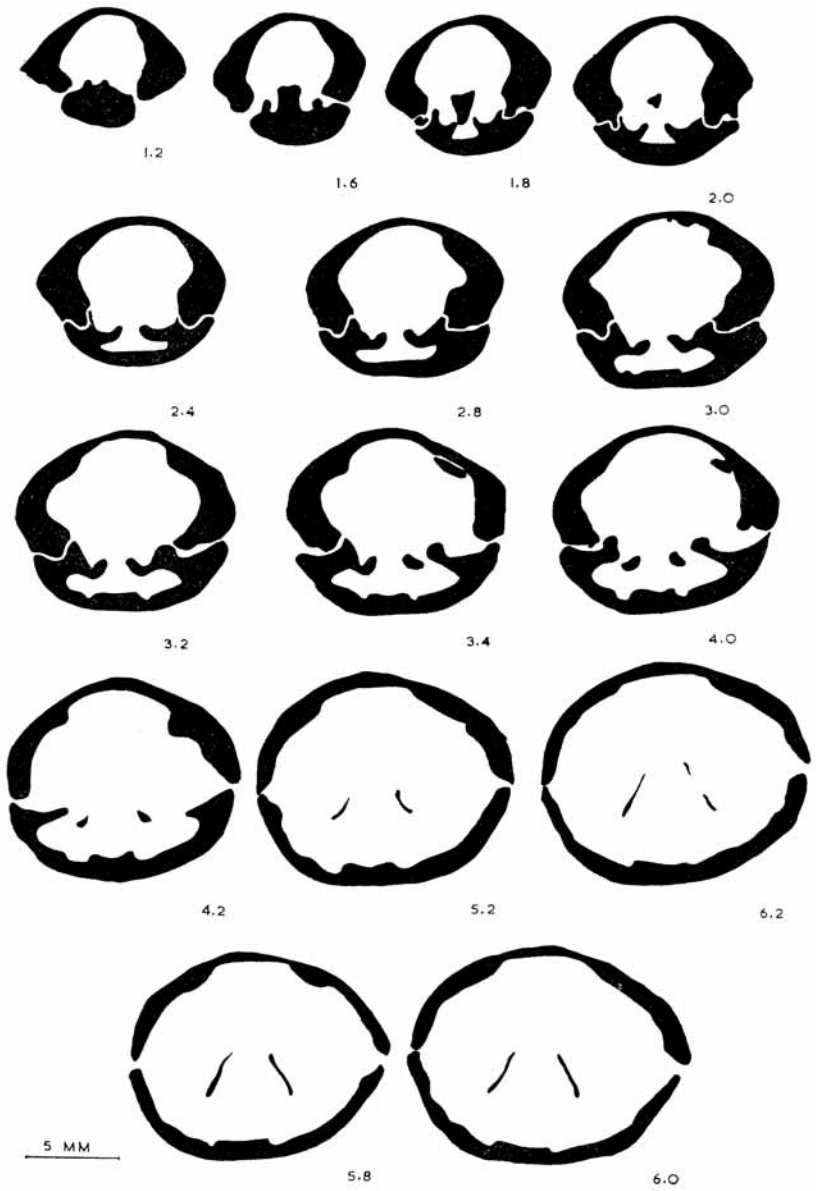
Type. Meyer's three syntypes SM B.16738–40. B.16739, Bargate Pebble Beds, Tuesley, Surrey, is chosen lectotype (dimensions: length 26, breadth 13, thickness 12).

Diagnosis. Elongate oval *Rhombothyris* with P/A ratio about 2. Brachial valve with greatest convexity near to umbo, pedicle valve regularly convex with maximum convexity about the centre. Beak nearly straight. Angle of truncation *c*. 105°; foramen attrite. Symphytium wide but short. Development of anterior commissure sulcate to rectimarginate to uniplicate, and to sulciplicate in some cases. Cardinal process oval. Inner socket ridges massive. In brachial valve anterior adductor muscle scars elongated pear-shaped; posterior portion of them deeply incised. Posterior adductor scars obscure smooth areas on postero-lateral sides of anterior adductors. Euseptoidum absent or poorly developed.

Description. In the typical uniplicate forms the brachial valve usually shows a low but distinct fold extending back about half the length of the valve, but there is no corresponding sulcus in the pedicle valve. On both sides of the fold the surface of the valve appears very slightly concave, giving a pinched appearance; in biplicate forms a shallow sulcus appears in the centre of the fold. A characteristic feature is the strong, sometimes almost bulbous convexity of the brachial valve near the umbo, but a median groove may be developed in this part of the valve; the groove is occasionally well developed, beginning about 1 mm. from the umbo and extending anteriorly about 5 mm. In lateral profile some individuals, particularly from the Bargate Beds, show a concavity in the anterior part of the brachial valve, the pedicle valve being carried down by the uniplication of the anterior commissure to form an overhanging beak.

In ventral profile the pedicle valve may be squarish anteriorly but many specimens are perfectly rounded. In many the pedicle valve is very slightly carinate at and near the umbo which, together with the frequent presence of a groove in the earlier-formed part of the brachial valve, suggests that the neanic stage of this species tends to be sulcate, although in the majority of individuals the sulcate stage is missing.

Remarks. Variation occurs in three main directions: (1) towards biplication by sulciplication—the biplicate forms sometimes resemble *R. microtrema* but differ from it in the feebler development of biplication, the absence of strong lateral compression and the absence of any anterior thickening; (2) towards loss of the uniplicate stage, giving a rectimarginate to slightly sulcate adult shell not easily distinguishable from *R. meyeri* but differing from that species in having a smaller foramen and in being less distinctly sulcate; (3) towards a broad oval form sometimes mistaken for '*Terebratula depressa*'



TEXT-FIG. 4. Transverse sections through *Rhombothyris extensa* (Meyer). The cardinal process (enlarged by callus) is seen in the first four sections, the concave clubbed hinge plates best at 3·0, the deep muscle impressions at 4·0, and the crural processes in the last three sections. BM BB.16235, CWW Coll., Bargate Beds, Compton, Surrey.

in the past but identifiable as *R. extensa* by the deep incision of, and form of, the dorsal muscle scars.

Distribution. Abundant at Upware and Brickhill and the commonest fossil in the Bargate Beds of Surrey. It is rare at Shanklin, in the '*Exogyra*' Beds, which Fitton (Sowerby 1836) correlated with Group XIII of the Atherfield coast section; a crushed specimen from Sevenoaks (BM B.21949) probably belongs to this species.

Rhombothyris microtrema (Walker)

Plate 15, figs. 3–5; text-fig. 5

Terebratula microtrema Walker 1868, p. 401, pl. 19, figs. 7–7*c*, 8–8*a*.
Terebratula microtrema Walker; Davidson 1874, p. 37, pl. 5, figs. 18, 18*a–c*, 21.

Type. Walker figured two specimens, of which that figured as pl. 19, fig. 7 (BM BB.16216), Upware, Cambridgeshire, is designated lectotype (dimensions: length 30, breadth 20·25, thickness 19).

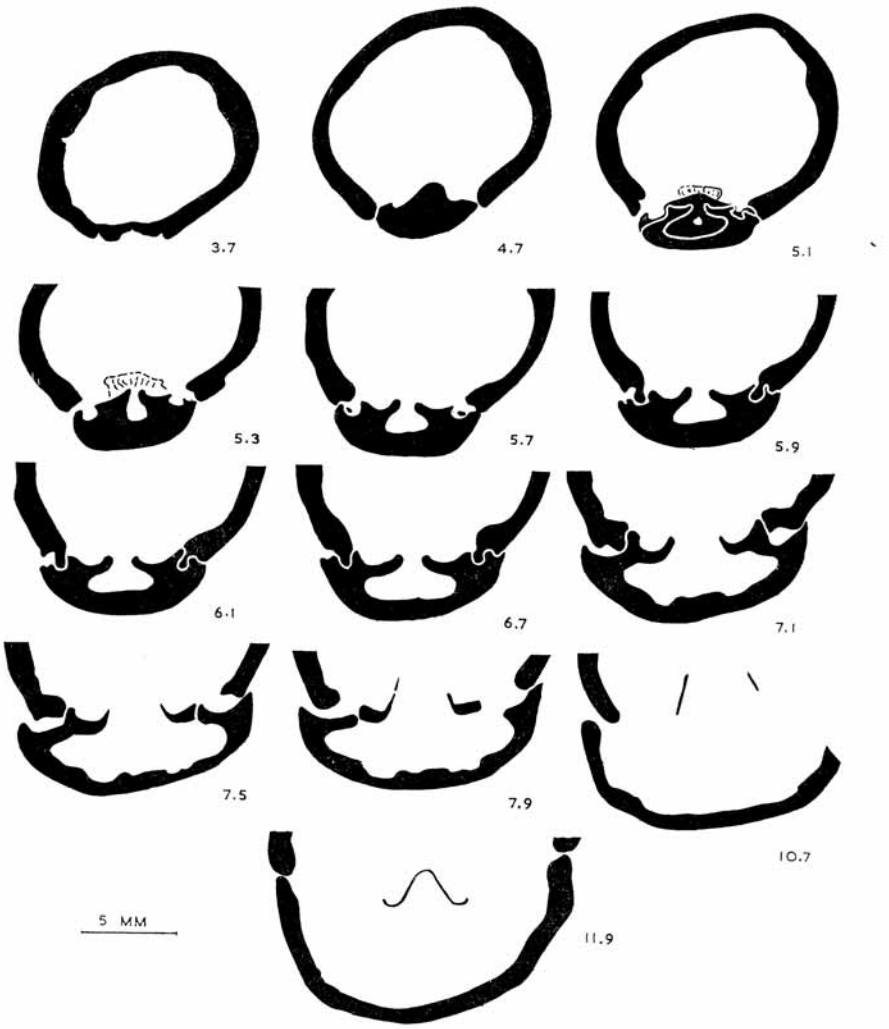
Diagnosis. Rhombothyris with ventral profile oval, truncated anteriorly, to rounded triangular. P/A ratio more than 2. Brachial valve has greatest convexity near umbo, strongly folded anteriorly. Pedicle valve very slightly carinate near umbo, posterior part of valve regularly convex, anterior part strongly folded. Both valves laterally compressed. Beak short, sub-erect. Angle of truncation *c.* 110°. Foramen attrite. Symphytium wide but short. Development of anterior commissure rectimarginate to uniplicate to strongly sulciplicate. Cardinal process oval. Crural processes high, reaching half-way to internal surface of pedicle valve. Loop narrower than space between anterior ends of inner socket ridges. Muscle scars deeply incised.

Description. The laterally compressed appearance, due to the vertical parallel or subparallel sides, is characteristic and may be sufficient to make the shell thicker than broad, especially in old individuals, which also show thickening of the anterior region. Young individuals are usually thinner in proportion to their breadth.

Although rare individuals do not pass beyond the uniplicate stage, sulciplication is typically well developed, with the apex of the median sinus reaching to or beyond the level of the lateral commissure. The plication of the commissure is typically reflected to some extent in folding of the shell, but this does not affect a very large part of the valves; thus in adult specimens not more than the anterior third of each valve is affected, usually less; in neanic specimens only the extreme anterior end is affected. Adult individuals are often deformed and asymmetrical.

Since grooving of the posterior convex part of the brachial valve has not been seen it seems that this species does not normally pass through a sulcate stage, if the doubtful premise that all changes during growth are retained in the adult shell be accepted.

Remarks. The chief variation is towards a uniplicate or only very slightly sulciplicate form with a resemblance to *R. extensa.* Some specimens in this condition have a concavity in the anterior part of the brachial valve as seen in lateral profile, giving a projecting beak-like appearance to the anterior end, as in some specimens of *R. extensa. R. microtrema*, however, is always thicker in proportion to its breadth than *R. extensa*



TEXT-FIG. 5. Transverse sections through *Rhombothyris microtrema* (Walker). 3·7 shows the symphytium, 4·7 the cardinal process. The hinge plates are enclosed by callus at 5·1 but are concave and clubbed at 6·1–6·7. The crural processes are seen at 7·9 and 10·7 and the transverse lamella of the loop at 11·9. SM B.80771, Brickhill.

and always shows some recognizable sign of the characteristic laterally compressed appearance.

R. microtrema is distinguished from *Praelongithyris praelongiforma* by its laterally compressed appearance and sub-parallel sides, its much blunter and less produced beak, its mesothyrid foramen and smaller angle of truncation. In addition the symphytium is much shorter and the folds and sulci affect a smaller proportion of the surface of the valves in *R. microtrema* than in *P. praelongiforma*.

Distribution. Abundant at Upware and Brickhill. Meyer's (1868*a*) specimens from the Bargate Beds (SM B.16773–8) are regarded as *R. extensa* and those from Shanklin (SM B. 14911–2) as *Praelongithyris praelongiforma* (Davidson 1874). The species has not been found at or from Faringdon, Meyer's record from there being based upon a single valve (Davidson 1874). Keeping's (1883) specimens from Schöppenstedt, Brunswick (SM F4617–18), appear to be long-looped.

Rhombothyris meyeri (Walker)

Plate 15, fig. 6; text-fig. 6

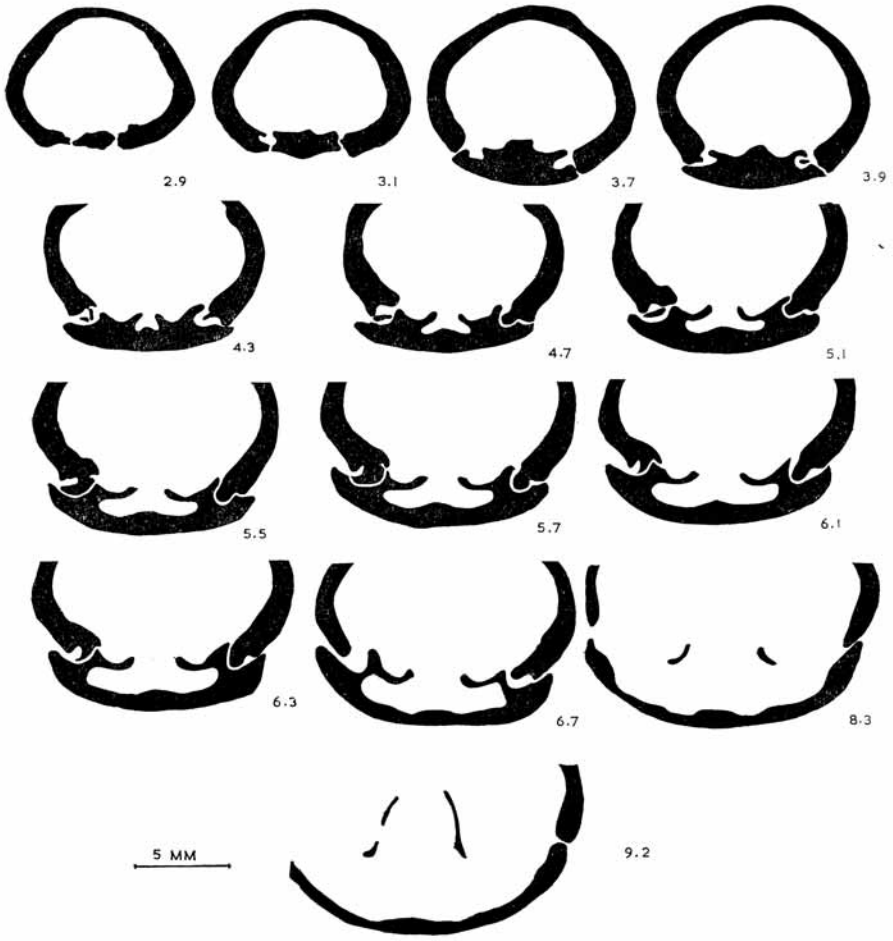
Terebratula meyeri Walker 1868, p. 401, pl. 19, figs, 6–6*b*.
Terebratula meyeri Walker; Davidson 1874, p. 44, pl. 3, figs. 6–8.

Holotype. BM 67598, Upware, Cambridgeshire (dimensions: length 36, breadth 28·5, thickness 20·5).

Diagnosis. Elongate oval *Rhombothyris*, squarely truncated anteriorly; P/A ratio about 1. Valves fairly regularly convex; greatest convexity of brachial valve about the middle, of pedicle valve slightly nearer the umbo. Pedicle valve very slightly carinate near umbo. Beak nearly straight. Angle of truncation *c*. 105°. Foramen large, transverse, attrite. Symphytium wide but very short. Development of anterior commissure rectimarginate to sulcate. Cardinal process prominent, slightly bifid. Loop of rounded triangular shape, width approximately equal to distance between anterior ends of socket ridges.

Description. The foramen is of the same type as that of *R. extensa* and *R. microtrema* but is larger and more transverse. In some ways the shell resembles that of *R. extensa* in reverse; in *R. extensa* the pedicle valve is regularly convex while the brachial valve is most convex near the umbo and develops a fold anteriorly, in *R. meyeri* the brachial valve is regularly convex while the pedicle valve tends to be most convex nearer to the umbo than half-way and develops a fold anteriorly. The brachial valve does not normally show a sulcus corresponding to the sinus in the commissure but more commonly has a fold which runs up into the sinus giving to the anterior end a characteristic 'bulldog' appearance. Rare specimens may show a sulcus in the extreme anterior part of the brachial valve. The well-developed sulcate condition is seen only in fully adult or gerontic individuals, most specimens being rectimarginate and there is no trace of any grooving of the brachial valve such as is seen in *R. extensa*. Typically *R. meyeri* is marked by prominent concentric growth-lines which cluster at the anterior end of gerontic specimens to give it a blunt and thickened appearance.

