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XII. *On the Internal Structure of some Mesozoic Brachiopoda.*

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[Plates 62–63.]

I. Introduction.

Discussion of Modern Methods of Investigating the Internal Structure of Fossil Brachiopod Shells.

The present paper shows how a method of research hitherto but tentatively used by a few workers on the internal characters of Brachiopod shells has been elaborated and applied to certain Mesozoic genera of different families, and has resulted in establishing the relationships of the forms examined more satisfactorily than by methods hitherto employed. It embodies some results of two years' research on the identification and classification of such numerous species of the Brachiopod families Rhynchonellidæ, Terebratulidæ, and Terebratellidæ, as are found in Jurassic and Cretaceous rocks. At the present time less than half of the Mesozoic Brachiopods are specifically determinable,

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and little or nothing is known of their internal structure, their mutual relationship, or their evolution. This is probably because internal casts are rare, and in Jurassic and Cretaceous species the two valves are not as a rule found detached from one another.

Comparatively little advance has been made in the study of Jurassic and Cretaceous forms since Davidson's monumental work (1851–1884), until the appearance of S. S. Buckman's (1901–1915) numerous papers on British Jurassic species. The last culminated in 1917 in the memoir on the Jurassic Brachiopoda of the Namyau Beds, Northern Shan States, Burma, in which a new classification of the Jurassic Rhynchonellids and Terebratulids was proposed. Buckman defined many new genera which he based on the external shape and folding of the shell, beak characters, shape of the muscle-scars, and, in the Rhynchonellids, on the character of the dental lamellæ. No consideration was taken of the form of the loop or crura in the brachial valve, or the cardinalia, consisting of hinge-plates, cardinal process, etc.

Buckman's classification may be criticized for being based mainly on a single internal structure. It is therefore not to be compared with that of Palæozoic genera as defined by Hall and Clarke (1892–94), Beecher (1893, *a-c*), Weller (1910, 1911, 1914), and other American authors; or with that of Tertiary and Recent genera, as proposed by Thomson (1915, *a-d*, 1916, 1925–27), Jackson (1912, 1916, 1918) and others. In these the whole internal structure of the shell has been considered, and the importance of the shape and development of the brachial loop, hinge-plate, cardinal process, etc., has been well demonstrated. In Buckman's classification specimens having similar external shape and folding of the shell and somewhat similar muscle-scars have been grouped together as related forms, although it can often be proved that these superficially similar forms are only homœomorphs, and have totally different internal hinge-characters. Too little is at present known about the internal structure of Mesozoic Brachiopods for any definite statement to be made as to the extent and importance of homœomorphy, either in internal or external form, but similar trends in parallel lineages have probably resulted in a large number of externally similar forms. Forms externally homœomorphic were described by Buckman (1901, 1906, *a*, *b*, 1907, *a*) from the Jurassic, but no attempt was made to distinguish them by internal characters.

A practical objection to Buckman's classification is the difficulty of preparing good internal casts of Terebratulid and Rhynchonellid genera, and even when prepared, of determining the exact outline of the muscle-scars, and so distinguishing the various genera.

Following on Buckman's work came Sahni's researches (1925, *a*, *b*, 1929) on the Chalk Terebratulids. He criticized Buckman's classification for being based on the muscle-scars alone, and himself investigated the muscle-scars of various Chalk species. As a result of this work Sahni stated that the muscle-scars were similar in shape in externally different forms, and therefore of no use in classification. He diagnosed twelve new genera on the external shell-characters and on the form of the brachial loop

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and cardinal process. Unfortunately, SAHNI examined insufficient material to give any description of the development of the loop, which certainly does undergo resorption and redeposition in successive growth-stages.

Much work remains to be done on the Cretaceous species before SAHNI's classification can be safely adopted.

SAHNI (1928) extended his investigation to certain of BUCKMAN's Jurassic Terebratulid genera, namely, *Lobothyris*, *Plectoidothyris*, *Plectothyris*, etc., and dissected out the loops of several genera. From a similarity of the dorsal adductor muscle-scars of *Lobothyris* and *Plectoidothyris*, and of the shape of the brachial loop in these two genera, SAHNI erroneously assumed *Lobothyris* to be identical with *Plectoidothyris*, having failed to take into consideration the external shape and folding of the two genera, or any other internal characters of the shell, except the loop and muscle-scars. He also showed that the loop in such genera as *Plectoidothyris* and *Plectothyris* was of different form and greater length than that of the Chalk specimens examined by him.

The examination of the interior of Brachiopod shells by preparing a small number of polished serial sections of a single specimen has been practised by BELANSKI (1928, *a* and *b*), WELLER (1910, 1911, 1914), KOZLOWSKI (1929), GEORGE (1927, 1930, 1932, 1933), DUNBAR (1932), SCHUCHERT and COOPER (1932), and others, on Palæozoic species, and by ROTHPLETZ (1886), KITCHIN (1900), and WIŚNIEWSKA (1932) on Mesozoic species. With the exception of KOZLOWSKI and WIŚNIEWSKA, no author has attempted to make reconstructions of the internal structure of the specimens sectioned.

No previous description has been given of the articulation of the two valves of Mesozoic forms, and no attempt has been made to figure the detailed structure of the hinge-plate. Most of the serial sections in the works above referred to are depicted as small diagrams showing the position of dental lamellæ, septa, and spondylia, but these are not as a rule accurately drawn from the actual specimens. No idea of the relationship of the various plates can be obtained from the sections, and the actual articulation of the two valves is frequently not shown.

Two of the Jurassic genera, namely, *Lobothyris* and *Plectoidothyris*, originally diagnosed by BUCKMAN, and even described as synonymous by SAHNI, have now proved to be totally unrelated. Equally interesting results were obtained in the investigation of the five other genera, namely, *Ornithella*, *Obovothyris*, *Kallirhynchia*, *Terebrirostra*, and *Digonella* gen. nov. Both the external and internal characters of the seven genera have been investigated in detail, and the genera have been re-defined on the external and internal characters collectively. A full description of the method employed is given in Part II.

II. IMPROVED METHOD OF INVESTIGATION.

Its application to Jurassic and Cretaceous Genera.

One or two specimens, preferably topotypes, which are identical in external characters with the type of the species which is either the genoholotype or genolectotype, are

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carefully selected, measured, and either photographed or drawn, or, with rare specimens, an external cast of the shell is prepared in plaster. The specimens are heated to redness in a Bunsen flame, better results being obtained with this than with a methylated spirit lamp or with an oxy-acetylene flame, and the specimens are then allowed to cool without being plunged into water. When cold the specimens are painted with a solution of amyl acetate and collodion, and this process is repeated after twelve hours, or when the hardening solution is dry. Three or four coats of this solution are applied until the shell is again hardened. If this process is omitted the shells tend to split and much of the internal detail may be lost. Longitudinal and horizontal axes are marked on the shell, and the specimens are embedded in a rectangular block of plaster, and transverse sections are then prepared by grinding the specimens either on a large carborundum wheel worked by a dental engine; or by hand, when they are rubbed down on ground glass with carborundum powder, or on a flat slab of carborundum. The shells are ground down from the umbones, and care must be taken to keep the longitudinal axis of the specimen vertical and the transverse section exactly horizontal. The grinding is continued until the whole of the internal structure of the shell is exposed. A more elaborate apparatus, such as that used by SOLLAS (1903) or SIMPSON (1933), may be used if serial sections are required. KOZLOWSKI (1932) described a method of preparing serial sections by embedding the specimen to be sectioned in a cylinder of cement formed within a steel ring. The cement cylinder is rubbed down to the level of the top and bottom margins of the ring to ensure that both the upper and lower surface of the cement cylinder are horizontal. The cylinder of cement is then removed from the steel ring and sectioned. A rectangular block of plaster, however, is easier to orientate than a cylinder when making drawings or photographs, and is readily prepared in a wooden or metal mould made in two sections.

Drawings of the transverse sections are made whenever there is the slightest change in the internal structure, and usually from 5—10 drawings are required to every millimetre of shell removed by grinding. The exact thickness of shell removed by each successive grinding is measured with a vernier gauge.

Owing to the heating of the shell, the test and internal plates, cardinalia, etc., are calcined and appear white in contrast to the dark matrix. The details of the internal structure can, therefore, be readily drawn or photographed without the labour of polishing the surface of the section. In sections of specimens which had not previously been calcined, it was found that much of the structure was quite indeterminable, especially in those which had a limestone matrix. In silicified specimens the skeleton is not affected by heating, but the matrix infilling the shell is frequently darkened.

The transverse sections have been drawn with the pedicle valve above and the brachial valve below. This orientation of the valves was adopted because Brachiopod shells are normally viewed from the dorsal side, with the brachial valve nearest to the observer.

The drawings are made by means of an apparatus which was constructed on the principle of that form of epidiascope invented by Mr. TAMS, of the Entomological

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Department, British Museum (Natural History). An enlarged image of the sections is thrown on the paper, and is readily traced. As the sections are all drawn with the same magnification, it is possible to reconstruct the specimen either by modelling in plasticine or wax, or by preparing diagrams on squared paper.

In Rhynchonellids with much incurved umbones, the transverse sections must be ground at right angles to the hinge-plate, etc., and true horizontal sections can only be used as "identification" sections and not for reconstruction of the shell, since the umbonal incurvature will result in the reversal of the sequence of the sections.

Transverse sections show the shape and size of hinge-teeth and sockets; the shape of the umbonal cavity of the brachial valve; and of the dorsal side of the hinge-plate, etc., which cannot be obtained from the examination of separated valves of the shell. It is impossible to investigate the relationship of teeth and sockets even in perfectly-preserved detached valves, as the teeth tend to split across when the two valves are separated, and a portion of each tooth is frequently left in contact with the sockets of the brachial valve.

A certain amount of information about the length and shape of the brachial loop can also be obtained from these transverse sections. In Terebratulids and Ornithellids, however, it is often difficult to distinguish the thread-like descending branches of the loop from the matrix in the anterior transverse sections of the shell.

In order to gain some further idea of the form of the brachial loop two other specimens are selected, corresponding in external characters with the shell already sectioned. These are also heated in the Bunsen flame, and when cool hardened with amyl acetate and collodion. Longitudinal sections approximately parallel to the plane of symmetry of the shell are then prepared by grinding the half of one specimen. A few drawings are made to show the articulation of the two valves, and the relationship of loop, crura, etc., to the hinge-plate. The loop may either be reconstructed from successive longitudinal sections, or, as soon as any portion of the loop is exposed in grinding, the remainder may be completely dissected out with the aid of a needle. The latter process is found to be more profitable, since the loop is permanently retained.

The dorsal and ventral views of the loop are obtained from another specimen, which is ground longitudinally at right angles to the plane of symmetry of the shell, and the loop dissected out from the hard matrix by chisels worked by a dental engine. The loop appears as a white thread against the darker matrix, and is readily seen during dissection. In some of the specimens the loop is encrusted with calcite crystals,* which, however, can be removed by careful grinding and the perfect loop exposed. Excellent preparations were made in this way of the loop of *Digonella digona*, with its accompanying spines (fig. 12, section 20). The heating of the shell tends to loosen the calcite crystals, and the shell frequently tends to split open, exposing the loop with the crystals removed.

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* The methods employed by the Rev. NORMAN GLASS (1888) and described by DAVIDSON (1881), could also be used for such specimens.

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Internal casts showing the muscle-scars of the two valves are obtained by heating a fourth specimen of the same species; or, if material is scarce, the test of a specimen can be split off and the muscle-scars exposed before the longitudinal sections are ground to show the dorsal and ventral views of the loop, as already described.

If material for investigation is not readily obtained, transverse serial sections can be cut from a single specimen, and the sections subsequently heated to bring out the structure. A permanent record of the internal structure of the specimen is thus obtained, but the relationship of the various internal plates cannot be satisfactorily shown, as it is impossible to prepare sufficiently thin sections.

In all the seven species examined, abundant duplicate material was available for investigation. By examining several examples of each species and carefully correlating the internal structure seen in the longitudinal and transverse sections and internal casts, it was ensured that a single species was described, and not two or more homœomorphous forms.

It is believed that careful examination of the interior of Brachiopod shells by the method employed by the author would not only be the means of building up a practical classification, but would also help to establish relationships, to work out lineages, and should give much needed information about the evolution of the whole group.

III. Results of Investigation.

Morphology and new Terminology for internal structures of Mesozoic Telotremata.

In describing the various structures seen in the transverse and longitudinal sections, and in the internal casts of the Mesozoic Telotremata which have been studied, it is necessary to establish a definite terminology. Reference is made to figs. 2—14, and also to the enlarged diagram, fig. 1, for explanation of the terms employed.

The following abbreviations have been used in the figures throughout the paper :—

ad = adductor muscle-scar,
al = ascending branch of loop,
b = attachment of dental lamellæ,
br = beak-ridge,
c = denticular cavity between tooth and denticulum,
ca = cardinal area,
cb = crural base,
cp = cardinal process,
cr = crura,
crp = crural process,
d = dental lamella,
dd = ventral end of dental lamella,
did = diductor muscle-scar,
dl = descending branch of loop,

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dp = deltidial-plate,
f = false area,
for = foramen,
g = cavity of pedicle valve,
h = hinge-plate,
ih = inner hinge-plate,
isr = inner socket-ridge,
j = insertion of septum,
k = spine,
l = loop,
m = denticulum,
oh = outer hinge-plate,
osr = outer socket-ridge,
p = outer periphery of shell,
pb = ,, ,, ,, of brachial valve,
pv = ,, ,, ,, of pedicle valve,
q = accessory socket in outer socket-ridge,
s = median septum of brachial valve,
sp = septalium,
spl = septalial plate,
sw = shell wall,
t = hinge-tooth,
tr = transverse band of loop,
u = umbo,
uc = umbonal cavity of brachial valve,
x = socket,
xf = socket-floor,
y = ridge on septum of brachial valve,
z = pedicle-collar,
zs = septum supporting pedicle-collar.

In the enlarged transverse section of the shell of *Digonella digona* (SOWERBY) fig. 1, the *pedicle* or *ventral* valve is shown above, and the *brachial* or *dorsal* valve below. The outer surface of the pedicle valve is labelled (*pv*), and of the brachial valve (*pb*). In the pedicle valve the slender *dental lamellæ* (*d*) are in contact with the *teeth* (*t*), but have split away from the inner surface of the pedicle valve to which, however, a part of each dental lamella (*dd*) is still attached. In the more posterior sections the *cavity of the pedicle valve* (*g*) is divided into three chambers by the dental lamellæ.

The *hinge-teeth* (*t*) are inserted into the crenulated *sockets* (*x*), which are bounded and supported by the *inner socket-ridges* (*isr*) and *outer socket-ridges* (*osr*). Articulation of the shell is also effected by the tooth-like terminations of the *false area* (*f*), which are

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described in this paper as the *denticula* (*m*). Each *denticulum* fits into a depression or cavity in the outer socket-ridge, which has been described in this paper as the *accessory socket* (*q*). A small projection from the outer socket-ridge is inserted between the hinge-tooth and denticulum into a cavity which may be termed the *denticular cavity* (*c*).

The united *hinge-plates* (*h*) are demarcated from the inner socket-ridges by a shallow depression, and from one another by a median sulcus, or *septalium*. The floor of the septalium is formed by two plates, referred to in this paper as *septalial plates*, which fuse together to form a septum supporting the hinge-plates. The true *median septum* (*s*) is short and the apex is inserted within the septalial plates. The median septum and fused septalial plates are clearly distinguishable in specimens which have been burnt. Beneath each hinge-plate is the *umbonal cavity* (*uc*), bounded by the hinge-plate, septalial plate, shell-wall, and *socket-floor* (*xf*).

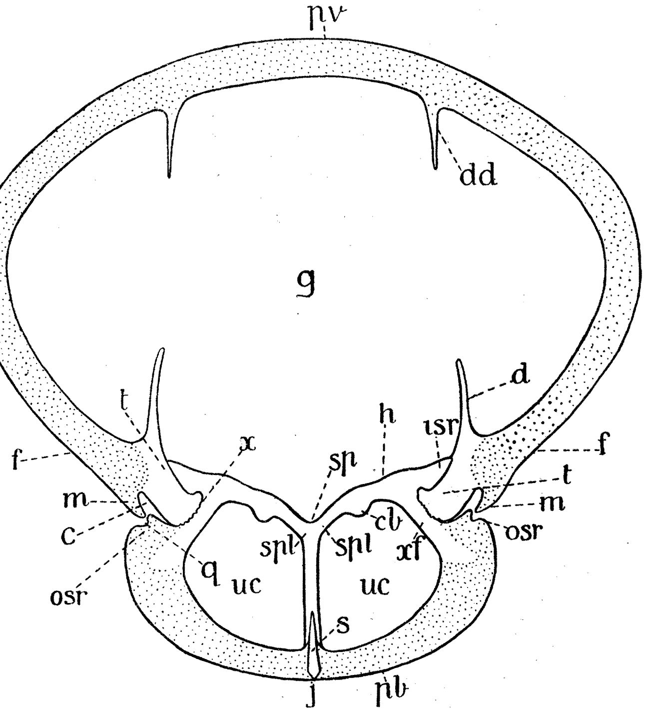

FIG. 1.—Enlarged drawing of transverse section of *Digonella digona* (J. SOWERBY) showing hinge-teeth in contact with sockets. × approximately 8. The punctate parts of the shell are dotted. The key to the lettering will be found on p. 516.

The *crural-bases* (*cb*) are seen as rounded swellings on the dorsal side of the hinge-plate, which in more anterior sections of *Digonella digona* (fig. 11, sections 29–38) project dorsally into the umbonal cavity, and finally unite with the loop.

The shell-wall and callus thickening in specimens of *Digonella digona* are found to be punctate, but punctæ are usually absent from the teeth, hinge-plates, and median septum. Scattered punctæ are seen on the ventral portion of the dental lamellæ. The punctate portions of the shell are dotted in fig. 1, and impunctate parts are left white.

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Internal Structure of the Pedicle Valve.

Dental lamellæ.—In internal casts of Rhynchonellids and Ornithellids these two plates diverge from the umbo of the pedicle valve at an angle varying slightly in different genera, but more or less constant for one species. They appear on the cast as two slits extending for a distance of 2–10 mm. In transverse sections the dental lamellæ are seen to extend across the cavity of the pedicle-valve dividing it into three chambers posteriorly, but they gradually recede from the shell-wall and remain in contact with the hinge-teeth anteriorly. The height of the dental lamellæ dorso-ventrally varies not only in specimens of one species, but the two lamellæ may vary in development in a single specimen, as shown in *Kallirhynchia yaxleyensis*, fig. 2, sections 11, 12. The dental lamellæ may be more strongly developed in the adult than in young specimens, or conversely they may become obsolete, or embedded in a thick callus deposit in the gerontic stage, as in *Ornithella bathonica*, fig. 7, and *Obovothyris magnobovata*, fig. 9. In the seven species examined dental lamellæ were developed in *Kallirhynchia yaxleyensis*, *Ornithella bathonica*, *Obovothyris magnobovata*, *Digonella digona*, and *Terebrirostra lyra*. In *Terebrirostra*, figs. 13, 14, the dental lamellæ extend the whole length of the much elongated umbo. Posteriorly, fig. 13, sections 1–4, the lamellæ extend across the cavity of the valve from the inner margin of the fused deltidial plates, but anteriorly they recurve sharply towards the thickened lateral margins of the pedicle valve, to which they are attached (fig. 13, sections 5–10, fig. 14, sections 1–5).

In the longitudinal sections ground either parallel, or at a small angle, to the plane of symmetry of the shell, the postero-anterior extension of the dental lamellæ is well shown. In *Ornithella*, fig. 8, sections 3–6, the dental lamella is seen to unite with the false area, and the actual line of fusion of the two structures is faintly seen. In *Obovothyris*, fig. 10, section 1, and *Digonella*, fig. 12, section 2, however, the dental lamella does not appear to fuse with the false area, and the two plates, although adjacent, are clearly demarcated.

Hinge-teeth.—These are rarely distinguishable in artificially prepared internal casts, but are well shown in longitudinal and transverse sections. The angle of insertion of the teeth within the sockets is usually remarkably constant for any species, although the teeth may vary in size in adult individuals of one species, according to the amount of callus thickening.

The long, slender tongue-like teeth of *Lobothyris* form a marked contrast to the massive teeth of *Plectoidothyris* with their hammer-shaped termination. The depth of insertion of the teeth posteriorly within the sockets is well shown in *Kallirhynchia*, fig. 2, sections 10, 11, and *Plectoidothyris*, fig. 4, sections 7–11, in which the posteriorly inserted portion of the tooth appears to be detached from the remainder.

Denticula.—Articulation is effected not only by the teeth and sockets, but in addition

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by the false areas. These usually terminate in a small tooth which is described in this paper as a denticulum. The denticula vary in size in different genera. In *Lobothyris*, fig. 5, sections 12, 13, they are long, slender, and finger-like, and fit completely into a cavity, or accessory socket, in the outer socket-ridges of the brachial valve. In *Kallirhynchia*, fig. 2, section 12, *Digonella*, fig. 11, section 23, and *Plectoidothyris*, fig. 4, section 12, the denticula are short and massive, and the rounded apex rests in a shallow depression in the outer socket-ridge. In *Terebrirostra* there is no false area and consequently no denticula are developed. The part of the outer socket-ridge forming the inner margin of the accessory socket may also interlock with the cavity between the hinge-tooth and denticulum as seen in *Lobothyris*, fig. 5, section 12. In the latter genus articulation of the two valves is therefore effected by three different structures: (1) hinge-tooth and socket; (2) denticulum and accessory socket; and (3) outer socket-ridge and denticular cavity.

Denticula are distinct from the small processes on the posterior surface of the hinge-socket in the Palæozoic Orthoidea which are described as "denticles" by SCHUCHERT and COOPER (1932). The denticles like the denticula assist in the articulation of the two valves.

Pedicle-collar.—The term pedicle-collar was proposed by JACKSON in 1916 (p. 24) for a plate on the inner side of the apex of the pedicle-valve. This structure is probably secreted by the mantle of the pedicle valve. The pedicle-collar is described as being "a kind of continuation of the deltidial plates, is free in front, and separated from the shell by a narrow cavity." This structure was observed by JACKSON in twenty-four recent Terebratulid species, but it was not found in forms having an advanced type of long loop, such as *Magellania*, *Terebratella*, *Dallina*, and *Macandrevia*. In some of these long-looped forms, however, there is a thickening in the umbo round the foramen resembling a pedicle-collar, but this is always fused to the shell, and never free anteriorly. This thickening round the foramen was described later by JACKSON (1918, p. 196) as a *pseudo-pedicle-collar*, and is the same as the *sessile pedicle-collar* of THOMSON (1927, p. 74).

A true pedicle-collar is said (JACKSON, 1916, p. 25) to occur in the fossil species *Terebratula grandis*, *Cyclothyris latissima*, and *Megathyris decollata* (= *detruncata*). In the last species the pedicle-collar is supported by a median septum.

The pedicle-collar was described by FISCHER and OEHLERT (1891) as "doublure sous-apicale et sous-cardinale," and before JACKSON's description of the pedicle-collar appeared in 1916, THOMSON (1915 *b*, p. 390) had observed and figured a similar structure in *Hemithyris psittacea*. In a later publication THOMSON (1927, p. 75) discussed the development of a pedicle-collar in Tertiary and Recent species and stated that "In general, species with a marginate or labiate foramen possess a well-developed pedicle-collar within the beak, forming a complete tube extending forward some little distance. . . ."

WIŚNIEWSKA (1932, p. 7) in a monograph on the Upper Jurassic Rhynchonellids of Poland stated that a pedicle-collar was developed in every species examined by her.

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In the seven genera examined by me a pedicle-collar was observed in *Digonella*, *Obovothyris*, *Lobothyris*, *Plectoidothyris*, and *Kallirhynchia*, but it varies considerably in form in the different genera. In *Digonella*, fig. 11, sections 1–7, the pedicle-collar forms a complete ring, well separated from the inner wall of the pedicle valve anteriorly, and it is supported posteriorly by a short septum. This septum can be seen in internal casts of *Digonella digona*, and its postero-anterior extension is shown in the longitudinal section, fig. 12, sections 15, 16. In *Obovothyris*, fig. 9, sections 1–4, the pedicle-collar is masked by posterior deposits of callus, but the septum supporting the pedicle-collar is prominently developed. Although the transverse sections of *Ornithella* were carefully examined a pedicle-collar was only observed in one specimen, so that if normally developed in this genus it must be embedded in the thick callus deposits filling the apex of the shell. No trace of a pedicle-collar was seen in young shells of *Ornithella*, or in young or adult shells of *Terebrirostra*. In *Lobothyris* the pedicle-collar is supported by a rudimentary septum, while in *Plectoidothyris* the pedicle-collar is developed as a thickened disk on the inner side of the deltidial plates. In longitudinal sections of *Kallirhynchia*, fig. 3, sections 13–15, the pedicle-collar is seen as a thickening on the ventral side of the umbo of the pedicle valve. At a short distance from the apex of the shell the pedicle collar becomes detached from the inner wall of the pedicle valve and projects into the cavity of the pedicle-valve like a short spine.

Further research is needed before anything definite can be said about the importance for generic diagnoses of the development or non-development of the pedicle-collar, and of its supporting septum.

Deltidial Plates.—In six of the seven genera examined the deltidial plates are conjunct, and no line of junction of the two plates is distinguishable in the transverse sections. In some genera belonging to the Zeilleriinæ the two deltidial plates may become conjunct, and further growth result, either in the overlapping of the two plates, or, in their being spirally coiled on the inner dorsal surface of the pedicle valve. In *Kallirhynchia*, fig. 2, sections 5–7, the deltidial plates are disjunct.

