

SILURIAN LEPTAENIDS (BRACHIOPODA)

by F. B. KELLY

ABSTRACT. Following the work of Poulsen (1943) the paper discusses the standing of *Leptaena rhomboidalis* (Wahlenberg 1821) and *Leptaena depressa* (James Sowerby 1825). The two species are redescribed and neotypes selected. Two new species of *Leptaena* are described: *Leptaena poulseni* and *Leptaena arberae* from the Wenlock Limestone of England. A new genus of leptaenid brachiopods is erected and the type species, *Ludfordina pixis* sp. nov., is described. This species is from the Lower Ludlow of Shropshire, England.

THE authorship and identity of *Leptaena rhomboidalis* have been subjects of considerable uncertainty. In order to make possible the description of related forms, it was necessary to determine the nature of the species. This paper examines and supports the argument propounded by Poulsen (1943).

(a) *Leptaena rhomboidalis* (Wahlenberg 1821). The name attributed to Wilckens (1769) is invalid, since it fails to conform to the binary convention and the species must, therefore, be ascribed to Wahlenberg, as *Anomites rhomboidalis* Wahlenberg 1821. In describing his species, Wahlenberg cited figures from two authors: Wilckens 1769 and Hüpsch 1781. Wilckens's specimens were collected near Stargardt, in Pomerania, probably from Gotlandian erratics, which are not uncommon in that district (Poulsen 1943, p. 20). Hüpsch (1781) described a species from the Eifel, which may be of Devonian age.

The author has not been able satisfactorily to recognize Hüpsch's species either from description or figures and excludes it from the present restricted description, which is based upon Wilckens's figures. It is suggested that their comparison with those of Poulsen (1943) fig. 7 and with Plate 98, fig. 1 of the present paper leaves no reasonable doubt regarding the identity of the species Wilckens illustrated.

James Sowerby (1825) described a generally similar species from Dudley, England, under the name *Producta depressa* and such specimens were, until the publication of Davidson's (1871) monograph, variously described as *Producta*, *Leptaena*, or *Strophomena depressa*. Davidson regarded Sowerby's species as synonymous with *Anomites rhomboidalis* Wahlenberg, which he attributed to Wilckens, and the name *Leptaena depressa* fell into disuse. Many specimens in our older collections are, however, still so labelled.

Hisinger (1827, p. 333) published, without description, the name *Terebratula rugosa*, which remained *nomen nudum* until Dalman (1828) adopted it. The *Terebratula rhomboidalis* preceding it in Hisinger's list is not a *Leptaena* (Dalman 1827, p. 146), although it may be surmised that its presence may have influenced Dalman to adopt the trivial name *rugosa* in place of the older *rhomboidalis* in naming his species. He was, at this time, publishing his new genus *Leptaena*, under which he described, with figures, *Leptaena rugosa* and *Leptaena depressa* (Sowerby). Under each of these he gave *Anomites rhomboidalis* Wahlenberg in his synonymy, under the former as 'cum *L. depressa* commixta' and under the latter as 'cum *L. rugosa* commixta'. It may then be argued that he regarded *Leptaena rhomboidalis* (Wahlenberg) as composite and partly referable to *Leptaena*

depressa (Sowerby). By inference he referred the remainder to *L. rugosa*, a newer name which would then, in modern practice, become a junior synonym of *L. rhomboidalis* (Wahlenberg) under Article 31. King (1846) selected *L. rugosa* Dalman as the type species of *Leptaena* Dalman, but it has not frequently been used, due to doubt as to its status and identity.

Spjeldnæs (1957) rediscovered Dalman's specimens of *L. rugosa*, selected a lectotype and redescribed the species. It is clearly not conspecific with *L. rhomboidalis* (Wahlenberg) as here restricted, which is a Silurian species; *L. rugosa* Dalman is from the Ordovician.

(b) *Leptaena depressa* (James Sowerby 1825). Sowerby, in describing his *Producta depressa*, presented a composite figure (pl. 459, fig. 3) showing two exteriors, one ventral and one dorsal interior. He said: '—they are all taken from two masses of Dudley limestone, but are grouped together so as to occupy less space, and the essential parts are made rather conspicuous.' He described his species as follows: 'Nearly semi-circular, depressed, corrugated, longitudinally striated: upper portion convex near the beak, concave near the margin; front abruptly descending.'

The two upper specimens in his figure, the exteriors, are undoubtedly referable to *Leptaena*, as is probably the lower right-hand one, a dorsal interior. The lower left-hand specimen, a ventral interior, shows a denticulate hinge-line and is probably, therefore, a *Strophonella* (?*funiculata*) since the trail is ventrally directed.