Remarks. The typical form is characterized by its large transverse foramen, blunt



TEXT-FIG. 6. Transverse sections through *Rhombothyris meyeri* (Walker). The cardinal process (enlarged by callus) is seen in the first four sections, the concave clubbed hinge plates at 5·5–6·3 (the peculiar tooth structure here is probably pathological). The muscle impressions can be seen at 8·3 and the crural processes at 9·2. SM B.80772, Upware.

sulcate anterior, and well-marked growth-lines. The species is very close to *R. extensa* and an elongated rectimarginate individual of *R. meyeri* may resemble a rectimarginate variety of *R. extensa*, the essential distinction lying in the foramen. Typically, however, *R. meyeri* is broader in proportion to its length than *R. extensa*.

Thickened individuals may resemble *R. microtrema* but never show any biplication; in addition, in *R. microtrema* the foramen is relatively smaller and the sides of the shell

more compressed. Blunt-fronted, almost rectimarginate varieties of *Praelongithyris praelongiforma* have been mistaken for *R. meyeri* but the foramen in the former is very different and the beak has quite a different shape. Within the typical forms of *R. meyeri* the relative proportions of length, breadth, and thickness undergo a certain amount of minor variation.

Distribution. R. meyeri was fairly abundant at Upware but has not been found at Brickhill. Specimens recorded by Meyer as rare in the Bargate Beds of Surrey have on re-examination been found to be *R. extensa.*

Rhombothyris conica sp. nov.

Plate 15, figs. 7, 8; text-fig. 7

Holotype. BM BB.16217 (Walker Coll.), Brickhill, Buckinghamshire (dimensions: length 32, breadth 22, thickness 19).

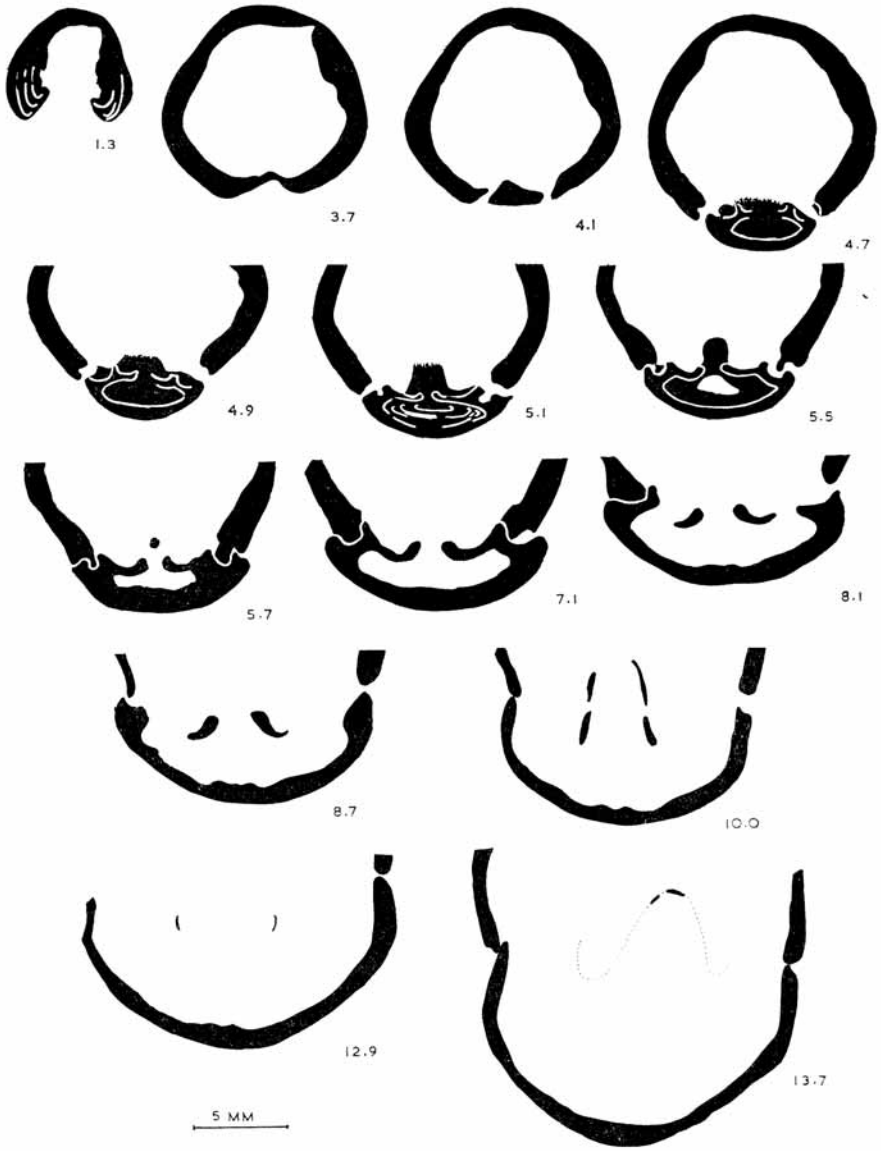
Diagnosis. Rhombothyris of oval ventral profile, more or less elongated. P/A ratio slightly greater than 1. Pedicle valve uniformly convex, brachial valve most convex in posterior half; greatest thickness slightly posterior to mid-line. Anterior commissure sulciplicate with sharp to angular median sinus, apex of which is level with lateral commissure. Beak short, nearly straight, rather narrow and conical; beak ridges rounded but visible. Foramen fairly small, circular, slightly attrite; angle of truncation *c.* 110°. Development of anterior commissure rectimarginate to uniplicate to sulciplicate. Cardinal process small, bifid.

Description. The distinctive characters of this species are those of the beak and foramen and the type of plication. Variation extends in two main directions: (1) towards a broad form, almost as broad as long and rather bluntly truncated anteriorly in ventral profile, tending to become obese in the posterior part of the brachial valve; (2) towards a thick form which may become thicker than wide while retaining the more typical elongated shape; this form tends to possess a more uniformly convex lateral profile in the brachial valve. The characteristics of the beak and the anterior commissure are retained.

Many neanic specimens are distinctly grooved in the posterior part of the brachial valve and carinate in the umbonal region of the pedicle valve, suggesting a nepionic sulcate stage, but no nepionic sulcate specimens have been seen and individuals of about 12 mm. long are uniplicate or rectimarginate; thus the grooving may be a subsequent modification.

Remarks. R. conica differs from *R. extensa* in the narrower and more conical beak and smaller foramen, the well-developed median sinus of the anterior commissure and the tendency to gerontic thickening, giving a slightly compressed appearance, and especially to gerontic thickening of the anterior part of the shell, not seen in *R. extensa.*

R. conica can be distinguished from *R. microtrema* in that the latter is more noticeably compressed, possesses better-developed biplication at an equivalent growth-stage (lacking the sharp emphasis upon the median sinus over the lateral plicae which *R. conica* shows), and has a slightly larger foramen and broader beak. From *R. meyeri* the chief points of distinction are: (1) *R. meyeri* is sulcate, *R. conica* sulciplicate as an



TEXT-FIG. 7. Transverse sections through *Rhombothyris conica* nov. The foraminal margin is shown at 1·3, the symphytium at 3·7, the cardinal process (enlarged by callus to enclose the hinge plates) at 4·1–5·5. The concave clubbed hinge plates can be seen at 7·1, the muscle impressions at 8·7, crural processes at 10·0, descending lamellae of the loop at 12·9, and transverse lamella at 13·7. BM BB.16200, Brickhill.

adult; (2) the shell of *R. conica* shows slight folding in the extreme anterior part, hardly ever seen in *R. meyeri*; (3) the beak is narrower and more conical and the foramen smaller in *R. conica* than in *R. meyeri*. From *Praelongithyris praelongiforma* this species differs in the characters of the beak and foramen and the shape of the anterior commissure.

Distribution. Brickhill only.

Genus PLATYTHYRIS gen. nov.

Type species *P. comptonensis* sp. nov. (= *Terebratula moutoniana* auctt. pars)

Diagnosis. Beak very short to fairly short, sub-erect; beak ridges rounded and ill-defined. Foramen mesothyrid to permesothyrid; angle of truncation 115–120°. Symphytium very short. Shell elongate, oval, or pear-shaped; maximum convexity posterior to mid-line. Development of anterior commissure rectimarginate to uniplicate, thence rarely to sulciplicate. Cardinal process small. Hinge plates horizontal, tapering. Crural processes strongly curved inwards. Loop short and compact, close beneath the crura; arch of transverse lamella low. In brachial valve posterior adductor scars ovoid, with outline concave inwards; anterior adductors triangular, continuous with posterior impressions on inner side of anterior ends of the latter. In pedicle valve adductors form one median elliptical scar. Diductors large, enclosing adductors, not clearly distinguishable from ventral pedicle adjustor scar, which forms a rounded depression. Euseptoidum very well developed and continuous from base of the cardinal process almost to the anterior end of the muscle scars.

Remarks. The name refers to the characteristic horizontal hinge plates. No species referable to the genus are known with certainty from outside England.

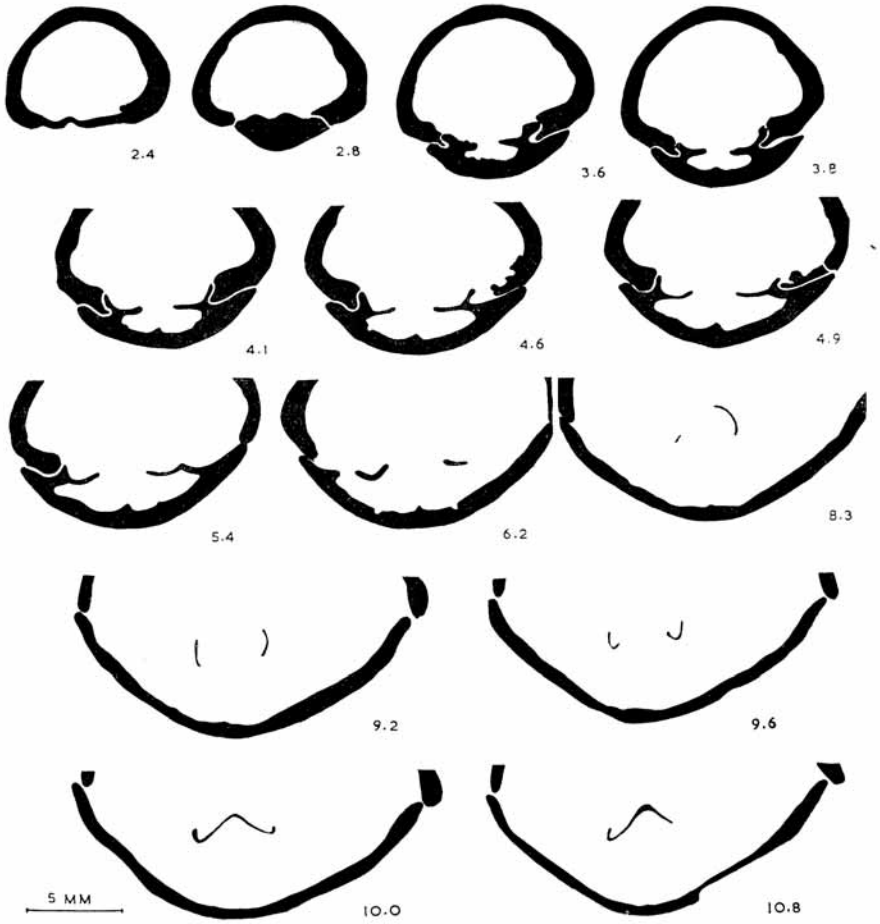
Platythyris comptonensis sp. nov.

Plate 15, figs. 9–11; text-figs. 2, 3, 8

Waldheimia moutoniana (d'Orb.); Meyer 1864, p. 251, pl. 12, figs. 14*a–c*.
Terebratula moutoniana d'Orb.; Walker 1868, p. 403, pl. 18, figs. 6–6*b*.
Terebratula moutoniana d'Orb.?; Davidson 1874, p. 42, pl. 4, figs. 11–13.

Holotype. BM BB.16230, Bargate Beds, Compton, Surrey (dimensions: length 24, breadth 16·5, thickness 13).

Diagnosis. *Platythyris* of elongated pear-shape in ventral profile. P/A ratio more than 1. Apical angle acute; cardinal slopes straight or very slightly convex, ventral profile anterior to line of maximum breadth a parabolic curve. Brachial valve uniformly convex but with a broad median fold in about the anterior third. Pedicle valve has maximum convexity distinctly in posterior half, anterior half somewhat flattened. Brachial valve more obese than ventral. Beak very short. Foramen fairly large, circular, slightly permesothyrid, usually attrite; angle of truncation *c*. 115°. Symphytium short. Lateral commissure much arched and anterior commissure strongly uniplicate. Development of anterior commissure rectimarginate to uniplicate. Cardinal process oval. Loop considerably narrower than space between anterior ends of socket ridges.



TEXT-FIG. 8. Transverse sections through *Platythyris comptonensis* nov. The symphytium is shown at 2·4, cardinal process at 2·8, horizontal tapering hinge plates at 3·6–4·9, strong euseptoidum at 3·8–8·3, incurved crural processes at 8·3, descending lamellae of the loop at 9·2 and 9·6, and the low-arched transverse lamella at 10·0–10·8. SM B.80767, Upware.

Description. This species has a very uniform and characteristic general shape, the main elements of which are: (1) the ventral profile, which is reminiscent of a triangle plus a parabola, representing the posterior and anterior parts respectively; (2) the lateral profile of the pedicle valve, the obese brachial valve seeming almost to enclose the pedicle valve by the strong arching of the lateral commissure; (3) the beak and symphytium characters.

Variations affect the relative proportions of length, breadth, and thickness, not the elements of the general shape just mentioned. Thus Upware and Brickhill specimens tend to be thicker (thickness up to 0·9 of breadth), specimens from the Weald to be wider and flatter. Brickhill specimens tend to be smaller, more elongated and narrower and more compressed anteriorly than those from any other locality.

Very rarely specimens from Upware and Brickhill have a slight median sulcus, giving a gerontic sulciplicate stage.

Remarks. This species has always been identified, with or without a mark of interrogation, with *Terebratula moutoniana* d'Orbigny 1849, a species from the Upper Neocomian and Aptian of Western Europe (Lankester 1863; Meyer 1864; Walker 1868; Davidson 1874; Teall 1875; Lamplugh and Walker 1903; Dines and Edmunds 1929; Wright 1939). Nevertheless, this English form seems to be quite distinct from that described by d'Orbigny. Several points in his description refer to characters never seen in English forms; the most important is the statement, borne out by his figure, that the beak is strongly recurved; Schloenbach (1866) also insists on this character. D'Orbigny's statement that the pedicle valve is more convex than the brachial, repeated by Pictet (1872), is also quite out of accord with the English species. The ventral profile is different, d'Orbigny's figures showing a regularly oval shape with the greatest width at about the mid-line and shallow plication; the anterior end is somewhat truncated in the continental form, boldly produced in the English. D'Orbigny's specimens and numerous topotype specimens have been examined and found to differ markedly from the English species in the particulars mentioned above. The English forms are therefore regarded as forming a separate species, *P. comptonensis*, which differs externally from *T. moutoniana* as discussed above and internally in having horizontal hinge plates, whereas those of *T. moutoniana* are keeled. *P. comptonensis* differs from *Sellithyris sella* externally in having a shorter and less incurved beak and in lacking any true sinuses of the commissure or any sulcus in the pedicle valve; from *Cyrtothyris uniplicata* in having a much shorter beak and symphytium and in having a deeper brachial valve compared with the pedicle valve.