In the longitudinal sections the deltidial plate may appear as a narrow curved plate in contact with the outer edge of the false area, or as a small semicircular plate anterior to the pedicle opening or foramen.

In *Terebrirostra* the conjunct deltidial plates or symphytium extend the whole length of the elongated umbo.

Cardinal Area or Interarea.—In the seven genera specially investigated a true cardinal area is only developed in the genus *Terebrirostra*. In longitudinal sections of *T. incurvirostrum*, fig. 14, sections 5–8, the cardinal area is seen to be fused with the dorsal end of one of the curved dental lamellæ. The outer surface lacks the prominent costation of the remainder of the shell, but is marked by numerous growth-lines which cross the two inter-areas at an angle of about 45°.

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Muscle-scars.—To the pedicle valve of the Telotremata are attached three sets of muscles—the adductors for closing the shell, the diductors for opening the shell, and the pedicle muscles which serve to retract the pedicle, and also attach the pedicle to the posterior part of the valve. The three sets of muscles leave scars which mark the region of their attachment to the shell, and these scars appear as more or less prominent ridges on the internal cast of the shell. The adductors have a double attachment to the pedicle valve and the scars of their attachment are usually enclosed by those of the diductor muscles. The pedicle muscles consist as a rule of two pairs of muscles known as the dorsal and ventral adjustors, and a single muscle which leaves a scar posterior to those of the adductors and diductors. The dorsal adjustors are usually attached to the hinge-plate of the brachial valve, and the two ventral adjustors leave a scar on the outer side of each of the diductor muscle-scars of the pedicle valve. In most of the genera examined the outline of the whole muscle-area was distinguishable, but the outlines of the individual muscle-scars were obscure. Better results, however, were obtained with the Ornithellids and Rhynchonellids than with the Terebratulids.

Buckman (1917) gave no description of the muscle-scars of the pedicle valve in any of his Terebratulid genera owing to the difficulty of preparing internal casts of this valve.

In *Lobothyris* the muscle-area is elongated and narrow, and extends from the umbo as a prominent ridge, about 12 mm. long, and 3 mm. wide at the anterior end. In *Plectoidothyris* the muscle-area is obscure and does not form a prominent ridge. The posterior end of the diductor and adductor scars are situated about 8 mm. anterior to the umbo, and the scars form an oval area about 11 mm. in width and 10 mm. in length.

After removing a thick deposit of callus, the muscle-scars were satisfactorily exposed in *Ornithella*, fig. 23, Plate 62. The diductor scars are elongated and narrow, and enclose two small oval adductor scars. The anterior adjustors are seen as small oval scars outside the posterior end of the diductors. In *Obovothyris*, *Digonella*, and *Terebrirostra*, the shell flakes off very readily when the specimens are heated, but the muscle-scars are usually obscure. An attempt has been made to figure the ventral muscle-scars of *Obovothyris* and *Digonella*, figs. 18*b*, 27, Plate 62, but the outline of the adductor and diductor scars is difficult to distinguish. The muscle-scars in these two genera are posteriorly situated. In *Kallirhynchia yaxleyensis* the muscle-area lies below the anterior end of the dental lamellæ and extends for about half the length of the pedicle valve. The two adductor scars are in contact along their inner margins, and together form an elongated oval area which is in contact on its lateral and anterior margins with the broad crescentic diductors. The adjustors leave a narrow linear scar on the outer margin of the diductors, fig. 16, Plate 62.

Vascular markings.—These are referred to in a paragraph describing this structure in the brachial valve (p. 530).

Internal Structure of the Brachial Valve.

Hinge-sockets and Socket-ridges.—The depth and width of the hinge-socket and the amount of overlap of the socket by the inner and outer socket-ridges are characters

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which vary considerably in the seven genera investigated. In the Terebratulid genera *Lobothyris* and *Plectoidothyris* the sockets do not appear to be crenulated. In *Lobothyris* the sockets are narrow and deeply excavated for the reception of the elongated linguiform teeth, and the elaborate processes for the articulation of the two valves (described on p. 520) probably render unnecessary any crenulation of teeth and sockets. In *Plectoidothyris* the sockets are broad and shallow, and the socket floor tends to split away from the outer socket-ridge while the anterior portion of each tooth is still in contact with the socket and inner socket-ridge, fig. 4, sections 13–15.

The crenulæ of the teeth and sockets in the genera *Ornithella*, *Obovothyris*, and *Digonella*, fig. 1, are so minute that they are only perceptible with a high-powered lens. In these three genera the outer socket-ridge does not play an important part in the articulation of the two valves, but the inner socket-ridge overlaps the socket and interlocks with a sulcus on the ventral side of a lip-like projection of each tooth. In *Kallirhynchia*, on the contrary, the crenulæ are clearly seen with a magnification of five diameters, and they interlock with corresponding crenulæ on the teeth.

The sockets in *Terebrirostra* are shallow and coarsely crenulated, and are only slightly overlapped by the outer socket-ridges which fit into a depression in the dorsal margin of the teeth. The inner socket-ridges, however, project for a short distance across the socket and interlock with a sulcus on the ventral surface of each tooth.

Additional information about the sockets, and inner and outer socket-ridges, can be obtained from the longitudinal sections ground approximately parallel to the plane of symmetry of the shell. In the sections farthest from the median line the outer socket-ridge is first seen as a slight thickening of the umbonal portion of the shell of the brachial valve. This thickening is increased to form a rounded lobe with a shallow depression on its anterior ventral margin. The depression deepens and forms the hinge-socket which is bounded posteriorly and anteriorly by a rounded lobe. The anterior lobe is the inner socket-ridge and the posterior the outer socket-ridge. In longitudinal sections near a median line through the shell the inner socket-ridge is seen to be deflected posteriorly and so to enclose the tooth within the socket. In longitudinal sections of some genera, such as *Obovothyris*, fig. 10, section 8, the inner socket-ridge is seen to persist as a posteriorly directed lip, when teeth and sockets can no longer be observed.

Cardinal Process.—This structure, which serves for the attachment of the diductor muscles in the brachial valve, is developed in the genera *Lobothyris*, *Plectoidothyris*, and *Terebrirostra*. In *Lobothyris* the cardinal process is developed as a small laterally elongated boss which is sessile on the inner wall of the brachial valve. It is never prominent and is only about 0·6 mm. long postero-anteriorly. The ventral surface is concave posteriorly, but slightly trilobate anteriorly. In *Plectoidothyris* the cardinal process is considerably larger and more prominent than in *Lobothyris*, and projects ventrally beyond the hinge-plates into the cavity of the pedicle valve. It is separated from the shell wall by a deep umbonal cavity. Posteriorly the ventral surface is medianly depressed and the depression is bounded on each side by a projecting lobe.

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Anteriorly, however, the outer lobes broaden and the median depression becomes correspondingly narrower and finally a low median ridge is developed and the cardinal process becomes slightly trilobed. In *Terebrirostra* the cardinal process is even more prominently developed than in *Plectoidothyris* and curves upwards away from the hinge, and projects ventrally into the cavity of the pedicle valve, appearing in transverse sections as a trilobed hollow boss with a short stalk which is entirely detached from the brachial valve. In *T. lyra* the trilobation and posterior denticulation of the cardinal process are well developed, fig. 3, sections 4–9, but in the geologically older species, *T. incurvirostrum* the cardinal process is simpler, the denticulation is not apparent, and the trilobation is less marked. No cardinal process is developed in the Ornithellid genera, *Ornithella*, *Obovothyris*, *Digonella*, or in the Rhynchonellid genus, *Kallirhynchia*.

Hinge-plates.—These plates serve for the attachment of the dorsal adjustor-muscles of the pedicle, and also for the diductor muscles in genera in which no cardinal process is developed. In the seven genera specially investigated the hinge-plate is not divided by the crural base into an inner and outer hinge-plate. Inner and outer hinge-plates are developed in the Tertiary Terebratulid shells in which the crural bases are given off ventrally and intersect the hinge-plate. The hinge-plates are among the most important structures in the brachial valve, as they are more constant in development and exhibit less variation in subsequent growth-stages than other internal characters. The difference between the hinge-plates of the various genera is best studied in the transverse sections. In *Kallirhynchia* the hinge-plates are thin, dorsally concave plates extending more or less horizontally and separated from one another by a narrow cavity. They are well demarcated from the inner socket-ridges by a shallow sulcus. In the more anterior transverse sections of *K. yaxleyensis*, fig. 2, sections 18, 19, the crural bases are seen as small angular projections from the dorsal surface of the hinge-plates. In *Lobothyris* and *Plectoidothyris* the hinge-plates are ventrally concave, and the inner extremities of each plate which are sharply deflected ventrally are extended anteriorly to form the crural bases. In *Lobothyris* the hinge-plates are not sharply demarcated from the inner socket-ridges, and posteriorly are sessile on the inner wall of the valve. Anteriorly, however, a narrow elongated umbonal cavity is developed beneath each hinge-plate, fig. 5, sections 12–20. A deep umbonal cavity separates the hinge-plates from the floor of the brachial valve in *Plectoidothyris*, and the inner socket-ridges and hinge-plates are well differentiated. The hinge-plates become free and detached from the cardinal process about 6 mm. below the apex of the valve.

A somewhat unusual type of hinge-plate is seen in *Terebrirostra*, in that each plate extends dorso-ventrally, fig. 13, section 11, and projects for a considerable distance into the cavity of the pedicle valve. The hinge-plates are separated by a narrow, deep septalium and are differentiated from the inner socket-ridges by a sulcus. In this genus the hinge-plates are united and supported by a median septum.

The hinge-plates of *Ornithella*, *Obovothyris*, and *Digonella* resemble one another in

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extending medio-laterally, but a careful examination of these plates in the three genera reveals various minor differences. No cardinal process is developed and the hinge-plates are united throughout, and supported by a median septum. In *Ornithella* the hinge-plates are approximate posteriorly and are separated by a deep V-shaped septalium. They tend to flatten and increase in width medio-laterally away from the umbones. The septalium becomes shallower, until it is scarcely distinguishable, and it is finally replaced by a rounded median ridge. The hinge-plates are separated from the inner socket-ridges by a shallow depression. In adult specimens of *O. bathonica* and other species of *Ornithella* the posterior part of the shell is much infilled by callus, and these deposits tend to mask the outline of the hinge-plates, fig. 7, sections 8–16. In transverse sections of burnt specimens, however, the outline of hinge-plates, teeth, and sockets, etc., can be readily distinguished from the secondary thickening. The septum supporting the hinge-plates and umbonal cavity is scarcely distinguishable in the adult shell owing to the callus infilling. The crural bases are seen as rounded swellings on the ventral side of the hinge-plates.

In *Obovothyris* the septalium is shallow even near the umbo of the brachial valve, and anteriorly is scarcely distinguishable. The ventral side of the hinge-plates is convex posteriorly, but tends to flatten out horizontally away from the umbo. The inner socket-ridges are not clearly differentiated from the hinge-plates. In adult shells of this genus the umbonal cavity is only infilled with callus for a distance of about 0·5 mm. from the umbo, and the septum supporting the hinge-plates is clearly defined. The crural bases are given off from the dorsal side of the hinge-plates.

The hinge-plate of *Digonella* shows a certain resemblance to that of *Obovothyris* in the early growth-stages, but in the adult is sufficiently distinct to warrant the description of the two species *D. digona* and *D. digonoides* as belonging, either to a distinct genus, or to a subgenus of *Obovothyris*. Posteriorly the hinge-plates are narrow and approximate, and are separated by a deep septalium, as in *Ornithella*. Anteriorly they increase in width medio-laterally and flatten, but the septalium is always distinguishable. The inner socket-ridges are deflected ventrally at a slight angle to the hinge-plates, and the crural bases are first seen as swellings on both the dorsal and ventral sides of the hinge-plate, fig. 11, section 16. The swellings on the ventral surface become less apparent, while the dorsal swellings increase in size anteriorly and form angular points which project into the umbonal cavity.

Crura and Brachial Loop.—The crural bases seen in transverse sections through the shell have already been described in the section entitled “ Hinge-plates.” Additional information about the relationship of these structures to the hinge-plate and inner socket-ridges can be obtained from the longitudinal sections parallel to the plane of symmetry of the shell.

In *Kallirhynchia* the crural bases which are given off from the dorsal side of the hinge-plate project ventrally and unite with the crura. The crura consist of two flattened, curved, posteriorly concave laminæ which project from the hinge-plate into

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the cavity of the pedicle valve. Each primary lamina unites at the ventral end with a second curved lamina, which is suspended from it and projects dorsally like a spur. A ventral extension of this second lamina beyond the point of attachment with the primary lamina terminates in a hook-shaped process, the apex of which is directed posteriorly, fig. 3, section 15. In immature specimens the crura appear to be longer than in senile individuals, and to extend almost across the entire cavity of the pedicle valve. The primary and second lamellæ are not clearly differentiated. The spur-like extension of the second lamella is anterior to, but almost in contact with, the primary lamella. The ventral extension of the second lamella is thread-like and curves round so that the apices of the two crura are practically in contact. The hook-shaped process, which terminates the crura in the gerontic form, is considerably less developed in immature specimens. This type of crura, which has not been previously described, may be known as calcarifer. Little is known at present of the interior of Jurassic Rhynchonellids, so no comparison can be made with other genera until further work on similar lines has been undertaken. From the differences of the shape of the hinge-plates of such genera as *Rhactorhynchia*, *Burmirhynchia*, and *Kutchirhynchia* when compared with those of *Kallirhynchia* it is reasonable to suppose that the crura of these genera will also differ in outline.

Owing to the poor state of preservation of the interior of the shell of *Terebrirostra lyra* it was only possible to make out details of the loop in one of the specimens examined. The crural bases are given off ventrally, and are a direct anterior continuation of the hinge-plates. The slender crural processes in *Terebrirostra incurvirostrum* are about 3·5 mm. in length in the adult, and curve anteriorly away from the crural bases. The loop in adult specimens of *T. incurvirostrum* extends as a narrow ribbon scarcely visible to the naked eye, parallel to, and about 4 mm. from, the outer surface of the brachial valve. The two descending branches of the loop are about 4 mm. apart. About 4 mm. from the anterior margin the loop recurves, and the ascending branch of the loop is directed posteriorly, almost in the same dorso-ventral plane as the descending branch, and at a distance of about 2 mm. from it. From the dorsal or ventral view only one branch of the loop is distinguishable anteriorly. About 11 mm. from the anterior margin the ascending branch of the loop is directed inwards, and bends round towards the pedicle valve and finally unites with the curved transverse band about 15 mm. from the anterior margin. A few small spines were seen projecting from the loop of one specimen. In the adult specimen illustrated in fig. 14, section 10, the brachial valve is 23·5 mm. long and the loop is entirely free from the septum. In an immature specimen [B. 84534] with a brachial valve 19·5 mm. long the loop is attached by slender connecting bands to a ridge on the septum about 0·5 mm. from the anterior end of the septum. In this specimen the connecting bands are 1·4 mm. long and project horizontally from the septum, and are then deflected at right angles and join the descending lamellæ. In the longitudinal section of a still younger specimen [B. 84535] having a brachial valve 14 mm. long the connecting bands are about 1·5 mm. long and extend almost horizontally from loop to septum. The deflection of the band

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in the slightly older specimen probably indicates that the connecting band is about to be detached from the descending lamellæ by resorption. This resorption of the connecting bands was seen in a transverse section of a brachial valve 20 mm. long, in which one connecting band is still attached to the septum but has split away from the descending lamella, while the other band has become detached from the septum but is still united with the loop.

The loop of *Ornithella* is given off from the ventral side of the hinge-plate. The descending branches curve forward following the contour of the lateral margin of the shell, and are about 10 mm. apart. The ribbon is narrow and flattened dorso-ventrally, and is broadest in lateral view. Small spines spring from one edge of the ribbon, but are rarely preserved. The anterior part of the descending branches is directed towards the ventral valve and the loop recurves upwards about 4 mm. from the anterior margin. The ascending branches are short and curve at first dorsally, then recurve ventrally and unite with the broad horizontal transverse band about 15 mm. from the anterior margin. The ascending branches and the transverse band form a pentagonal figure. The crural processes are small and project forward into the cavity of the pedicle valve, converging slightly towards the median septum. No spines were observed on the ascending branches of the loop of *Ornithella,* or of any the genera specially investigated.

In *Obovothyris* the loop is rather similar in shape to that of *Ornithella*, but the spines on the descending branches are longer and usually well preserved. In both *Obovothyris* and *Digonella* spines are developed on the outer margin of the descending branches and are even seen on that portion which unites with the crural bases (fig. 9, section 26, and fig. 11, sections 37, 38). In *Obovothyris* the crural processes are short and converge towards one another. The slightly curved descending branches of the loop are about 10 mm. apart, and usually extend to within 3 or 4 mm. of the anterior margin, but in some specimens they are almost in contact with the margin. The anterior portion of the ascending branches is practically in the same dorso-ventral plane as the descending branches, but they are deflected ventrally and unite with the transverse band about 10 mm. from the anterior margin. The transverse band is horizontal in adult specimens, and ascending branches and transverse band form a broad pentagonal figure.

In *Digonella* the descending branches diverge at a low angle from the hinge-plate, but do not converge anteriorly. Spines are usually preserved on the descending branches and in one specimen, fig. 12, section 20, they are fine and hairlike, about 1·5 mm. in length, and eight spines occupy a vertical distance of 5 mm. The descending branch of the loop in this specimen is flattened dorso-ventrally, and the spines project dorsally, curving round from under the loop anteriorly where the ribbon twists. The loop in *Digonella digona* extends almost to the anterior margin of the shell. The ascending branches either may be abruptly recurved upwards in the same dorso-ventral plane as the descending branches, or they may project laterally

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beyond the descending branches. They unite with the slightly curving transverse band about 8 mm. from the anterior margin. The transverse band is bounded at each end by a small flange which projects posteriorly. The ascending branches and transverse band form a rounded arch, which is never pentagonal in outline. The crural processes are large and project well forward into the cavity of the valve.

In *Obovothyris* and *Digonella* the loop is given off from the dorsal side of the hinge-plate, and in neither of these genera, or in *Ornithella*, is the loop attached to the median septum in the adult.

In a specimen of *Digonella digona* having a brachial valve 10 mm. long the loop resembled that of the adult shell, and was not attached to the septum. Examination of a smaller specimen with a brachial valve 5·5 mm. long showed that the loop resembled that of the adult, but the descending lamella was much thickened for about 2 mm. below the dorsal umbo. A narrow connecting band was seen attached to the descending lamella about 2·5 mm. below the umbo, but it did not extend across to the median septum. In still younger forms the loop was no doubt attached to the septum by narrow connecting bands. A similar terebratellid stage has not yet been observed in young specimens of *Ornithella* and *Obovothyris*.

In *Lobothyris* and *Plectoidothyris* the crural bases are given off ventrally, and project almost at right angles to the more or less horizontal hinge-plates. In both these genera the descending branch of the loop is a broad ribbon, flattened dorso-ventrally, and in dorsal or ventral view the edge of the ribbon appears as a thin thread. In *Lobothyris punctata* the loop is usually about 8·5 mm. long, while in *Plectoidothyris polyplecta* it is about 18·5 mm. long. The descending branches in both these genera are abruptly deflected upward to form the ascending branches. In *Plectoidothyris* the ascending lamellæ slope gently towards the ventral valve and unite with the transverse band about 5 mm. from the anterior end of the loop. The transverse band is rather narrow and slightly curved, and is demarcated from the ascending lamellæ by a bend in the loop. The crural processes are given off about 7 mm. below the umbo.

In *Lobothyris* the ascending lamellæ unite with the curved transverse band about 2·5 mm. above the anterior end of the loop.

In the longitudinal section of *L. punctata*, fig. 6, section 12, the broad ribbon of the descending lamellæ obscures the ascending lamellæ and transverse band. The crural processes project ventrally in the same plane as the descending lamellæ, of which they appear to be triangular extensions.

Median septum, Septalium, and Septalial Plates.—The V-shaped cavity between the united hinge-plates of many Rhynchonellid and Zeilleriid species was described by LEIDHOLD (1920, p. 354) as the septalium. Before the publication of this work, however, WELLER (1910, p. 502) had described this cavity in Palæozoic Rhynchonellid species as the crural cavity. As the term crural cavity is thought to be misleading, since the cavity is not connected with the crura, LEIDHOLD's term, septalium, has been adopted. The floor of the septalium is formed by two plates, the septalial plates, which converge

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and fuse together to form a septum. This septum supports the hinge-plates, and appears to be distinct from the true median septum in many species. In the transverse section of *Digonella*, fig. 1, it was found that the dorsal end of the so-called median septum tended to split along the centre, as though composed of two separate plates, and also to become detached from a short septum, the dorsal end of which is inserted in the wall of the brachial valve. This short septum is the true median septum. The actual splitting away of the septalial plates from the median septum is shown in *Digonella digona*, fig. 11, sections 30–34, in *Terebrirostra lyra*, fig. 13, section 21, and in *Kallirhynchia yaxleyensis*, fig. 2, sections 7, 8.

It has been found that the calcining of the shell tends to separate the true median septum fairly readily from the septalial plates. The division of the septum into the true median septum and septalial plates can be seen equally well in transparent transverse sections of the brachial valve, as was shown by WIŚNIEWSKA in 1932 (p. 6, fig. 1, A–C) in the Rhynchonellid species, *Rhynchonella loxia* (FISHER DE W.), *Septaliphoria pinguis* (ROEMER), and *S. astieriana* (D'ORBIGNY). In the transparent sections of these species the true median septum appears as a short rudimentary structure, at the base of, and enclosed by, a second septum which unites with the hinge-plates.

In transverse sections of Rhynchonellid species which have a much incurved umbo in the brachial valve the septalium appears to be reversed, and the two septalial plates, which are only fused together and in contact with the median septum in the posterior part of the shell, project freely as two diverging plates into the umbonal cavity, fig. 2, sections 8–10.

The true median septum in *Kallirhynchia* only extends across the umbonal cavity for a distance of about 0·5 mm. from the umbo of the valve, anterior to this it is of such a low elevation as to be almost indistinguishable in the transverse sections of *K. yaxleyensis*.

No septalium is developed in Terebratulid species in which a cardinal process is developed, since the hinge-plates are not united. A rudimental septum is observed in the anterior transverse sections of *Lobothyris punctata*, but this septum is probably formed as a thickening along the inner margin of the adductor muscle-scars. FREDERICKS (1918, 1927, p. 2) suggests the term "euseptoidum," for a similar development in the pedicle valve of *Spirifer*, *Schizophoria*, etc. In *Terebrirostra*, however, in which the hinge-plates remain united at the base of the cardinal process, a deep septalium is seen. The septum in *Terebrirostra* bears a low rounded ridge, in fig. 14, section 10, *y*, springing from the dorsal edge near the umbo and extending across the septum to its anterior margin. The slender connecting bands joining loop and septum in immature forms unite with this ridge about 1·5 mm. above the anterior termination of the septum. A septalium, varying in depth in different species, is developed in many genera of the Zeilleriinæ as the hinge-plates are united.

Vascular sinuses.—These are extensions of the cœlome, or visceral cavity, into the

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dorsal and ventral mantle-lobes which line the shell, and they contain the circulatory fluid or blood. The shell secreted by the mantle is usually thinner along the vascular sinuses so that their position can often be traced as furrows on the interior of fossil shells, or as ridges on internal casts. The vascular sinuses consist usually of two or more main trunks which branch more or less frequently towards the shell margin. The disposition of the sinuses varies in different genera, and may differ also in the two valves of a single species. The arrangement of the sinuses appears to be sufficiently constant for this character to be considered in the description of Brachiopod genera and families. A special study has been made of the vascular sinuses in the genus *Zeilleria*, in connection with a piece of research on the Jurassic Zeilleriids. The disposition of the four main trunks and the number of bifurcations of the trunks was found to be similar in different species, but the angle of divergence of the inner trunks from the end of the septum, and of the divergence of the two secondary sinuses formed by bifurcation of the two outer main trunks, varied in shells of different width and convexity. In the pedicle valve there are also four main trunks, the outer two of which bifurcate once.

In most of the artificially prepared casts of Terebratulids no trace of vascular sinuses can be seen, owing, no doubt, to the difficulty of separating the shell from the internal cast, since on naturally formed internal casts the vascular markings are usually preserved. Better results are obtained with artificially prepared casts of the Zeilleriids, but in Rhynchonellids the position of the sinuses is often masked by the longitudinal costation.

In the internal casts of the brachial valve of *Kallirhynchia yaxleyensis* traces of branching canals can be seen on some of the costæ anterior to the muscle-scars, but in no specimen of *Kallirhynchia*, so far examined, are the vascular sinuses perfectly preserved. In most Rhynchonellid genera there are two main trunks given off from the anterior end of the median septum, and curving outwards and backwards round the outer margin of the adductor muscle-scars. Numerous secondary sinuses which frequently bifurcate are given off anteriorly and laterally from the main trunks.

No traces of vascular sinuses are seen on the artificially prepared internal casts of *Lobothyris* and *Plectoidothyris*. In a specimen of *Lobothyris punctata* from the French Middle Lias which has the two valves separated, the vascular sinuses are seen as two main trunks in the brachial and pedicle valves. In the brachial valve the two main trunks are given off from between the anterior ends of the adductor muscle-scars. They diverge slightly and each sinus bifurcates a short distance below its point of origin, and each of these secondary sinuses also bifurcates anteriorly, but the four resultant sinuses remain in close proximity to one another near the anterior margin. In the pedicle valve the two main trunks are given off along the lateral margin of the diductor muscle-scars and each splits into two at the anterior end of the scar. Each lesser sinus bifurcates anteriorly as in the brachial valve.