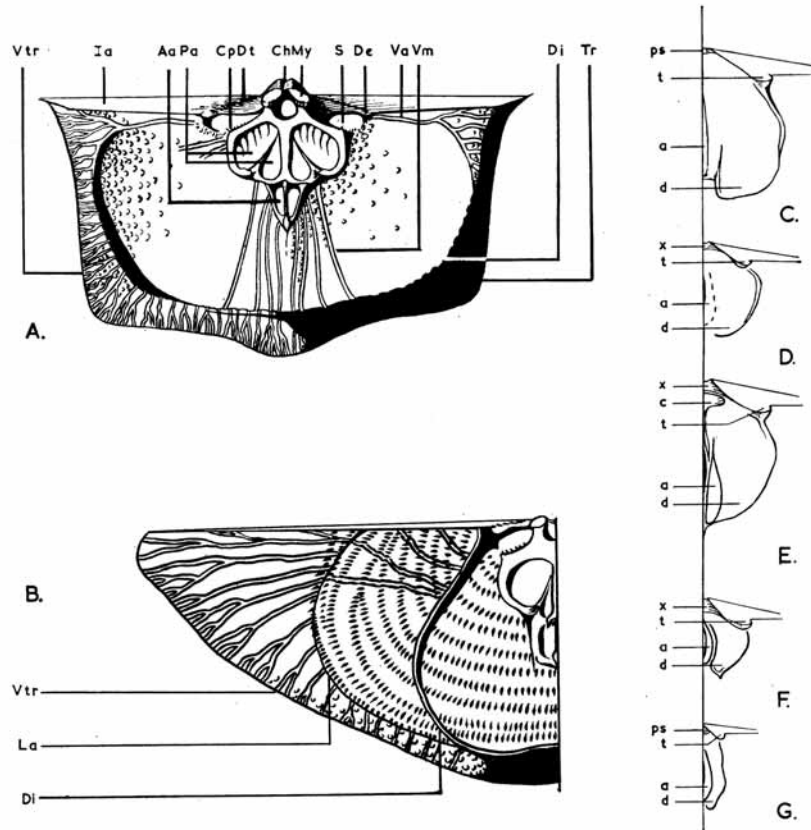
In both *Leptaena* and *Strophonella* the dorsal valve is initially concave and the ventral valve convex. Hence, Sowerby's 'upper portion convex near the beak' can only apply in these genera, to the ventral valve. 'Concave near the margin' applies to some species of *Leptaena* and all species of *Strophonella*. He then, however, says 'front abruptly descending' and, since it has been shown that he is describing a ventral valve, he can only mean that the front, i.e. the trail, is deflected dorsally. But the lower left-hand figure shows a trail unmistakably deflected ventrally and is therefore to be excluded as disagreeing with his description. The remaining figures and the description agree closely with a species of *Leptaena* common in the Dudley (Wenlock) limestone, Sowerby's type-locality. The depressed region inside the periphery of the ventral exterior is characteristic and there is general agreement in size. The original specimens figured by Sowerby are no longer to be found, but several specimens identified by him are in the possession of the British Museum (Natural History). From these a neotype has been chosen (B60949) and is figured here.

Descriptions of *Leptaena rhomboidalis* (Wahlenberg 1821) and *Leptaena depressa* (James Sowerby 1825) are offered in the present paper to amplify those of their authors and to describe their internal characters.

Terminology. Text-fig. 1 illustrates the terminology used in this paper; one new term is introduced. At the line of geniculation in *Leptaena* a ridge of secondary shell-substance is developed, which surrounds and defines the visceral disc. The ridge is here called the *apophragm* (*apo*—away, *phragm* from *phrassain*—to fence). It is usually present only in the dorsal valve, but may be developed in the ventral valve of alate species such as *Leptaena poulsenii* sp. nov.

Williams and Rowell (1965, fig. 74) have applied the term diaphragm to this structure, but by definition (*ibid.*, p. 144) this seems inapt. Diaphragm has been variously used by

Girty (1910), Muir-Wood (1928), and Ulrich and Cooper (1938). As defined by the two former authors it is, strictly, to be applied to *Productus* and *Diaphragmus*, where it is a



TEXT-FIG. 1. A. *Leptaena depressa* (J. Sowerby). Diagrammatic dorsal interior ($\times 2$); B. *Leptaena poulseni* sp. nov. Diagrammatic dorsal interior ($\times 2$). Vtr. Vasculature on trail. Ia. Interarea. Aa. 'Anterior scars'. Pa. Adductor scars. Cp. Socket Plates. Dt. Track of denticle. Ch. Chilidium. My. Myophore. S. Socket. De. Denticle. Va. Vascula cruralia. Vm. Vascula media and myaria. Di. Apophragm. Tr. Trail. La. Lamellar wall (one young adult only); C-G Delthyrial and muscular arrangement in ventral valves of: C. *Leptaena depressa* (James Sowerby). D. *Leptaena rhomboidalis* (Wahlenberg). E. *Leptaena poulseni* sp. nov. F. *Leptaena arberae* sp. nov. G. *Ludfordina pixis* gen. et sp. nov. ps. Pedicle callist. t. Tooth. a. Adductor scar. d. Divaricator scar. x. Pseudodeltidium. c. Pedicle collar.

thin, crescentic plate, tangential to the visceral disc, and may be costate. The apophragm in *Leptaena* is normal to the visceral disc, is unornamented, and is not crescentic in shape. As used by Ulrich and Cooper (1938) the diaphragm is exemplified in *Leptellina*,

where it is a more or less semi-circular or bilobate visceral disc, elevated above the anterior part of the valve. Williams and Rowell (1965) have redefined this as a lophophore platform.