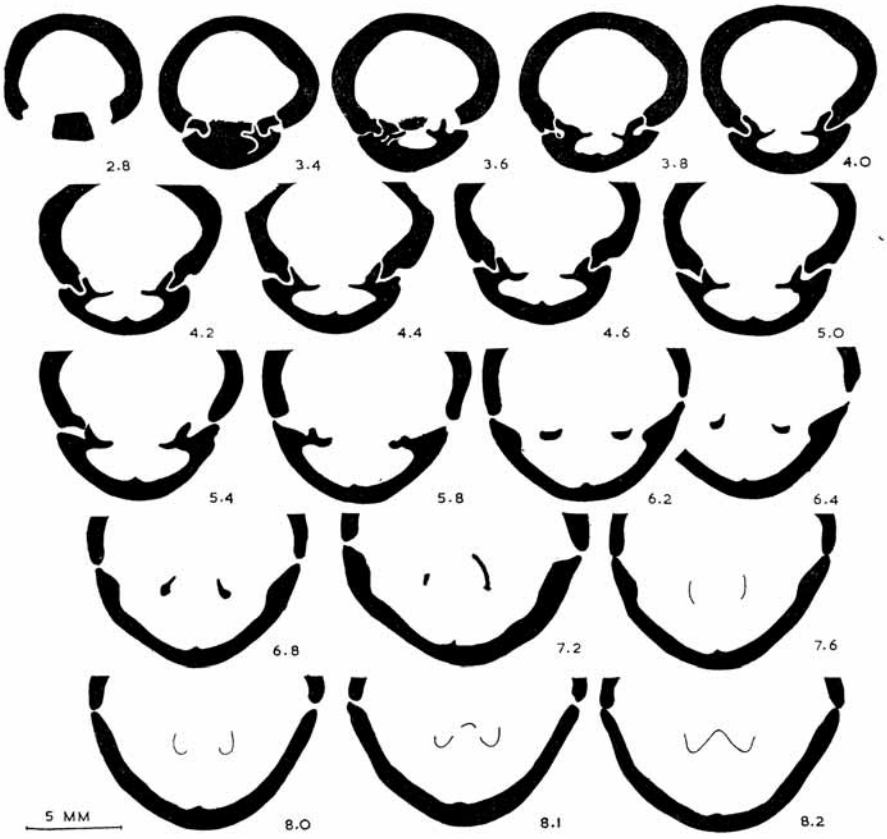
Distributon. Very abundant at Upware and Brickhill and also occurs in the Bargate Beds. At other localities it is rare. Single valves which may belong to the species occur at Faringdon. Meyer (Davidson 1874) recorded it from the Hythe Beds of Hythe, Kent, but his specimens (SM B.58782–5) are varieties of *Sellithyris sella*. It occurs rarely in the upper part of the Ferruginous Sands at Shanklin, Isle of Wight (BM B.25797), and of the Hythe Beds at Maidstone (BM BB.3444 and GS 96848). Forms in the Lower Albian deposits at Leighton Buzzard, Bedfordshire, resembling this species differ from it in beak characters and in internal morphology.

Platythyris minor sp. nov.

Plate 15, figs. 12–14; text-fig. 9

Holotype. BM BB.16220, Walker Coll., Brickhill, Buckinghamshire (dimensions: length 23, breadth 14, thickness 13).

Diagnosis. Platythyris of elongated oval ventral profile, slightly produced at anterior and posterior ends. P/A ratio about 1, or slightly more. Both valves regularly convex,



TEXT-FIG. 9. Transverse sections through *Platythyris minor* nov. The cardinal process is seen at 2·8 and is enlarged by callus to enclose the hinge plates at 3·4 and 3·6. The narrow horizontal hinge plates are best shown at 4·2–5·0, the strong euseptoidum at 3·8–7·6, the incurved crural processes at 7·2, descending lamellae of the loop at 7·6 and 8·0, and low-arched transverse lamella at 8·1 and 8·2. BM B.16201, Brickhill.

with maximum convexity slightly posterior to mid-line. Brachial valve possesses anteriorly a low but often distinct and rather square-cut fold; no sulcus in pedicle valve. Beak fairly short, sub-erect. Beak ridges rounded. Symphytium very short. Foramen mesothyrid to permesothyrid; angle of truncation *c.* 120°. Lateral commissure much arched. Anterior commissure strongly uniplicate but slightly sulciplicate in some specimens; development rectimarginate to uniplicate to sulciplicate. Socket ridges well developed and massive. Hinge plates distinctly narrow.

Description. This is a small species with maximum adult length about 25, width 15; some apparently gerontic individuals do not exceed 21. The most characteristic feature is the strong uniplication combined with some pinching in of the sides of the anterior part of the shell, giving it a distinctly 'nosed' effect. Uniplication develops when the shell is about 10 or 12 mm. in length and strong uniplication at an early stage of growth is characteristic.

Remarks. This species is very close in external characters to *P. comptonensis*, especially to some Brickhill varieties of the latter, but it differs (1) in being smaller, relatively deeper and more compressed; (2) in showing a tendency towards greater incurvature of the beak and towards a permesothyrid rather than mesothyrid foramen; (3) in possessing distinctly narrower hinge plates. Proportions vary a little in *P. minor*; some gerontic (perhaps stunted?) forms with close-set and well-marked growth-lines have thickness as much as two-thirds the length, and a beak approaching the erect condition.

Distribution. Brickhill only.

Genus SELLITHYRIS gen. nov.

Type species *Terebratula sella* J. de C. Sowerby 1823

Diagnosis. Beak short or moderately short; beak angle variable. Foramen mesothyrid to permesothyrid, usually marginate. Angle of truncation 95–110°. Shell squat, not much longer than wide, strongly biplicate in the adult stage. Development of anterior commissure rectimarginate–uniplicate–sulciplicate–episulcate but with a strong tendency towards omission of the two middle stages. Cardinal process small but distinctly bifid. Hinge plates concave, tapering. Crural processes sharp-pointed, inclined towards mid-line, approximately upright in lateral view; lamellae of loop distinctly narrow. Posterior and anterior adductor impressions in brachial valve separate, posterior lying along outer margin of anterior; both rather triangular in shape, diverging from the midline, the posterior at a greater angle than the anterior. Euseptoidum not always present. Adductor scars may be bounded in posterior part by low septum-like ridges.

Remarks. The characters of the beak and foramen cover quite a wide range in the different species but the genus is homogeneous in the general shell shape, type of plication, and characters of the hinge plates, loop, and muscle scars. In addition to the species described below the genus contains some European continental species ranging from the Valanginian to the Cenomanian, including *Terebratula carteroniana* d'Orb., *T. essertensis* Pictet, *Rectithyris tornacensis* d'Archiac sp. (Sahni 1929), and probably *T. campichei* Pictet.

Sellithyris sella (J. de C. Sowerby)

Plate 16, figs. 1–4; text-figs. 2, 10

Terebratula sella J. de C. Sowerby 1823, p. 53, pl. 437, fig. 1.
Terebratula sella J. de C. Sow.; Davidson 1855, p. 59, pl. 7, figs. 4–10.
Terebratula sella J. de C. Sow.; Davidson 1874, p. 78, pl. 202, fig. 19

Holotype. BM B.61547, Sowerby Coll., Hythe, Kent (dimensions: length 27·5, breadth 25·5, thickness 14).

Diagnosis. Rhomboidal to pentagonal *Sellithyris* with P/A ratio more than 1; breadth may almost equal length. Brachial valve regularly convex near the umbo, strongly

folded anteriorly. Pedicle valve strongly convex posteriorly, maximum convexity near the umbo, with anteriorly two lateral folds separated by wide sulcus, with, or without a median fold. Beak sub-erect to erect. Angle of truncation *c.* 110°; foramen circular, may be slightly telate; mesothyrid to very slightly permesothyrid. Beak ridges rounded; sometimes well-defined adjacent to foramen. Symphytium wide, moderately short. Development of anterior commissure rectimarginate–uniplicate–sulciplicate–episulcate. Hinge plates thin. Crural processes thin, inclined towards midline at about 20°, slightly incurved at tip, base thickened. Descending lamellae of loop diverge at about 60°; loop wide and triangular. Euseptoidum feeble. Posterior portions of dorsal adductor scars bounded by septum-like ridges.

Description. The posterior lateral angles of the pentagonal ventral profile correspond to the greatest breadth of the shell and to the outer extremities of the lateral sinuses of the commissure. The cardinal slopes are always longer than the other three sides of the pentagonal shape.

The anterior commissure is typically very markedly episulcate, the plicae and sinuses of the commissure reflecting the folds and sulci of the shell. The lateral sinuses are typically wide and strongly arched, giving that winged appearance which is so characteristic of adult individuals from Atherfield and the Kentish Rag. The median sinus is typically smaller and narrower than the lateral. The development of the plications in the anterior commissure can be traced in young individuals from the Atherfield coast. A series of such stages can be observed in BM BB.3591–9 and BB.3577–90, which show that the shell remains rectimarginate up to about 15 mm., when it becomes slightly uniplicate, but by 20 mm. it is already distinctly episulcate, this stage having been apparently reached through a transitory sulciplicate stage. Further development consists of increasing emphasis of the plicae and sinuses and, with them, of the folds and sulci of the valves, so that gerontic individuals of typical form have an acute bi-rostrate appearance, with a great distance from the base of the lateral sinus to the apex of the plica.

EXPLANATION OF PLATE 15

All figures are natural size.

Figs. 1, 2. *Rhombothyris extensa* (Meyer). 1*a–c*, Lectotype, SM B.16739, Bargate Beds, Tuesley, Surrey. 2*a–c*, BM 67592, Upware, Cambs., figured Walker 1868, pl. 18, fig. 5.

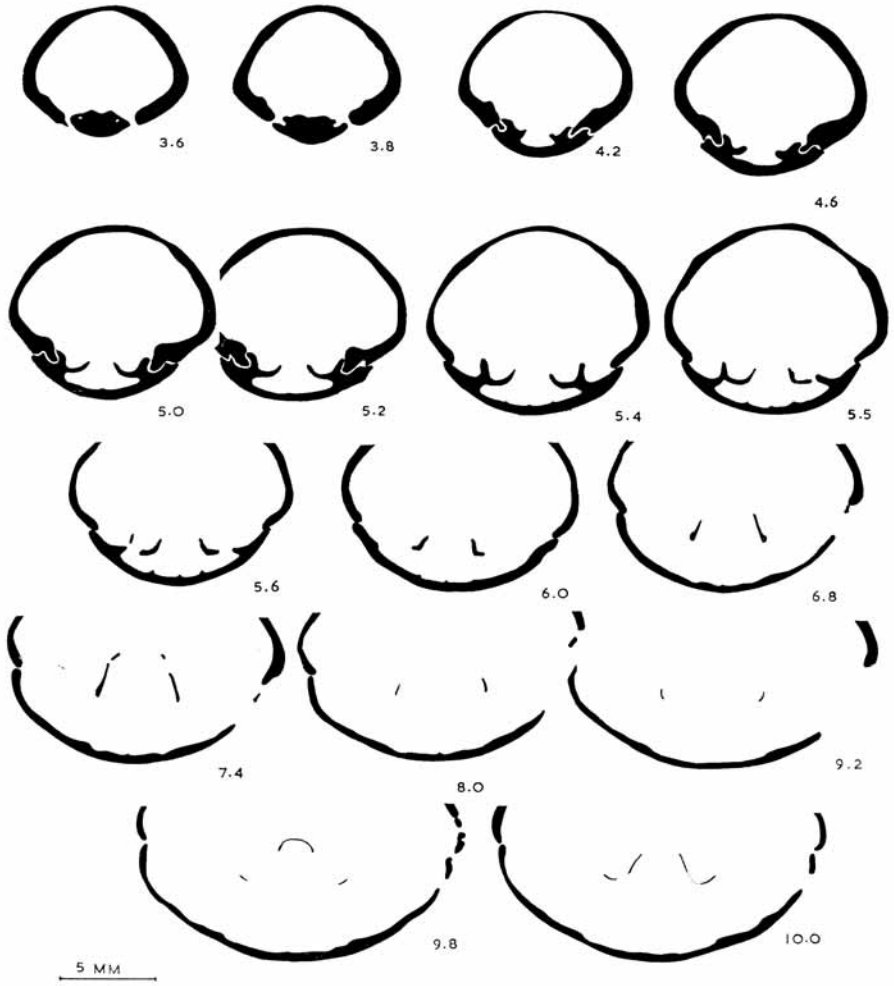
Figs. 3–5. *Rhombothyris microtrema* (Walker). 3*a–c*, Lectotype, BM BB.16216, Walker Coll., Upware, Cambs. 4*a–c*, A thick specimen, BM B.25571, Walker Coll., Upware. 5*a–c*, A specimen showing concavity in the anterior part of the brachial valve, BM BB.16232, Walker Coll., Upware.

Figs. 6*a–c*. *Rhombothyris meyeri* (Walker), Holotype, BM 67598, Walker Coll., Upware, Cambs.

Figs. 7, 8. *Rhombothyris conica* sp. nov. 7*a–c*, Holotype, BM BB.16217, Walker Coll., Brickhill, Bucks. 8*a–c*, A smaller specimen showing well the characteristic shape of the anterior commissure, BM BB.16219, Walker Coll., Brickhill, Bucks.

Figs. 9–11. *Platythyris comptonensis* sp. nov. 9*a–c*, Holotype, BM BB.16230, Bargate Beds, Compton, Surrey (CWW 12077). 10*a–c*, BM BB.16233, Walker Coll., Upware, Cambs. 11*a–c*, BM B.1848, Caroline Birley Bequest, Brickhill, Bucks.; 11*b* shows well the longitudinal striae in the shell (ventral view).

Figs. 12–14. *Platythyris minor* sp. nov. 12*a–c*, Holotype, BM BB.16220, Walker Coll., Brickhill, Bucks. 13*a–c*, BM BB.20444, Brickhill. 14*a–c*, A small compressed specimen, BM B.25466, Walker Coll., Brickhill.



TEXT-FIG. 10. Transverse sections through *Sellithyris sella* (J. de C. Sowerby). The cardinal process and the beginnings of the sockets are seen at 3·6 and 3·8, the concave tapering hinge plates at 5·4 and 5·5 and the ridges bounding the muscle scars at 5·4–6·0. 7·4 shows the maximum height of the crural processes, 8·0 and 9·2 the thin descending lamellae of the loop, and 9·8 and 10·0 the transverse lamella. BM B.16202, Hythe Beds, Hythe, Kent.

Parasulcate adults, lacking the median sinus, are common both in the Hythe Beds and in the Ferruginous Sands of the Isle of Wight. Hythe Bed specimens in particular show considerable variation in the beak angle, some having an erect beak, whereas in

typical forms it is sub-erect. The degree of production of the beak also varies. A study of any large collection of *S. sella* from one locality shows considerable variation in the detail of the shape, e.g. the P/A ratio or the degree of development of the 'wings' formed by the lateral sinuses. There is also considerable variation in the ratios of length, breadth, and thickness; in particular there is a tendency, both in the Isle of Wight and in the Weald, for specimens from low horizons, especially those from the *Perna* Bed, to be thinner than those from higher horizons.

In the Bargate Beds *S. sella* is rare and the few specimens known (e.g. Shaw Coll. in GS and BM) are distinctive and might be regarded as a separate subspecies. They show a strong tendency towards the verticality of the lateral commissure characteristic of *S. upwarensis*.

A collection (GS) from the base of the Sandgate Beds of Sellinge, Kent, shows another late Aptian local race of the species. Most of these specimens are rather narrow and elongate, sharply episulcate but with wings less developed than in Atherfield types. The central sinus is small and low; the plicae tend to be angular, the sinuses rounded. There is a tendency towards a vertical lateral commissure, although not as marked as in *S. upwarensis*. Specimens of average size are very slightly globose and the plications are not much reflected in the folding of the shell. Fully adult forms have the anterior third folded. A thoroughly gerontic individual (GS Ca 4622) is thick, angular, with hardly any median sulcus; the lateral commissure turns very sharply into the lateral sinus, almost as in *S. upwarensis*. Another specimen (Ca 4616) is flattened and more like the Bargate Bed specimens mentioned above, although the lateral commissure is rather less vertical and the general shape long and narrow with the front much produced and very little median sinus, i.e. the ventral profile is very different from that in the Bargate Bed material; here again the plicae are angular, the sinuses rounded.

Remarks. It must be emphasized that *S. sella*, although variable, is distinctive, not closely resembling any other English Cretaceous species except some forms of *S. coxwellensis*, but Sowerby's figure and description have been misunderstood by some European authors, who have ascribed other forms to Sowerby's species or vice-versa. The chief European continental species which have been confused with *S. sella* are *Terebratula acuta* auctt., *T. valdensis* de Loriol, and *T. russillensis* de Loriol.

These species occur, along with *S. sella*, in the Lower Cretaceous of the Jura and are all biplicate terebratulids of very similar general external shape. Several other Lower Cretaceous biplicate species of southern Europe and North Africa remain undescribed.

T. acuta is more elongated and has a more acute umbonal angle than *S. sella* but there is a close external resemblance between the two species and Pictet remarked (1872, p. 74) that there is almost a transition between them in the Hauterivian of the Jura and the Hils Conglomerate of Brunswick. There are, however, several differentiating characters:

(1) In *S. sella* breadth is typically not much less than length; in *T. acuta* length is up to 1½ times breadth. (2) In *T. acuta* P/A ratio is much higher than in *S. sella*; the resulting posterior elongation has caused *acuta* to be frequently confused with *T. praelonga* J. de C. Sow. *S. sella*: P/A ratio of twelve specimens, Hythe Beds, near Ashford, Kent, 1·32. *T. acuta*: P/A ratio of twelve specimens, Aptian, La Glappe, Narbonne, 1·94. (3) *T. acuta* usually shows a strong, almost bulbous convexity in the posterior part of the brachial valve, not present in *S. sella*. (4) *T. acuta* possesses strong ventral biplication at a much smaller stage than *S. sella*, the adult form being already developed by a length of 12 mm. (5) *T. acuta*

has a straighter beak and a longer and better-exposed symphytium than *S. sella*. (6) In *T. acuta* the beak ridges are sharper, the cardinal area more clearly defined and the symphytium is bordered by distinct marginal ridges. (7) Internally *T. acuta* differs from *Sellithyris* particularly in its hinge plates, which are deeply concave, almost virgate, and somewhat clubbed. It is hoped to discuss the systematic and nomenclatural position of this species in a later publication.