In *Terebrirostra* the vascular markings are usually obscure. In the brachial valve one sinus follows the outer margin of each of the posterior adductor muscle-scars. Two

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other sinuses appear to extend vertically across the adductor muscle-scars, and to converge towards the median septum, and then to extend, parallel to, and at a short distance from, it. In the pedicle valve also, there appear to be four main trunks, two extending from the anterior end of the dental lamellæ, and one extending along each outer margin of the muscle area. All four trunks bifurcate frequently.

In adult shells of *Ornithella* it is seldom possible to prepare internal casts to show all the vascular markings, owing to the difficulty of removing the thick deposits of callus. Four main trunks can be distinguished in each valve. In the brachial valve the two outer trunks follows the outer margin of the adductor muscle-scars and diverge outwards from their anterior lateral margin, and then bifurcate. The two inner main trunks are given off from the anterior end of the median septum, and diverge slightly towards the anterior margin. In the pedicle valve the two outer main trunks are given off just above the anterior end of the dental lamellæ, and the two inner main trunks from the umbo; the latter extend along the inner margin of the diductor muscle-scars. The outer main trunks bifurcate shortly below their point of origin, the branch curving outwards and extending parallel to the lateral margin of the shell.

In the brachial valve of *Digonella digona* the two outer main trunks are given off from the posterior end of the adductor muscle-scars, and extend along the outer margin of the anterior adductor scar, as in *Ornithella*. The two inner trunks extend across the adductor muscle-scars, and extend vertically downwards towards the anterior margin. No bifurcations were observed. In the pedicle valve the two outer main trunks extend along the outer margin of the dental lamellæ, and the two inner main trunks extend from the anterior end of the diductor scars, but no bifurcations were observed.

In *Obovothyris* the vascular markings are usually obscure but there are apparently four main trunks in each valve. In the brachial valve two inner main trunks are given off from the anterior end of the median septum. The two outer main trunks extend, as in *Digonella*, but converge inwards at the anterior end of the muscle area and bifurcate, the bifurcations curving inwards towards the inner main trunks. In the pedicle valve the four main trunks are similarly placed to those of *Digonella*, but no bifurcations were observed.

Muscle-scars.—In the brachial valve each of the two adductor muscles is split into two parts, and consequently leaves two scars of attachment, which are known as the posterior and anterior adductor muscle-scars. The relative position and shape of these two scars varies in different genera. The diductor muscles are attached to the cardinal process, or to the hinge-plates in genera in which no cardinal process is developed. The dorsal adjustors of the pedicle are also attached to the hinge-plate.

In Rhynchonellids and Zeilleriids the posterior and anterior adductor-scars are usually well demarcated, but in Terebratulids the two parts of the scar are not as a rule distinguishable in internal casts. In *Kallirhynchia* the subtrigonal anterior adductor scars are almost in contact with the median septum along their inner margin and with the posterior adductors along part of their outer margin. The posterior adductors

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project posteriorly beyond the anterior scars, but are less extended anteriorly. They are linear in outline, increasing slightly in width anteriorly.

The adductor muscle-area in *Lobothyris punctata* is narrow and spatulate in outline, tapering rapidly posteriorly, and usually about 2 mm. in width anteriorly. The muscle-scars rarely exceed 8 mm. in length, and usually diverge from the umbo at an angle of about 40°. In *Plectoidothyris polyplecta* the adductor muscle-scars are strap-shaped and do not narrow rapidly towards the umbo. They are usually about 14 mm. in length and 2·5 mm. in width, and diverge from the umbo at an angle of about 20°. In *Terebrirostra* the adductor muscle-area is trigonal in outline and tapers posteriorly to an acute extremity. The longer side is almost in contact with the median septum. The posterior and anterior lateral margins are sub-rounded. The division between the posterior and anterior scars is obscure, but the anterior adductors appear to be narrow and linear in outline. In *Ornithella*, *Digonella*, and *Obovothyris* the adductor muscle-scars are somewhat similar in outline. In *Digonella* and *Obovothyris* the outer margin of the scars is marked by a vascular sinus which extends nearly vertically. In *Digonella* the outer or posterior adductor scars are elongate-oval in outline and project posteriorly for a short distance beyond the anterior scars, with which they are in close contact along their inner margin. The anterior adductors are subtrigonal in outline and increase slightly in width anteriorly, while their inner margin remains in contact with the median septum. In *Obovothyris* the anterior adductors are broader than in *Digonella*, and the posterior and anterior adductors are about the same length. In both these genera the longitudinal axis of both adductor-scars are approximately vertical. In *Ornithella* the anterior adductors are elliptical in outline, and the posterior adductors are crescentic. The longitudinal axis of both the scars is inclined at an angle of about 20° to the median septum.

Punctation of shell.—No study has been made of the shell structure, although it was observed that in the transverse sections of *Digonella*, *Obovothyris*, and *Ornithella* the number of punctæ varied in different parts of the section, and that no punctæ were developed on the teeth, hinge-plates, and septum, although sparingly developed on the dental lamellæ. This character has been investigated by CARPENTER (1845, 1848), PERCIVAL (1916), LEIDHOLD (1922, 1925), THOMSON (1927), KING (1869), and other authors who have shown that the number and size of the punctæ do vary in different species. This character might be of use in distinguishing species, provided a similar area of shell surface were studied for each species, since the density of the punctæ is known to vary in different parts of the same shell.

Calcareous spicules.—The development of minute calcareous spicules in the mantle and brachia of some Recent Brachiopods has been studied by HANCOCK (1859), VAN BEMMELEN (1883), DESLONGCHAMPS (1860, 1865), THOMSON (1927), JACKSON (1912), BLOCHMANN (1906, 1908), and others. THOMSON (1927) states that spicules are developed in the Recent Protremata, and among the Telotremata in the Terebratulidæ and some

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Terebratellidæ. The presence or absence of these spicules and their arrangement is of considerable help in establishing the relationship of recent species and genera. The spicules are formed of crystals of calcite which vary in shape and size in different species, and are often branched or fused together to form a network. They apparently formed an additional internal skeleton for reinforcing the soft parts, and are especially found along the walls of the vascular sinuses.

These spicules may be preserved in the interior of fossil Brachiopod shells as gray powdery matter, and they have already been studied in the Thecidiidæ. DESLONGCHAMPS (1865, p. 21) records their occurrence in a Liassic species *Kingena* [*Pseudokingena*] *deslongchampsi*, in which the spicules were evidently very numerous in the mantle.

Traces of small spicules were observed by the author when dissecting out the loops of the Terebratulid species under the microscope, but their significance was not realized at that time. A careful examination may reveal the presence of these spicules in fossil as well as in recent species.

External Morphology.

No new terms have been used in the description of the external shell characters in Part IV, and the terms employed have been defined by BUCKMAN (1917, 1919) and THOMSON (1915a, 1927).

As BUCKMAN has made a thorough study of the external morphology of Jurassic species it is not proposed to duplicate his work in giving detailed descriptions of the exterior of the shell in the seven species specially examined.

Homœomorphy.

Forms which are superficially similar but which differ structurally were described by BUCKMAN (1901) as homœomorphs. These were said to be either isochronous, which occur in deposits of approximately the same age, or heterochronous, which occur in beds of different ages.

The question of homœomorphy has been touched on in the "Introduction" and further reference is made to the subject in the "Systematic Descriptions" (p. 541).

As examples of isochronous homœomorphs may be mentioned the Middle Liassic species, *Lobothyris punctata* which is similar in external form to two undescribed species, belonging to different genera. These three forms are only distinguishable externally by the different folding of the shell and by slight differences in beak characters, but are readily distinguished by their internal structure. Other examples of isochronous homœomorphs are provided by *Ornithella bathonica* and "*Ornithella*" *cadomensis* from the Fullers Earth Rock; and *Obovothyris* sp., and *Microthyridina lagenalis* from the Upper Cornbrash.

Excellent examples of heterochronous homœomorphs are provided by "*Terebrirostra*" [*Terebratulina*] *neocomiensis* and species of *Terebrirostra* from the Albian and Cenomanian.

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Lobothyris punctata and *Plectoidothyris polyplecta* are distinct from one another in external characters, but have rather similar dorsal adductor-scars and brachial loops and are to a certain extent internal homœomorphs. Further investigation of internal characters, however, has shown these two species to be totally unrelated.

Such a list can be added to indefinitely and will serve to show the importance of a careful examination of internal as well as external characters.

IV. Systematic Descriptions.

Emended diagnoses of the genera Kallirhynchia, Lobothyris, Plectoidothyris, Ornithella, Obovothyris, *and* Terebrirostra, *and description of a new genus* Digonella.

As a result of my researches on the genotypes of *Kallirhynchia*, *Lobothyris*, *Plectoidothyris*, *Terebrirostra*, *Digonella*, *Obovothyris*, and *Ornithella*, much additional information about the internal structure of the two valves has been obtained, and described in Part III. Several internal structures, which have not previously been investigated, have been found to be of diagnostic importance, and are therefore included in the generic diagnoses. In consequence of this, it is necessary to redefine Buckman's genera, *Kallirhynchia*, *Lobothyris*, *Plectoidothyris*, *Obovothyris*, on the internal and external characters of the genotype collectively, and to assign to these genera only those species which are similar in structure to the genotype, and are obviously related forms.

The internal structure of the Cretaceous genus *Terebrirostra* is more fully described, and one new genus, *Digonella* from the Bathonian is defined.

As no specimens of the genotype of *Ornithella* were available, examination has been made of the common Fullers Earth Rock species, *O. bathonica*, which is closely related to the type both in external form and in internal structure.

No attempt is made to assign these genera to sub-families on account of the confusion prevailing in existing classifications.

Family Rhynchonellidæ, Gray.

Genus *Kallirhynchia*, Buckman.*

Emended H. M. Muir-Wood.

Figs. 15–17, Plate 62; fig. 32, Plate 63; and figs. 2, 3.

Kallirhynchia, Buckman (1914), p. 1.
Kallirhynchia, Buckman (1915), p. 76.
Kallirhynchia, Buckman (1917), p. 31.

Emended diagnosis.—Shell posteriorly norelliform, anteriorly everted, pedicle valve with well-defined sinus, linguiform extension of pedicle valve with approximately

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* Unless otherwise stated the reference is to S. S. Buckman.

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rectangular termination, brachial valve with flattened median fold. Hypothyrid, beak suberect, foramen elliptical to circular, deltidial plates disjunct to just conjunct. Shell smooth near umbones, ornamented with sub-angular costæ on remainder of shell. Dental lamellæ subdivergent. Median septum short, low, only supporting hinge-plates

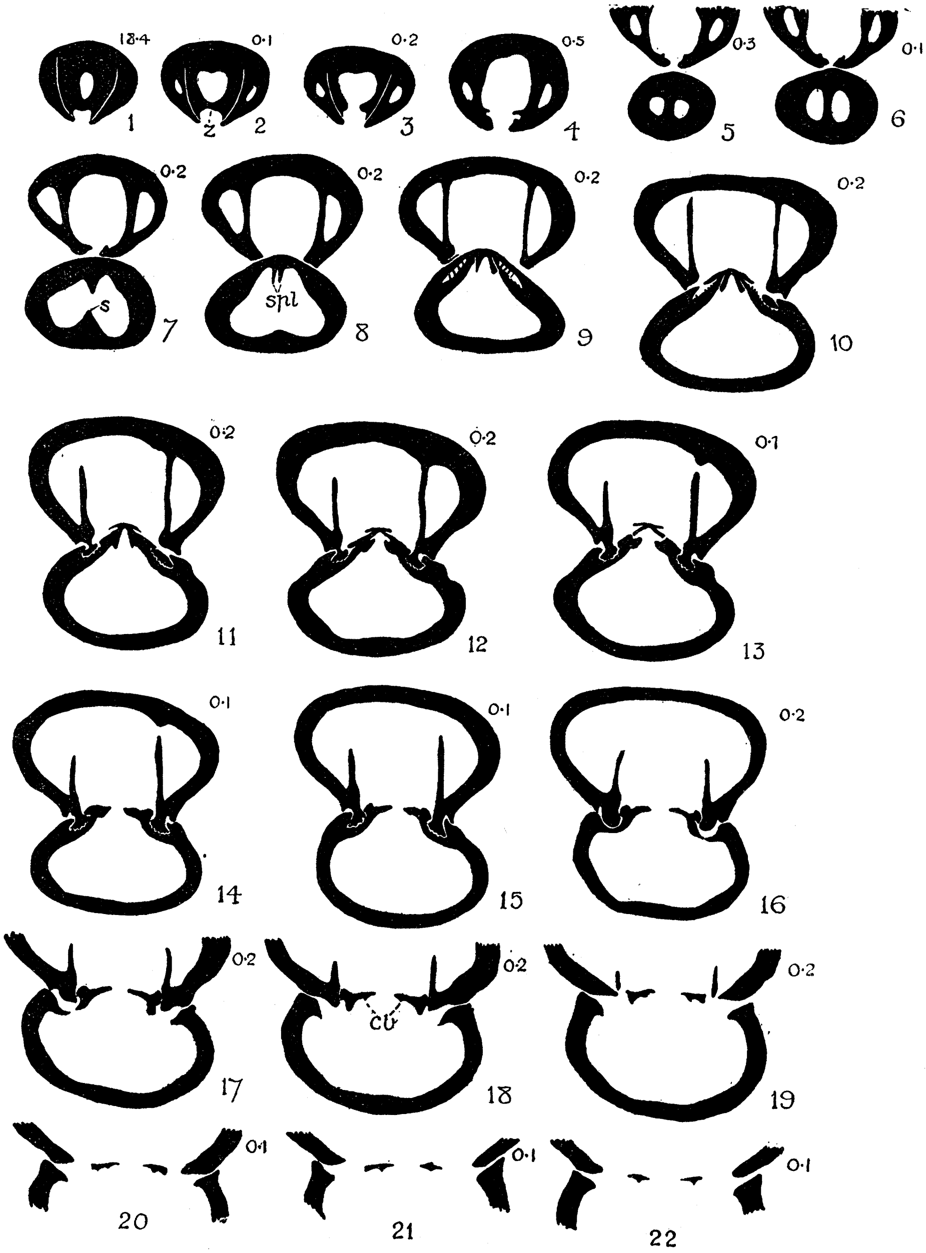

FIG. 2.—Twenty-two transverse sections* through the posterior part of the shell of *Kallirhynchia yaxleyensis* (DAVIDSON), Lower Cornbrash, Yaxley, Peterborough [B. 82276.] × 2½. Original height of shell = 18·8 mm. Sections 1–4 show the pedicle valve only.

The key to the lettering will be found on page 516.

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* The numbers at the top right-hand corner of the transverse sections represent the thickness of shell in mm. removed in the successive grindings.

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posteriorly. Hinge-plates curved, sharply differentiated from inner socket-ridges. Crural bases given off dorsally. Teeth terminally flabellate. Crura long, curved, in adult slender laminæ, terminating ventrally in a hook-shaped process (Calcarifer). Pedicle collar developed. Posterior adductor-scars of brachial valve narrow, linear, anterior adductor-scars subtrigonal extending anteriorly beyond posterior adductors.

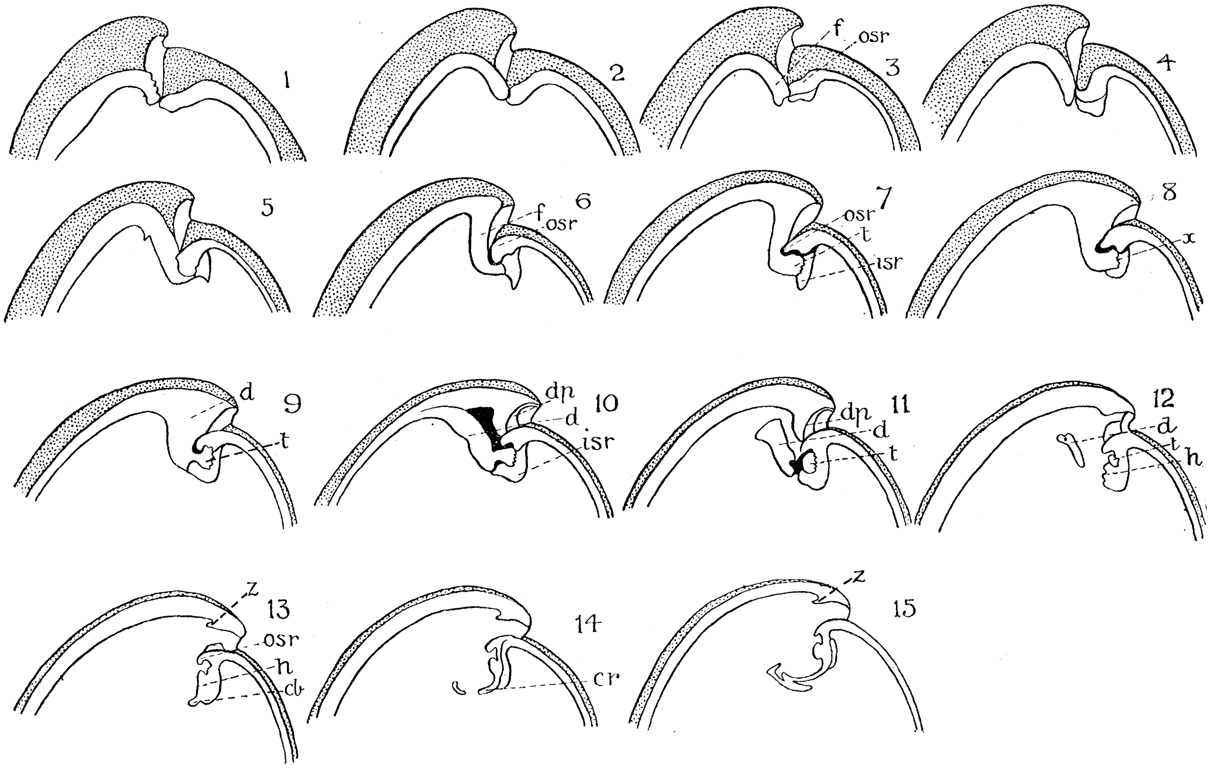

Fig. 3.—Fifteen longitudinal sections through the shell of *Kallirhynchia yaxleyensis* (Davidson) approximately parallel to the plane of symmetry of the shell. Lower Cornbrash, Yaxley, Peterborough. [B. 81639.] $\times 2\frac{1}{2}$. The sections are ground at varying distances from one another. In section 15 the complete crus was excavated with the aid of a dissecting needle.*

The key to the lettering will be found on p. 516.

Genotype.—*Rhynchonella yaxleyensis* Davidson, 1878.

Species (at present recognized).—*K. yaxleyensis* (Davidson) ; *K. concinna* (Sowerby) ; *K. crassicosta* Buckman ; *K. multicosta* Douglas and Arkell ; and other variants of *K. yaxleyensis* described as distinct species by Buckman.

Range.—Jurassic. ? Great Oolite, Cornbrash, ? Callovian.

Remarks.—Buckman's original diagnosis of this genus was :—" Hypothyrid (beak stout, rather flattened, suberect, rarely incurving, apex short, but distinct, foramen elliptical, deltidial plates trigonal, disjunct), slightly trilobed ; median fold often more or less strangulate ; multiplicate, dental plates somewhat strong, subdistant, divergent ;

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* Outer shell-surface stippled.

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ventral muscle-area fairly large, pyriform ; dorsal septum not strong ; dorsal muscle-scars elongate, anterior scars well in front of posterior scars and suboblong."

The distinguishing characters of the genus are not very clear from BUCKMAN'S diagnosis, and he included several species which, even from external characters, are obviously unrelated to the type. He expressed a doubt, however, whether the Vesulian and Great Oolite species were really related to the Cornbrash forms, but included them on account of the similarity of the muscle markings. He cited *Rhynchonella yaxleyensis* DAVIDSON as the genotype, but on another page (1917, Plate 15, fig. 23) he figured a specimen in his own collection from the Cornbrash of Yetminster, Dorset, as the "genotype." DAVIDSON'S unique specimen, and therefore the holotype, figured in 1878, his Plate 27, fig. 23, was obtained from the Cornbrash of Yaxley, Peterborough, and this specimen is preserved in the British Museum (Nat. Hist.) Coll. [B. 82289]. In accord with the rules of Zoological nomenclature I have taken DAVIDSON'S species *Rhynchonella concinna* var. *yaxleyensis* as the genotype of *Kallirhynchia* and have investigated the structure of topotypes in the Davidson collection from the Cornbrash of Yaxley. BUCKMAN'S specimen figured by him as the "genotype" is a variety of *K. yaxleyensis*.

BUCKMAN included certain forms described by many authors as the *Rhynchonella concinna*-group in his list of species of *Kallirhynchia*. The name *Rhychonella concinna* has been applied to species ranging from the Inferior Oolite to the Cornbrash, and there is still some doubt about the exact horizon of SOWERBY'S type-specimen. The holotype of *R. concinna*, Brit. Mus. (Nat. Hist.) [B. 71570], is said (SOWERBY, 1815, Feb., p. 192) to have come from the Great Oolite at Aynhoe [Northants]. The two specimens on the tablet which were not figured are undoubtedly Great Oolite forms belonging to BUCKMAN'S genus *Burmirhynchia*. The type, however, appears to be a typical *Kallirhynchia* and closely related to *K. yaxleyensis*. In the Davidson Collection, one specimen labelled *Rhynchonella yaxleyensis* from the Cornbrash of Yaxley is indistinguishable from the type of *R. concinna* SOWERBY, and other specimens though smaller in size have similar ornament and folding.

BUCKMAN (1917, Plate 15, fig. 24) figured a poor plaster cast of *R. concinna*, and stated that it was from the Lower Cornbrash between Ardley and Aynhoe, Northants. DOUGLAS and ARKELL (1932, p. 153) (ARKELL, 1933), on the other hand, state that *K. concinna* is a Great Oolite species, and that specimens indistinguishable from the type could be obtained in a Great Oolite quarry a quarter of a mile E. of Aynhoe. They also state that WALFORD (1917, p. 10) found typical specimens of *R. concinna* in Aynhoe Allotments Quarry in 1883, and that he considered it to be from a bed a little above the Stonesfield Slate. If genuinely a Great Oolite species, *K. concinna* must have persisted practically unchanged until the Lower Cornbrash times. Owing to lack of material no investigation was made of the internal structure of *K. concinna*.

ROTHPLETZ (1886) stated that the crura of *Rhynchonella concinna* are radulifer in shape, but from illustrations of radulifer crura given by ROTHPLETZ and by WIŚNIEWSKA

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there do not appear to be any spur-like lamellæ projecting dorsally from the primary lamellæ, as in *Kallirhynchia*.

Family Terebratulidæ, Gray.

Genus *Plectoidothyris*, Buckman.

Emended H. M. Muir-Wood.

Figs. 30, 31, Plate 62; fig. 35, Plate 63, and fig. 4.

Plectoidothyris, Buckman (1914), p. 2.
Plectoidothyris, Buckman (1915), p. 78.
Plectoidothyris, Buckman (1917), p. 122.
Plectoidothyris, Buckman: Sahni (1928), p. 134.

Emended diagnosis.—Shell sulco-convex in neanic stage becoming biconvex, elongate-oval in outline, anterior commissure plane to uniplicate, to multiplicate. Umbo short, erect, slightly incurved in gerontic stage, obliquely truncate, foramen subapical, circular, marginate, epithyrid, beak-ridges obscure. Symphytium short. Pedicle-collar developed. Cardinal process prominent, bilobed, separated from shell floor by deep umbonal cavity. Hinge-plates narrow, concave, demarcated from inner socket-ridges and ventrally deflected crural bases. Loop extending for approximately two-thirds of length of brachial valve, descending branches broad, flat dorso-ventrally directed plates. Teeth mallet-shaped, deeply inserted. Outer socket-ridges interlocking between teeth and massive denticula. Dorsal adductor scars elongated, narrow, strap-shaped.

Genotype.—*Terebratula polyplecta* Buckman, Oolite Marl, *bradfordensis* zone.

Species.—*P. polyplecta* (S. S. Buckman), *P. plicata* (J. Buckman).

Range.—Inferior Oolite.

Remarks.—S. S. Buckman's original diagnosis of this genus was "Permesothyrid (young), epithyrid (adult), (beak short, obliquely truncate, incurved only in old age, foramen somewhat large, almost apical, attrite, symphytium broad, very short); morphogeny concavo-convex to elongately biconvex, to fimbriate (multiplicate); muscle-tracks long, sub-approximate, subdivergent."

Buckman points out the similarity of growth-stages, before multiplication, of *Plectoidothyris* with those of *Lobothyris*, and this led to confusion of the two genera by Sahni as already stated on p. 513.

Plectoidothyris polyplecta is distinguished from *Plectothyris fimbria* (Sowerby), the genotype of Buckman's genus *Plectothyris*, by its more erect umbo and subapical foramen, more elongate shell; less divergent and narrower dorsal adductor muscle-scars, and by the differences in internal characters, shape of hinge-plate, teeth and sockets, etc.

Buckman (1917, p. 122) cites *P. polyplecta* as the genotype of *Plectoidothyris*, and on Plate 20, fig. 14*a*, of the same work figures a specimen from the Oolite Marl, Notgrove Station, Glos. as the "genotype." The holotype of this species was described by Buckman (1901, p. 242) from the same horizon and locality.