The erection of the apophragm commences after geniculation and apparently continues throughout the life of the brachiopod. It may thus be said progressively to limit the degree of closure of the conjoint valves in response to increasing spatial requirements of the developing visceral and mantle cavities.

In describing the articulatory structure of the dorsal valve of *Leptaena* the author has preferred to follow the terminology of Spjeldnæs (1957) in using the term socket-plate, rather than that of Williams and Rowell (1965), who used the term inner socket ridge. The latter is defined as: 'Ridge of secondary shell commonly overhanging dental socket and forming its inner or anterior margin.'

In *Leptaena* the socket is formed by an elongate plate originating beneath the chilidium. The plate is concave in transverse section and forms both the floor of the socket and its inner margin. It is crenulated and is supported by lateral ridges from the notothyrial platform which form the posterior boundaries of the muscle scars.

Dorsal muscle scars in Leptaena. The central part of the mature dorsal valve of *Leptaena* bears a quadripartite impression symmetrically divided by the median septum, thus forming a pair of posterior and a pair of anterior scars. The posterior scars are sub-circular in outline and in well-preserved specimens are themselves seen to be bilobate. The anterior scars are almost triangular and terminate about the end of the median septum, which is here elevated to a delicate point. They are laterally bounded by a varying system of parallel and converging ridges. The bilobation of the posterior scars indicates that they consist of a pair of postero-lateral and a pair of antero-mesial adductor scars. The function of the anterior scars is not, however, clear.

The anterior scars resemble muscle scars, but their development as, for example, in *L. depressa*, makes such a function improbable. In the young adult shell the posterior boundary of the adductors is defined by an anchor-shaped ridge immediately in front of the cardinalia, whilst the anterior extension of the scars is concealed by the internal repetition of the external rugae and costellae. The median septum is indicated by the slightly greater development of one costella, whilst two lateral costellae are discernibly emphasized and later become the lateral bounds of the anterior scars. The mature dorsal shell shows these scars as a pair of depressions in a platform of secondary shell. The platform necessarily narrows as its height increases and in gerontic valves the depressions are filled, leaving only the crest of the median septum visible, whilst the platform falls abruptly away to the anterior floor of the valve. This may suggest the atrophy of some function at present unknown. The elevation of these scars into a platform must imply folding of the dorsal outer epithelium, which would have the effect of dividing the mantle cavity into two parts. In the ventral valve there is frequently selective deposition of shell material antero-laterally to the divaricator scars and indicating the presence of dorsally directed spirolophes. It is inferred from the position of these that the anterior body-wall and the mouth were located over the anterior scars.

Mature and gerontic specimens of *L. depressa* and *L. poulsoni* are shown, Plate 98, figs. 7, 11, 12, and 9.

Vasculature in Leptaena. The majority of specimens examined for the purpose of the paper showed little indication of the origin and course of the main vasculature. Traces of the vascula media and vascula myaria are not uncommon. Occasionally the vascula cruralia are detectable and appear to curve forward from the lateral parts of the hinge-line, thus suggesting the commencement of the arcuate form necessary to the accepted saccate pattern. Complete vascula arcuata have not, however, been seen. The figured dorsal valve of *L. depressa*, Plate 98, fig. 7 shows a number of vascula originating immediately anterior to the sockets and from the postero-lateral adductor scars whence they partially cross the disc. Specimens of *L. poulsenii* suggest that these vascula genitalia may reach the apophragm. In *L. arberae* the vascula myaria, when seen, appear to reach and surmount the apophragm and no suggestion of vascula arcuata has been observed.

From this composite and somewhat tentative evidence it seems probable that the dorsal valve in *Leptaena* departs from the accepted saccate pattern and may in fact be lemniscate.

The figured dorsal valve of *L. poulsenii*, Plate 98, fig. 12, has an almost complete lateral trail which carries good impressions of the vascula terminalia. These have reached a stage when they may reasonably be equated with the external costellation.

Specimens numbered BU are deposited in the Department of Geology, Birmingham University; those labelled BMNH are in the British Museum (Natural History).

SYSTEMATIC DESCRIPTIONS

Superfamily STROPHOMENACEA King 1846
Family LEPTAENIDAE Hall and Clarke 1894
Genus LEPTAENA Dalman 1828

Leptaena rhomboidalis (Wahlenberg 1821)

Plate 98, figs. 1-3

- 1821 *Anomites rhomboidalis* Wahlenberg, p. 65.
non 1828 *Leptaena rugosa* Dalman, p. 106, fig. 1.
non 1871 *Strophomena rhomboidalis* (Wilckens); Davidson, pl. 39, figs. 1-21.
1943 *Leptaena rhomboidalis* (Wilckens); Poulsen, pp. 19-21, fig. 7a-d.
non 1965 *Leptaena rhomboidalis* (Wilckens); Williams and Rowell, fig. 252, 5d-e.