S. sella differs from *T. valdensis* chiefly in the following:

(1) *T. valdensis* is nearly always considerably longer than broad. (2) *T. valdensis* has a greater P/A ratio so that, like *T. acuta*, it has been mistaken for *T. praelonga*. *T. valdensis*: P/A ratio of twelve specimens, Valanginian, Carrière d'Arzier, Vaud, 1·69. (3) In *T. valdensis* the lateral sinuses are less distinct from the lateral commissure and the lateral sulci of the brachial valve less developed than in *S. sella*. (4) In *T. valdensis* the beak is more incurved, being usually erect, and is more produced in ventral profile; the foramen verges on the permesothyrid condition and the angle of truncation is slightly greater than in *S. sella*. (5) Internally *T. valdensis* differs from *Sellithyris* principally in having piped hinge plates.

T. russillensis differs from *S. sella* chiefly in:

(1) its large, thick, and completely erect beak and short, almost hidden symphytium; (2) its very large foramen with angle of truncation about 130°; (3) in being relatively thicker, lacking well-developed wing-like lateral sulci and bearing only a very small median sinus; (4) in possessing piped hinge plates similar to those of *T. valdensis*, with which it is probably congeneric.

Distribution. In the lower part of the Aptian in England *S. sella* is the typical and most abundant brachiopod which flourished in the Lower Greensand sea before the latter joined with the boreal sea in *Parahoplites nutfieldensis* times. It is common in the *Perna* Bed of the Isle of Wight and the equivalent bed at the base of the Atherfield Clay in Surrey, in the calcareous Hythe Beds of Kent and in the Ferruginous Sands of the Isle of Wight, where it is very abundant in the lower part but apparently dies out before the top of the series. The species becomes much less abundant before or about the beginning of *nutfieldensis* times; it is rare in the Bargate Beds and in the equivalent Sandgate Beds of Kent, in both of which local races, distinct from the Lower Aptian form, occur. Among the specimens from Seend, Faringdon, Brickhill, and Upware which have been referred to *Terebratula sella* there are some which are not easy to distinguish from that species but, nevertheless, these grade imperceptibly into the biplicate forms more typical of those localities, described here as *S. coxwellensis* and *S. upwarensis*, and should be regarded as *sella*-like variants of one or other of these.

On the European continent, too, *S. sella* appears to reach its acme in the Lower Aptian, after which it is not known (Pictet 1872).

Sellithyris sella shanklinensis subsp. nov.

Plate 16, figs. 5, 6

Terebratula sella J. de C. Sow.; Davidson 1874, p. 36, pl. 5, figs. 12–16 (*non* fig. 11).

Holotype. BM BB.16234, Walker Coll., Shanklin, Isle of Wight (dimensions: length 23, breadth 18, thickness 12).

Diagnosis. S. sella globose as adult. Plication less developed than in typical forms of species, folding shallower and affecting smaller proportion of shell. Beak nearly straight to sub-erect; symphytium well exposed; beak ridges moderately sharp.

Remarks. That the biplicate terebratulids occurring in the fossiliferous bands of the Ferruginous Sands about Shanklin are distinct from *S. sella* s.s. was realized by Meyer (Davidson 1874, p. 34). In the points of difference set out above, particularly the smaller development of plication which causes the characteristic lateral 'wings' of *S. sella* to be rare in the Shanklin form, the latter approaches *S. coxwellensis*. It was, in fact, upon Meyer's recognition of the similarity between the Shanklin forms and the Faringdon forms that Davidson (1874) based his identification of the latter as varieties of *Terebratula sella*. Nevertheless, there are certain differences between the Shanklin forms and the typical *S. coxwellensis* of Faringdon, the chief of which is the small size and frequent absence of the median sinus among the Shanklin forms. In many ways the latter are morphologically intermediate between *S. sella* and *S. coxwellensis*. The internal structures closely resemble those of the typical *S. sella*.

Distribution. Isle of Wight, in Group XIII of the Ferruginous Sands near Shanklin and Group X near Atherfield.

Sellithyris upwarensis (Walker)

Plate 16, figs. 7–9; text-figs. 11, 12

Terebratula sella, J. de C. Sow.; Walker 1868, p. 403, pl. 18, figs. 7–7*b*.
Terebratula sella var. *upwarensis* Walker 1870, p. 562.
Terebratula sella var. *upwarensis* Walker; Davidson 1874, p. 35, pl. 5, figs. 3–10*a*.

Holotype. BM 67594, Walker Coll., Upware, Cambridgeshire (dimensions: length 27, breadth 20, thickness 21).

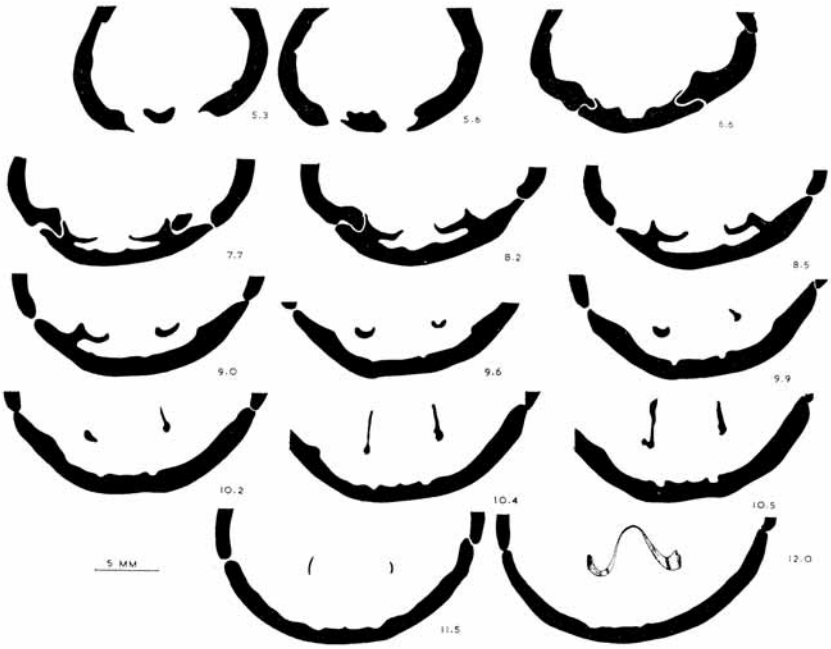
Diagnosis. *Sellithyris* of rounded rhomboidal ventral profile; typical ratio of length to breadth 5:4. P/A ratio slightly more than 1. Brachial valve flattened posteriorly, or slightly grooved in midline near umbo, anteriorly sharply folded with narrow median sulcus and wide and deep lateral sulci. Pedicle valve strongly convex and somewhat carinate posteriorly, with strong folds anteriorly occupying half to two-thirds of length of valve in adults. Anterior commissure strongly episulcate with angular plicae and sinuses, median sinus large. Lateral commissure approximately vertical. Development of anterior commissure rectimarginate–episulcate. Beak sub-erect to erect, usually nearer the latter. Angle of truncation *c*. 110°. Foramen large, circular, may be slightly telate or attrite. Beak ridges rounded, but well defined immediately adjacent to foramen. Symphytium very wide, moderately to very short. Teeth inserted at 30–40° to the commissural plane. Hinge plates thin, close to floor of brachial valve; dorsal umbonal cavity low. Crural flanges present. Loop a wide, somewhat squat triangle. Dorsal adductor scars very large, angular.

Description. Typical specimens of this species, most of which come from Upware, have a highly characteristic appearance: distinctly globose, with thickness three-quarters or more of width (but rarely equalling width), with bold, blunt, angular plication and a laterally compressed appearance.

The anterior commissure in many individuals almost reaches the quadriplicate stage by development of an external plica lateral to each lateral sinus. It is characteristic of the species that the lateral commissure is almost vertical in its passage forwards from the umbo and turns abruptly into the lateral sinus through almost a right angle, but in

some specimens the commissure turns slightly dorsally before entering the steep turn into the lateral sinus, thus forming a shallow external plica.

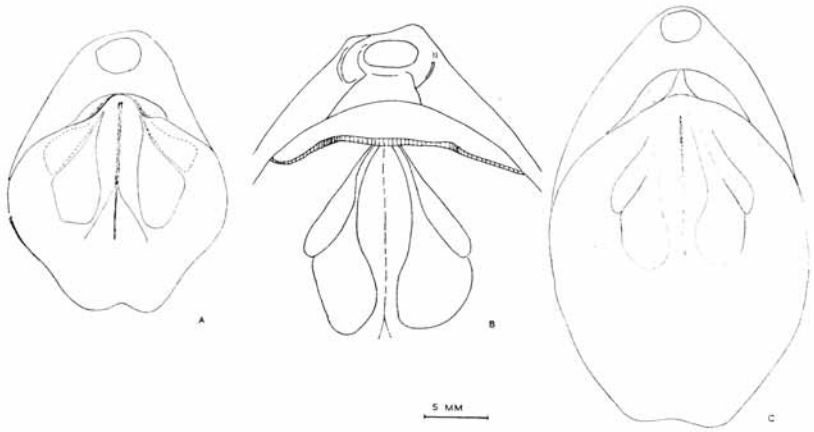
The carinate posterior part of the pedicle valve and the frequent occurrence of a groove



TEXT-FIG. 11. Transverse sections through *Sellithyris upwarensis* (Walker). The cardinal process can be seen at 5·3 and 5·6, the concave tapering hinge plates at 7·7 and 8·5, the crural processes at maximum height at 10·5, and descending lamellae of the loop at 11·5. The transverse lamella has been dissected out at 12·0. SM B.80776, Upware.

in the posterior part of the brachial suggest a sulcate nepionic stage but the earliest growth stage actually seen (BM B.25597) is 15 mm. long and rectimarginate. The rectimarginate to episulcate transition seems to be abrupt, the plicae and sinuses appearing at once, without intervening uniplicate, paraplicate, or sulciplicate stages, at about 15 mm., since there are also specimens of that length (BM B.25597) showing all the plication present, although very small. Neanic individuals (18–22 mm.) have well-developed and typical plication, the sub-vertical course of the lateral commissure between the umbo and the lateral sinus being evident, but the whole shell is relatively thin, average ratio of thickness to breadth for ten specimens in that length range from Upware being 0·56 as compared with 0·75–0·85 for adult specimens. In neanic specimens the beak is noticeably straighter than in adults. Growth from the neanic stage results in a relative increase in thickness, coupled with increasing emphasis on the plication and a slight tendency towards incurvature of the beak.

Adults of the species vary considerably, even at Upware, the home of the globose type, the chief variable factor being the relative thickness and the consequent depth of the plication, since there is good correlation between these characters well shown in those exceptional specimens which are actually thicker than wide and have extremely exaggerated plication. At Brickhill, although gerontic specimens are globose and laterally compressed with very deep plication, like those from Upware, the majority of the adults resemble rather the neanic stages from Upware in being relatively thin and in not



TEXT-FIG. 12. Camera lucida drawings of calcite internal casts of three species of Aptian terebratulids in dorsal view, to show muscle impressions. A, *Sellithyris upwarensis* (Walker). The euseptoidum is quite well developed. The posterior and anterior adductor scars are separate. SM B.80775, Upware. B, *Cyrtothyris cantabridgiensis* (Walker), BM BB.16212, Upware. C, *Praelongithyris praelongiforma* nov., BM BB.16213. In B and C the posterior adductor scars lie close against the postero-lateral sides of the anterior adductor scars; the euseptoidum is just visible.

showing strong lateral compression. Average thickness: breadth ratio of ten specimens from Brickhill in the 21–28 mm. length range 0·62; that of ten specimens from Upware in the same length range 0·82. Occasional examples of the Brickhill type occurred at Upware, however. The characters of the commissure remain constant.

Remarks. S. upwarensis does not resemble any other English species except *S. sella* and *S. coxwellensis*. From *S. sella* this species differs typically in being thicker in relation to breadth, much more globose in appearance and in lacking the prominent 'wings' and the acute produced appearance of the central portion of the anterior margin seen in *S. sella*.

In less typical examples of the two species other characters must be taken into account: (1) The central sinus in *S. upwarensis* is invariably better developed than in *S. sella* and may almost, in rare cases quite, equal in depth the lateral sinuses. In *S. sella* the central sinus is always much smaller than the lateral. (2) In *S. sella*, although the beginning of the lateral sinus is usually formed by a sharp ventral bend of the lateral commissure, the latter drops from the umbo to the lateral sinus at a distinct angle to

the vertical, the angle varying with the proportions of the shell but reaching a maximum of 40° in some specimens. In this the species contrasts with *S. upwarensis*.

There are three European continental species which to some extent resemble *S. upwarensis*: *Terebratula carteroniana* d'Orb., *T. campichei* Pictet, and *T. russillensis* de Loriol. *T. carteroniana* has a straighter beak, a smaller and narrower median sinus, and characteristically strongly marked growth lines. *T. campichei*, according to Pictet (1872, p. 63), has a much straighter beak. *T. russillensis* is narrower compared with its length, has a larger and more inflated beak and larger foramen and possesses piped hinge plates; it is no doubt to be referred to a different genus.

Distribution. Upware and Brickhill only, very abundant at the former, slightly less so at the latter.

Sellithyris coxwellensis sp. nov.

Plate 16, figs. 10–12; text fig. 13

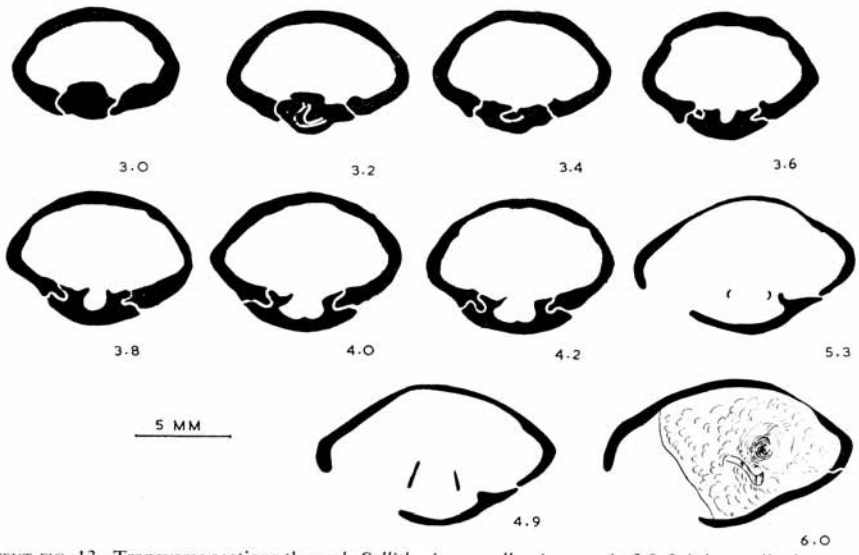
Terebratula tornacensis d'Archiac var. *roemeri* Davidson 1855, p. 61, pl. 7, figs. 11–16; pl. 9, figs. 1–8, 36–37; ?pl. 6, figs. 45–49.
Terebratula sella J. de C. Sow. var.; Davidson 1874, p. 36.

Holotype. BM B.26007, Walker Coll., Faringdon, Berkshire (dimensions: length 20, breadth 18·5, thickness 11).

Diagnosis. Sellithyris of pentagonal ventral profile with rounded angles. Breadth typically 0·8–0·9 of length, thickness *c.* 0·6 of breadth. P/A ratio (average of twenty adult specimens from Faringdon) 1·50. Brachial valve has maximum convexity about the centre; pedicle valve more evenly convex but rather inflated near posterior end. Anteriorly both valves folded but this usually affects less than one-third of the shell. Pedicle valve slightly carinate near the umbo. Anterior commissure typically episulcate, the sinuses and plicae gently angular; median sinus well developed, often approaching or equalling the lateral sinuses in depth. Beak sub-erect; symphytium well exposed; beak ridges fairly well defined. Foramen large, circular, precisely mesothyrid. Angle of truncation *c.* 95°. Development of anterior commissure rectimarginate–sulciplicate–episulcate. Teeth inserted at 20–30° to the commissural plane; accessory articulation fairly well developed. Hinge plates narrow. Dorsal umbonal cavity high. Crural flanges present. Loop small and relatively narrow.

Description. Adults are characteristically globose, with the folds affecting the anterior part of the shell only and in some cases even that very little, but the species is variable, the variation affecting chiefly the following characters: (1) the relative proportions of length, breadth, and thickness. Occasional elongated specimens occur and there is a rather distinctive transverse variety, as broad as long, at Faringdon (e.g. Davidson 1855, pl. 9, figs. 5, 7); (2) the development of folding in the shell. Even in those individuals with quite well-developed plications of the anterior commissure both valves usually remain smoothly convex except in the extreme anterior part. The holotype shows about the maximum depth of folding in which approximately one-third of the shell is involved; (3) the anterior commissure. Typically the median sinus is well developed, more so than in *S. sella*, but in some individuals from both Faringdon and Seend it is so large as to

equal or even exceed the lateral sinuses in depth and prominence while remaining comparatively narrow. The lateral sinuses are never as well developed as in *S. sella* and may be lacking. There are also variants in which the median sinus is poorly developed or absent; these approach *Cyrtothyris cyrta* in superficial appearance; (4) An obvious character of many individuals from Faringdon is the presence of well-emphasized concentric growth lines or growth halts forming little steps upon the surface of each valve.