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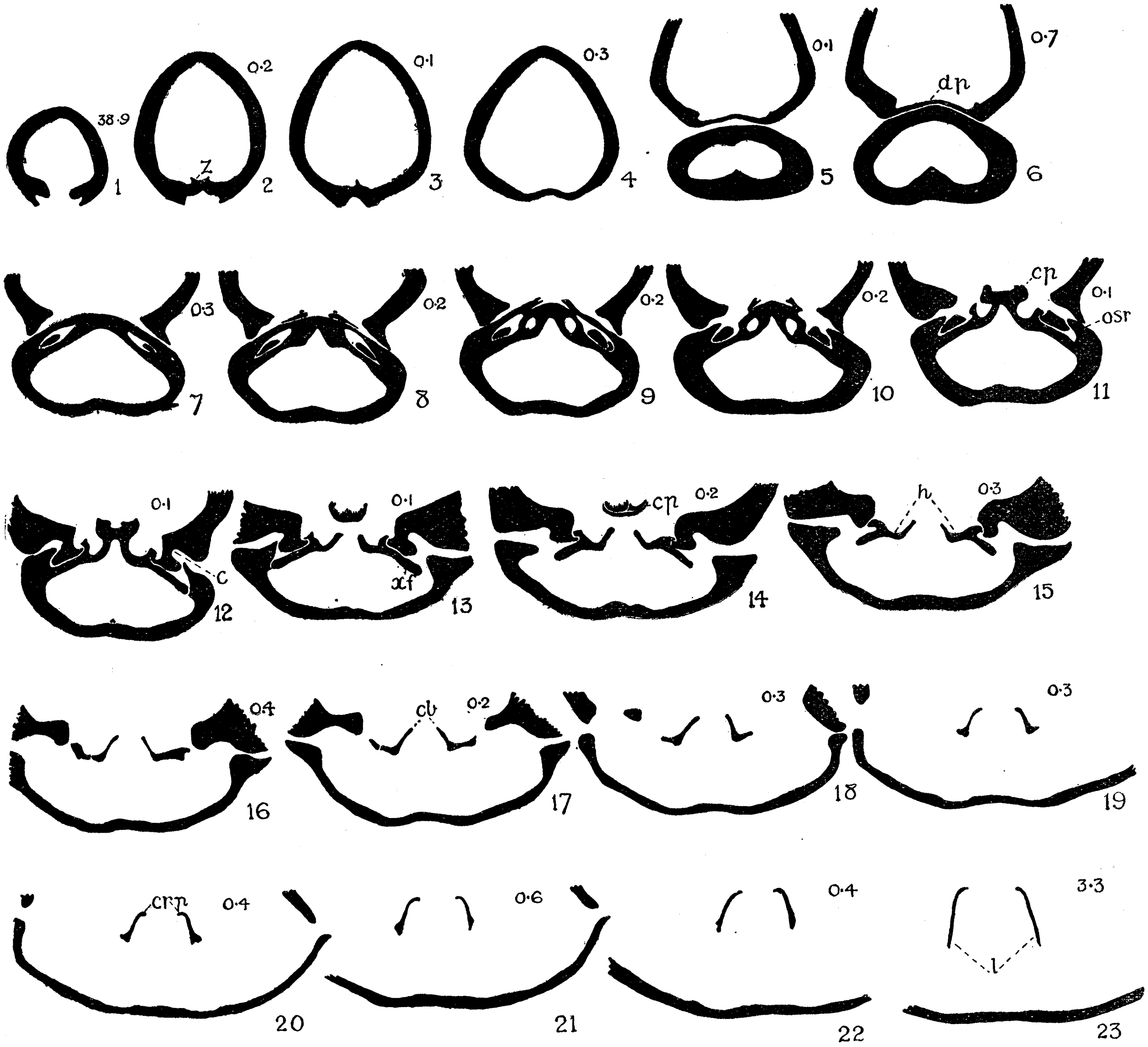

Fig. 4.—Twenty-three transverse sections through the posterior part of the shell of *Plectoidothyris polyplecta* (Buckman). Inferior Oolite, Oolite Marl, Notgrove, Glos. [B. 67617.] × $2\frac{1}{2}$. Original height of shell = 42·1 mm. Sections 1–4 show the pedicle valve only.

The key to the lettering will be found on page 516.

Genus *Lobothyris*, Buckman.

Emended H. M. Muir-Wood.

Figs. 28, 29, Plate 62 ; fig. 37, Plate 63, and figs. 5, 6.

Lobothyris, Buckman (1914), p. 2.
Lobothyris, Buckman (1915), p. 78.
Lobothyris, Buckman (1917), p. 107.
Plectoidothyris, Buckman : Sahni (1928, in part), p. 120.

Emended diagnosis.—Shell plano-convex in neanic stage, becoming biconvex, elongate-oval in outline, anterior commissure plane to uniplicate to ? sulciplicate. Umbo rounded,

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suberect to incurved; foramen circular to oval labiate; epithyrid, beak-ridges angular. Cardinal process small, trilobed, not separated from shell floor by umbonal cavity. Hinge-plates concave, fused with inner socket-ridges. Crural bases sharply recurved ventrally from hinge-plates. Descending branches of loop forming broad plates extending dorso-ventrally. Loop approximately one-third of length of brachial valve. Pedicle collar supported by short septum. Symphytium narrow anterio-posteriorly. Teeth linguiform, deeply inserted, denticula interlocking with outer socket-ridges.

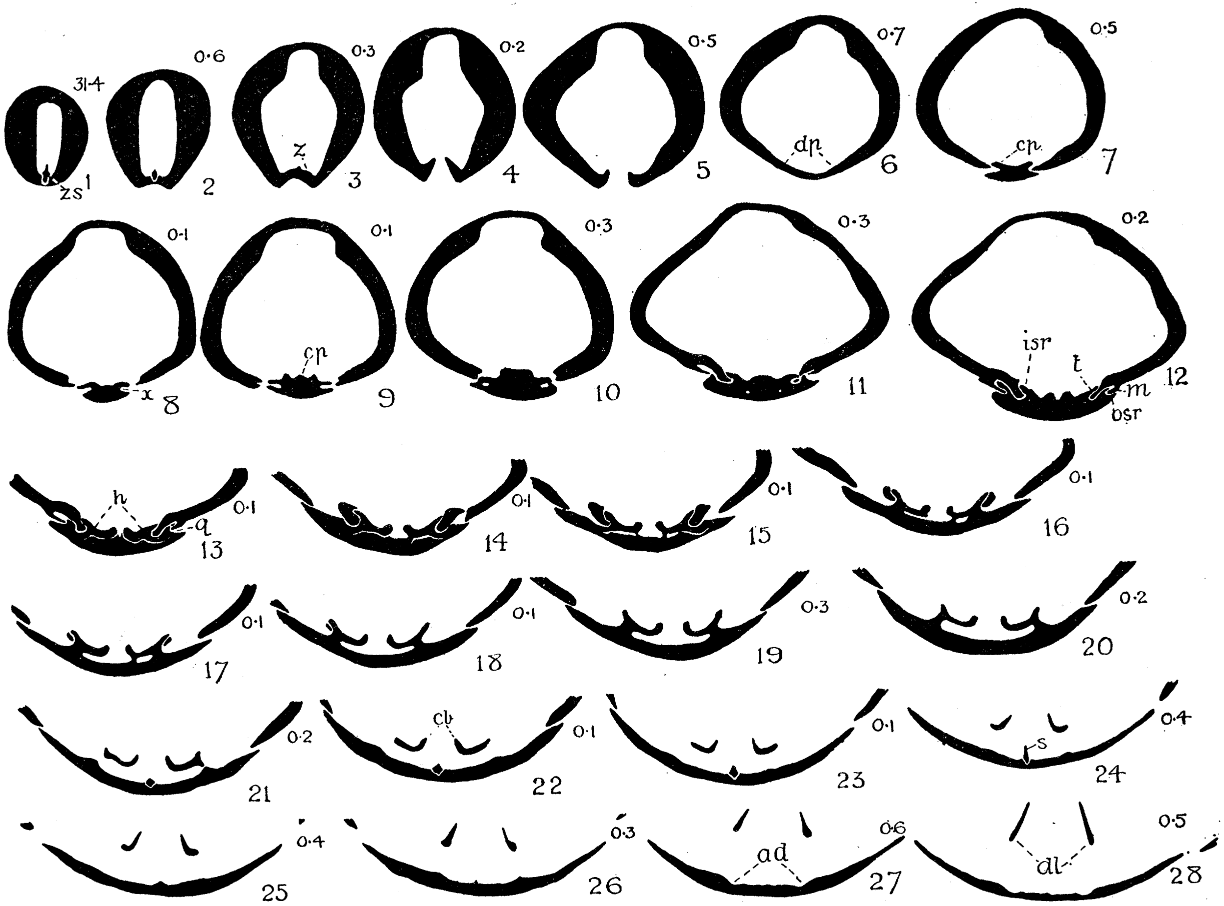

FIG. 5.—Twenty-eight transverse sections through the posterior part of the shell of *Lobothyris punctata* (SOWERBY). Middle Lias, Tilton, Leicestershire. [B. 65240.] × 2½. Original height of shell = 31·8 mm. Sections 1–6 show the pedicle valve only.

The key to the lettering will be found on page 516.

Adductor muscle-scars of brachial valve short, narrow, spatulate, diverging at angle of about 40°.

Genotype.—*Terebratula punctata* J. SOWERBY, 1813.

Species (at present recognized).—*L. punctata* (SOWERBY), *L. subpunctata* (DAVIDSON in part), *L. edwardsi* (DAVIDSON).

Range.—Lias— ?

Remarks.—S. S. BUCKMAN's original diagnosis of this genus was " Epithyrid (beak

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overhanging dorsal umbo, foramen more or less elliptical, in old forms labiate, symphytium broad); morphogeny, subconcavo-convex to biconvex, to elongate, to uniplicate, to sulciplicate—centronella to terebratula stage; muscle-tracks, narrow, sub-approximate."

A large number of species ranging from the Lower Lias to the Kimeridgian were listed by Buckman as belonging to *Lobothyris*, but he suggested that these species might

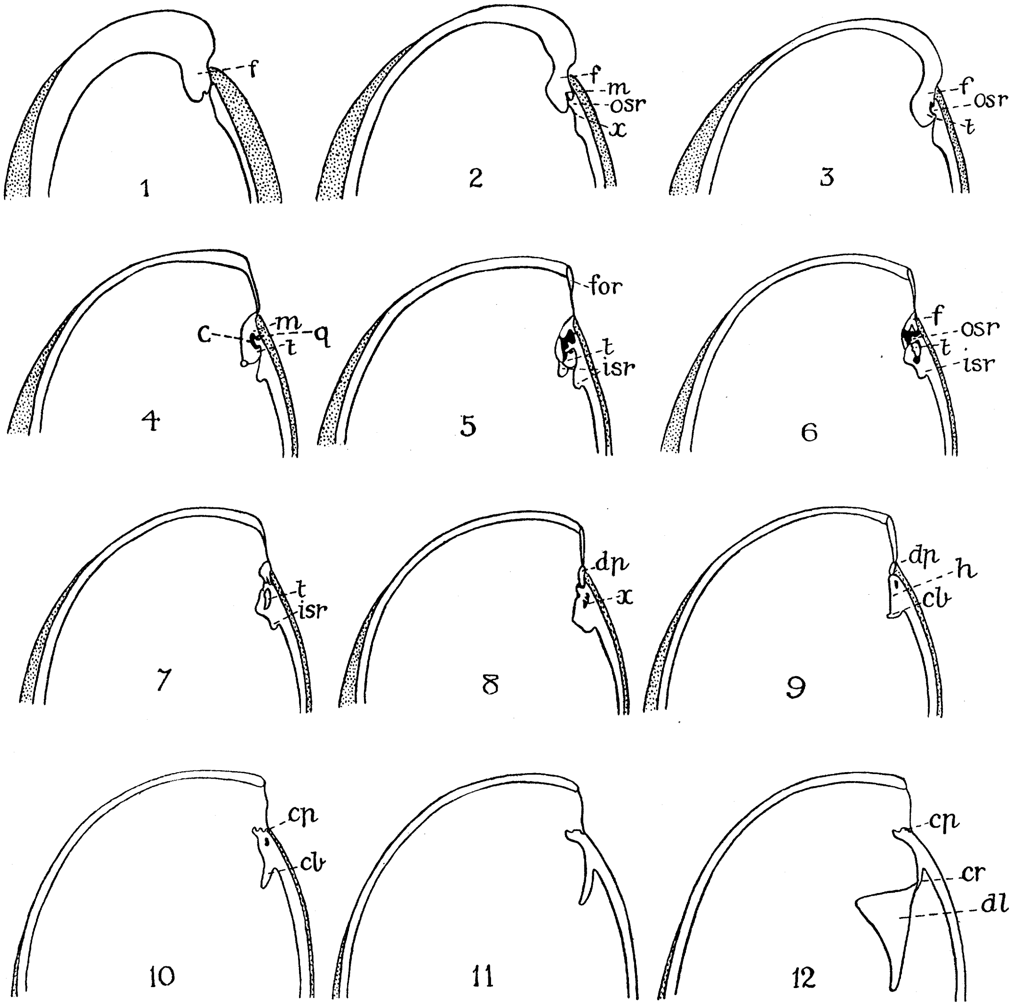

Fig. 6.—Twelve longitudinal sections through the shell of *Lobothyris punctata* (Sowerby), approximately parallel to the plane of symmetry of the shell. × 2½. Middle Lias, Halstead, Leicestershire. [B. 81638.] In section 12 the complete loop was dissected out with the aid of a dissecting needle. The key to the lettering will be found on page 516.

be successive offshoots from a plano-convex or circular biconvex stock, and that they might not belong to one genetic series. Many of these species can be distinguished from *L. punctata* by marked differences in external characters, and in the shape of the dorsal adductor scars, and will, no doubt, prove to have a totally different internal structure. Investigation of the Liassic species *Lobothyris punctata* (Sowerby) and *L. subpunctata* (Davidson) has shown that they are homœomorphous with forms having

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a different internal structure. Some of these homœomorphs differ from *Lobothyris punctata* in having sulcation of the posterior portion of the brachial valve; a more incurved beak and broader adductor muscle-scars, and differences in the hinge-plates as well as a longer loop in the adult shell. Other homœomorphs of *L. punctata* having anterior sulcation of the brachial valve may belong to BUCKMAN's genus *Euidothyris*, or to a genus apparently homœomorphous with *Sphœroidothyris*, but with the anterior commissure sulcate.

DUBAR (1925, 1931) figures specimens with a silicified brachial loop belonging to the group of *Terebratula punctata* and *T. davidsoni* from the Lias of the French Pyrenees. Careful examination of DUBAR's plates shows that the species of the *punctata* and *davidsoni* group belong to two or possibly three distinct series differing slightly in external and internal characters. The narrow elongated form figured as *T. davidsoni* HAIME has a sulcate brachial valve, a much incurved carinate umbo in the pedicle valve, and a longer loop than in *Lobothyris*, and belongs to another genus, although included by BUCKMAN in *Lobothyris*. *Terebratula radstockiensis* DAVIDSON, identified as belonging to the genus *Lobothyris* by BUCKMAN, has a sulcate brachial valve and a different internal structure from *L. punctata*, and may belong to the same undescribed genus as *T. davidsoni*.

SAHNI (1928, p. 135) copied one of DUBAR's figures (1925, Plate 6, fig. 18) showing the loop of *Terebratula punctata*, var. *lata*, and pointed out the similarity in form to that of *Plectoidothyris polyplecta* (BUCKMAN). He also figured somewhat inaccurately the adductor muscle-scars of *Plectoidothyris* and *Lobothyris*, and from the close resemblance of the brachial loops and muscle-scars of the two genera he stated that *Lobothyris* was synonymous with *Plectoidothyris*.

The marked difference in beak characters and the differences in the internal structure, cardinal process, hinge-plate, teeth and sockets, etc., shown in the transverse sections of *Plectoidothyris polyplecta*, and *Lobothyris punctata*, show conclusively that we are concerned with two totally distinct and unrelated genera.

Although the brachial loops of the two genera are similar in form, the loop of *Lobothyris* is always shorter than that of *Plectoidothyris*. In adult specimens of *Lobothyris punctata* about 30 mm. in length from the British Middle Lias the loop averages 9 mm. in length, as compared with 18 mm. in *Plectoidothyris polyplecta*, in adult shells about 38 mm. long. SOWERBY figures (1813, Plate 15, fig. 2) a young specimen of *Terebratula punctata* having a brachial valve 21 mm. in length in which the loop is only 8·5 mm. in length. Another specimen from the same locality and collection, but not figured by SOWERBY, has a brachial valve 23 mm. in length and a loop 9 mm. in length. In a homœomorph of *Lobothyris punctata* from the British Middle Lias the loop averages 14 mm. in length in an adult shell 30 mm. long. The crura in this form are considerably longer than in *L. punctata*.

The lectotype of *Terebratula punctata* SOWERBY (1813, Plate 15, fig. 4) was obtained from the [Middle] Lias of Hornton [Oxfordshire], and is not identical with the specimen

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figured as "genotype" of *Lobothyris* by Buckman (1917, Plate 20, fig. 7, *a*) from the Middle Lias of Le Pont Rouge, Vendée, France. Investigation of an externally similar specimen from the same French locality shows that Buckman's form is congeneric, and that it is probably a more massive and elongated variety of Sowerby's species.

As Buckman cites *T. punctata* Sowerby as the genotype of the genus *Lobothyris*, this species has been accepted as such by me, and investigation has been made of the internal structure of specimens externally similar to the lectotype of Sowerby's species.

Deslongchamps (1884, p. 249) in his classification of *Terebratula* divided the genus into a number of species groups, and *T. punctata* is the type of "group C." The species belonging to this group are described as "allongées, renflées, à crochet épais et court." Deslongchamps (1884, Plate 10, figs. 1, 2) also figured the loop of a French specimen of *T. punctata* which does not agree in form with that of the English species. In the lateral view of the loop of the English species the transverse band is concealed by the broad ribbon of the descending lamellæ, while in the French form the descending lamellæ are narrow and the transverse band is well exposed.

Alkins (1923) measured 300 specimens of "*Terebratula punctata*" from the Middle Lias of Stathern, Leicestershire, and worked out the ratios of width/length and depth/length. After plotting his results in the form of graphs, he stated that the species as represented by these shells was perfectly homogeneous.

Family Terebratellidæ, King.

Genus *Ornithella*, Deslongchamps.

Emended H. M. Muir-Wood.

Figs. 22–24, Plate 62; fig. 38, Plate 63, and figs. 7, 8.

Ornithella, Deslongchamps (in part), 1884. pp. 273, 292, 293.
Ornithella, auctt. in part.

Emended diagnosis.—Shell plano-convex in neanic stage, becoming biconvex; elongate-oval to pentagonal in outline; truncated or strangulate anteriorly. Anterior commissure plane. Maximum width about half-way down length of shell. Umbo rounded, suberect to incurved, frequently in contact with the brachial valve in the gerontic stage; permesothyrid. Dental lamellæ embedded in callus in adult. Median septum less than half length of brachial valve, short, stout, supporting hinge-plate. Septalium shallow. Crural bases given off ventrally. Inner socket-ridges separated from hinge-plates by shallow depression. Loop with short spines, long, not attached to septum in adult. Muscle-area of brachial valve lens-shaped with longitudinal axis inclined at an angle of about 20° to median septum. Posterior adductors crescentic, anterior adductors lenticular. Pedicle-collar rarely observed.

Genotype.—*Terebratula ornithocephala* J. Sowerby, 1815.

Species.—*O. ornithocephala* (J. Sowerby), *O. bathonica* Rollier, *O. brutonensis*

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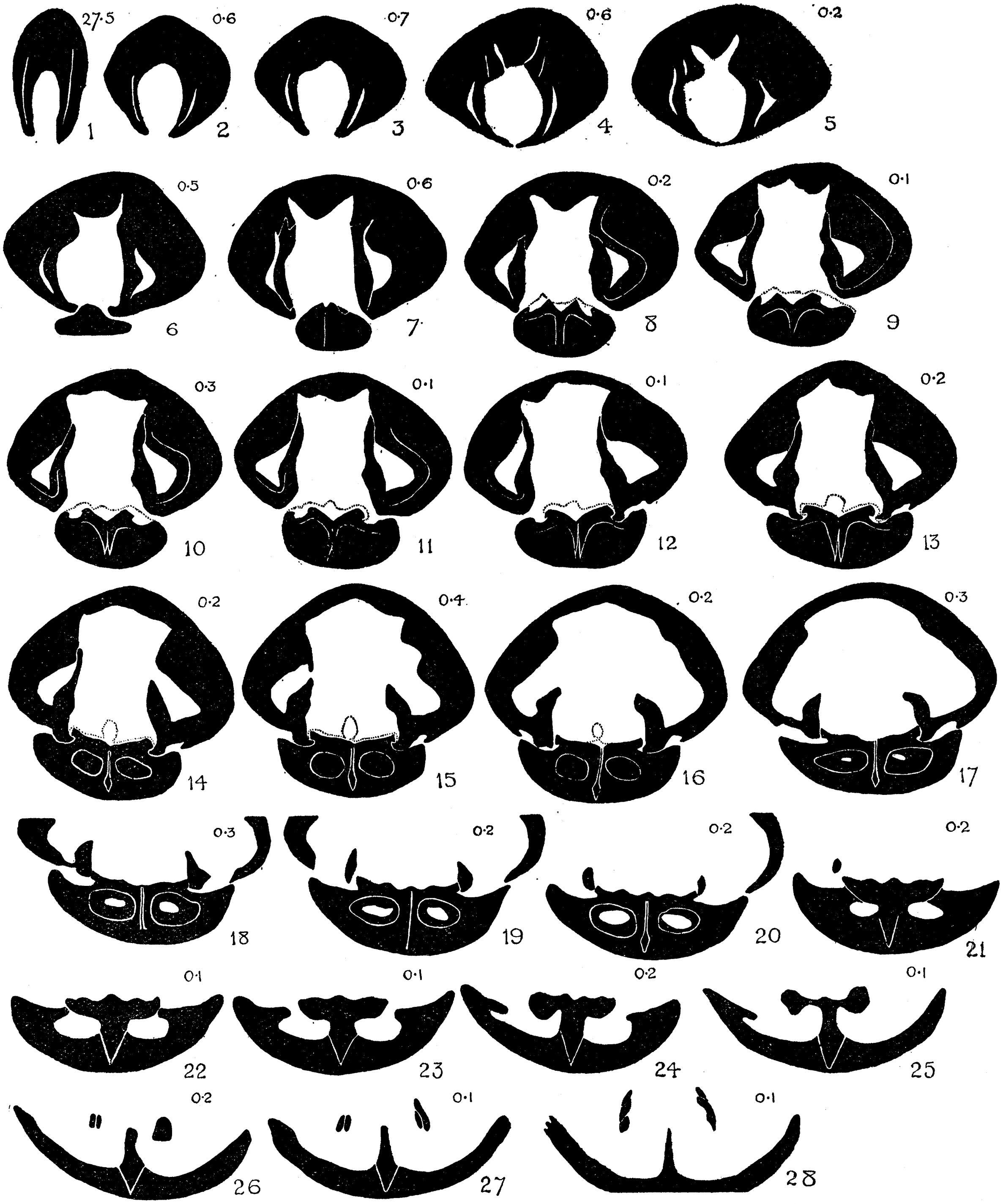

Fig. 7.—Twenty-eight transverse sections through the posterior part of the shell of *Ornithella bathonica* Rollier. Fullers Earth Rock, Box Tunnel, Wilts. [B. 82278.] × 2½. Original height of shell = 29·8 mm. Sections 1–5 show the pedicle valve only. Deposits of callus on the hinge-plates are indicated by means of a dotted line. The thick callus deposits in the umbonal region of the pedicle valve cause the apparent obsolescence of the dental lamellæ.

The key to the lettering will be found on page 516.

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ROLLIER, *O. triquetra* (J. DE C. SOWERBY) [= *O. subtriquetra* D'ORB. *sp.*], *O. bathiensis* ROLLIER; **O. haydonensis* and *O. pupa* MUIR-WOOD MS.

Range.—Bathonian—Fullers Earth—Cornbrash, and ? Upper Jurassic.