Diagnosis. Semi-oval to rhomboid, with fine radial costellae and very deeply incised rugae. Foramen large, truncating the pseudodeltidium which covers the entire delthyrium. Ventral muscle scar sub-pentagonal; adductors poorly defined, not enclosed by diductors.

Neotype. Here selected, BU 878. *Paratypes.* BU 879, BU880.

Locality and horizon. Upper Visby Marl, Visby, Gotland. I am informed by Professor Regnéll, now of Lund, that there is frequently some doubt regarding the provenance of many specimens bearing the name *L. rhomboidalis*, the locality Visby often being synonymous with Gotland. The possible horizons seem to be Upper Valentinian-Lower Wenlock, i.e. Upper Visby Marl or Hogklint group. The species is thus from horizons lower than those providing the British species described below, which are from the Wenlock Limestone and lower Ludlow.

Description. Disc transversely semi-oval to rhomboid, its greatest width, a little anterior to the hinge-line, about 24 mm., but may reach 37 mm. in old specimens. Trail geniculated more or less abruptly, curving dorsally, laterally produced into ears. Trail forms half the total length, which is 24–27 mm.

Radial ornament of fine costellae, increasing by intercalation and bifurcation. Concentric rugae 8–12, deeply incised and widely spaced. Foramen penetrates the beak, truncating the pseudodeltidium which covers the delthyrium. Chilidium high, grooved. Contour of ventral valve convex about the beak, becoming flatter towards the edge of the disc. Contour of dorsal valve follows generally that of the ventral and is gently concave.

Dorsal interior. Apophragm outlines an almost completely oval disc, truncated towards the middle of the hinge-line, and is relatively low and sharp crested. Cardinal process bifid, myophores narrow and slender, shafts slightly diverging. Socket-plates small, crenulated; opposite each one is a denticle, carried on the edge of the interarea. Adductor scars sub-circular, faintly bilobate, bounded by ridges produced from the notothyrial platform. Anterior scars not strongly defined, about half the width of the adductor scars. Median septum extending to two-thirds of the length of the disc, dividing anterior scars which are laterally bounded by fine ridges.

Ventral interior. Diductor scars sub-pentagonal, bounded by a strong ridge; adductor scars poorly defined, not enclosed by diductors. Teeth small, supported by receding dental lamellae.

Comparisons. This species is most easily recognized by its strongly rugose exterior, which no other species has so well-developed. In radial ornament it is nearly approached by *L. poulsoni* sp. nov., which has a similar development of foramen and pseudodeltidium. The latter species is, however, so strongly alate that no confusion of entire specimens is possible. As in all the species here described, the ventral muscle scars are distinguishing features. They are shown in text-fig. 1 c–g. *L. rhomboidalis* (Wahlenberg) is usually slightly larger than *L. arberae* sp. nov. which also has a similar foramen and pseudodeltidium; the latter is less rugose and its radial ornament is not thread-like.

Leptaena depressa (James Sowerby 1825)

Plate 98, figs. 4–9

1825 *Producta depressa* James Sowerby, p. 86, pl. 459, fig. 3.

1871 *Strophomena rhomboidalis* (Wilckens); Davidson, pl. 39, figs. 3, 5, 12, 14 only.

Diagnosis. Semi-circular to quadrate or rhomboid, having radial costellae with small interspaces and rugae not coarsely developed. Foramen small, often cicatrized; pseudodeltidium small covering only umbonal part of delthyrium. Ventral valve depressed immediately inside line of geniculation. Ventral muscle scar large, widely cordate. Adductors anteriorly elevated, shorter than diductors.

Neotype. Here selected, BMNH B60649. *Paratypes.* BU 882, BU 881, BMNH B43364.

Locality and horizon. Wenlock Limestone, Dudley, England.

Description. Outline semi-circular to quadrate or rhomboid, widest at the hinge-line, about 40 mm. Total length approximately equal to the width, trail forming half the length. Small acute ears developed at the cardinal extremities, from which the trail is abruptly geniculated all round. Rugae relatively fine, 13–18 in number; radial costellae closely spaced. Ventral valve convex about the beak but typically depressed immediately before the line of geniculation. A small foramen may be present but is usually sealed internally or cicatrized. Pseudodeltidium small, chilidium high.

Dorsal interior. Disc outlined by a strong apophragm, highest anteriorly, curving inwards posteriorly to the hinge-line. Cardinal process bifid, myophores and shafts subparallel in young adults, but divergent in gerontic specimens. Socket-plates crenulated. Outer wall of each socket formed by inner edge of interarea from which a denticle is produced.

Adductor scars bilobate, outlined by sub-circular ridges from the notothyrial platform. Median septum extends for about three-quarters of the length of the disc, where it is pointed and where the anterior scars terminate. Latter about one third as wide as the adductor scars, bounded by lateral ridges meeting at an acute angle at the termination of the median septum.