TEXT-FIG. 13. Transverse sections through *Sellithyris coxwellensis* nov. At 3·0–3·4 the cardinal process (enlarged by callus) encloses the hinge plates, the concave tapering shape of which is seen best at 4·0–4·2. 4·9 shows the maximum height of the crural process and 5·3 the descending lamellae of the loop, the transverse lamella of which is partly dissected out at 6·0. Sections 3·0–4·2 BM BB.20462, Bowler's Pit, Faringdon, Berkshire. Sections 4·9–6·0 BM B.26019, Faringdon, Berks.

Prominence of these growth lines varies greatly. They seem to be, to some extent, a gerontic character, appearing crowded together near the anterior margin of really large old individuals (21–22 mm.), but they occur even more commonly on comparatively small shells which, from their small size, thinness, and poorly developed plication, appear to be quite young. The deeply cut growth lines seem to be evidence of stunting of the shell by unfavourable conditions.

Remarks. This form has been ascribed to the Tourtia species *Terebratula roemeri* d'Archiac (Sharpe 1854) and *T. tornacensis* d'Archiac (Davidson 1855). The name *T. tornacensis* has been most used for it, in spite of the fact that Davidson later (1874) withdrew his identification, on the advice of Meyer, and described the form instead as a variety of *T. sella* J. de C. Sow.

S. coxwellensis resembles *T. tornacensis* in its well-exposed symphytium and its well-developed median sinus. It differs in several respects: the beak is straighter and the

symphytium still better exposed in *T. tornacensis*; in the latter the plicae are angular, the median sinus characteristically rounded, a combination occasionally, but rarely, seen in *S. coxwellensis*. Above all the dorsal profile is different; in *T. tornacensis* the P/A ratio is markedly smaller than in *S. coxwellensis* and it becomes more so as the shell grows older; also the cardinal slopes are concave in *T. tornacensis*, convex in *S. coxwellensis*; these two factors together give a characteristic 'high-shouldered' appearance to *T. tornacensis*, not seen in *S. coxwellensis*.

S. sella resembles *T. tornacensis* in its general proportions and in being episulcate, but in little else. *T. tornacensis* has a straighter beak, much more exposed symphytium and larger foramen than *S. sella*. *S. sella* has a considerably larger P/A ratio; its cardinal slopes are convex; its lateral sinuses are better developed and its median sinus less well developed than those of *T. tornacensis*.

S. coxwellensis and *S. sella* resemble each other considerably and are in rare cases not clearly distinguishable. The essential points of distinction are: (1) *S. coxwellensis* has a straighter beak, a longer and better-exposed symphytium, and sharper beak ridges. (2) In *S. coxwellensis* the median sinus is better developed, the lateral sinuses less well developed, and it lacks the wide lateral 'wings' of *S. sella*. (3) *S. coxwellensis* is more globose as an adult and the folds affect a smaller proportion of the shell. *S. coxwellensis* is, typically, markedly convex with shallow folds affecting the anterior part only, while in *S. sella* the shape is, typically, thinner with deep folds which may affect half or more of the shell. (4) In late adult and gerontic stages *S. coxwellensis* tends to become more and more globose whereas in *S. sella* development tends to be towards emphasis of the folds of the shell.

In both species neanic individuals are relatively thinner than adults and have a straighter beak and better-exposed symphytium, but these latter are more marked in the young of *S. coxwellensis* than in those of *S. sella*. Both species are variable in certain characters, variants of *S. coxwellensis* including some with a slight resemblance to the Brickhill form of *S. upwarensis* imparted by the relatively large median sinus. Young individuals of *S. coxwellensis* at Faringdon may resemble young forms of *Cyrtothyris* but differ in being more transverse and in having much sharper beak ridges.

Distribution. Abundant and varied at Faringdon and Coxwell (Berkshire) and also known at Seend (Wiltshire).

Genus CYRTOTHYRIS gen. nov.

Type species *Terebratula depressa* var. *cyrta* Walker 1868

Diagnosis. Foramen large, circular, mesothyrid; marginate to slightly labiate. Angle of truncation 110–120°. Beak ridges rounded. Shell depressed, may become more inflated, with or without folding, in later growth stages. Cardinal process essentially small, becoming enlarged by callus deposited around and along posterior parts of hinge plates. Accessory articulation sometimes present but never strongly developed. Socket ridges well developed, hinge sockets deep. Hinge plates virgate, at least in mature condition; clubbed; sometimes keeled. Crural flanges and crural keels typically present. Loop broad, triangular; transverse lamella strongly recurved and high-arched in centre.

Posterior and anterior dorsal adductor scars separate, posterior closely juxtaposed to postero-lateral margins of anterior; posterior elongated, strap-shaped; anterior elongated flask-shaped, with long narrow posterior portion, expanding anteriorly towards mid-line. Euseptoidum not a constant character.

Remarks. Three of the species included here have formerly been ascribed to *Terebratula depressa* Lamarck, now type species of *Rectithyris* Sahni 1929, and between these two genera there are points of resemblance.

The loop is similar in its wide triangular shape and high-arched transverse lamella. The dorsal muscle scars have the same general arrangement and the anterior adductors a similar shape. The socket ridges have the same tendency to bend over laterally so as to enclose the hinge teeth, although this tendency is better developed in *Rectithyris*. Externally there is a close resemblance between some shorter-beaked variants of *Rectithyris depressa* and some longer-beaked variants of *Cyrtothyris uniplicata*, but the latter grades towards the other two Aptian species formerly ascribed to *T. depressa*, namely *C. cyrta* and *C. cantabridgiensis*, and these three species are shown by their internal characters to be closely related to one another and readily distinguishable from *R. depressa*. A further point of resemblance between the two genera is in the ontogeny, during which some species of *Cyrtothyris* are known to pass through a rectimarginate, straight-beaked, rhomboidal stage much resembling *Terebratula viquesneli* d'Archiac 1846 which Davidson (1855, p. 71) regarded as a young stage of *T. depressa*.

The essential differences between the genera lie in the hinge plates and crura. Although both possess virgate hinge plates, those of *Cyrtothyris* form a fairly equilateral V in cross-section and are distinctly clubbed, while those of *R. depressa* form a more open V, with the inner lamina smaller than the outer, and are tapering. Furthermore, the hinge plates in *R. depressa* are keeled for their whole length, which in itself seems sufficient to divide the two genera. In *Cyrtothyris* the keel is typically a crural one, although not always present, and is associated with a flange more or less at right angles to the crus to give the 'golf-club' shape of the crura typical of this genus in transverse section. In *Rectithyris* the keel has moved back to give a keeled hinge plate while the flange resembles rather a curved trough forming an anterior extension of the outer lamina of the hinge plate. As the flange does not extend as far as the region of maximum height of the crural processes there cannot strictly be said to be a crural flange or keel. The crural processes in *Rectithyris* are in fact inwardly curved structures with their curvature parallel to that of the cross-section of the descending lamella of the loop, quite different from those of *Cyrtothyris*. Species of *Cyrtothyris* include variants in which the crural keel had moved back somewhat so that the anterior parts of the hinge plates are keeled, and also variants in which the flange does not extend forwards to the crural process, but the association of fully keeled hinge plates and flangeless crural processes appears to be constant and diagnostic in *R. depressa*. The resemblances suggest relationship between the Aptian *Cyrtothyris* and the Cenomanian *Rectithyris* but the nature of this relationship is obscure in the present state of knowledge of the Albian terebratulids.

The clubbed hinge plate in *Cyrtothyris* often shows a slight double rim on its inner margin and this may just possibly indicate the incipient development of an 'inner hinge plate' such as Sahni described in *R. depressa*. It seems, however, to be a random and inconstant feature and may have no special significance. It may be noted here that no

sign of an inner hinge plate has been seen in *R. depressa* during this investigation although numerous topotypes were examined and some sectioned.

Cyrtothyris cyrta seems to occupy a central position in the genus. On either side of it are two main groupings of species; on one hand the depressed forms *C. uniplicata* and *C. seeleyi*, on the other the biplicate form *C. cantabridgiensis*. *C. dallasi* stands apart from the others but its relationship to *C. uniplicata* (then called *T. depressa*) was realized by Walker (1868, p. 404).

Cyrtothyris cyrta (Walker)

Plate 16, fig. 13; Plate 17, fig. 1; text-figs. 2, 14

Terebratula depressa var. *cyrta* Walker 1868, p. 404, pl. 18, figs. 1–1*b*.
Terebratula depressa var. *cyrta* Walker; Davidson 1874, p. 41, pl. 4, figs. 6, 7.

Holotype. BM 67597, Walker Coll., Upware, Cambridgeshire (dimensions: length 44·5, breadth 41, thickness 26).

Diagnosis. *Cyrtothyris* almost as broad as long; in ventral profile sub-circular. In lateral profile maximum convexity distinctly near to posterior end, brachial valve tending to flatten anteriorly. Beak short, nearly straight to sub-erect. Angle of truncation *c*. 120°. Symphytium visible but short and broad. Lateral commissure straight or gently curved. Development of anterior commissure rectimarginate to gently uniplicate.

Description. The distinctive characters of this species are those of the beak and commissure, combined with the broad, depressed shell. Young forms are rectimarginate and distinctly depressed, the rectimarginate stage being retained until the shell is at least 30 mm. in length, in many cases more. Further growth is marked by two main changes in shape: (*a*) the appearance of a uniplicate stage, (*b*) increase in convexity until old individuals have a very rotund appearance compared with juvenile stages, an appearance imparted especially by the strongly marked convexity of the brachial valve close to the umbo, with the symphytium almost overhung by the nearly vertical posterior wall of the obese brachial valve. In young individuals of about 20 mm. the brachial valve may be almost flat and the remarkable increase in the convexity of this valve with growth is a striking characteristic of the species. Accompanying this development of the brachial valve is a reduction in relative length of the symphytium, so that the latter is better-exposed in young specimens than in old. Some very adult individuals from Faringdon are distinctly transverse. Internally the dorsal umbonal cavity varies with growth, being relatively higher in gerontic, thickened specimens.

Remarks. This species differs from *C. uniplicata* chiefly in the much shorter and more erect beak and much shorter symphytium, characters which seem to be constantly associated with the comparatively weak development of uniplication and retention of the rectimarginate condition to a late stage, and also with the tendency to great increase in the convexity of the posterior part of the brachial valve. Uniplication in *C. cyrta* is gerontic but occurs to a varying extent. Really gerontic forms may occasionally be confusable with *C. uniplicata*, especially if crushed.

In some specimens the state of preservation is such that the longitudinal striae appear very prominently and this, together with the short beak, may give a resemblance to *Terebratula capillata* d'Archiac; the specimen of *T. capillata* recorded from the Hythe Beds of Jacket's Hill, Sussex (Kirkaldy and Bull 1940), may possibly have been a *C. cyrta* of this type.

TEXT-FIG. 14. Transverse sections through *Cyrtothyris cyrta* (Walker). Enclosure of the hinge plates by the enlarged cardinal process is well shown at 4·6–5·4, the virgate clubbed hinge plates and euseptoidum at 6·6–8·2, and the keeled and flanged crura at 13·5. The descending lamellae of the loop can be seen at 14·6 and high-arched transverse lamella at 16·6. BM B.25627, Upware, except section 13·5, which is from SM B.80777, Upware.

Distribution. Abundant at Upware, Potton, Brickhill, and Faringdon. Internal casts in the basal Sandgate Beds of Great Chart and Sellinge, Kent, and in the basal Carstone of Hunstanton (e.g. BM B.60975) are probably this species, as are a few silicified forms from the Hythe Beds of Godstone, Surrey (e.g. BM B.85930–2). One or two incomplete and doubtful specimens indicate that it probably occurs rarely in the Bargate Beds of St. Martha's, Surrey (e.g. SM B.16727). Forms which, pending investigation of their internal structures, seem referable to this species occur in the Claxby Ironstone and the Tealby Series of the Lower Cretaceous (Hauterivian) of Lincolnshire.

Poorly preserved specimens probably of this species have been examined from the Aptian of Ste. Croix, Switzerland (BM B.35744), and from the Hils Conglomerate of Berklingen, Brunswick (BM B.35629).

Cyrtothyris uniplicata (Walker)

Plate 17, figs. 2, 3; text-fig. 15

Terebratula depressa Lamarck; Walker 1868, p. 403, pl. 18, figs. 2–2*a*.
Terebratula depressa var. *uniplicata* Walker 1870, p. 561; p. 563, figs. 1, 2.
Terebratula depressa var. *uniplicata* Walker; Davidson 1874, p. 40, pl. 4, figs. 1, 2, 4, 5.

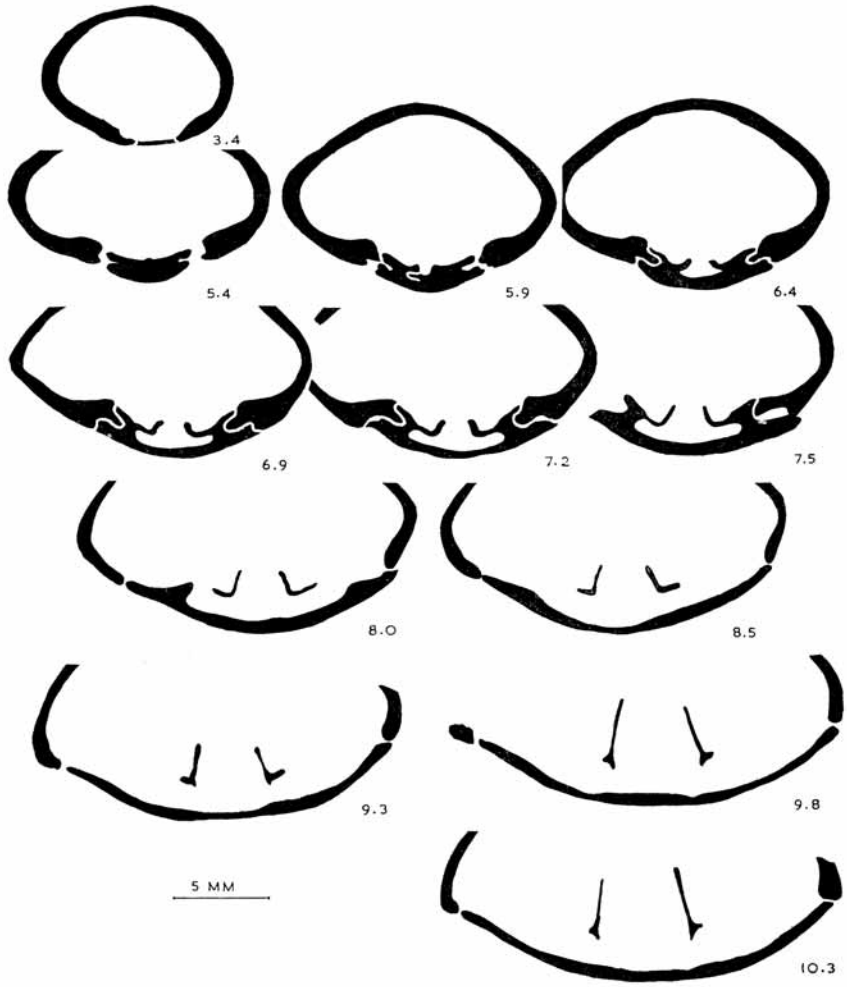
Holotype. BM 67843, Walker Coll., Upware, Cambridgeshire (dimensions: length 61, breadth 52, thickness 28).

Diagnosis. *Cyrtothyris* of rounded ventral profile, oval anteriorly, triangular posteriorly; cardinal slopes straight or very slightly concave, lateral slopes strongly rounded and continuous with front margin. P/A ratio rather more than 2. In lateral profile pedicle valve very regularly convex; brachial valve has maximum convexity about one-third of total length from posterior end and flattens towards anterior margin; pedicle valve somewhat deeper than brachial. Beak straight or nearly straight; symphytium large and well exposed. Foramen slightly telate. Angle of truncation *c*. 115°. Lateral commissure gently arched. Development of anterior commissure rectimarginate to uniplicate.

Description. The wide, depressed shape, ventral profile and characters of the beak and symphytium are the dominant features of this species. Variation mainly affects simple length–breadth–thickness ratios. A more important type of variation is in the length of the beak, e.g. at Upware, although the general form remains reasonably constant. Specimens from Brickhill tend to be thinner and to have shorter beaks than most Upware specimens, while the beak remains straight and the symphytium well exposed. Those from Faringdon tend to be smaller than elsewhere and to have the beak somewhat more incurved, verging on sub-erect, although the symphytium is large and well exposed and the foramen of the same general type. Those from Shanklin, on the other hand, have straight beaks.

The young of this species show a straight beak and well-exposed symphytium. The general form is rhomboidal and the shell tapers in thickness to the anterior margin, which is at first rectimarginate but soon acquires gentle uniplication, the characteristic stage of the adults. The gerontic stage is marked by deepening and squaring of the uniplica, almost into a parasulcate stage, and by increasing obesity of the shell as a whole and especially of the brachial valve, the deepening of which close to the posterior end has the effect of appearing to shorten the beak and symphytium, as in *C. cyrta*.