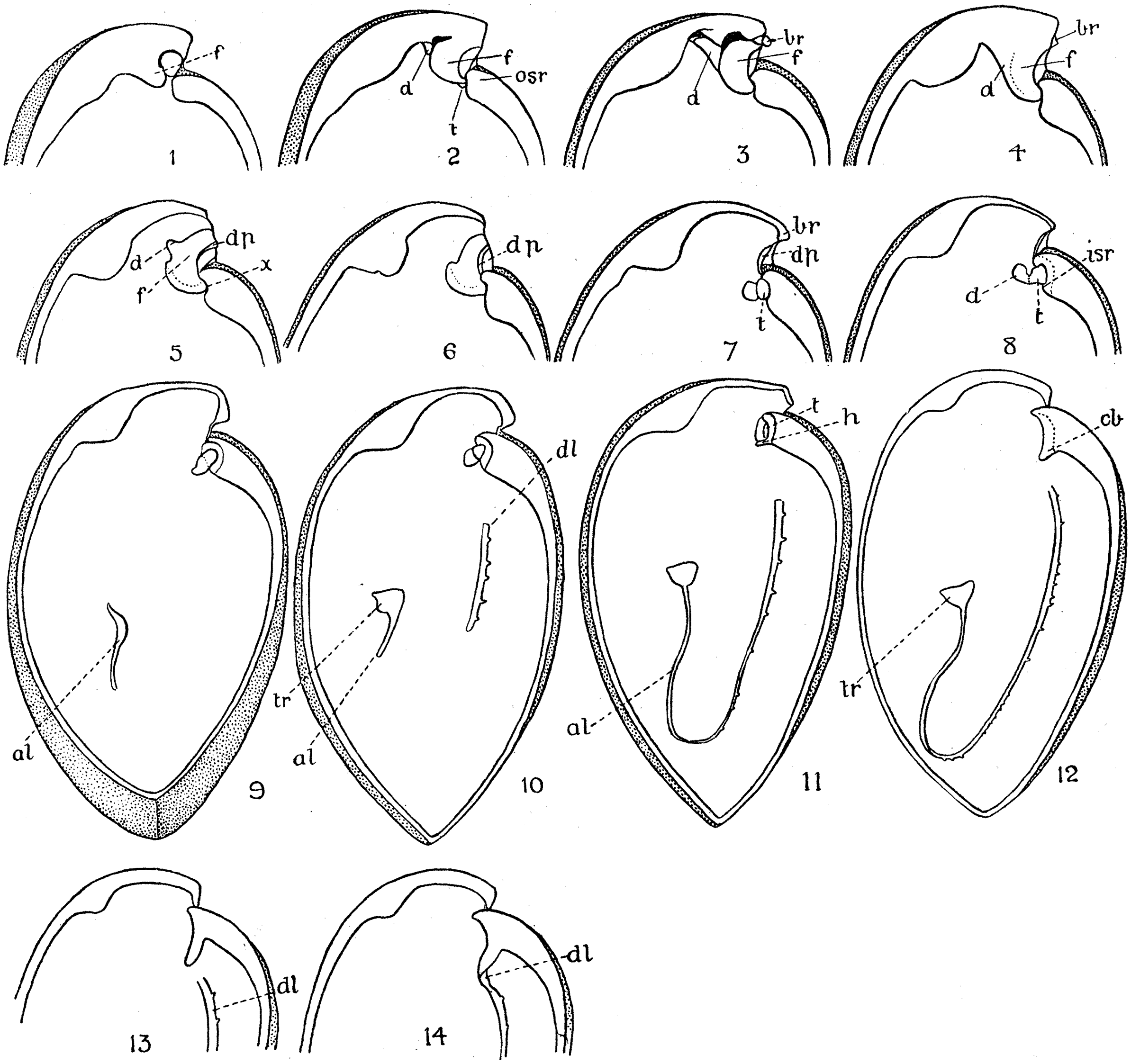

FIG. 8.—Fourteen longitudinal sections through the shell of *Ornithella bathonica* ROLLIER. Fullers Earth Rock, Box Tunnel, Wilts. [B. 82277.] × 2½. Sections 1–6 were ground at an angle of about 25° to the plane of symmetry of the shell. Sections 7–14 were ground so as to expose one-half of the complete loop and its relationship to the crus.

The key to the lettering will be found on page 516.

Remarks.—DESLONGCHAMPS (1884, pp. 273, 292, 293) described *Ornithella* as a section of *Zeilleria*, BAYLE, with *Terebratula ornithocephala* SOWERBY, as the type. He included the species *T. indentata* SOWERBY, *T. umbonella* (LAMARCK), *T. bucculenta* SOWERBY,

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* Descriptions of these species will appear shortly in another paper by the author.

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and *T. celtica* MORRIS, in his description of the genus. All these species, however, have a different muscle-arrangement and a different hinge-plate from that of *O. ornithocephala* and are not congeneric.

The genotype of *Ornithella*, *Terebratula ornithocephala* was described by SOWERBY in 1815 (Plate 101, figs. 1, 2, 4). He figured three specimens of which the specimen depicted in Plate 101, fig. 1, from Chatley, Somerset, probably from the Lower Cornbrash, has been selected as lectotype. The specimen represented by fig. 2 of the same plate from an unknown locality has been renamed *Ornithella fullonensis* by RICHARDSON (1907, p. 430). SOWERBY'S third specimen (Plate 101, fig. 4) from the Lower Lias of Pickeridge, Somerset, is the type of *Terebratula sarthacensis* D'ORBIGNY.

The question of the genotype of *Ornithella* was discussed by BUCKMAN in 1907*b* (p. 379), while the identity of the species *Ornithella ornithocephala* was discussed by the same author in 1904 (p. 396), and by DOUGLAS and ARKELL in 1928 (p. 165).

DOUGLAS and ARKELL (1928, p. 165) were unable to find any trace of Upper Cornbrash at Chatley in their recent mapping of Cornbrash outcrops, and no specimens of *O. ornithocephala* were collected by these authors from the Lower or Upper Cornbrash of any locality, nor are any Cornbrash specimens preserved in the British Museum collections. A careful comparison of the type-specimen of *O. ornithocephala* has been made with the numerous species of *Ornithella* occurring in the Fullers Earth Rock. *O. ornithocephala* is not identical with the Fullers Earth forms, and must be regarded as a distinct species. In the absence of material from the Cornbrash, investigation has been made of the internal structure of *O. bathonica* ROLLIER, the common Fullers Earth Rock species.

A specimen of *O. ornithocephala* in the duplicate Sowerby collection, possibly from Chatley, was dissected to show the loop, fig. 38, Plate 63, which agreed with that of *O. bathonica*.

It is probable that *Microthyris* [= *Microthyridina*, SCHUCHERT and LE VENE] will prove to be closely related to, if not synonymous with, *Ornithella*. Examination of specimens of *Microthyridina lagenalis* (SCHLOTH.) from the uppermost Brown Jura of Beggingen, Schaffhausen, Switzerland, showed that they had essentially similar internal structure, hinge-plate, etc., as *Ornithella*. The muscle-scars are also very similar in the two genera. The specimens investigated agreed in size and external shape with that figured by VON BUCH in 1834 (Plate 3, fig. 43) from Aarau, Switzerland, the type locality for *Terebratula lagenalis*.

In the British Upper Cornbrash there appear to be *lagenalis*-like forms with at least three distinct types of internal structure, one belonging to *Obovothyris*, another probably to *Microthyridina*, and the third to an undescribed genus. The matter is further complicated by the selection of DESLONGCHAMPS' figure of *Terebratula lagenalis* in Paléontologie franç., Plate 107, fig. 1, from an unknown locality, as geno-holotype of *Microthyridina* by SCHUCHERT and LE VENE (1929, p. 84).

ROLLIER (1919, p. 321) refers to *Ornithella* as being a synonym of *Microthyris*, a

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subgenus of *Zeilleria*, and restricts the application of the name *Ornithella* to the "*emarginata*" group of species. As *Z. emarginata* is not mentioned by Deslongchamps in his original description of *Ornithella* Rollier's interpretation of the genus is incorrect.

Genus *Obovothyris*, Buckman.

Emended H. M. Muir-Wood.

Figs. 25–27, Plate 62; fig. 33, Plate 63; and figs. 9, 10.

Obovothyris, Buckman (1927), p. 32.
Ornithella, Douglas and Arkell (in part) (1928), p. 160.
Ornithella, auctt. (in part).

Emended diagnosis.—Shell sulco-carinate in neanic stage, becoming biconvex; subpentagonal in outline; antero-lateral margins with subangular carinæ; anterior margin truncate or excavate, anterior commissure plane or slightly waved dorsally. Maximum width occurring at about two-thirds of the length of shell. Umbo carinate, suberect to incurved. Permesothyrid. Median septum about two-thirds of length of brachial valve, thin and plate-like supporting hinge-plate. Septalium shallow. Inner socket-ridges and hinge-plates fused. Crural bases and loop given off dorsally. Loop spinose, long, not attached to septum in adult. Muscle-area of brachial valve lens-shaped, anterior scar almost in contact with septum. Pedicle-collar supported by stout septum.

Genotype.—*Obovothyris magnobovata* Buckman, 1927.

Species (at present recognized).—*O. obovata* (Sowerby), *O. grandobovata* and *O. magnobovata* Buckman, also a new species from the Upper Cornbrash and homœomorphous with *Microthyridina lagenalis* (Schloth.).

Range.—Lower Cornbrash—Upper Cornbrash.

Distinctions.—*Obovothyris* is distinguished from *Ornithella* by differences in the shape of the hinge-plate; by the more spinose loop which is given off from the dorsal side of the hinge-plate; by the development of a pedicle-collar supported by a septum; by its longer median septum; and by the development of subangular carinæ at the antero-lateral margins of the shell.

Remarks.—In the original diagnosis of this genus, Buckman did not clearly define the characters by which it could be distinguished from *Ornithella*, and subsequent authors* have, therefore, not adopted his genus, but have preferred to retain the name *Ornithella* for the "*obovata*" group. No internal characters were described by Buckman with the exception of the muscle-scars which are indistinguishable in his figure of the type, and the long septum of the brachial valve. Investigation of internal characters, however, indicates that *Obovothyris* should be regarded as a distinct genus,

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* Douglas and Arkell (1928), p. 160.

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although related to *Ornithella* and *Digonella*, as shown by a similarity in the shape of the muscle-scars, in the form of the loop which in each type is spinose, and in the shape of the hinge-plate. The differences in internal characters have already been discussed

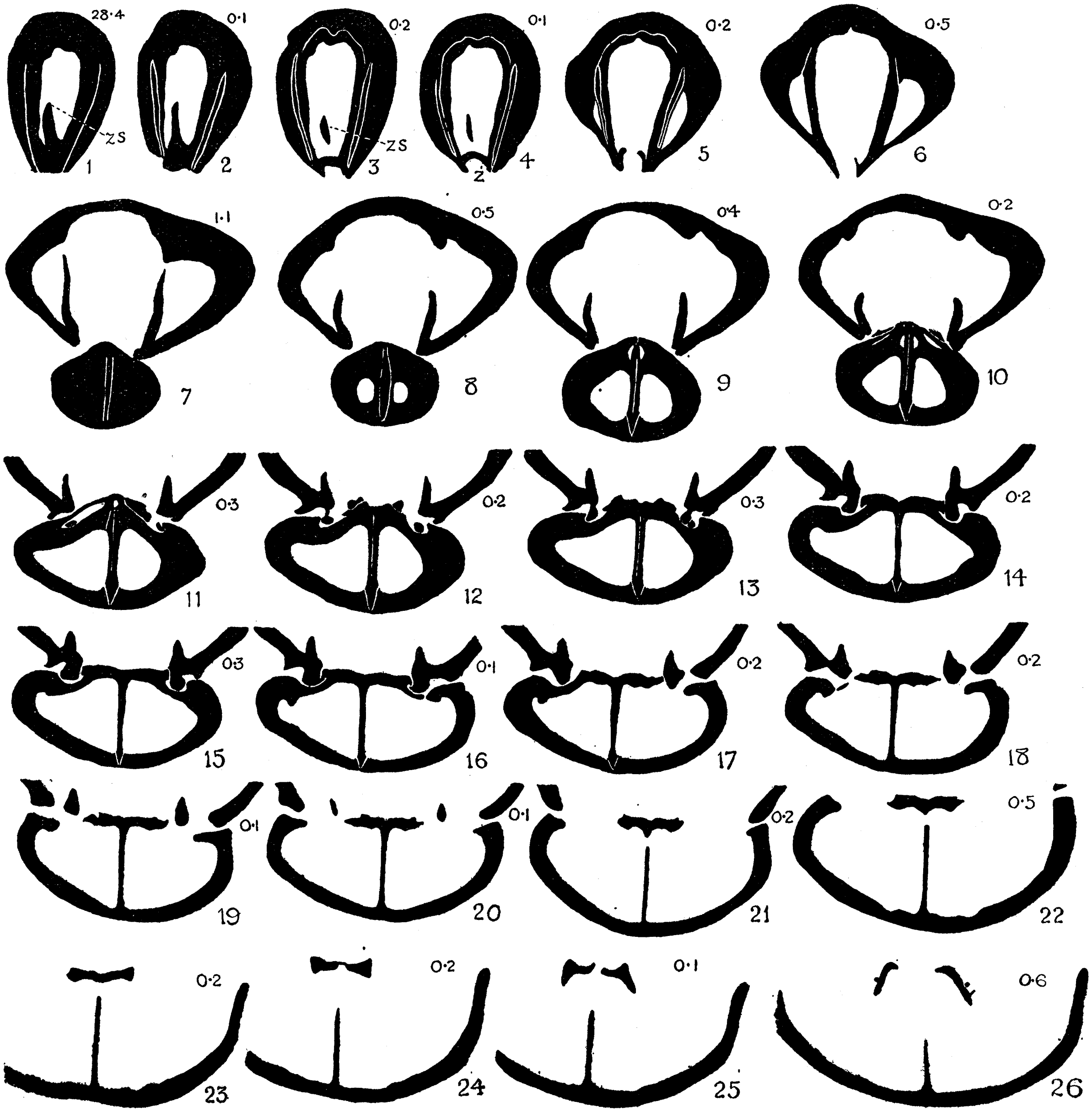

Fig. 9.—Twenty-six transverse sections of the posterior part of the shell of *Obovothyris magnobovata* S. S. Buckman. Cornbrash, Blackthorn Hill, Bicester. [B. 68325.] × 2½. Original height of shell = 29·6 mm. Sections 1–6 show the pedicle valve only.

The key to the lettering will be found on page 516.

in the section on "Morphology and Nomenclature." The genera *Ornithella*, *Digonella*, and *Obovothyris* should probably be grouped together in one subfamily.

The sulcate umbo of the brachial valve and corresponding carination of the pedicle

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valve of *Digonella* and *Obovothyris* indicate derivation from a sulcate ancestor, and in this connection it is interesting to mention that the internal structure and hinge-plate of "*Aulacothyris*" *meriani* (Oppel) from the Inferior Oolite, Lower Trigonia Grit are remarkably similar to those of *Ornithella* and *Obovothyris*. Although possessing a sulcate

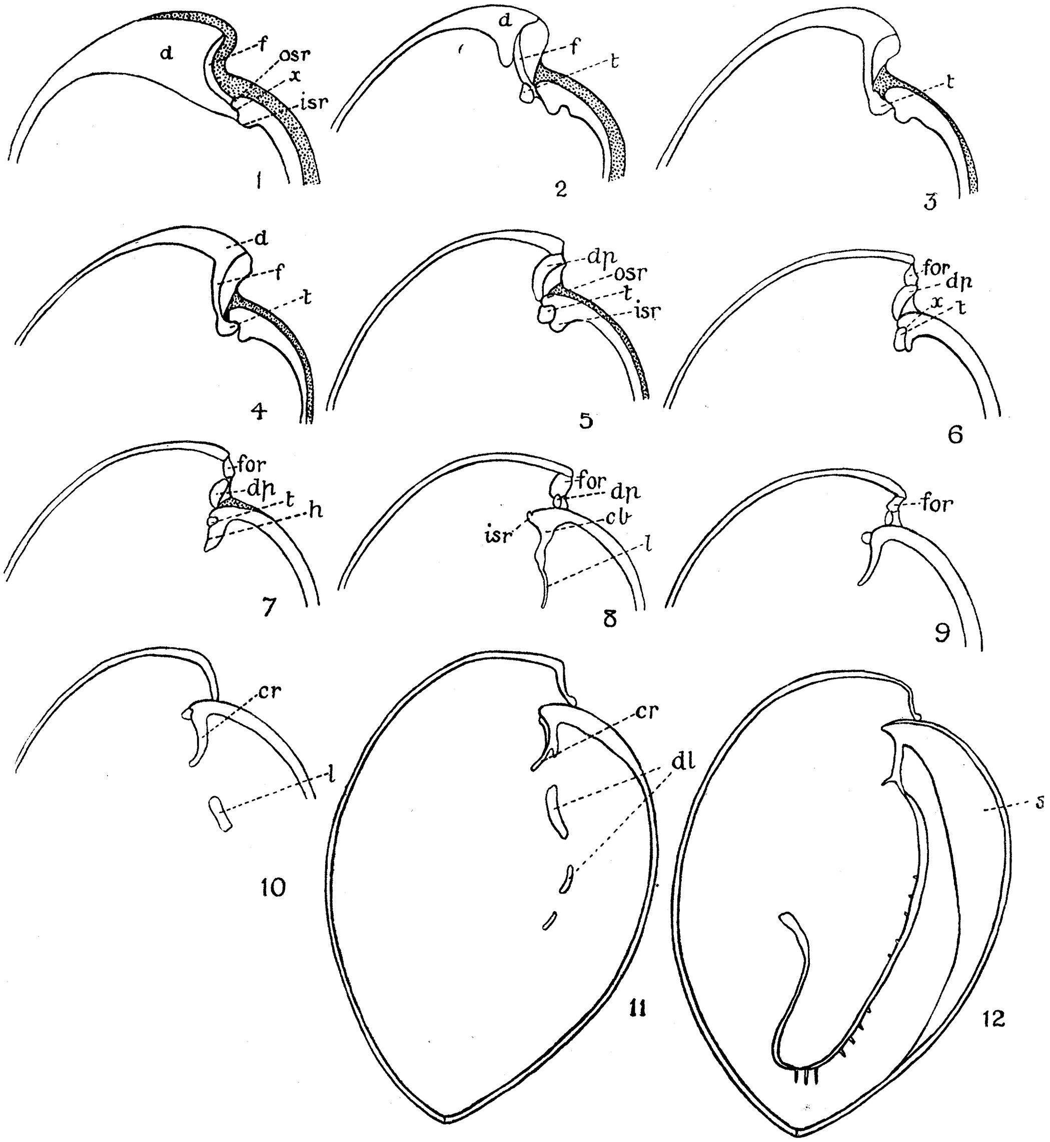

Fig. 10.—Twelve longitudinal sections through the shell of *Obovothyris magnobovata* S. S. Buckman, Lower Cornbrash, Blackthorn Hill, Bicester. [B. 57807.] × 2½. Sections 1–11 were ground at an angle of about 25° to the plane of symmetry of the shell. Section 12 shows the spinose loop and median septum dissected out in a second specimen from the same horizon of Rushden, Northants. [B. 81636.] The key to the lettering will be found on page 516.

brachial valve and a carinate pedicle valve, this species is totally unrelated to *Aulacothyris resupinata* (Sowerby), the genotype of *Aulacothyris*, from the Middle Lias. More research is needed before any attempt can be made to work out the lineages of the species at present grouped together in the subfamily Zeilleriinæ.

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It is possible that some of the more globose forms at present included in the "*obovata*" group may be found to have a similar internal structure to that of "*Ornithella*" *umbonella* (LAMARCK). This species belongs to a new genus which is being described by the author in another paper.

DESLONGCHAMPS (1884, p. 274) subdivided the genus *Zeilleria* into a number of species groups of which *Terebratula obovata* and *Terebratula digona* are examples of group "*h*" which, however, was not given a special name.

The holotype of *O. magnobovata* was described by BUCKMAN (1927, Plate 1, figs. 9, *a*, *b*) from the Lower Cornbrash of Blackthorn Hill, Bicester, Oxon. This specimen is preserved in the Buckman collection, British Museum (Nat. Hist.) [B. 58321].

Genus *Digonella* gen. n.

Figs. 18, 19, Plate 62; fig. 34, Plate 63; and figs. 1, 11, 12.

Syn. *Ornithella* auctt. (in part).

Diagnosis.—Shell sulco-carinate in neanic stage, becoming biconvex, elongate-oval to trigonal in outline; antero-lateral margins with angular carinæ, anterior commissure plane or dorsally waved. Maximum width occurring at, or near, anterior margin. Umbo flattened, suberect. Mesothyrid. Dental lamellæ slender, sub-parallel. Median septum slightly greater than half length of brachial valve, thin and plate-like supporting hinge-plate. Septalium shallow. Inner socket-ridges separated from hinge-plates by shallow depression. Crural bases and loop given off dorsally. Loop with numerous long spines, long, unattached to septum in adult. Muscle-area of brachial valve linear, adjacent to septum. Pedicle-collar forming a complete ring detached from shell wall and supported posteriorly by septum.

Genotype.—*Terebratula digona* J. SOWERBY, 1815.

Species (at present recognised).—*Digonella digona* (SOWERBY), *D. digonoides* (BUCKMAN).

Range.—Bathonian. Bradford Clay.

Distinctions.—*Digonella* is distinguished from *Ornithella* by differences in the internal structure shown in transverse sections; by its more spinose loop, longer median septum; and by its trigonal shell outline, and prominent lateral carinæ. From *Obovothyris* it is distinguished by differences in the shape of the hinge-plate; shorter median septum; more persistent and slender dental lamellæ; and by its trigonal shell outline, and more erect, flattened umbo.

Remarks.—SOWERBY (1815, p. 217) figures four specimens as *Terebratula digona* of which figs. 1–3 of Plate 96 are from the Bradford Clay of Bradford (Wilts.) or Pickwick (Wilts.). Of these the specimen represented as fig. 1 is selected as lectotype. This specimen is preserved in the British Museum (Nat. Hist.) collection [B. 71586]. The

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specimen represented by figs. 4, 5 of the same plate from Felmersham (Bedfordshire), probably from the Great Oolite, should be referred to *Digonella digonoides* (Buckman).

Davidson (1878, Plate 22, fig. 22) figured the interior of the brachial valve of "*Waldheimia*" *digona* showing the spines on the loop exceptionally well preserved. Much restored drawings of the spines in this species were also given by Deslongchamps (1884).

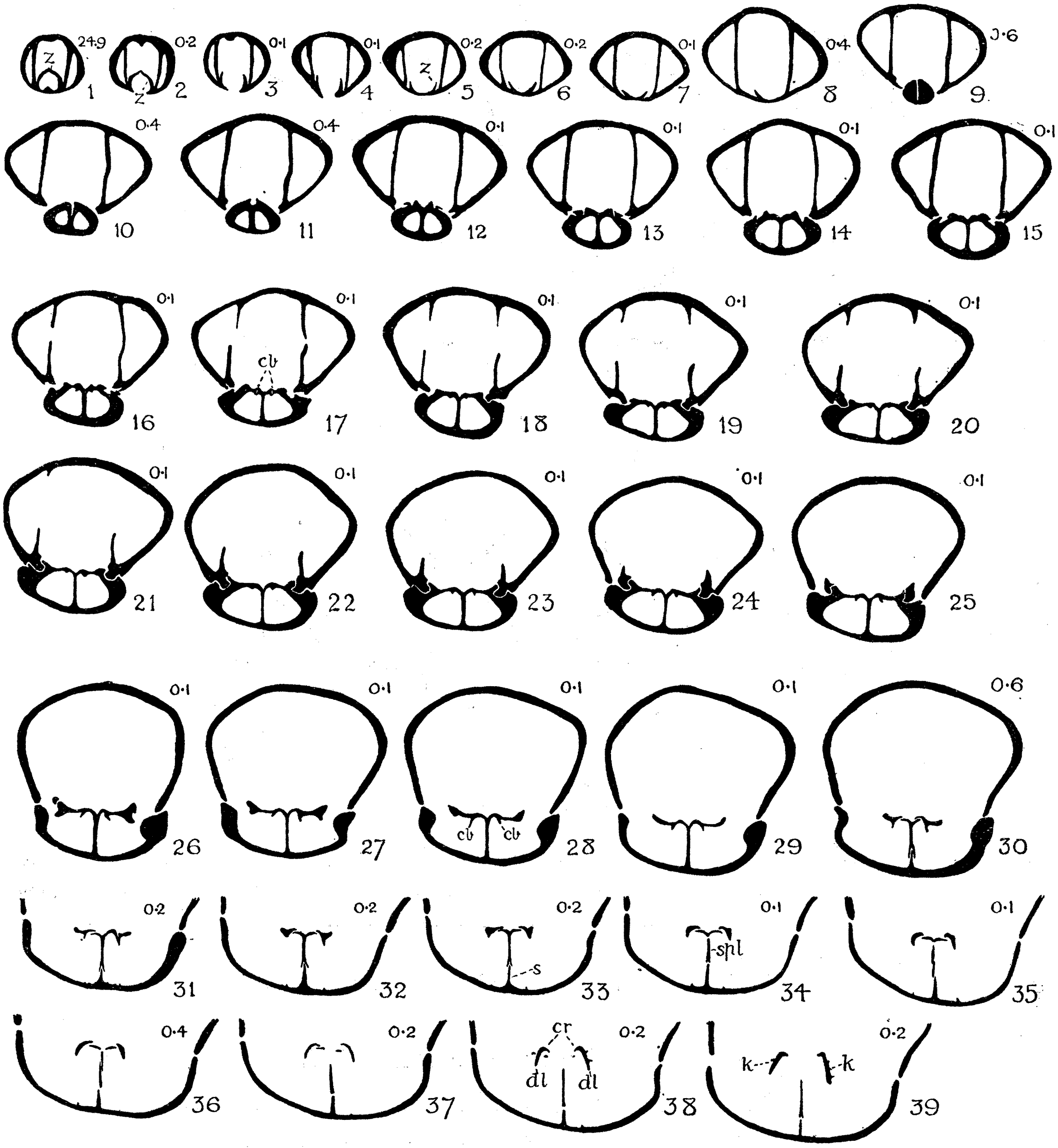

Fig. 11.—Thirty-nine transverse sections through the posterior part of the shell of *Digonella digona* (Sowerby). Bradford Clay, Bradford-on-Avon, Wilts. [B. 82279.] × 2½. Original height of shell = 25·9 mm. Sections 1–8 show the pedicle valve only.