Ventral interior. Muscle scar cordate, diductors wide. Adductor scars elevated, shorter than the diductors, which do not enclose them. Teeth strong, crenulated except in old specimens and supported by dental lamellae which are produced forwards and are continuous with the ridges outlining the muscle scars. A transverse plate is present in the apex of the delthyrial cavity. A low ridge is developed round the inside face of the trail, marking the line of contact of the articulated valves. On specimens having a quadrate or rhomboid outline the trail frequently shows three lobes.

EXPLANATION OF PLATE 98

- Figs. 1–3. *Leptaena rhomboidalis* (Wahlenberg). Upper Visby Marl or Hogkint Group, Gotland. 1, Ventral exterior of neotype ($\times 2$), BU 878. 2, Interior of ventral valve ($\times 2$), BU 880. Incompletely cleaned due to crystallization in the floor of the valve. 3, Interior of a large dorsal valve ($\times 1$), BU 879.
- Figs. 4–9. *Leptaena depressa* (James Sowerby). 4, 5, Ventral and dorsal exteriors of neotype ($\times 1$), BMNH B60949. Wenlock Limestone, Dudley, England. 6, Ventral exterior of topotype ($\times 1$), BU 881. Wenlock Limestone, The Wren's Nest, Dudley, England. 7, Dorsal interior of topotype ($\times 1$), BU 882. Locality and horizon as fig. 6. 8, Ventral interior, showing trilobation of trail. Topotype ($\times 1$), BMNH B43364. Wenlock Limestone, Dudley, England. 9, Part of dorsal interior, showing gerontic development of scars ($\times 2$), BU 877. Locality and horizon as fig. 6.
- Figs. 10–13. *Leptaena poulsenii* sp. nov. 10, Ventral exterior of an almost complete specimen. The interrupted hinge-line and irregular rugae show that the specimen suffered injury from which it recovered ($\times 1$), BU 890. Wenlock Limestone, The Wren's Nest, Dudley, England. 11, Dorsal interior of young adult ($\times 1$), BMNH B43361. Wenlock Limestone, Dudley, England. 12, Dorsal interior of holotype ($\times 1$), BU 889. Wenlock Limestone, The Wren's Nest, Dudley, England. 13, Fragmentary ventral interior showing pedicle collar ($\times 2$), BU 891. Locality and horizon as fig. 12.
- Figs. 14–16. *Leptaena arberae* sp. nov. 14, Ventral exterior of holotype ($\times 2$), BU 887. Locality and horizon as fig. 12. 15, Dorsal interior ($\times 2$), BU 886. Locality and horizon as fig. 12. 16, Ventral interior ($\times 2$), BU 888. Locality and horizon as fig. 12.
- Fig. 17–19. *Ludfordina paxis* gen. et sp. nov. Lower Ludlow Mudstones, Upper Millichope, Shropshire, England. 17, Ventral exterior of holotype ($\times 2$), BU 883. 18, Ventral interior (mould) ($\times 2$), BU 884. 19, Dorsal interior (mould) ($\times 2$), BU 885.
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Comparisons. *L. depressa* differs from the other species described here in the poor development of the foramen and pseudodeltidium. In radial ornament it is most closely approached by *L. arberae* sp. nov. which is, however, much smaller and has a large pseudodeltidium and an open foramen. *L. 'rhomboidalis'* var. *eta* Reed (1917, pl. 13, figs. 5-7) shows a depression of the ventral exterior inside the line of geniculation. The latter lacks the abrupt geniculation of *L. depressa* and seems never to develop the quadrate or rhomboid shape common in the latter. The ventral musculature of *L. depressa* is most closely approached by *L. 'rhomboidalis'* var. *gamma* Reed (1917, pl. 12, figs. 2-3), but the latter is more strongly rugose. *L. rugosa* Dalman differs in its flabellate ventral muscle scar and greatly depressed region of the ventral exterior.

Discussion. *L. depressa* is the commonest of the species of *Leptaena* found at Dudley, although in some exposures it may be outnumbered by *L. poulsenii* sp. nov. or *L. arberae* sp. nov. The species, or its varieties, extends throughout the Wenlock and into the Leintwardinian. The above description is applied to specimens from the horizon and locality specified, since Sowerby's specimens were collected from these beds.

A single specimen examined, BU 892, shows slightly aberrant articulation in that it has developed a series of minor denticles between the antero-lateral edge of the chilidium and the normal denticle developed at the lateral edge of the socket. Professor Spjeldnæs informs the writer (*in lit.*) that he has found such a development not uncommon in gerontic valves. Since, however, this specimen shows a growth-track preceding each of the minor denticles, they must clearly have been present at all stages of growth. Reed (1917, p. 873) claimed to have seen minute denticles along the entire hinge-line in *L. zeta* Lamont 1947. The writer has not observed this in any of the species described in the present paper.

Leptaena poulsenii sp. nov.

Plate 98, figs. 10-13

1871 *Strophomena rhomboidalis* (Wilckens); Davidson, pl. 39, figs. 1, 10, 11, 15 only.

Diagnosis. Transversely semi-oval in outline, having highly alate lateral extensions. Ornament of thread-like radial costellae and coarse concentric rugae. Foramen large, open, pseudodeltidium large, covering the entire delthyrium. Ventral muscle scar sub-circular, adductors and diductors of equal length.