Remarks. This species includes the 'typical *Terebratula depressa*' and *T. depressa* var. *uniplicata* of Davidson (1874). Some specimens resemble *Rectithyris depressa* (Lamarck) of the Cenomanian Tourtia and on external characters could be confused with that species, the chief differences being that the Tourtia forms are more distinctly rhomboidal in dorsal profile, the beak longer and more produced, and the symphytium longer (in some cases extremely so) and more distinctly concave in lateral profile; the beak ridges are slightly more distinct but the telae formed by them in the foraminal margin rather less so; the umbonal part of the pedicle valve is much more decidedly carinate. The Tourtia species, in late adult or gerontic stages, tends to pass into slight but angular biplication, not seen in *C. uniplicata*, whose gerontic individuals possess massive and



TEXT-FIG. 15. Transverse sections through *Cyrtothyris uniplicata* (Walker). The symphytium can be seen at 3·4 and cardinal process at 5·4. The typical cyrtothyrid inner socket ridges are shown at 6·4–7·2, the virgate clubbed hinge plates at 6·9–7·5, and keeled and flanged crura at 9·3–10·3. BM BB.16211, Upware.

squarish uniplication. It is noteworthy that the characters in which the Tourtia form differs from *C. uniplicata* are in the main possessed also by juvenile forms of the latter.

Distribution. Abundant at Upware, Brickhill, and Faringdon. Occurs at Shanklin, Isle of Wight, in the upper part of the Ferruginous Sands.

Cyrtothyris cantabridgiensis (Walker)

Plate 17, figs. 4, 5; text-figs. 12, 16

Terebratula depressa var. *cantabridgiensis* Walker 1870, p. 561; p. 563, figs. 3–5.
Terebratula depressa var. *cantabridgiensis* Walker; Davidson 1874, p. 41, pl. 4, figs. 8–10.

Holotype. BM 67844, Walker Coll., Upware, Cambridgeshire (dimensions: length 43, breadth 31·5, thickness 25).

Diagnosis. Cyrtothyris of oval ventral profile; in lateral profile depressed, juvenile individuals much so. Both valves uniformly convex. Beak short, nearly straight to sub-

TEXT-FIG. 16. Transverse sections through *Cyrtothyris cantabridgiensis* (Walker). The symphytium and dorsal umbo can be seen at 5·4, the cardinal process, enlarged by callus which has enclosed the hinge plates, at 5·8–7·0. The virgate clubbed hinge plates are shown at 9·0–11·0, keeled and flanged crura at 14·2, and high-arched transverse lamella at 17·5. BM BB.16212, except the last section, which is from BM BB.20461 (both from Upware).

erect. Angle of truncation *c.* 120°. Symphytium short and broad, but visible. Lateral commissure strongly arched; anterior commissure sulciplicate. Hinge plates concave posteriorly, virgate anteriorly; distinctly clubbed.

Description. The beak resembles that of *C. cyrta* but is rather more erect at all stages of growth. The young stages are depressed but have a general resemblance to those of *C. cyrta* except that they are clearly sulciplicate. In adult individuals the plication

becomes the most obvious character and is reflected in considerable folding of the shell; the central sinus is always well developed, with its ventral limit on a level with that of the lateral commissure on each side. The gerontic stage is marked by obesity of the anterior part of the shell, with crowding together of growth-lines. In a few gerontic individuals there is a tendency towards a labiate foramen (e.g. Davidson 1874, pl. 4, figs. 9, 10).

This species does not vary much, perhaps because so few specimens are known. In Brickhill specimens the plication is shallower than in those from Upware, although the relative proportions are the same, including the good development of the median sinus. This difference is retained into old age. Upware forms are rather rhomboidal in ventral profile, the largest specimens (47·5 mm. long) being strongly sulciplicate. Their foramen is large, mesothyrid to slightly permesothyrid, the symphytium exposed but short, the beak nearly straight to sub-erect. In general appearance they resemble *C. cyrta* except for the biplication. Brickhill forms are more ovoid in ventral profile and thinner, with biplication less well developed. The beak is rather more incurved than in the Upware forms, being definitely sub-erect.

Remarks. This species is clearly separate from *C. cyrta* since it is biplicate at an early stage (before 25 mm. in length), whereas *C. cyrta* is rectimarginate at this stage and never attains biplication. Walker (1870) remarks that this species 'approaches *Terebratula praelonga* in the plication', although the resemblance is seen only in older individuals of *C. cantabridgiensis*, in which it may be reinforced by the labiate foremen; nevertheless the two species can be distinguished by the foramen, which is mesothyrid in *C. cantabridgiensis*, permesothyrid in *Praelongithyris praelongiforma* (*T. praelonga* of Walker 1870), by the relatively greater breadth of *C. cantabridgiensis*, and by the early and constant development of biplication in the latter species.

Distribution. Rather rare at Upware, Potton, and Brickhill. A specimen from the Bargate Beds of Surrey probably referable to this species is in the Shaw Collection (GS) and a specimen from Faringdon (SM B.18290) may possibly belong to it.

Cyrtothyris seeleyi (Walker)

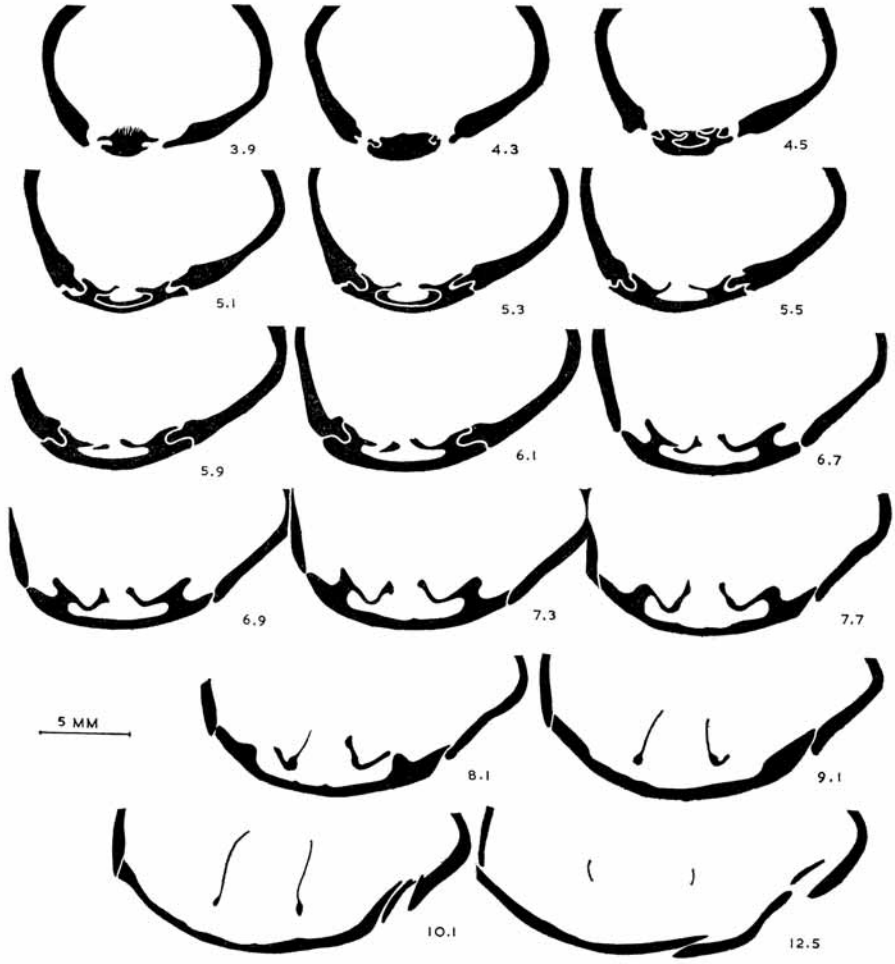
Plate 18, figs. 3, 4; text-fig. 17

Terebratula seeleyi Walker 1870, p. 561; p. 563, figs. 6–8.
Terebratula seeleyi Walker; Davidson 1874, p. 43, pl. 7, figs. 3, 4.

Lectotype. BM 67845, Upware, Cambridgeshire (Walker 1870, figs. 6, 7) (dimensions: length 38, breadth 23, thickness 16).

Diagnosis. Cyrtothyris of elongated oval ventral profile; P/A ratio about 1. In lateral profile both valves regularly and gently convex, flattening anteriorly with greatest thickness well posterior to mid-line, shell tapering towards both front and sides. Beak nearly straight to sub-erect. Symphytium large and well exposed. Angle of truncation *c.* 110°. Lateral commissure very gently curved, anterior commissure typically rectimarginate. Hinge plates concave posteriorly to markedly virgate anteriorly.

Description. The ventral and lateral profiles and symphytium characters of this species are its distinctive features. Variation is mainly confined to the length/breadth ratio and



TEXT-FIG. 17. Transverse sections through *Cyrtothyris seeleyi* (Walker). The first three sections show enclosure of the hinge plates by the enlarged cardinal process. The hinge plates can be seen to become clubbed at 5·9 and virgate at 6·7. Sections at 9·1 and 10·1 show the form of the crura and at 12·5 the descending lamella of the loop. BM BB.16214, Upware.

to various asymmetries shown by individuals. Apart from this the most important variable character is the anterior commissure which, although typically rectimarginate, may be incipiently uniplicate or incipiently sulcate.

Juvenile stages are thin, oval, less elongated than the adults, so that, with their fairly

straight beak, well-exposed symphytium, and rectimarginate anterior commissure, they much resemble equivalent growth stages of *C. uniplicata*. Further growth is accompanied by relative elongation, while individuals verging on the gerontic tend to develop slight uniplication or sulcation and a slightly more incurved beak. The characteristics of the symphytium and the tapering form of the shell are retained throughout growth.

Remarks. Walker's (1870) and Davidson's (1874) descriptions differ slightly; Davidson describes the beak as 'incurved', Walker as 'very slightly recurved'; Walker describes the anterior commissure as 'not plicated' but Davidson speaks of slight plication. In both of these particulars Walker is the more accurate.

The only species to which *C. seeleyi* bears much resemblance is *C. uniplicata*, to which some younger individuals appear very close externally. Some of the flatter and more elongated varieties of *Platythyris comptonensis* at Upware have been mistaken for *C. seeleyi* in the past but they possess a much shorter symphytium and more definite uniplication.

Distribution. The species is probably confined to Upware and Brickhill and is nowhere abundant, but a crushed specimen, rather juvenile, from the Bargate Beds of St. Martha's, Surrey, could possibly belong to it (BM B.8533).

Cyrtothyris dallasi (Walker)

Plate 18, figs. 5–7; text-fig. 18

Terebratula dallasi Walker 1867, p. 455, pl. 19, figs. 1*a–c*, 2*a–c*.
Terebratula dallasi Walker 1868, p. 404.
Terebratula dallasi Walker; Davidson 1874, p. 45, pl. 3, figs. 1–5.

Lectotype. BM 62204, Walker Coll., Upware, Cambridgeshire (Walker 1867, pl. 19, figs. 2*a–c*) (dimensions: length 27, breadth 20, thickness 25).

Diagnosis. Cyrtothyris of short, blunt pear-shaped ventral profile, regularly rounded anteriorly. In lateral profile pedicle valve gently convex for three-quarters or more of postero-anterior distance, whence it bends abruptly dorsalwards at about 80°. Brachial valve gently convex from the umbo to its extreme anterior extension whence it bends abruptly ventralwards and slightly posteriorly at a little more than a right angle to meet downturned portion of pedicle valve. Beak short, sub-erect; beak ridges fairly well defined, especially close to foramen. Symphytium short but visible. Angle of truncation *c.* 115°. Lateral commissure straight; anterior commissure rectimarginate to slightly sulciplicate. Hinge plates almost horizontal posteriorly, more distinctly virgate anteriorly. Crural flanges absent. Loop pear-shaped in plan. Muscle scars large.

Description. The appearance of diverging moderately convex valves connected by a sub-vertical anterior and lateral 'curtain' of shell, together with the short beak and large foramen, makes this species distinctive. It is variable in details of shape and proportion, many individuals showing asymmetry or deformity. The main variable character is the length/breadth ratio, some individuals becoming distinctly elongated while retaining the other diagnostic characters.

The rectimarginate anterior commissure is almost sufficiently constant to be diagnostic, slight development of biplication being rare and essentially gerontic.

The muscle scars are shown by an internal cast (BM B.25607). The principal impressions are broad, pear-shaped, slightly angular in outline and are very large, the impressions of the pallial sinus trunks diverging not from between the adductor scars but from

TEXT-FIG. 18. Transverse sections through *Cyrtothyris dallasi* (Walker). The cardinal process, enlarged by callus, is seen enclosing the hinge plates at 5·8 and 6·6. The clubbed hinge plates become virgate at 8·4. The form of the crura can be seen at 9·9 and the high-arched, strongly recurved transverse lamella can be reconstructed from the sections at 12·9–13·9. SM B.80781, Brickhill.

their anterior apices. The diductor scars in the pedicle valve also appear to be very large but are not well preserved.

Remarks. This is a puzzling species in that it exhibits a type of shell growth frequently seen as a gerontic condition in other species, e.g. in *Praelongithyris lankesteri* and *C. cantabridgiensis* and also in *Terebratula biplicata* var. *gigantea* Walker from the Albian (BM B.26146, Shenley Limestone, Leighton Buzzard). It would appear, however, that this shape in *C. dallasi* is a true specific character and not a gerontic development only, since specimens down to 23 mm. in length show it as clearly as larger individuals, if not more so.

Distribution. Largely confined to Upware, Potton, and Brickhill, but not common. A damaged specimen (BM B.25977) from Hythe, Kent (probably Sandgate Beds), may possibly belong to this species. Meyer's record at Faringdon (Davidson 1874) seems to be based only on a doubtful brachial valve (BM B.8317).

Genus PRAELONGITHYRIS gen. nov.

Type species *P. praelongiforma* nov. (= *Terebratula praelonga* auctt. pars)

Diagnosis. Foramen large or very large, circular, permesothyrid, slightly labiate in gerontic stage. Angle of truncation 120–130°. Beak sub-erect to erect; beak ridges rounded. In ventral profile elongated, drawn out posteriorly, truncated anteriorly. Anterior commissure sulciplicate in adult stage but rectimarginate condition retained late. Cardinal process small but enlarged by callus. Pedicle collar sometimes present. Accessory articulation developed. Hinge plates virgate, clubbed. Crural flanges present. Loop broad, triangular; transverse lamella high-arched. Dorsal muscle scars and euseptoidum as in *Cyrtothyris*.

Remarks. The species here ascribed to this genus much resemble internally, and are probably closely related to, *Cyrtothyris*. Evidence on this point may emerge from work on the Hauterivian fauna now in progress. For the time being these species are thought to be sufficiently distinct in external characters, especially of the general shell shape and of the beak and foramen, to justify inclusion in a separate genus.

Praelongithyris praelongiforma sp. nov.

Plate 17, fig. 6; Plate 18, fig. 1; text-figs. 2, 12, 19

Terebratula praelonga J. de C. Sowerby *in* Fitton 1836, p. 339.
Terebratula praelonga J. de C. Sowerby 1837, pl. 14, fig. 14*a*, non fig. 14*b*.
Terebratula praelonga J. de C. Sow.; Davidson 1855, p. 58, pl. 7, figs. 1, 2.
Terebratula praelonga J. de C. Sow.; Walker 1868, p. 403, pl. 19, fig. 1.
Terebratula praelonga J. de C. Sow.; Davidson 1874, p. 37, pl. 3, figs. 12, 13.

Holotype. BM 67590, Walker Coll., Upware, Cambridgeshire (Walker 1868, pl. 19, fig. 1) (dimensions: length 45, breadth 27, thickness 25·5).

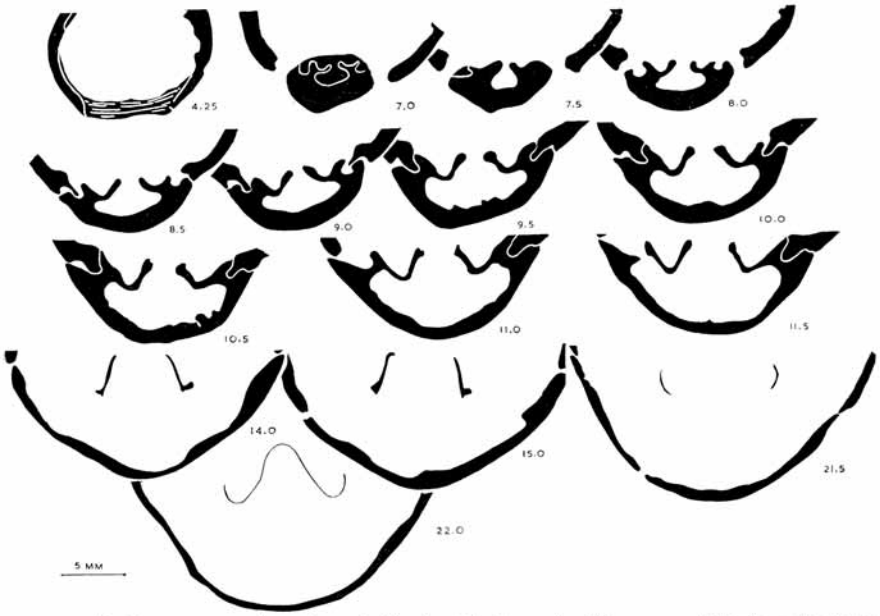
Diagnosis. Praelongithyris with P/A ratio distinctly more than 1. Both valves strongly and uniformly convex in lateral profile. Shell folded anteriorly in adults. Beak moderately long, sub-erect. Foramen slightly labiate in gerontic specimens. Angle of truncation 120–130°. Symphytium large, distinct and well exposed. Dorsal umbonal cavity large. Crural flange and keel present.