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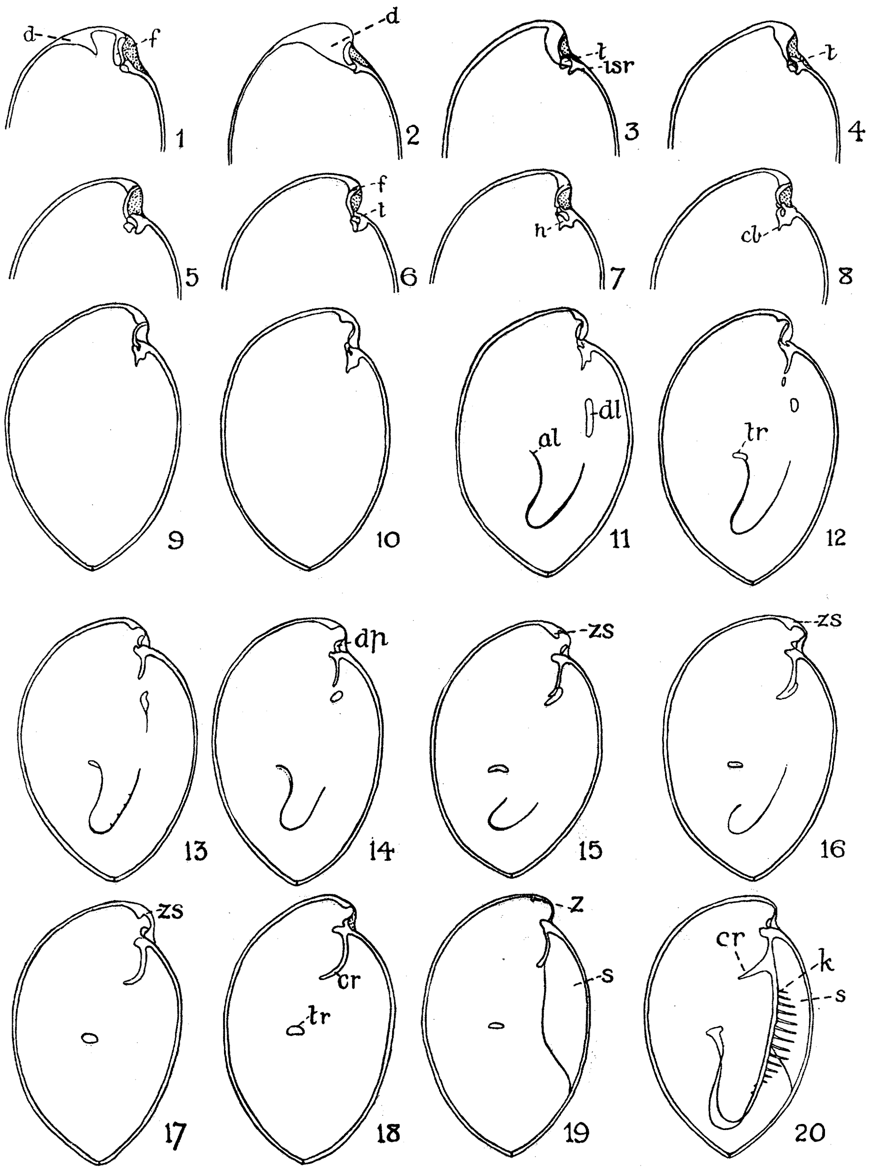

FIG. 12.—Twenty longitudinal sections through the shell of *Digonella digona* (SOWERBY), Bradford Clay, Bradford-on-Avon, Wilts. × 2½. Sections 1–19 were ground at an angle of about 15° to the plane of symmetry of the shell. Section 20 shows the spinose loop and median septum dissected out from a second specimen. [B. 84289.]

The key to the lettering will be found on page 516.

Genus *Terebrirostra*, D'ORBIGNY, 1847.

Figs. 20, 21, Plate 62; fig. 36, Plate 63, and figs. 13, 14.

Lyra, Cumberland MS. in SOWERBY (1816), p. 88 (*nom. nud.*).
Trigonosemus, KOENIG (in part) (1825), p. 3.
Terebrirostra, D'ORBIGNY (1847), p. 269.
Terebrirostra, D'ORBIGNY (1850a), p. 126.

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Terebrirostra, d'Orbigny (1850b), p. 345.
Terebrirostra, d'Orbigny (1850c), [1849-52], p. 85.
Terebrirostra, d'Orbigny (1851), p. 222.
Terebrirostra, d'Orbigny: Davidson (1852), p. 31.
Terebrirostra, d'Orbigny: Davidson (1853), p. 67.
Terebrirostra, d'Orbigny: Dall (1877), p. 72.
Lyra, Cumberland: Dall (1877), p. 45.
Lyra, Cumberland: Deslongchamps (1884), p. 266.
Lyra, Cumberland: Hall and Clarke (1894), p. 890.
Lyra, Cumberland: Schuchert and LeVene (1929), p. 78.

Diagnosis.—Shell biconvex, folding subintertext to incipiently ligate; brachial valve elongate-oval to subtrigonal in outline, pedicle valve resembling brachial valve

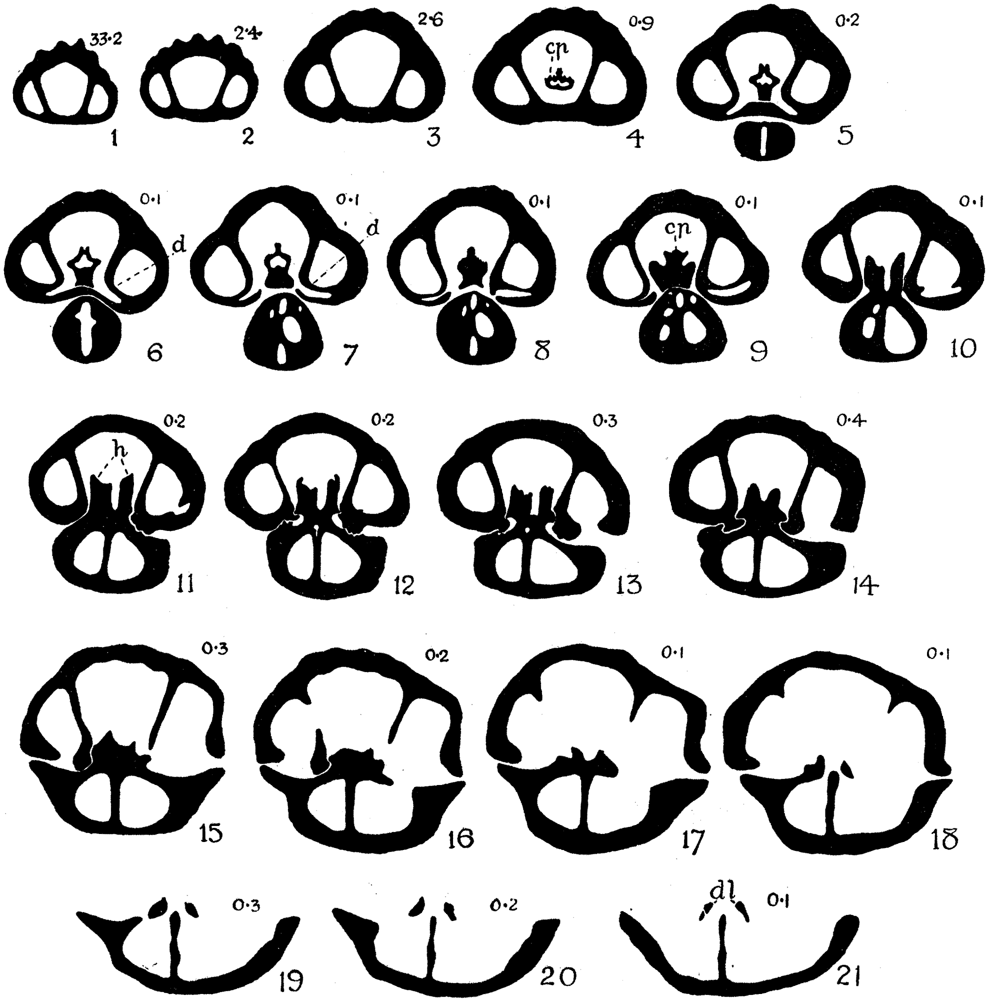

Fig. 13.—Twenty-one transverse sections through the posterior part of the shell of *Terebrirostra lyra* (Sowerby), Cenomanian, Warminster, Wilts. [B. 84531.] × 2½. Original height of shell = 35·2 mm. (umbo broken). Sections 1–4 show the pedicle valve only. The trilobed cardinal process projects into the cavity of the pedicle valve in sections 4–9.

The key to the lettering will be found on page 516.

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but with long curving, suberect umbo; anterior margin rounded, becoming truncate or excavate; anterior commissure slightly sulcate or plane; lateral commissure deflected towards pedicle valve anteriorly. Beak-ridges angular. Deltidial plates fused. Dental lamellæ extending whole length of umbo, anteriorly curved and uniting with lateral margin. Median septum extending about one-half of length of brachial valve, supporting hinge-plate. Septalium deep. Hinge-plates joined, extending dorso-ventrally. Loop spinose, long, not joined to septum in adult, attached to septum in young. Crural processes long and curved. Cardinal process large, trilobed, projecting ventrally into cavity of pedicle valve.

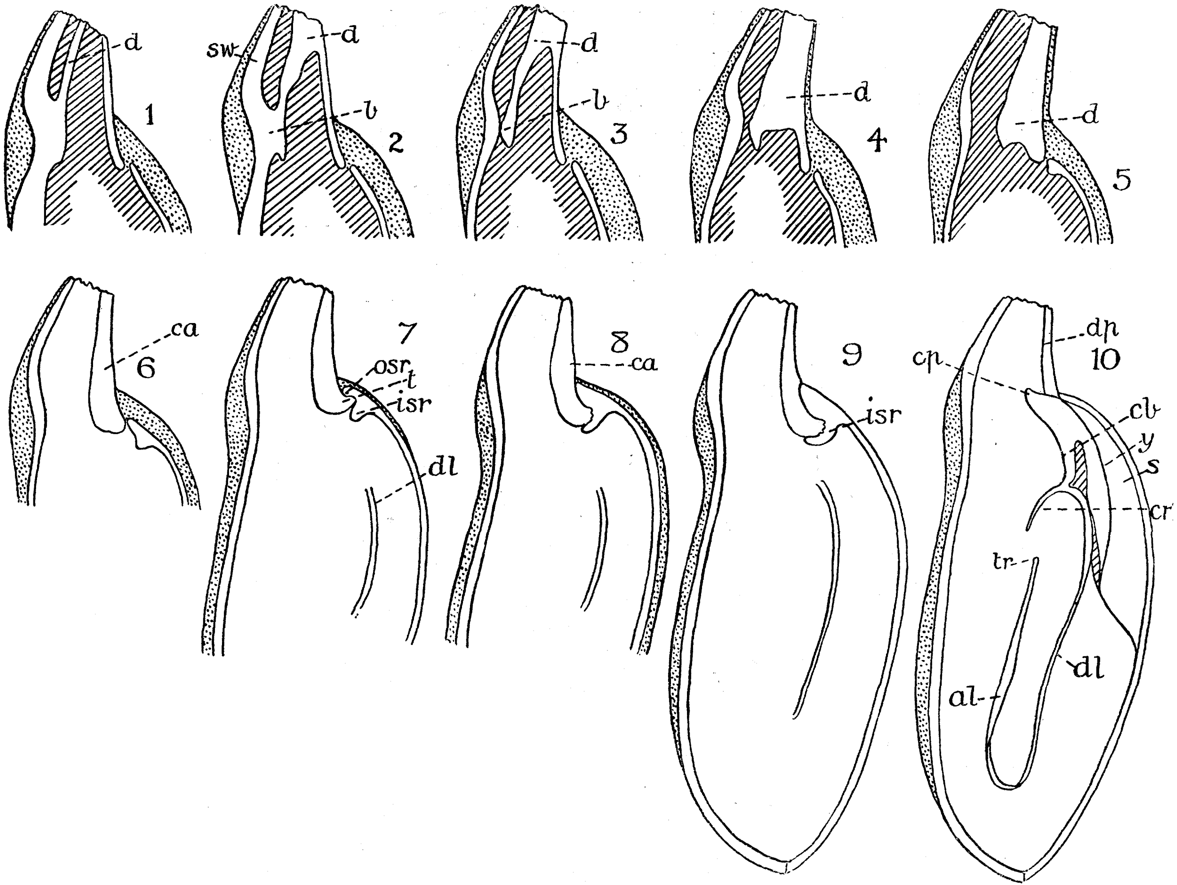

FIG. 14.—Ten longitudinal sections through the shell of *Terebrirostra incurvirostrum* LAMPLUGH and WALKER, Cretaceous, Shenley Hill, Leighton Buzzard, Bedfordshire. [B. 84532.] × 2½. The sections 1–9 were ground approximately parallel to the plane of symmetry of the shell. The loop and median septum shown in section 10 were exposed by dissection.

The key to the lettering will be found on page 516.

Genotype.—*Terebratula lyra* J. SOWERBY, 1816 = *Lyra meadii* Cumberland MS.: J. SOWERBY.

Species (at present recognized).—*T. lyra* (SOWERBY), *T. bargesiana* D'ORBIGNY, *T. arduennensis* D'ORBIGNY, *T. incurvirostrum* LAMPLUGH and WALKER.

Range.—Cretaceous.

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Remarks.—*Terebrirostra* is distinguished from Recent Terebratellas in having the brachial loop unattached to the median septum in the adult; and in having a larger cardinal process and different hinge-plate. The numerous fossil species at present described as *Terebratella,* vary considerably in their hinge-characters, but most of these forms have a Terebratellid or doubly attached loop in the adult. *Terebrirostra* is distinguished from *Trigonosemus* by the simpler form of the loop; by the differences in the hinge-characters, and by its angular beak-ridges.

The name *Lyra,* employed by so many authors, has never been definitely described or figured in any publication. The only mention of it was in the description of *Terebratula lyra* by JAMES SOWERBY in 1816 (p. 88), as follows :—" Mr. Cumberland, indeed, considered it a new Genus and named it *Lyra Meadi,* in compliment to our worthy friend, whom I esteem so much, but the term *Lyra* is so apt I could not resist applying it to the specific name."

The first published description of the genus was by D'ORBIGNY in 1847, who called it *Terebrirostra,* which name must be adopted, with genotype *Terebratula lyra* SOWERBY.

D'ORBIGNY did not describe or figure the loop of this genus in any of his publications. DESLONGCHAMPS (1884, p. 267), however, dissected out the loop of *Terebrirostra bargesiana* D'ORBIGNY, from the Albian of the Ardennes, and described it as being similar to that of *Waldheimia* and not terebratellid in the adult. In his description of this genus under the name of *Lyra,* DESLONGCHAMPS mentioned that the megerliform and terebratelliform stages persist in the early growth-stages of the shell. The terebratelliform stage of loop development was observed in immature specimens of *T. incurvirostrum.*

In most of the British specimens of *Terebrirostra* the umbo of the pedicle valve is imperfectly preserved, and the pedicle opening cannot be studied. This structure was seen, however, in a young specimen of *T. lyra* from the French Cenomanian in the British Museum (Nat. Hist.) collections [B. 82453], which has a complete umbo showing the oval terminal foramen surrounded by a slightly raised rim. In this specimen the umbo was somewhat curiously curved ventrally, and away from the brachial valve.

The folding of the shell in *Terebrirostra* is peculiar. In young forms of *T. lyra* the anterior commissure is slightly sulcate, but the sulcation of the brachial valve is not met by a corresponding fold in the pedicle valve. Such a condition is described as non-intertext by BUCKMAN (1917, p. 80). In the adult shell the anterior portion of the brachial valve becomes medianly depressed, and a shallow median sulcus is developed in the pedicle valve. The anterior commissure is now plane, and the folding of the shell approaches the ligate stage (BUCKMAN, 1917, p. 79), but the lateral carinæ do not extend up the shell.

Terebrirostra neocomiensis D'ORBIGNY (1850a, p. 127), has a shorter umbo than *T. lyra,* and has no dental lamellæ in the pedicle valve. The shell is dorsally uniplicate, and the ornament consists of fine thread-like costæ unlike that of *T. lyra.* From the external characters and folding of the shell as well as from the absence of dental lamellæ, this

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species appears to be allied to *Terebratulina* and is certainly not to be identified as a *Terebrirostra*.

Owing to lack of specimens of *T. lyra* from the Cenomanian, and also to the poor state of preservation of the interior of the shell of this species, it was necessary to dissect out the loop of adult specimens of *T. incurvirostrum* LAMPLUGH and WALKER (1903), from the Cretaceous, ? Albian of Shenley Hill, Leighton Buzzard. Attempts to dissect out the loop of *T. lyra* from the Cenomanian of Warminster were usually unsuccessful owing to the partial silicification of the interior of the shell. The cardinal process and hinge-plate of *T. incurvirostrum* are less advanced than those of *T. lyra*, and probably indicate an earlier age than the Cenomanian for the Shenley Hill deposits.

The remarkable elongation of the beak in the pedicle valve of *Terebrirostra* is paralleled to some extent in other genera of the Terebratulacea, and appears to be a trend in development, which is seen in species of Terebratulids in the Upper Jurassic, in ? *Terebratulina* in the Neocomian, in *Terebratella* in the Aptian, and in ? *Trigonosemus* in the Upper Chalk. This elongation of the umbo was probably favourable at first to the growth of the animal, but was finally carried to such an exaggerated pitch as to cause the extinction of the genus.

JAKOVLEV (1908, p. 31) discussed the length of the cardinal area in the genera *Terebratella*, *Trigonosemus*, and *Terebrirostra*, as well as that of Permo-Carboniferous genera of the Donez-Basin, and suggested that the high area was due to rapid accumulation of sediment.

V. CLASSIFICATION.

Until more research on the lines already described has been carried out on the Mesozoic Telotremata it is not proposed to put forward any new classification of the genera into families and subfamilies. When the external morphology, as well as the internal structure of these Mesozoic species, has been thoroughly studied it should be possible to outline trends, to build up lineages and so to construct some rational system of classification. Division of the genera into families and subfamilies will probably be based on internal characters, such as the form of the loop, and its developmental stages, and the form of the cardinalia. The genera will be defined by internal as well as external characters, and the species mainly by external shape, folding, and ornament.

In the genera specially investigated, the most important diagnostic internal characters were found to be those of the brachial valve. The form of the hinge-plates and cardinal process (cardinalia), size of the umbonal cavity, development of the septalium, size and shape of the hinge-sockets and angle of insertion of teeth, and additional articulation of denticula and socket-ridges, form of the loop, and position of crural bases are all characters which have been found to vary more or less in different genera, but which are fairly constant for one genus. The hinge-plate is found to vary less in form in successive growth-stages than the cardinal process and loop. The frequent asymmetry of the loop owing to injury during the life of the animal, or other causes, renders any

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classification relying on this character alone unsatisfactory. The median septum, or septum and fused septalial plates, is found to be variable in dorso-ventral height, but to be fairly constant in antero-posterior length in related species.

In the pedicle valve the dental lamellæ vary considerably in development not only in successive growth-stages of one specimen, but also the two lamellæ of one specimen may be unevenly developed. In the gerontic stage the lamellæ may either become embedded in thick deposits of callus, and therefore appear to be obsolete, as in *Ornithella*, or they may become more strongly developed than in the young specimens, or they may disappear entirely. For these reasons the dental lamellæ are not of much diagnostic importance.

The significance of the development of the pedicle-collar and its supporting septum is not at present known. This structure, without supporting septum, appears to be developed in many of the Jurassic Rhynchonellids and Terebratulids, and in *Obovothyris* and *Digonella* is accompanied by a supporting septum. It is interesting that this structure is found in many Recent Terebratulids and Rhynchonellids, but is not developed in most of the Recent Dallininæ and Magellaniinæ, although usually present in the less advanced long-looped genera.

In the external morphology, the folding of the shell and the ornament in successive growth-stages and the beak characters are found to be important diagnostic characters.

Each character evolves separately and at a different rate, so that it is necessary to take this into consideration in the diagnosis of genera. The present piece of research has emphasized the importance of not relying on a single character, but of diagnosing genera on the internal and external characters collectively.

The metamorphoses of the loop in successive growth-stages by resorption and redeposition have been worked out in Recent and Tertiary species by FRIELE (1877), DESLONGCHAMPS (1884), BEECHER (1893a-c), THOMSON (1927), FISCHER and OEHLERT (1892), and others. Although it is not likely that the Terebratulid loop undergoes a series of remarkable developmental changes similar to those of the Terebratellid loop, there is no doubt that its form must vary with the growth of the shell, and any classification based on the form of the loop must take this factor into consideration.

The primitive centronellid loop, consisting of two short descending lamellæ united in a triangular median plate in the Devonian Terebratulid genus, *Centronella*, forms the early growth-stage of the loop of the more advanced Palæozoic Terebratulid genus, *Dielasma* (WATSON, 1909), and probably occurs in young specimens of all Mesozoic Terebratulids. In the Recent Terebratulid genus, *Gryphus*, no mention of the centronellid stage is made by DESLONGCHAMPS (1884, p. 194), who describes the growth of the loop as a continuous development. In *Liothyrina* [*Gryphus*] *vitrea*, he found that it originated as short crural processes given off from the hinge-plate. The crural processes gradually elongated, and formed not only crura, which converged towards the median line, but also the two branches of the loop, which grew anteriorly, recurved upwards, and finally became united. This is confirmed by THOMSON (1927), who states that the

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Centronella stage is lost by tachygenesis. The centronellid loop is present also as an early stage of growth of the spiralia of some Spiriferidæ and is described by BEECHER and SCHUCHERT (1893) in the primitive Palæozoic genus *Zygospira*. In Recent species of *Terebratulina* the development of the loop is similar, as shown by MORSE (1871, a and b), but the crura unite in the adult stage to form a complete ring.

It is not known at present if the centronellid stage occurs in the immature stages of loop development of the Ornithellids. There is no evidence that the ornithellid loop was attached to the septum in the young stage, although traces of connecting bands were seen in *Digonella digona*, or that it ever passed through the complicated series of metamorphoses that are known to occur in the Dallininæ and Magellaniinæ. It is possible that the ornithellid loop may be derived from the Palæozoic long-looped genera, such as *Cryptacanthia* or *Harttina*, in which the loop is not joined to the septum. Further research on the long-looped genera is being undertaken by the author, and it is hoped to throw light on some of these doubtful points.

At least five distinct series of long-looped forms with dorsal septa are represented in the Mesozoic rocks :—(1) with ornithelliform loops ; (2) with ismeniform loops ; (3) with magadiform loops ; (4) with terebratelliform loops ; (5) with terebrirostriform loops. Group (5) differs from group (4) in having the loop attached to the septum in the early growth-stages only and also in having different cardinalia. Forms with ismeniform loops have been described from the Jurassic by MOORE (1860, 1863) in *Terebratella* [*Hamptonina*] *buckmani*, and by ZITTEL (1870) in *Megerlea* [*Trigonellina*] *pectunculus* and other species. The adult loops of these forms resemble the early growth-stages of the loop of the Recent Dallininæ. *Magas*, in section 3, has a loop somewhat resembling that of young stages of Recent Magellaniinæ. The relationship of fossil Terebratellas to the Recent genus is not clear. MEYER (1868, p. 269), who examined the loop of *Terebratella menardi* from the Cenomanian, stated that it was attached to the septum even in young forms, and he did not describe any change in the form of the immature loop.

Many schemes for the classification of the Terebratulids, Terebratellids, and Rhynchonellids into families and subfamilies have been outlined by successive workers on the Brachiopods, usually without any regard for the work of previous authors. Some of these classifications, such as that of VON BUCH (1834), QUENSTEDT (1871), ROTHPLETZ (1886), and BUCKMAN (1917), are based entirely on the shape and folding of the shell and on the shell ornament. BUCKMAN's four divisions are :—I. Læves, II. Capillatæ, III. Rugosæ, IV. Ornatæ. It has already been shown by SAHNI that " Læves " include genera with entirely different lengths of loop which probably indicate different phylogenetic development. The " Capillatæ " include the genera *Terebratulina*, *Disculina*, *Trichothyris*, and *Holcothyris*, all four of which are capillate but are totally unrelated in their internal characters. It is doubtful also if the " Rugosæ " and " Ornatæ " should be separated from one another or from the " Capillatæ." BUCKMAN criticizes the classification of ROTHPLETZ and DOUVILLÉ as being artificial, but his own system possesses all the defects of those earlier workers.

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Among classifications relying mainly on internal characters may be mentioned that of King (1850), Davidson (1853), Douvillé (1880), Dall (1870–1871), and Beecher (1893*a*).

Schuchert modified Beecher's classification in 1913 and again in 1929. In the latter publication the sub-family Zeilleriinæ is introduced to include *Zeilleria, Ornithella,* etc. The name Zeilleriinæ is attributed by Schuchert and Le Vene to Rollier (1919). The latter author, however, proposed the family Zeillérídés to replace the Waldheimiidæ of Douvillé and included in it all Jurassic long-looped genera. The name Zeilleriinæ should therefore be correctly attributed to Schuchert and Le Vene. Among genera with ornithelliform loops are included forms with ismeniform and terebratelliform loops which are obviously unrelated, and should be removed from the Zeilleriinæ to the Dallininæ or Magellaniinæ. *Obovothyris* and *Cincta,* which have ornithelliform loops, are placed by Schuchert and Le Vene in the Dallininæ, where they obviously cannot belong. A considerable amount of rearrangement of the genera will have to be made in Schuchert and Le Vene's classification before it can be adopted.

The Mesozoic, Tertiary, and Recent Terebratulids are left undivided in the subfamily Terebratulinæ by these authors with the exception of *Pseudoglossothyris, Tegulithyris,* and *Avonothyris* which are placed in the Nucleatinæ, presumably on account of the sulcation of the brachial valve. Examination of the species at present grouped together in *Pseudoglossothyris* shows, however, that we are dealing with a number of unrelated homœomorphous forms which will, no doubt, prove to be sulcate relations of various plano-convex or biconvex genera of the Terebratulinæ.

An improved classification based on Beecher's work was proposed by Thomson (1927) for the Tertiary and Recent forms. It introduces a number of new characters not previously used in any classification, and it should form a useful basis for the classification of Mesozoic genera.