Holotype. BU 889. *Paratypes.* BU 890, BU 891, BMNH B43361.

Locality and horizon. Wenlock Limestone, The Wren's Nest, Dudley, England.

Description. Outline transversely semi-oval, about 70 mm. wide at the hinge-line, the widest part of the shell, and about 40 mm. long at the median line, the trail forming about half the total length. Trail curved in front, geniculated through a right angle at the middle, angle of geniculation decreasing to zero at the cardinal angles. The disc forms the middle portion of the shell, about 30 mm. wide, 20 mm. long. Rugae number 13-18, extending on to the ears. Outer rugae directed towards the cardinal angles, those nearer the beak converging or intersecting the hinge-line at a right angle. Costellae fine, interspaces relatively wide with closely spaced growth-lines. Costellae increase by

intercalation. Foramen large, truncating the pseudodeltidium. The latter covers the entire delthyrium.

Ventral valve convex about the beak, flattening out laterally and towards the front. Dorsal valve concave.

Dorsal interior. Disc outlined by a thin, relatively high apophragm; widest towards the front, in shape oval to scutiform. Myophores and shafts of the cardinal process sub-parallel to divergent. Socket-plates crenulated. Posterior edge of socket formed by interarea, carrying a denticle opposite each socket-plate.

Adductor scars sub-circular, bilobate, outlined by ridges from the notothyrial platform. Low median septum extending a little over half the length of the disc, where it is pointed, defining the anterior extension of the anterior scars. The latter defined laterally by ridges from which offshoots converge at the termination of the septum. Anterior scars about half as wide as the adductor scars.

Ventral interior. Ventral disc similar in shape to dorsal, laterally defined by an apophragm. Teeth strong, supported by lamellae which continue forward with the ridges bounding the diductor scars. In older specimens secondary shell unites the pseudodeltidium, dental lamellae, and the floor of the valve, forming a pedicle-collar with the foramen at its apex. Diductors semicircular, a low median ridge carrying the adductor scars. Both pairs of muscles are of equal length. Inner face of teeth crenulated, except in old specimens.

Comparisons. In ornament, rugosity, and deltidial development *L. poulsoni* resembles *L. rhomboidalis* with which it is compared above. It is differentiated from others described here by its extreme alation and its ventral musculature. A similar form from the early Devonian (Birdson Shales, Tennessee) of the United States is figured by Cooper (1944, pl. 132, fig. 16) as *L. rhomboidalis*. The American species appears to be closely related to *L. poulsoni*.

Discussion. *Leptaena poulsoni* was figured by Davidson (1871), with other species, as *L. rhomboidalis*. Plate 39, fig. 15 was incorrect in that it showed a ventral interior of *L. poulsoni* having the muscle scars of *L. depressa*, i.e. having adductors shorter than diductors. The specimen is BMNH B8340 and has adductors and diductors of equal length. The pedicle-collar developed in the specimen figured in this paper is not, however, present in Davidson's specimen. His figure shows the ventral apophragm correctly.

Leptaena arberae sp. nov.

Plate 98, figs. 14–16

Diagnosis. Small *Leptaena* of sub-quadrate to ovate outline having a variable degree of alation, rugose, costellate. Foramen open, pseudodeltidium well-developed, covering the entire delthyrium. Ventral adductors shorter than diductors, scar semicircular.

Holotype. BU 397. *Paratypes.* BU 396, BU 398.

Locality and horizon. Wenlock Limestone, The Wren's Nest, Dudley, England.

Description. Disc sub-quadrate to ovate; ears small and acute in young specimens, well developed in older ones. Shell widest at the hinge-line, 25–40 mm. according to age.

Length of disc at median line about 10 mm. and the total length, including the trail, about 18 mm. Shell geniculated through 90° and at the median point of geniculation a slight lobation may be discernible, not extending to the trail. Foramen, chilidium, and pseudodeltidium well developed. Radial costellae closely spaced, increasing by bifurcation and intercalation. Immediately preceding bifurcation they tend to thicken and become flattened. Rugae never coarsely developed, becoming progressively finer from the line of geniculation to the beak. Outer ones diverging sharply towards hinge-line, inner ones parallel or tending to converge.

Dorsal interior. Disc transversely oval, defined by strong apophragm and truncated posteriorly by the hinge-line. The apophragm often shows a slight ventrally directed lobe at the middle line. Myophores and shafts of cardinal process sub-parallel. Socket-plates crenulated, posterior edge of socket formed by interarea and carrying a denticle opposite each socket-plate. Adductor scars defined by sub-circular ridges. Low median septum extends to about three-quarters of the length of the disc. Anterior scars triangular and pustulate. Young specimens show them bounded by thin, parallel or divergent ridges.

Ventral interior. Teeth fairly robust, crenulated, supported by receding dental lamellae. Adductor scars not prominent, separated by a thin ridge. Diductors, the longer of the two sets of scars, bounded laterally by curved ridges which give a pointed outline to each scar at its anterior extremity.