Description. In a typical adult the valves are strongly folded to correspond with the plication of the anterior commissure. Davidson aptly described the species as 'scuttle-shaped', to express the appearance given to the shell by the typical drawn out structure of the posterior and the wide, blunt, biplicate truncation of the anterior end. It is a large form, fully adult individuals ranging up to 58 mm. in length, and variable in some of its characters, but the shapes of the beak, foramen, and symphytium are constant. The angle of truncation is unusually high, so that the foramen appears to extend ventrally into the pedicle valve. The symphytium is well exposed not because the beak is remarkably straight, but because it is produced while remaining sub-erect.

Forms of *P. praelongiforma* at Brickhill differ from those occurring at Upware in the biplication, which tends to be very weak or absent at Brickhill but well developed at

Upware, although individuals with weak plication did occur at the latter. Those individuals in which biplication is absent are rectimarginate and not uniplicate. The characters of the beak and foramen remain constant.

Young specimens are thinner than older ones, the increase in obesity continuing into the gerontic stage. Biplication develops comparatively late in life. Out of a number of



TEXT-FIG. 19. Transverse sections through *Praelongithyris praelongiforma* nov. 4·25 shows the large symphytium. Enclosure of the hinge plates by the secondarily enlarged cardinal process is seen at 7·0, the virgate, strongly clubbed hinge plates at 9·0–11·0, the keeled and flanged crura at 14·0, descending lamellae of the loop at 21·5, and the high-arched transverse lamella at 22·0. SM B.80778, Upware.

young specimens of this species from Shanklin (SM B.14903–10) the youngest (13 mm.) are not very clearly distinguishable from the equivalent stages of *Cyrtothyris uniplicata* except perhaps by greater relative thickness; they have the same fairly straight beak, well-exposed symphytium and rather rhomboidal shape with rectimarginate anterior commissure. Some of the larger specimens (20 mm.) show a slight early development of biplication, without intervening uniplicate stage.

The development of biplication remains the most variable character, since occasional adult individuals over 40 mm. long remain rectimarginate. The symphytium is variable in length, although always well exposed. There is also a good deal of variation in minor details of shape and proportion.

Remarks. Sowerby described his species *Terebratula praelonga* as 'ovate, much elongated, gibbose; front slightly elevated, with a depression in its middle; beak prominent, large;

surface smooth' and figured two specimens, giving only one view of each. The first was a dorsal view, taken 'from a drawing by the Rev. G. E. Smith', so that there is no definite indication that Sowerby even saw the specimen, which is presumed to be now lost. This is the figure which has always been taken by authors as the type of *T. praelonga*. As a result, interpretation of the species has always been confused, especially on the European continent, where several distinct species with rather elongated beaks have been referred to it, in particular *T. acuta* auctt. and *T. valdensis* de Loriol.

Sowerby's second figure was a ventral view of a small form which showed nothing of diagnostic value and has apparently been ignored by subsequent authors. The original specimen of this figure is, however, preserved (GS 2008) and, since the original of the first figure is presumed lost, is the sole surviving type specimen. On re-examination it can be seen that this specimen is not the form which has always been known as *T. praelonga* on the basis of Sowerby's first figure but is, in fact, a long-looped form rather close to Walker's '*Waldheimia*' *juddi*. Since this specimen is here chosen as lectotype of *T. praelonga* J. de C. Sow., the form which has usually gone under that name must become a new species for which the name *praelongiforma* is proposed.

T. acuta differs from *P. praelongiforma* in several respects: (*a*) its biplication develops at a much earlier stage; (*b*) its foramen is less strongly permesothyrid; (*c*) it is altogether smaller, really large gerontic specimens reaching little more than 30 mm. in length; (*d*) its symphytium is distinctly 'bordered' (de Loriol *in* Pictet 1872); (*e*) it does not possess the strongly virgate hinge plates and keeled crura of *Praelongithyris*. Pictet (1872, p. 76) discusses the confusion of these two species and concludes that the true *T. praelonga* (*Praelongithyris*) is not present in the Neocomian of Switzerland. *T. valdensis* differs from *P. praelongiforma* principally in its more incurved beak and shorter and more hidden symphytium and in having piped concave hinge plates.

Distribution. The true *P. praelongiforma* is possibly confined to the English area. It occurred fairly abundantly at Upware, more rarely at Brickhill. Elsewhere it is rare but undoubted examples have been found in the Bargate Beds of Surrey, at Maidstone (Davidson 1854, pl. 7, figs. 2–2*c*), and at Shanklin (Upper Ferruginous Sands) (SM B.14903–12). Less typical specimens have been found at Faringdon, at Sandgate, Kent (Sowerby's original figure), in the Hythe Beds of Borough Green, Kent, and Godstone, Surrey (CWW), and at Pulborough, Sussex (BM 9287). A form very similar externally occurs in the Claxby Series of Lincolnshire and the Hils Conglomerate of Brunswick.

Praelongithyris lankesteri (Walker)

Plate 18, fig. 2; text-fig. 20

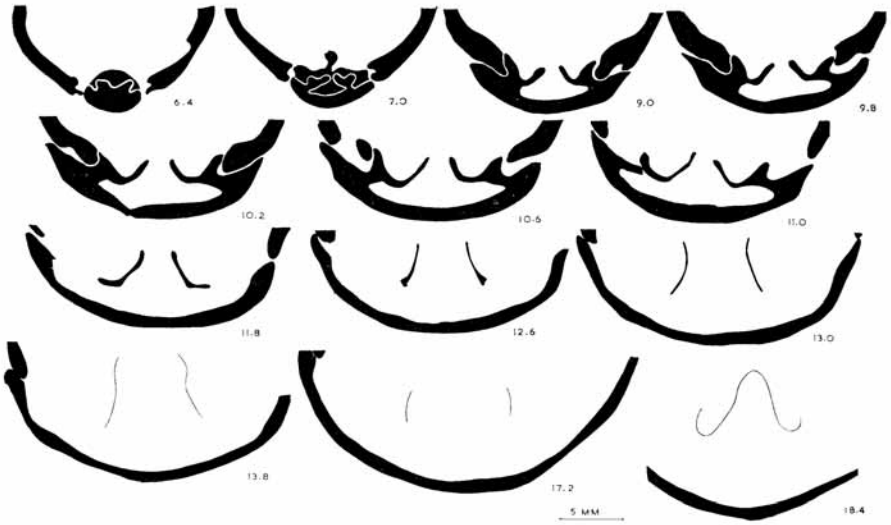
Terebratula lankesteri Walker 1868, p. 402, pl. 19, figs. 2–2*b*.
Terebratula lankesteri Walker; Davidson 1874, p. 38, pl. 3, figs. 9–11.

Holotype. BM 67591, Walker Coll., Upware, Cambridgeshire (a deformed individual) (dimensions: length 41, breadth 26, thickness 26).

Diagnosis. *Praelongithyris* of oval ventral profile or slightly truncated anteriorly. In lateral profile both valves very convex. P/A ratio about 1. Maximum thickness towards anterior end, especially in gerontic individuals. Beak moderately short, sub-erect to

erect, usually more nearly the latter. Angle of truncation *c.* 120°. Symphytium moderately short but distinctly visible. Anterior commissure sulciplicate but not strongly so; shell little folded. Crural flange present but not crural keel.

Remarks. This species has the same general shape, beak, and foramen structure as *P. praelongiforma*. The chief differences are that in *P. lankesteri*: (*a*) the beak is more



TEXT-FIG. 20. Transverse sections through *Praelongithyris lankesteri* (Walker). Secondary enlargement of the cardinal process by callus is seen at 6·4 and 7·0, the virgate hinge plates at 9·0–10·6, the passage into the crura at 11·0–13·8, descending lamellae of the loop at 17·2, and high-arched transverse lamella at 18·4. SM B.80780, Upware.

incurved and the symphytium shorter; (*b*) the beak is shorter and less obviously produced, although it varies in this respect; (*c*) the shell is globose anteriorly, at least in adult specimens, and little folded; (*d*) the anterior part of the shell becomes increasingly inflated in the gerontic stage, which does not occur in *P. praelongiforma*. Apart from the latter the only species to which any resemblance is shown by certain specimens is *Cyrtothyris dallasi*.

Walker laid stress on the fine longitudinal striae said to characterize this species but this is a character seen in any Lower Cretaceous terebratulid in the right condition of preservation. He also quoted the shell structure as a point of distinction from *T. praelonga* (*P. praelongiforma*), the punctations in *P. lankesteri* being smaller and wider apart.

Distribution. Rare at Upware, very rare at Brickhill. Some poorly preserved ferruginous casts from Potton probably belong to this species. It was apparently a local derivation from *P. praelongiforma*.

SUMMARY OF STRATIGRAPHICAL CONCLUSIONS

The stratigraphical value of English Aptian terebratulids is limited partly by the small geographical range of most of the species and partly by their sporadic occurrences, separated by large areas and thicknesses of barren sands, continuous fossiliferous limestone formations being absent.

The Albian and Aptian terebratulid faunas. The distinction between these is most clearly shown on the borders of Buckinghamshire and Bedfordshire where the unfossiliferous Woburn Sands separate the phosphatic deposits of Brickhill, at the base, from the Shenley Limestone, at the top; the former bears an Aptian, the latter an Albian fauna, with hardly a species in common. The Shenley Limestone fauna, never adequately

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EXPLANATION OF PLATE 16

All figures are natural size.

Figs. 1–4. *Sellithyris sella* (J. de C. Sowerby). 1*a–c*, Holotype, BM B.61547, Sowerby Coll., Hythe Beds, Hythe, Kent. 2*a–c*, BM B.61549, Sowerby Coll., Hythe Beds, Hythe. 3*a–c*, BM 31433, Davidson Coll., Ferruginous Sands, Isle of Wight. 4, Ventral view to show the longitudinal striae in the shell, BM B.25970, Hythe Beds, Lympne, Kent.

Figs. 5, 6. *Sellithyris sella shanklinensis*, subsp. nov. 5*a–c*, Holotype, BM BB.16234, Walker Coll., Ferruginous Sands, Shanklin, Isle of Wight. 6*a–c*, Specimen showing well the shape of the anterior commissure, BM B.15126, Slatter Coll., Ferruginous Sands, Shanklin.

Figs. 7–9. *Sellithyris upwarensis* (Walker). 7*a–c*, Holotype, BM 67594, Walker Coll., Upware, Cambs. 8*a–c*, Typical Brickhill specimen, BM B.25468, Walker Coll., Brickhill, Bucks. 9*a–c*, Juvenile specimen, BM B.25594, Walker Coll., Upware.

Figs. 10–12. *Sellithyris coxwellensis* sp. nov. 10*a–c*, Holotype, BM B.26007, Walker Coll., Faringdon, Berks. 11*a–c*, Specimen showing relatively little folding of the valves, BM B.26036, Walker Coll., Faringdon. 12*a–c*, A stunted specimen, BM B.21136, Addison Crofton Coll., Faringdon.

Figs. 13*a–c*. *Cyrtothyris cyrta* (Walker). Holotype, BM 67597, Walker Coll., Upware, Cambs.

EXPLANATION OF PLATE 17

All figures are natural size.

Figs. 1*a–c*. *Cyrtothyris cyrta* (Walker). A relatively juvenile specimen, BM B.25625, Walker Coll., Upware, Cambs.

Figs. 2–3. *Cyrtothyris uniplicata* (Walker). 2*a–c*, Holotype, BM 67843, Walker Coll., Upware, Cambs. 3*a–c*, Typical Faringdon specimen, BM B.26025, Walker Coll., Faringdon, Berks.

Figs. 4–5. *Cyrtothyris cantabridgiensis* (Walker). 4*a–c*, Holotype, BM 67844, Walker Coll., Upware, Cambs. 5*a–c*, A more juvenile specimen, BM B.6256, Davidson Coll., Upware.

Figs. 6*a–c*. *Praelongithyris praelongiforma* sp. nov. Holotype, BM 67590, Walker Coll., Upware, Cambs.

EXPLANATION OF PLATE 18

All figures are natural size except fig. 1*d*.

Figs. 1*a–d*. *Praelongithyris praelongiforma* sp. nov. BM BB.16231, Davidson Coll., Upware, Cambs.; 1*d* (slightly enlarged) is an oblique view to show the labiate foramen.

Figs. 2*a–c*. *Praelongithyris lankesteri* (Walker). Holotype, BM 67591, Walker Coll., Upware, Cambs.

Figs. 3–4. *Cyrtothyris seeleyi* (Walker). 3*a–c*, Lectotype, BM 67845, Walker Coll., Upware, Cambs. 4*a–c*, BM B.25462, Brickhill, Bucks.

Figs. 5–7. *Cyrtothyris dallasi* (Walker). 5*a–c*, Lectotype, BM 62204, Walker Coll., Upware, Cambs. 6*a–c*, BM 62203, Potton, Beds. 7*a–c*, Gerontic specimen with biplicate anterior commissure, BM B. 25463, Brickhill, Bucks.

described, seems to be essentially of an Albian-Cenomanian type whose affinities with the Cenomanian Tourtias are demonstrated by the abundance of *Terebratula capillata* d'Archiac and of types closely related to *T. dutempleana* d'Orb. and by the presence of *T. robertoni* d'Archiac, *T. boubei* d'Archiac, and *T. ovata* J. Sowerby. This affinity is underlined also by the long-looped terebratuloids and the rhynchonelloids (Lamplugh and Walker 1903; Kitchin and Pringle 1920). A similar brachiopod fauna is found in the remainder of the English Albian (Price 1874; Whitaker and Jukes Browne 1899; Kitchin and Pringle 1922), again with hardly a species which is found in the English Aptian. It should be noted that this English Albian-Cenomanian fauna, unlike that of the Aptian, is closely similar to faunas of the same age in north-west Europe.

The Upper Aptian. This fauna is characterized by the presence of *Rhombothyris* and *Platythyris*, of species and subspecies of *Sellithyris* other than *S. sella* s.s., and of certain species of *Cyrtothyris* (*C. uniplicata*, *C. seeleyi*, *C. cantabridgiensis*).

In the Weald and the Isle of Wight, where Lower as well as Upper Aptian deposits exist, the Upper fauna appears at a definite horizon, corresponding to the Bargate Beds of west Surrey and Sussex, the base of the Sandgate Beds in east Kent, and a glauconitic sand high in the Ferruginous Sands (Group XIII) at Shanklin, Isle of Wight. These three can be correlated also by the presence of the zonal ammonite *Parahoplites nutfieldensis*. Members of the same fauna occur in the upper part of the rag and hassock facies (Hythe Beds) in west Kent, although not until the base of the overlying Sandgate Beds in East Kent, and also in Group X of the Ferruginous Sands in the west of the Isle of Wight, thus the fauna may have entered the area during the deposition of the *Cheloniceras martini* zone, but the evidence is not clear before the succeeding *P. nutfieldensis* zone.

At Faringdon sedimentation commenced with beds containing both *P. nutfieldensis* and an Upper Aptian brachiopod fauna, clearly to be correlated with the Bargate Beds. To the north of London the richly fossiliferous deposits of Brickhill, Potton, and Upware are of more debatable age, lacking indigenous ammonites of precise zonal significance. The indigenous brachiopod fauna is unmistakably Upper Aptian and it can be stated that, on this evidence, there is no ground for assuming the presence of pre-Upper Aptian deposits, although derived Lower Aptian ammonites and derived Infra-Valanginian brachiopods occur. There were two fossiliferous levels at Upware (Keeping 1883), but whether there was any significant difference in fauna between the two is now impossible to say. None seems to have been noted when the sections were visible. Northwards from Upware brachiopods are extremely rare in the Aptian and of no stratigraphical value.

Appended are complete lists of species of Terebratulidae from the principal Upper Aptian localities, together with important species of other groups of brachiopods:

Upware: *Rhombothyris extensa*, *R. microtrema*, *R. meyeri*, *Platythyris comptonensis*, *Sellithyris upwarensis*, *Cyrtothyris cyrta*, *C. uniplicata*, *C. cantabridgiensis*, *C. seeleyi*, *C. dallasi*, *Praelongithyris praelongiforma*, *P. lankesteri*.

Brickhill: As at Upware but without *R. meyeri* and with the addition of *R. conica* and *Platythyris minor*.

Faringdon (Sponge Gravels): *S. coxwellensis*, *C. uniplicata*, *C. cyrta*, *C. cantabridgiensis*, *P. praelongiforma*. The first two species are by far the most abundant.

Significant species of other brachiopod groups common to Upware, Brickhill, and Faringdon: *Genmarcula aurea* Elliott, *Terebratella fittoni* Meyer, '*Ornithella*' *juddi* (Walker), '*O.*' *pseudojurensis*

(Leymerie), *Rhynchonella antidichotoma* Buvignier, *Rh. depressa* J. de C. Sow., *Cyclothyris latissima* (J. de C. Sow.).

Bargate Beds, West Surrey: Terebratulids: *R. extensa*, *P. comptonensis*, *S. sella* var., *C. cantabridgiensis*, *C. seeleyi*, *P. praelongiforma*. Other groups: *Terebratulina elongata* Davidson, *G. aurea*, *T. fittoni*, *Terebratella trifida* Meyer, *T. davidsoni* Walker (?), '*Ornithella*' *juddi*, '*O.*' *wanklyni* (Walker) (?), *R. antidichotoma*, *Rhynchonella cantabridgiensis* Davidson (?), *R. upwarensis* Davidson (?).