A brief outline of the history of the classification of the Rhynchonellidæ was given by Wiśniewska (1932), and need not therefore be repeated here. Reference, however, should be made to the tentative classification by Rothpletz (1886, p. 86) by means of the form of the crura in Mesozoic species which are described as (*a*) radulifer ; (*b*) falcifer ; (*c*) septifer. A fourth type (*d*) is described by Wiśniewska as arcuifer, and a fifth type (*e*) by the author in *Kallirhynchia* as calcarifer. Leidhold (1920) also describes what appears to be another distinct type in his genus *Thurmanella* from the Upper Jurassic.

VI. Summary.

(1) In this paper attention has been drawn to the importance of the question of homœomorphy in Brachiopoda due to parallel development. In consequence of this a careful examination of internal as well as of external characters is essential for the determination of genera and species.

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(2) Seven common Mesozoic species, six of which are the genotypes of previously described genera, have been selected for detailed examination, and their little known internal structure has been studied. This investigation has been by means of longitudinal and transverse sections, internal casts, and dissected specimens.

(3) It is found that by heating the specimens before sectioning or dissecting, the internal plates and brachial loop appear white against a dark matrix, and can be accurately drawn or photographed.

(4) Reconstructions have been made from the transverse and longitudinal sections of the interior of the brachial valve of *Kallirhynchia yaxleyensis*, *Lobothyris punctata*, *Plectoidothyris polyplecta*, *Ornithella ornithocephala*, *Obovothyris magnobovata*, and *Digonella digona* from the Jurassic, and of *Terebrirostra*, *incurvirostrum* from the Cretaceous.

(5) Much new information regarding the internal morphology of these genera has thus been obtained, and the previously unknown structures " accessory socket," " denticulum," " denticular cavity," and " septalial plate," are defined.

(6) The cardinalia and articulatory processes of the two valves in these genera have been described in detail, and illustrated by means of enlarged diagrams.

(7) The complete loop seen in dorso-ventral view and in contour has been dissected out in each of the seven species, and the minute spines springing from one edge of the loop of *Ornithella*, *Digonella*, *Obovothyris*, and *Terebrirostra*, have been investigated.

(8) The median septum in *Ornithella*, *Obovothyris*, and *Digonella* has been found to be composed of, (*a*) a short septum, (the true septum) springing from the floor of the brachial valve; (*b*) two plates (septalial plates) fused together dorsally to form a septum, but diverging from one another ventrally and uniting with the hinge-plates. The apex of the true septum is inserted within the dorsal end of the fused septalial plates.

(9) Growth-stages in the development of the brachial loop, due to resorption and redeposition, have been observed in specimens of *Terebrirostra incurvirostrum*, and also in the " calcarifer " crura of *Kallirhynchia yaxleyensis*.

(10) Five unrelated groups of long-looped Brachiopods are now known from the Mesozoic, some of which are ancestral forms of Recent species.

(11) The emended diagnoses of the above-mentioned six genera and the diagnosis of *Digonella* gen. n., are based on the internal and external characters collectively. The diagnostic importance of the internal characters of the brachial valve has been emphasized.

(12) A brief résumé has been given of modern methods employed in the investigation of Brachiopod shells, and of the defects of former classifications based only on external characters or on single internal characters.

Work on the lines described in this paper should make it possible to outline trends, to build up lineages, and to construct a natural system of classification.

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IX.—Index of Genera, Species, and Families.

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IX.—EXPLANATION OF PLATES.

(All specimens of natural size unless otherwise stated.)

PLATE 62.

FIG. 15, *a*.—*Kallirhynchia yaxleyensis* (DAVIDSON). Holotype. Dorsal view. Lower Cornbrash. Yaxley, Peterborough. [B. 82289.]

FIG. 15, *b*.—Ditto, lateral view of the same specimen.

FIG. 15, *c*.—Ditto, anterior view of same specimen.

FIG. 16.—Ditto, internal cast of pedicle valve showing adductor, diductor, and pedicle muscle-scars and dental lamellæ. Same horizon and locality. [B. 82299.]

FIG. 17.—Ditto, internal cast of brachial valve showing adductor muscle-scars. Same horizon and locality [B. 82298.]

FIG. 18, *a*.—*Digonella digona* (J. SOWERBY). Internal cast of brachial valve showing adductor muscle-scars and slit representing median septum. Bradford Clay, Bradford-on-Avon, Wilts. [B. 84527.]

FIG. 18, *b*.—Ditto, internal cast of pedicle valve of same specimen showing posteriorly situated muscle-scars.

FIG. 19, *a*.—Ditto, dorsal view of lectotype. Same horizon, and ? same locality. [B. 71586.]

FIG. 19, *b*.—Ditto, lateral view of same specimen.

FIG. 20.—*Terebrirostra incurvirostrum* LAMPLUGH & WALKER. Internal cast of brachial valve showing muscle-scars. Cretaceous, ? Albian, Shenley Hill, Leighton Buzzard, Bedfordshire. [B. 82256.] × 2.

FIG. 21, *a*.—*Terebrirostra lyra* (J. SOWERBY). Anterior view of topotype. Cenomanian, Horningsham, Warminster, Wilts. [B. 84525.]

FIG. 21, *b*.—Ditto, lateral view of same specimen.

FIG. 21, *c*.—Ditto, dorsal view of same specimen showing length of pedicle umbo.

FIG. 22, *a*.—*Ornithella ornithocephala* (J. SOWERBY). Lectotype. Dorsal view. Lower Cornbrash, Chatley, Somerset. [B. 49540.]

FIG. 22, *b*.—Ditto, lateral view of same specimen.

FIG. 22, *c*.—Ditto, anterior view of same specimen.

FIG. 23.—*Ornithella bathonica* ROLLIER. Internal cast of pedicle valve showing adductor, diductor, and pedicle muscle-scars. Fullers Earth Rock, Box Tunnel, Wilts. [B. 84526.]

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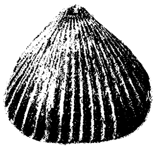
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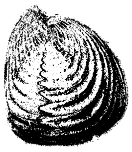
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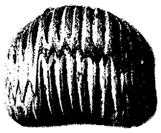
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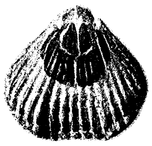
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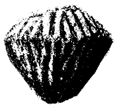
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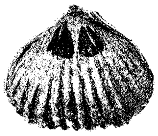
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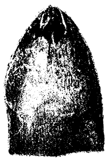
18 a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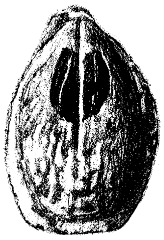
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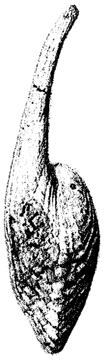
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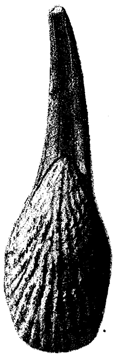
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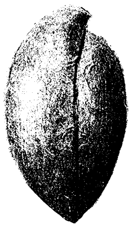
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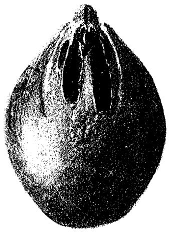
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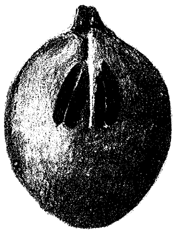
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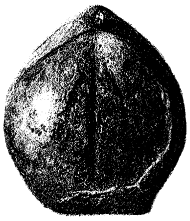
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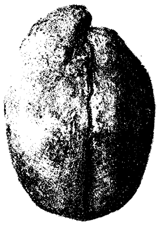
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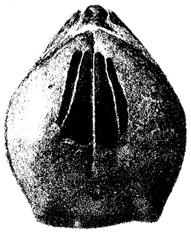
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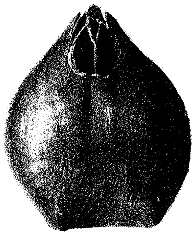
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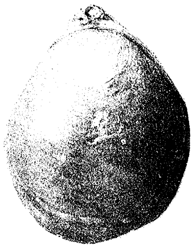
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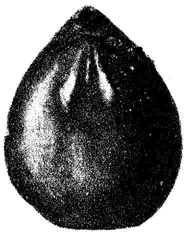
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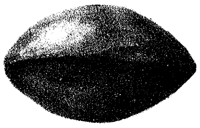
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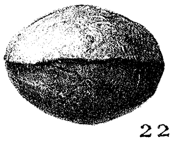
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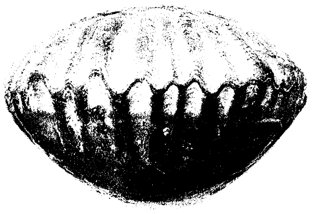
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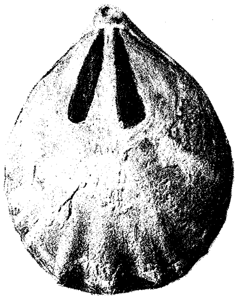
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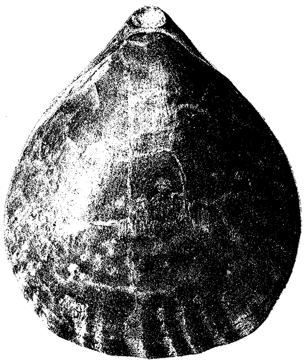
30 c

H.G. Herring photo.

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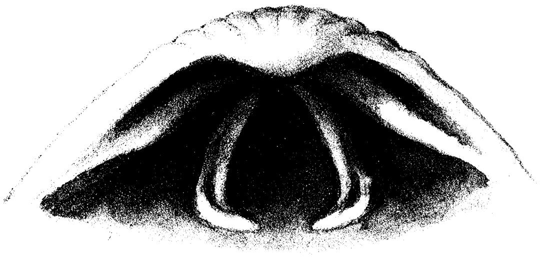

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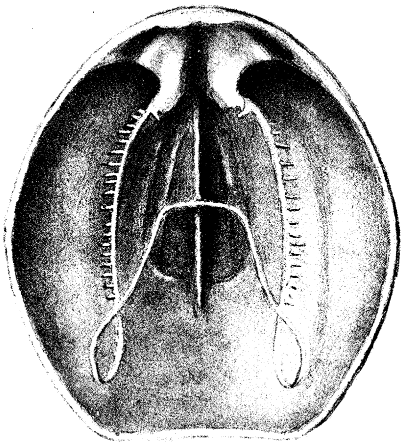

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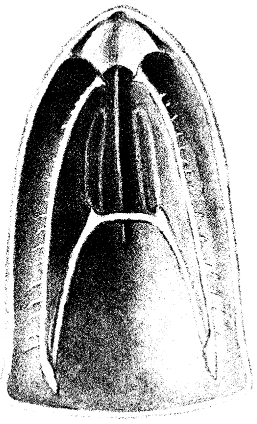

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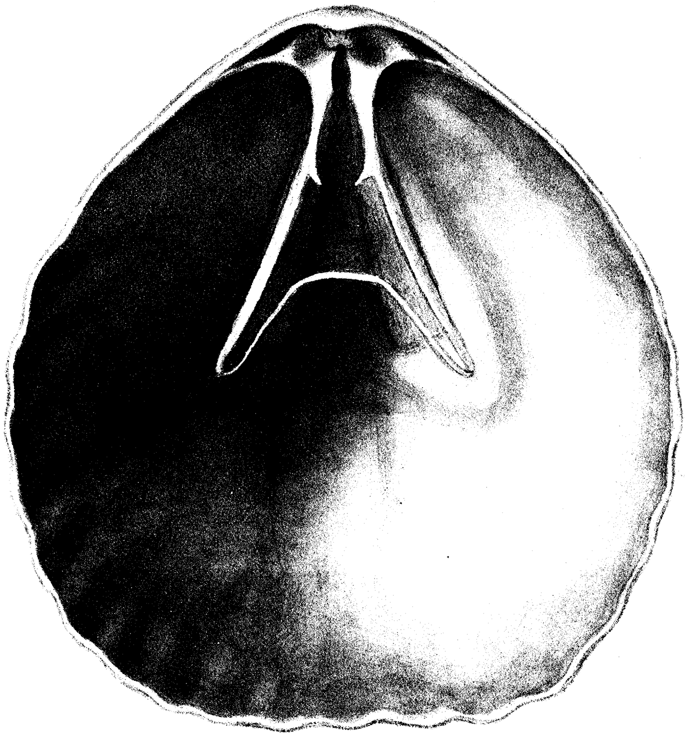

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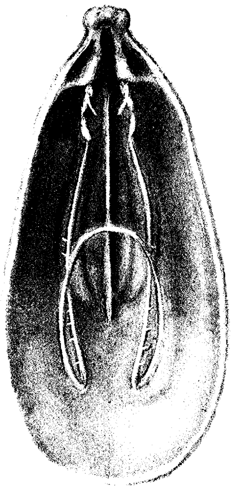

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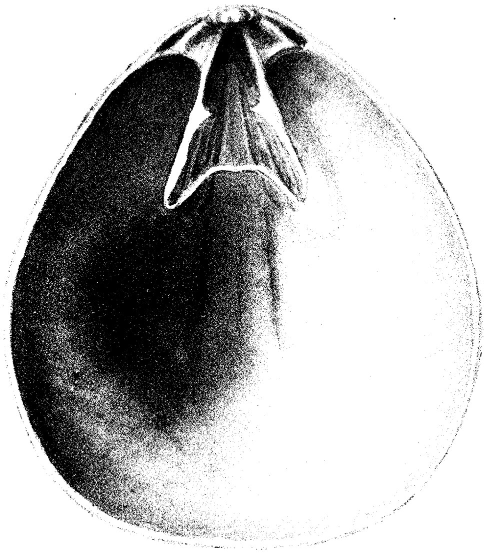

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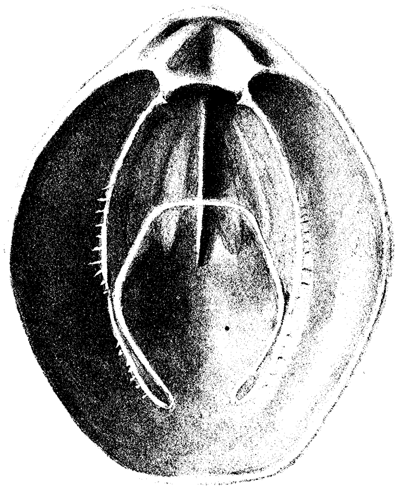

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G. M. Woodward del.

Huth coll.

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FIG. 24.—*Ornithella bathonica* ROLLIER. Internal cast of brachial valve showing adductor muscle-scars and slit representing median septum. Same horizon and locality. [B. 84529.]

FIG. 25, *a*.—*Obovothyris magnobovata* S. S. BUCKMAN. Holotype. Naturally formed internal cast of brachial valve showing trace of muscle-scars. Lower Cornbrash, Blackthorn Hill, Bicester. [B. 58321.]

FIG. 25, *b*.—Ditto, anterior view of same specimen.

FIG, 25, *c*.—Ditto, lateral view of same specimen.

FIG. 26.—Ditto, internal cast of brachial valve. Lower Cornbrash, Rushden, Northants. [B. 84530.]

FIG. 27.—Ditto, internal cast of pedicle valve. Lower Cornbrash, Rushden, Northants. [B. 84523.]

FIG. 28, *a*.—*Lobothyris punctata* (J. SOWERBY). Lectotype. Dorsal view. Middle Lias, Hornton, Oxon. [B. 61522.]

FIG. 28, *b*.—Ditto, lateral view of same specimen.

FIG. 28, *c*.—Ditto, anterior view of same specimen.

FIG. 29.—Ditto, internal cast of brachial valve showing adductor muscle-scars. Middle Lias, Tilton, Leicestershire. [B. 84524.]

FIG. 30, *a*.—*Plectoidothyris polyplecta* (S. S. BUCKMAN). Topotype. Anterior view. Inferior Oolite, Oolite Marl. Railway cutting, Notgrove Stn., Glos. [B. 47184.]

FIG. 30, *b*.—Ditto, lateral view of same specimen.

FIG. 30, *c*.—Ditto, dorsal view of same specimen.

FIG. 31.—Ditto, internal cast of brachial valve showing adductor muscle-scars. Same horizon and locality. [B. 84528.]

PLATE 63.

FIG. 32.—*Kallirhynchia yaxleyensis* (DAVIDSON). Reconstruction of posterior portion of interior of brachial valve from dissected specimens showing the upper surface of curved calcarifer crura, and hinge sockets. × 5.

FIG. 33.—*Obovothyris magnobovata* S. S. BUCKMAN. Reconstruction of interior of brachial valve from dissected specimens and transverse sections showing the fused hinge-plates and septalium, hinge-sockets, inner and outer socket-ridges, median septum and complete loop with spines on the descending branches. × $2\frac{1}{2}$.

FIG. 34.—*Digonella digona* (J. SOWERBY). Reconstruction of interior of brachial valve from dissected specimens and transverse sections showing the fused hinge-plates, shallow septalium, hinge-sockets, socket-ridges, and complete loop with long spines on the descending branches. × $2\frac{1}{2}$.

FIG. 35.—*Plectoidothyris polyplecta* (S. S. BUCKMAN). Reconstruction of interior of brachial valve from dissected specimens and transverse sections showing the incurved umbo, cardinal process, divided hinge-plates and long loop. × $2\frac{1}{2}$.

FIG. 36.—*Terebrirostra incurvirostrum* LAMPLUGH & WALKER. Reconstruction of interior of brachial valve from dissected specimens showing the prominent cardinal process and divided hinge-plates, hinge-sockets, median septum, and complete loop with spines on the descending branches. × $2\frac{1}{2}$.

FIG. 37.—*Lobothyris punctata* (J. SOWERBY). Reconstruction of interior of brachial valve from dissected specimens and transverse sections showing the small cardinal process, divided hinge-plates, and short loop. × $2\frac{1}{2}$.

FIG. 38.—*Ornithella ornithocephala* (J. SOWERBY). Reconstruction of interior of brachial valve from a dissected specimen showing slightly incurved umbo, fused hinge-plates, deep septalium, hinge sockets, hinge-plates, median septum and complete loop with short spines on descending branches. × $2\frac{1}{2}$.

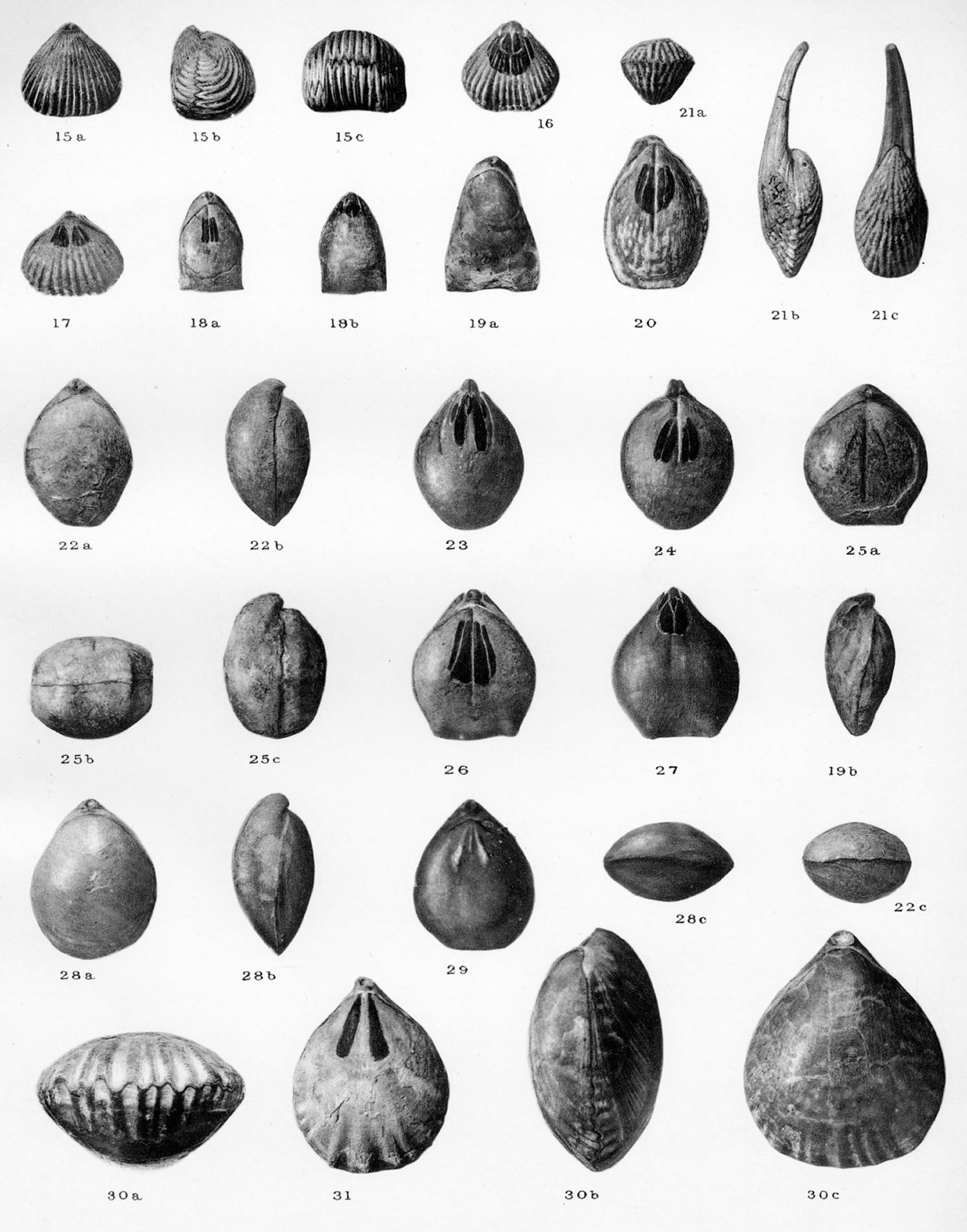

PLATE 62.

FIG. 15, *a.*—*Kallirhynchia yaxleyensis* (DAVIDSON). Holotype. Dorsal view. Lower Cornbrash. Yaxley, Peterborough. [B. 82289.]

FIG. 15, *b.*—Ditto, lateral view of the same specimen.

FIG. 15, *c.*—Ditto, anterior view of same specimen.

FIG. 16.—Ditto, internal cast of pedicle valve showing adductor, diductor, and pedicle muscle-scars and dental lamellæ. Same horizon and locality. [B. 82299.]

FIG. 17.—Ditto, internal cast of brachial valve showing adductor muscle-scars. Same horizon and locality [B. 82298.]

FIG. 18, *a.*—*Digonella digona* (J. SOWERBY). Internal cast of brachial valve showing adductor muscle-scars and slit representing median septum. Bradford Clay, Bradford-on-Avon, Wilts. [B. 84527.]

FIG. 18, *b.*—Ditto, internal cast of pedicle valve of same specimen showing posteriorly situated muscle-scars.

FIG. 19, *a.*—Ditto, dorsal view of lectotype. Same horizon, and ? same locality. [B. 71586.]

FIG. 19, *b.*—Ditto, lateral view of same specimen.

FIG. 20.—*Terebrirostra incurvirostrum* LAMPLUGH & WALKER. Internal cast of brachial valve showing muscle-scars. Cretaceous, ? Albian, Shenley Hill, Leighton Buzzard, Bedfordshire. [B. 82256.] × 2.

FIG. 21, *a.*—*Terebrirostra lyra* (J. SOWERBY). Anterior view of topotype. Cenomanian, Horningsham, Warminster, Wilts. [B. 84525.]

FIG. 21, *b.*—Ditto, lateral view of same specimen.

FIG. 21, *c.*—Ditto, dorsal view of same specimen showing length of pedicle umbo.

FIG. 22, *a.*—*Ornithella ornithocephala* (J. SOWERBY). Lectotype. Dorsal view. Lower Cornbrash, Chatley, Somerset. [B. 49540.]

FIG. 22, *b.*—Ditto, lateral view of same specimen.

FIG. 22, *c.*—Ditto, anterior view of same specimen.

FIG. 23.—*Ornithella bathonica* ROLLIER. Internal cast of pedicle valve showing adductor, diductor, and pedicle muscle-scars. Fullers Earth Rock, Box Tunnel, Wilts. [B. 84526.]

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FIG. 24.—*Ornithella bathonica* ROLLIER. Internal cast of brachial valve showing adductor muscle-scars and slit representing median septum. Same horizon and locality. [B. 84529.]

FIG. 25, *a.*—*Obovothyris magnobovata* S. S. BUCKMAN. Holotype. Naturally formed internal cast of brachial valve showing trace of muscle-scars. Lower Cornbrash, Blackthorn Hill, Bicester. [B. 58321.]

FIG. 25, *b.*—Ditto, anterior view of same specimen.

FIG, 25, *c.*—Ditto, lateral view of same specimen.

FIG. 26.—Ditto, internal cast of brachial valve. Lower Cornbrash, Rushden, Northants. [B. 84530.]

FIG. 27.—Ditto, internal cast of pedicle valve. Lower Cornbrash, Rushden, Northants. [B. 84523.]

FIG. 28, *a.*—*Lobothyris punctata* (J. SOWERBY). Lectotype. Dorsal view. Middle Lias, Hornton, Oxon. [B. 61522.]

FIG. 28, *b.*—Ditto, lateral view of same specimen.

FIG. 28, *c.*—Ditto, anterior view of same specimen.

FIG. 29.—Ditto, internal cast of brachial valve showing adductor muscle-scars. Middle Lias, Tilton, Leicestershire. [B. 84524.]

FIG. 30, *a.*—*Plectoidothyris polyplecta* (S. S. BUCKMAN). Topotype. Anterior view. Inferior Oolite, Oolite Marl. Railway cutting, Notgrove Stn., Glos. [B. 47184.]

FIG. 30, *b.*—Ditto, lateral view of same specimen.

FIG. 30, *c.*—Ditto, dorsal view of same specimen.