Comparisons. *L. arberae* is distinguished from *L. depressa* and from *L. poulsenii* by its smaller size and thicker costellae. The interspaces between costellae are much reduced and the costellae themselves tend to flatten and become thicker preceding bifurcation. The ventral muscle scars are broadly semi-circular, as in *L. poulsenii*, but the anterior production of each diductor scar into a point and the recession of the dental lamellae in *L. arberae* distinguish the two species. The dental lamellae, however, resemble those of *L. rhomboidalis*, which it also approaches in size and foraminal development. Their external ornament is, however, different and they appear at different horizons.

Genus LUDFORDINA gen. nov.

Type species. *Ludfordina pixis* sp. nov.

Diagnosis. Small leptaenid brachiopods having a more or less pronounced antero-median sulcus. Both valves sharply geniculate dorsally; radial ornament and rugae obsolescent. Ventral muscle-scars elongate, dorsal ones not strongly defined.

Range. As presently known the genus ranges from the Middle Ordovician (Norway) to the Ludlovian (England).

Discussion. *Ludfordina* embraces two species, *Ludfordina pixis* sp. nov. from the Ludlovian and *Leptaena minuta* Kiaer from the Middle Ordovician. Its erection is justified by the consistency of its diagnostic features as exemplified in these two species. Spjeldnæs (1957, p. 213) suspected that *Leptaena minuta* Kiaer might be placed in *Cyphomena* Cooper. The latter genus, however, is non-rugose on the disc, not sharply geniculate, and its ventral musculature is wider relative to its length. *Notoleptaena* Gill and

Rugoleptaena Havlíček are similar to the new genus, but are ventrally geniculate whilst having a dorsally directed median trail.

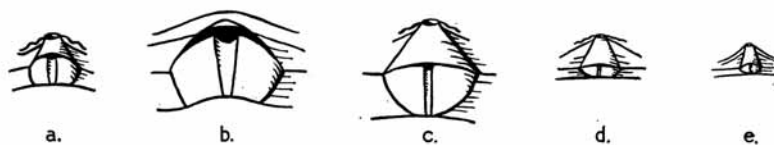
Ludfordina pixis sp. nov.

Plate 98, figs. 17-19

Holotype. BU 883. *Paratypes*. BU 884, BU 885.

Locality and horizon. Upper Millichope, Shropshire, England. Stream section in Lower Ludlow mudstones.

Description. Outline rhomboid, hinge-line forming widest part of the shell. Small acute ears developed at cardinal extremities from which the lateral margins converge and curve inwards towards the front. At the line of geniculation there is a well-marked median



TEXT-FIG. 2. Diagrammatic illustration of pseudodeltidia and chilidia in: *a*, *Leptaena rhomboidalis* (Wahlenberg); *b*, *Leptaena depressa* (J. Sowerby); *c*, *Leptaena poulsenii* sp. nov.; *d*, *Leptaena arberae* sp. nov.; *e*, *Ludfordina pixis* gen. et sp. nov. (All are to approximately the same scale.)

sulcus, characteristic of the genus. Trail sharply geniculated dorsally, about a quarter of the total length. Width at hinge-line of the holotype 15.5 mm., length at the median line 6.5 mm., lateral to the sulcus 8 mm., the depth of the sulcus is therefore 1.5 mm., but is greater in some other specimens.

From the cardinal angles a peripheral ridge follows outline of shell, increasing in height as it approaches the lobes which result from the sulcate outline. Ridge highest at these points, between them almost or entirely disappearing. Ventral valve is thus sulcate in both horizontal and vertical planes. Ventral valve convex in a narrow elongate zone about the beak, flattened and depressed towards antero-lateral margin inside peripheral ridge. Foramen and pseudodeltidium small, chilidium moderately developed. Contour of dorsal valve follows that of ventral. Ornament of poorly defined costellae and obsolescent rugae.

Dorsal interior. Components of cardinal process slender, closely set. Adductor scars faintly impressed, outlined by lateral ridges from notothyrial platform, divided by low median ridge. Latter extends as thin median septum to about two-thirds of the length of disc. Anterior scars ill-defined. Socket plates small; apophragm low, bilobate.

Ventral interior. Muscle scars relatively small, elongate, adductors occupying about one-quarter of total width, shorter than diductors and not enclosed by them. Diductors bounded by sharp sub-parallel ridges discontinuous with dental lamellae. Ridges curve inwards at anterior end, giving hook-shaped impression in casts. Low median ridge divides muscle scar in young adults, disappearing in old specimens. Teeth strong. In old specimens, beak contains a callist, longitudinally grooved.

Comparisons. *Ludfordina pixis* is distinguished by its sulcate anterior margin. In outline it therefore resembles *Rugoleptaena* [*Leptaena*] *emarginata* (Barrande), which is, however, recognized by the reversed deflection of its trail. *Ludfordina pixis* most closely resembles *Leptaena minuta* Kiaer, here included in the new genus, which is, however, smaller, and has converging ridges bounding the ventral diductors.