Upper part of Hythe Beds, Maidstone area, west Kent: *R. extensa*, *P. comptonensis* var.; *G. aurea*, *T. fittoni*.

Base of the Sandgate Beds, east Kent: *S. sella* var., *P. comptonensis* (?), *C. cyrta*, *C. dallasi* (?), *P. praelongiforma*; *Terebratella oblonga* (J. de C. Sow.), *Sulcirhynchia hythensis* Owen 1956 (= *Rhynchonella gibbsiana* auctt.), a zeillerid.

Glauconitic sand in Group XIII of the Ferruginous Sands, Shanklin, Isle of Wight: *R. extensa*; *P. comptonensis*, *S. sella shanklinensis*, *C. uniplicata*, *P. praelongiforma*; *T. oblonga*, '*O.*' *juddi* (?), '*O.*' *morrisi* (Meyer), '*O.*' *celtica* (Morris), '*O.*' *tamarindus* (J. de C. Sow.) var., '*O*'. *wanklyni*, *S. hythensis*, *Rhynchonella parvirostris* (J. de C. Sow.), *Lingula truncata* J. de C. Sow.

The Lower Aptian. This fauna is characterized by abundance of *S. sella* s.s. and by occasional forms comparable with *C. cyrta* and *P. praelongiforma*, these being the only terebratulid species. The rest of the brachiopod fauna is scanty: *T. oblonga* (J. de C. Sow.), *S. hythensis* Owen, *R. parvirostris* (J. de C. Sow.), *Lingula truncata* J. de C. Sow.

The Lower Aptian fauna occurs in the lower half of the Ferruginous Sands in the western part of the Isle of Wight (Atherfield), where the upper half is so sparsely fossiliferous that no definite upper boundary to the fauna can be stated. The fauna is also represented in the *Perna* Bed (base of the Atherfield Clay) on both sides of the Isle of Wight and along the northern crop of the Weald, and in the Hythe Beds of Kent, Surrey, and Sussex, especially east Kent, but not to the north of the Weald.

British and continental Aptian faunas. The Aptian brachiopod fauna of England has little in common with that of adjoining countries of Europe, in contrast to that of the Albian and Cenomanian, in which many species are common to Britain and Western Europe.

The Lower Aptian fauna is much poorer in species in England and many of the most characteristic species of the Lower Aptian of the Paris Basin (Corroy 1925), the Jura and north-west Germany do not appear. Such are: *Terebratula essertensis* Pictet, *T. acuta* auctt., *T. russillensis* de Loriol, *T. valdensis* de Loriol, *T. moutoniana* d'Orb., *T. collinaria* d'Orb., *T. moreana* d'Orb., *Terebratella astieriana* d'Orb., *Terebrirostra arduennensis* d'Orb.

The typical southern English Upper Aptian fauna does not appear at all on the Continent; of all the terebratulid species named above as occurring in the English Upper Aptian only *C. cyrta* seems to be known in that of the Continent. Among the long-looped forms, again, the typical English Upper Aptian species *G. aurea* Elliott, *T. trifida* Meyer, *T. davidsoni* Walker, and *T. fittoni* Meyer are not found on the Continent.

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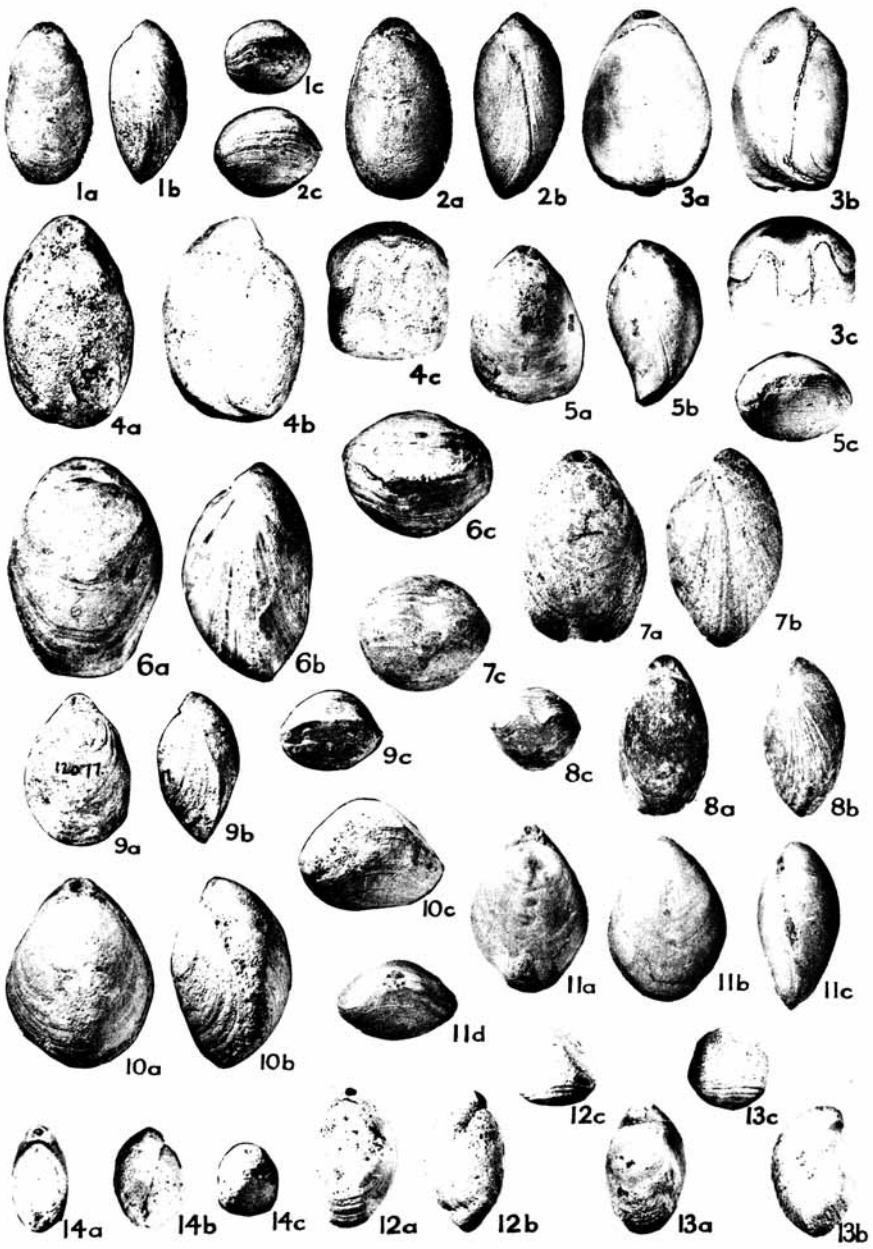

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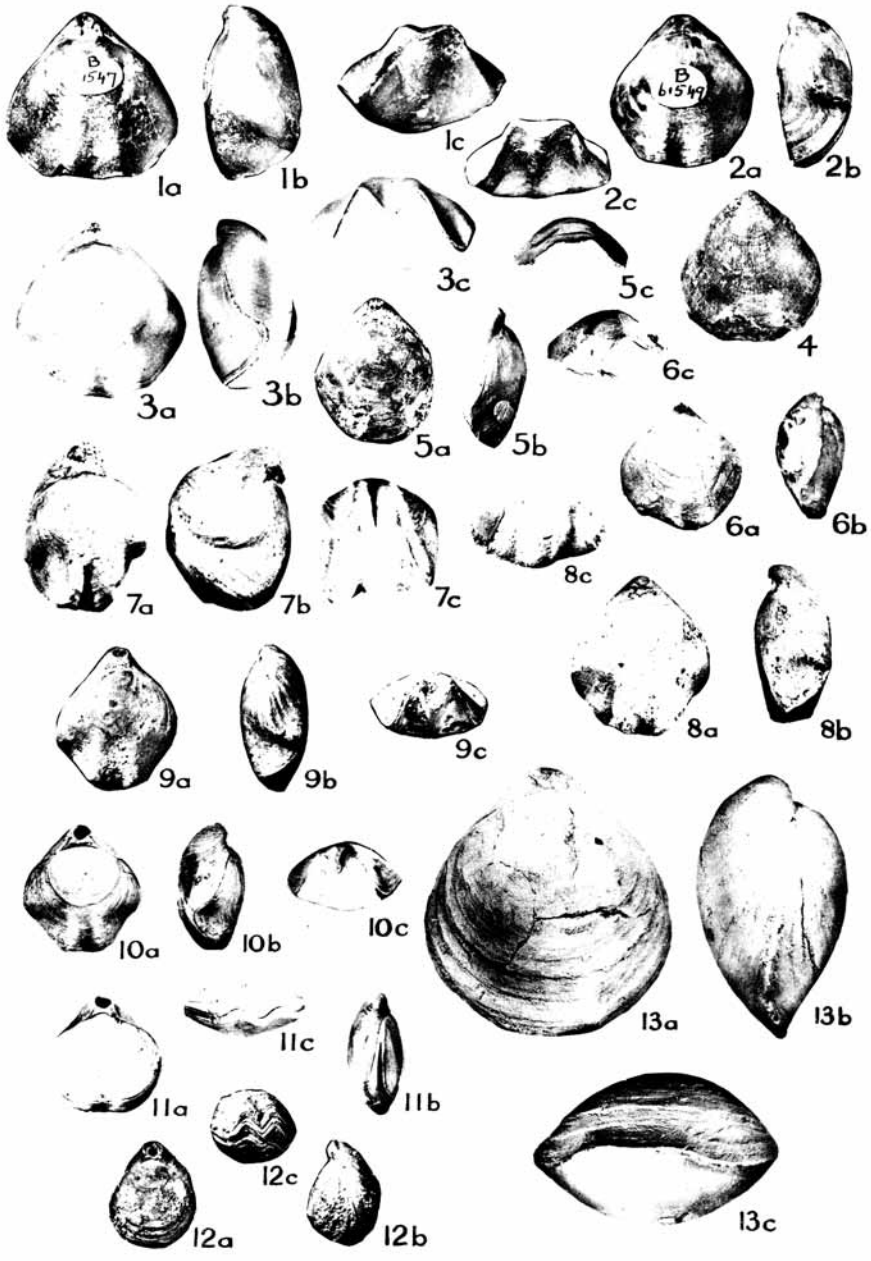

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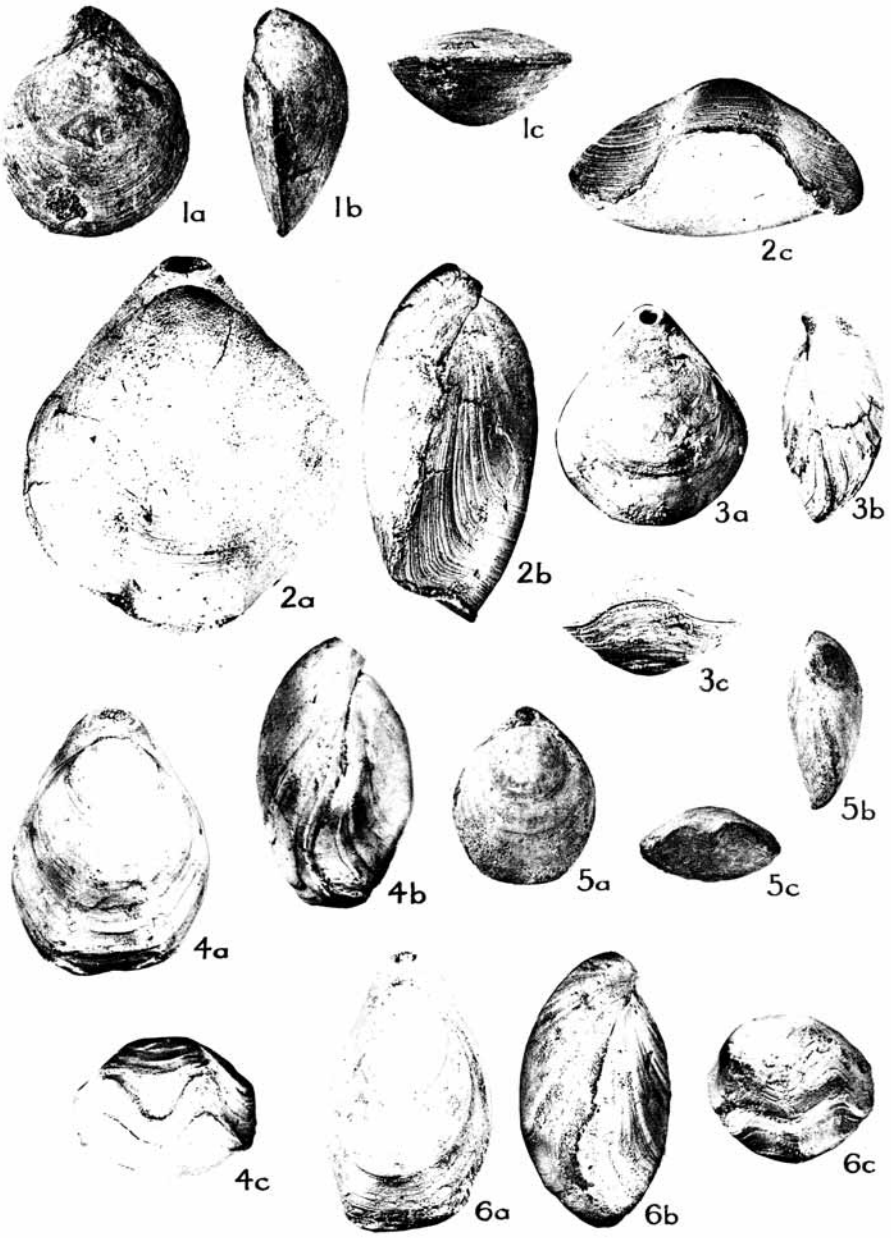

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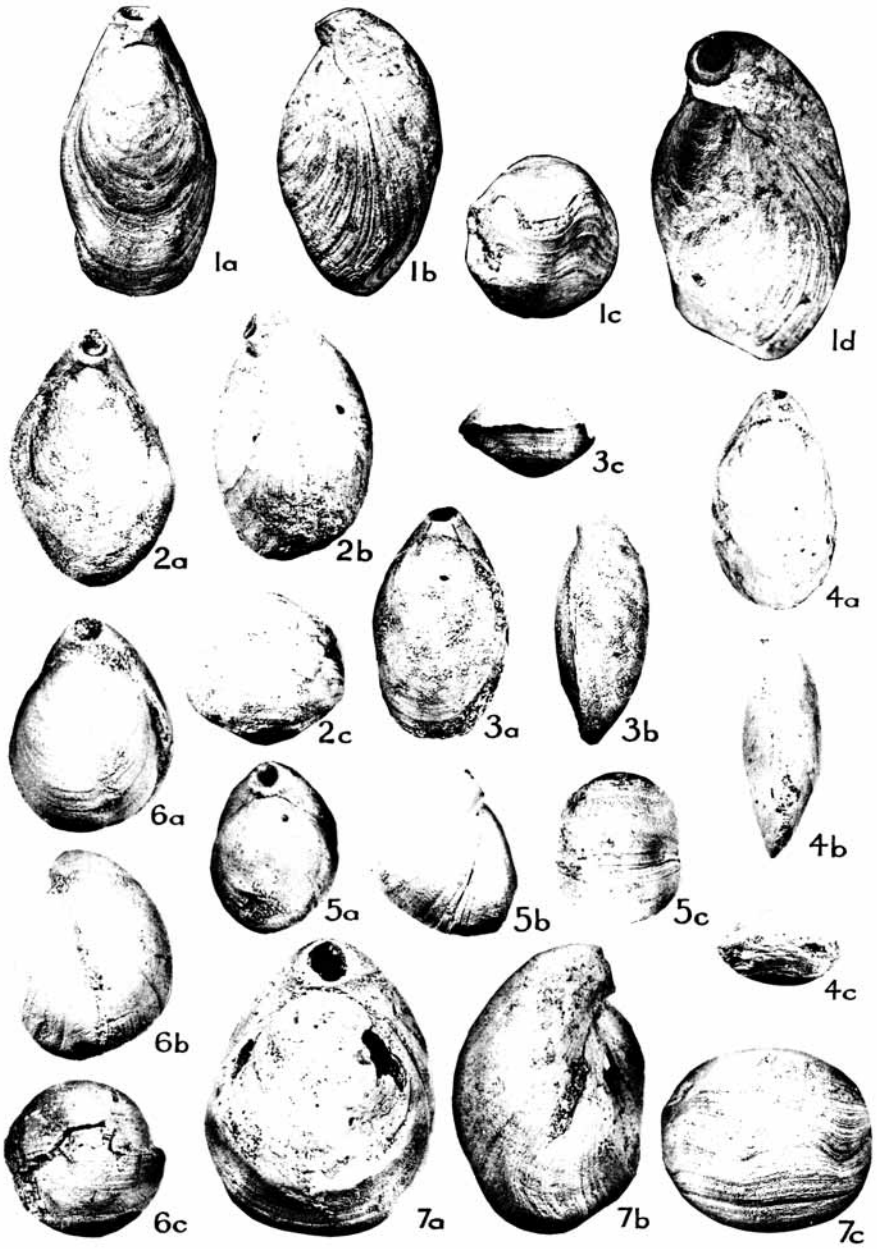

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