FIG. 31.—Ditto, internal cast of brachial valve showing adductor muscle-scars. Same horizon and locality. [B. 84528.]

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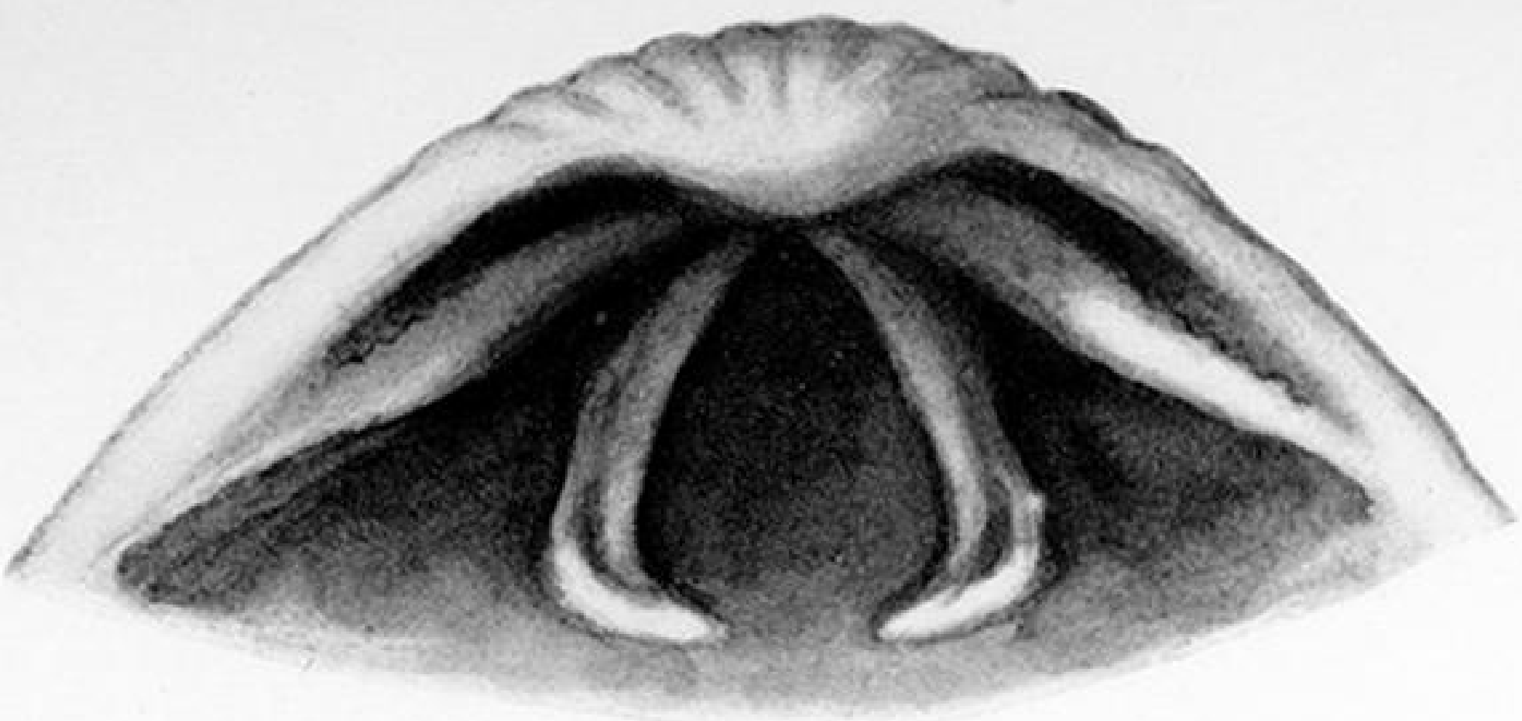

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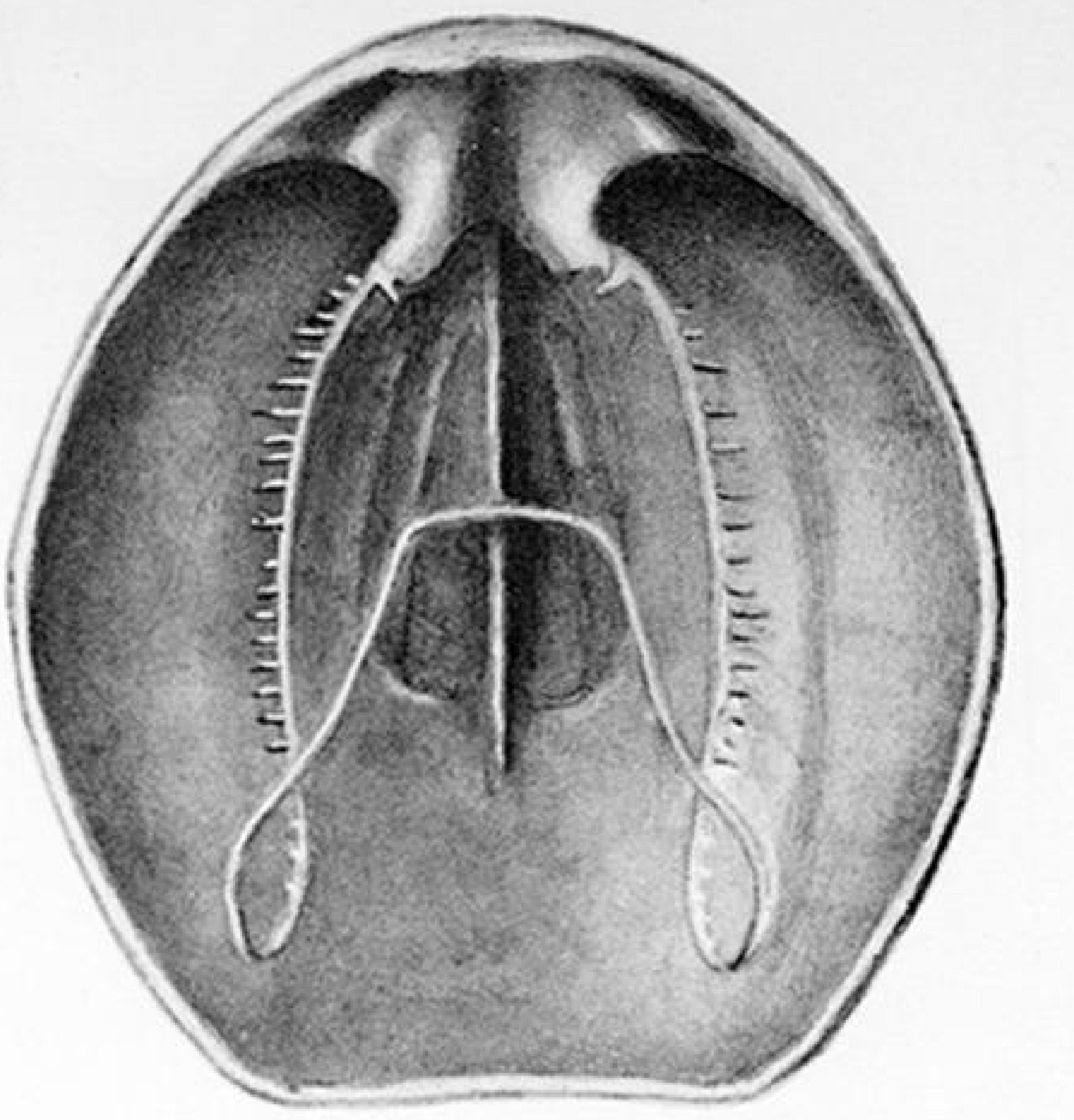

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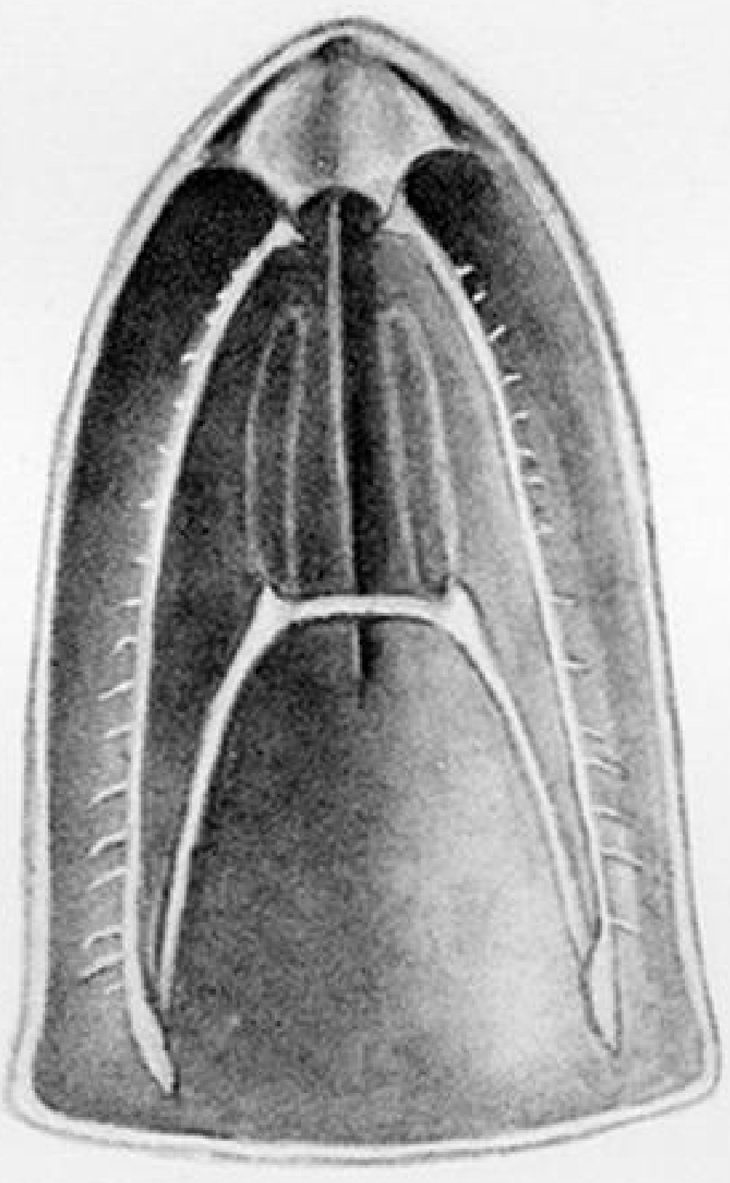

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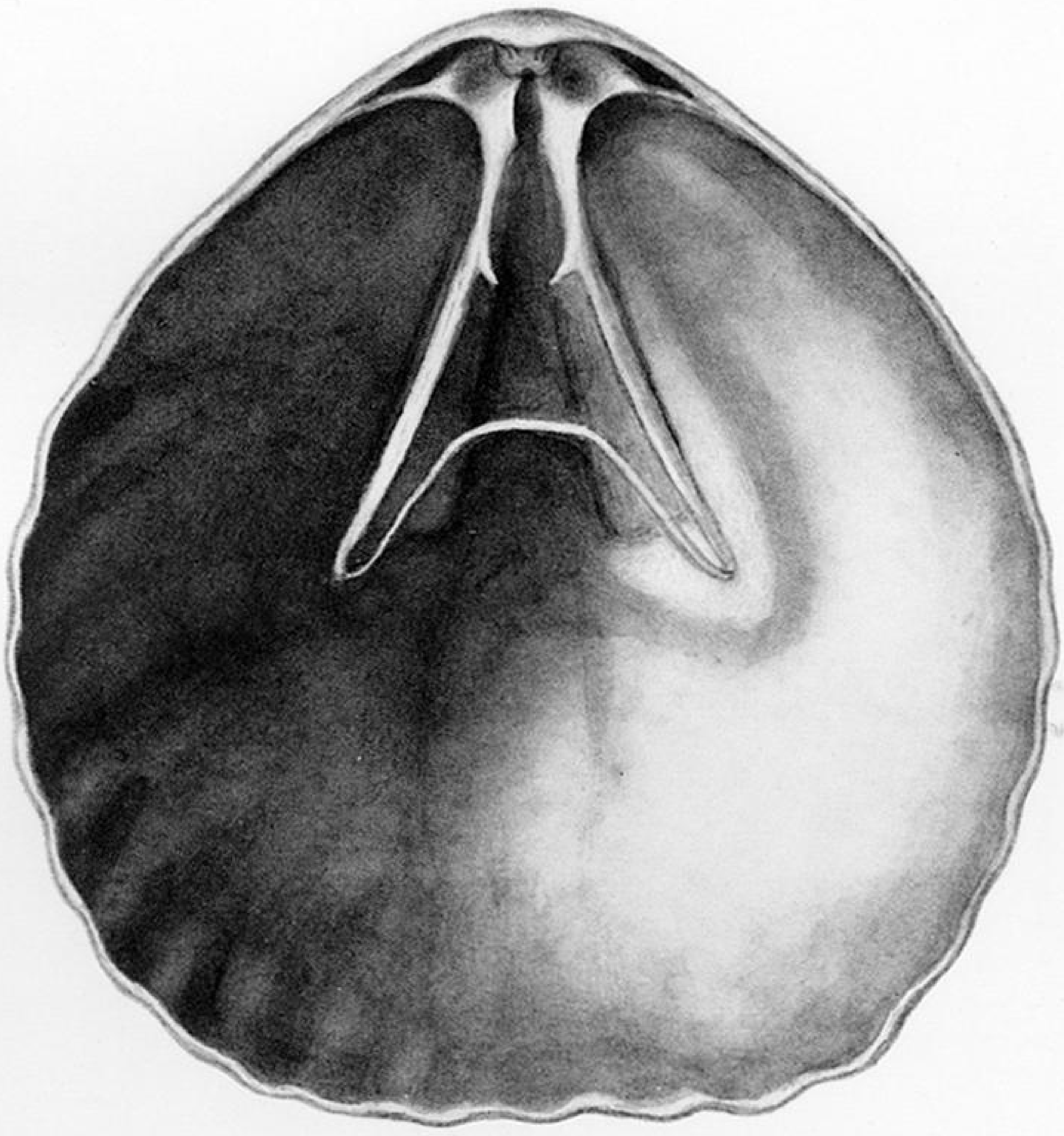

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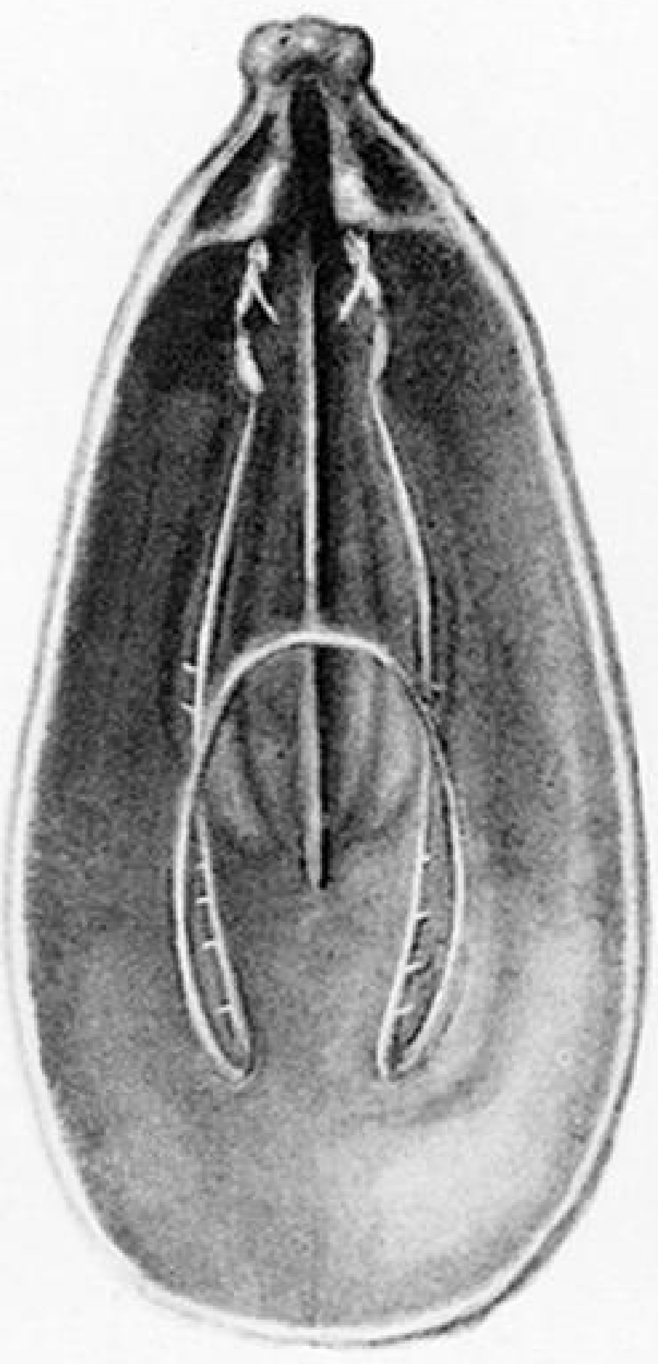

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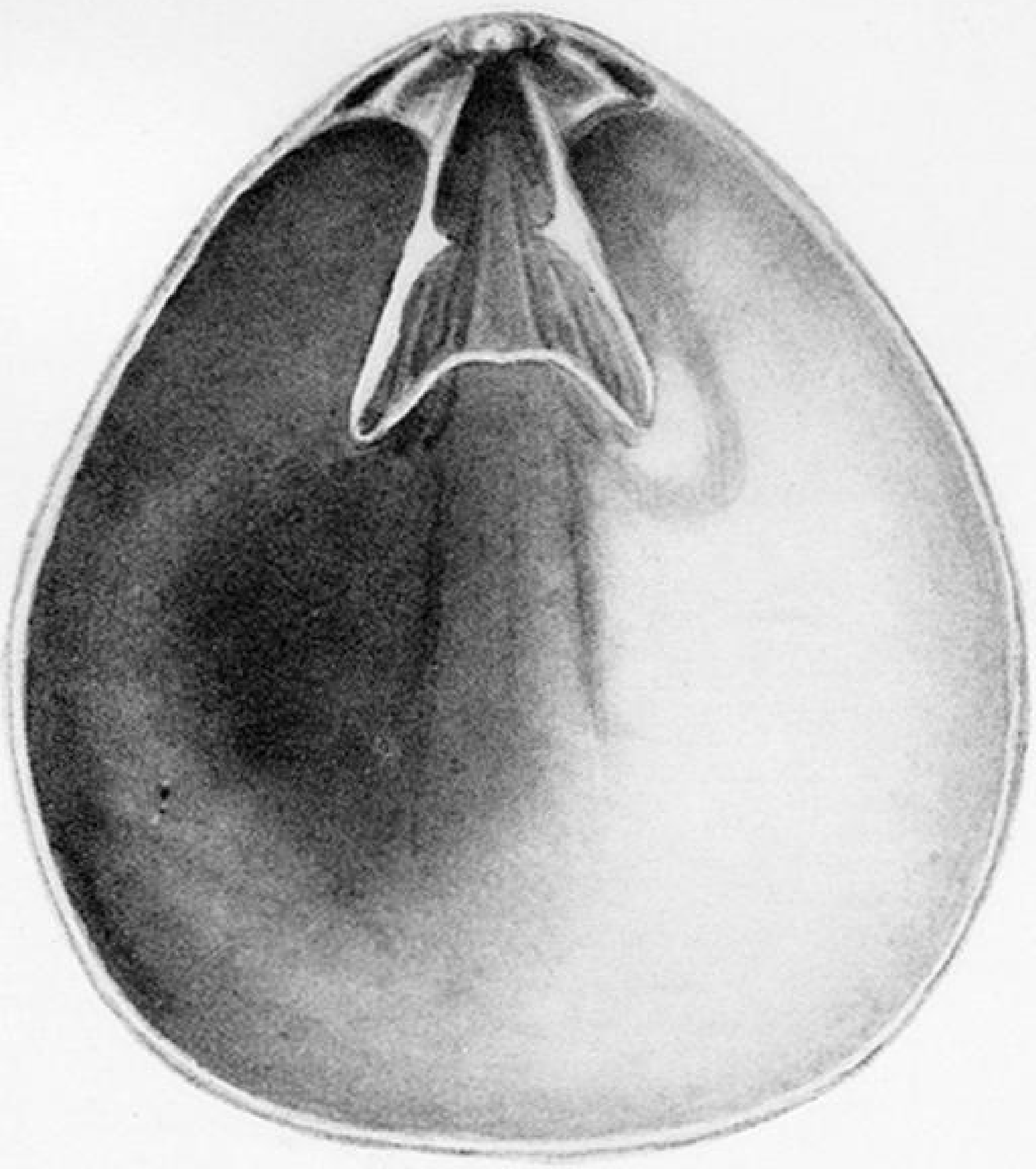

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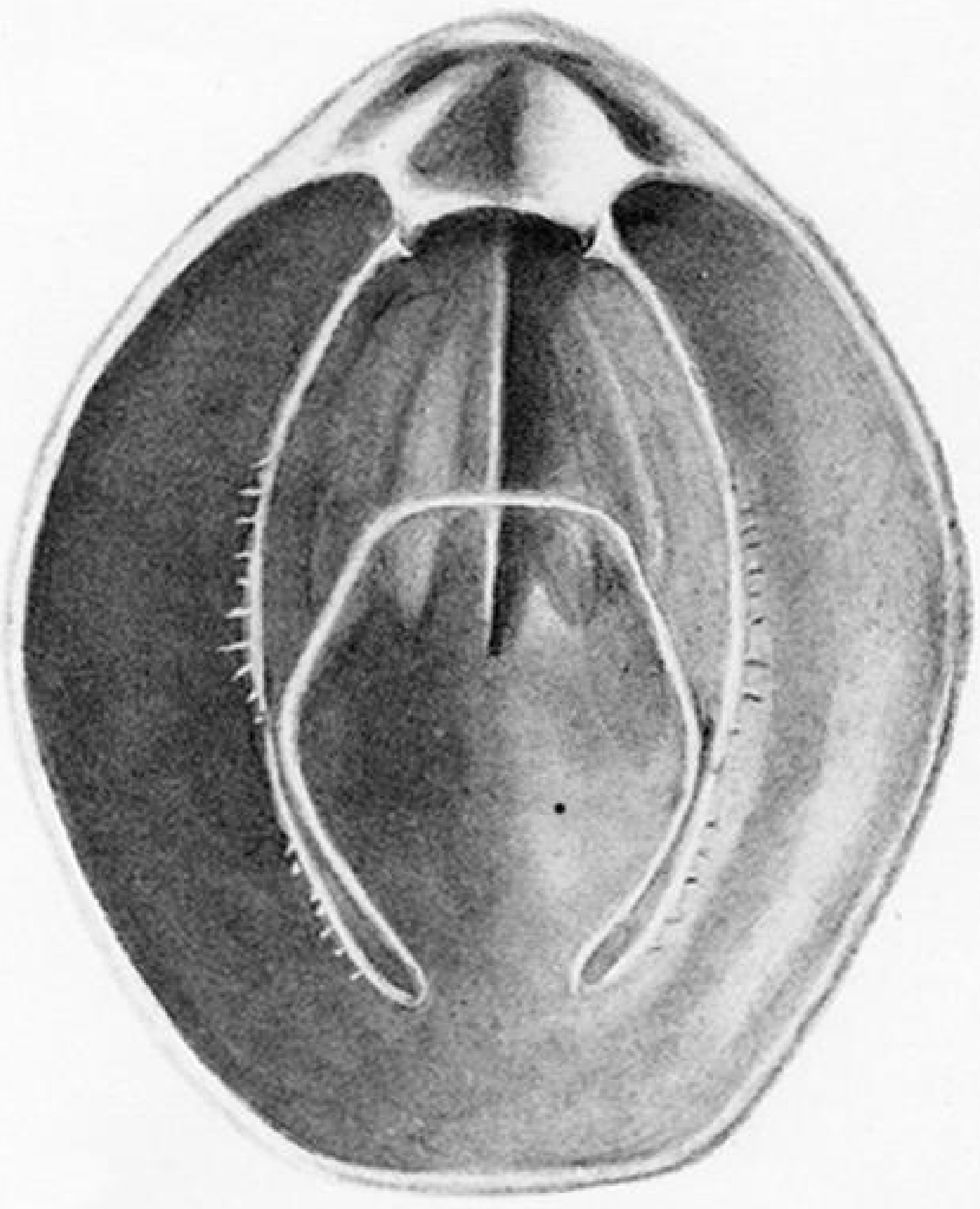

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PLATE 63.

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FIG. 33.—*Obovothyris magnobovata* S. S. BUCKMAN. Reconstruction of interior of brachial valve from dissected specimens and transverse sections showing the fused hinge-plates and septalium, hinge-sockets, inner and outer socket-ridges, median septum and complete loop with spines on the descending branches. × 2½.

FIG. 34.—*Digonella digona* (J. SOWERBY). Reconstruction of interior of brachial valve from dissected specimens and transverse sections showing the fused hinge-plates, shallow septalium, hinge-sockets, socket-ridges, and complete loop with long spines on the descending branches. × 2½.

FIG. 35.—*Plectoidothyris polyplecta* (S. S. BUCKMAN). Reconstruction of interior of brachial valve from dissected specimens and transverse sections showing the incurved umbo, cardinal process, divided hinge-plates and long loop. × 2½.

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FIG. 37.—*Lobothyris punctata* (J. SOWERBY). Reconstruction of interior of brachial valve from dissected specimens and transverse sections showing the small cardinal process, divided hinge-plates, and short loop. × 2½.

FIG. 38.—*Ornithella ornithocephala* (J. SOWERBY). Reconstruction of interior of brachial valve from a dissected specimen showing slightly incurved umbo, fused hinge-plates, deep septalium, hinge sockets, hinge-plates, median septum and complete loop with short spines on descending branches. × 2½.

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