Discussion. Spjeldnæs (1957), in describing *Ludfordina* [*Leptaena*] *minuta*, from the Upper Cyclocrinus Beds (Middle Ordovician, Norway), states that the species is known only from the type locality (Tonerudodden) where it occurs abundantly. The writer has found *Ludfordina pixis* only at Upper Millichope, Shropshire, where it is locally abundant.

The species appears to be indistinguishable from a specimen in the Manchester Museum, examined by courtesy of Dr. R. M. C. Eager. This specimen is labelled '*Strophomena pixis* Salter ms.' and is stated to be from the Wenlock Shales, Malvern Tunnel. It is preserved in a black shaley matrix in association with *Dicoelosia* [*Bilobites*] *biloba* (Linn.). Presumably the trivial name '*pixis*' is derived from the pitch-like appearance of the matrix. The writer has been unsuccessful in finding any description published by Salter which might define the species and it seems that the name has no validity. From respect to Salter, however, the name is retained here, although not aptly descriptive for the Upper Millichope specimens, which are preserved in olive-grey mudstone.

Should later investigation reveal that the Wenlock Shale form is not conspecific with *Ludfordina pixis* then a new name will be required for Salter's specimen.

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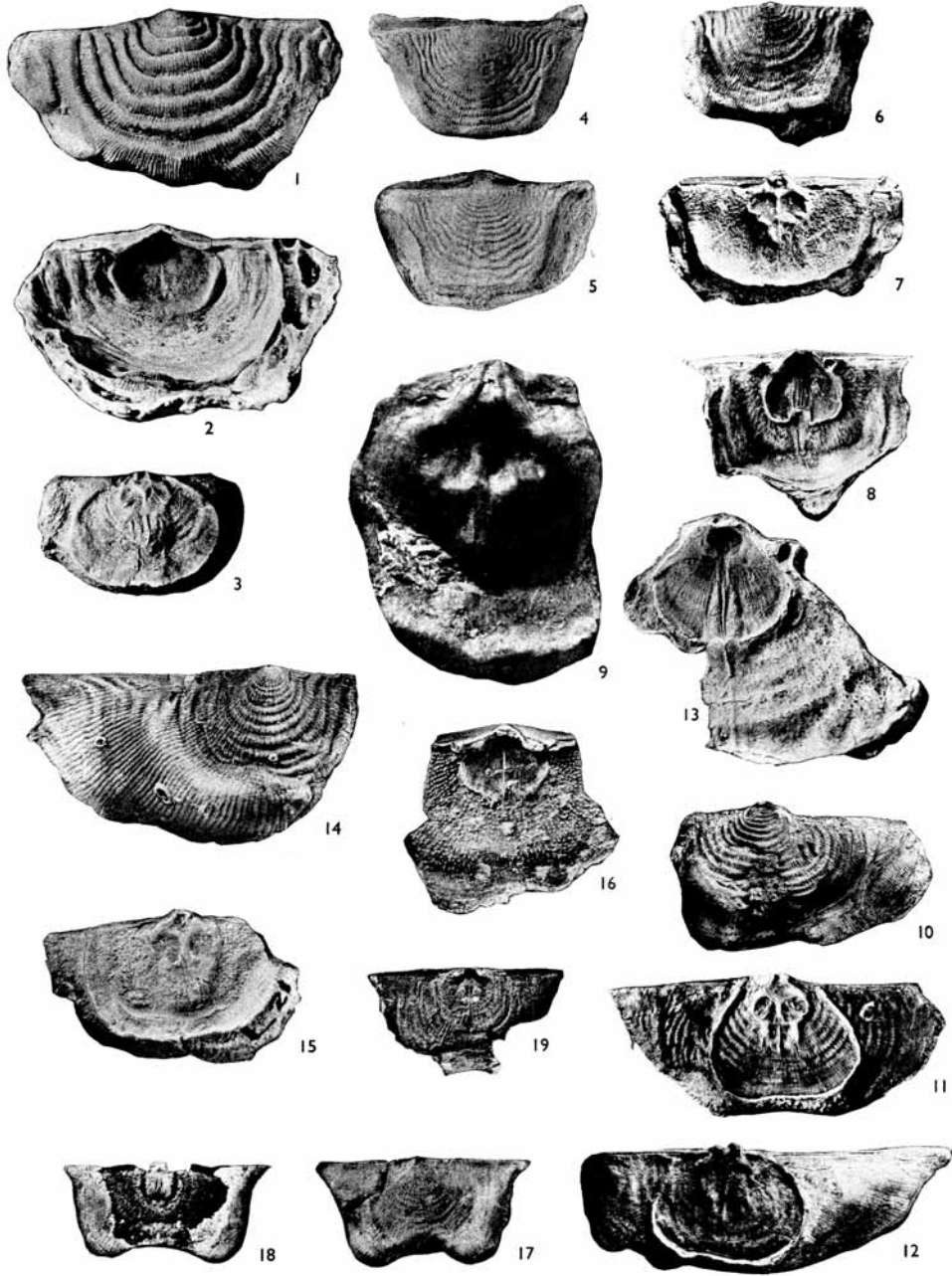
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