

LLANDOVERY STROPHEODONTIDS FROM THE WELSH BORDERLAND

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ABSTRACT. Eleven species and two subspecies in six genera of stropheodontid brachiopods are described from the Upper Llandovery (Lower Silurian) of the Welsh Borderland. Five species and one subspecies are new: *Leptostrophia ostrina*, *L. voraginis* and subspecies *palustris*, *Amphistrophia whittardi*, *Pholidostrophia salopiensis*, and *Megastrophia ethica*; the latter is also made the type of a new subgenus *Eomegastrophia*. New information has been gained on the phylogeny of the family.

OWING mainly to its early confusion with the Caradoc, which is better exposed, the fauna of the Llandovery series in the Welsh Borderland was not much collected and described in the first half of the nineteenth century, and subsequently most of the specimens were ascribed to Wenlock forms (apart from the pentamerids). Indeed, of the stropheodontid brachiopods, only '*Orthis*' *compressa* J. de C. Sowerby 1839 and '*Strophomena*' *arenacea* [Salter MS.] Davidson 1871 have ever been named from the Borderland, and from Wales itself only those species dealt with by Williams (1951) are known.

The specimens and species described here come from many parts of the Welsh Borderland, namely Shropshire, Ankerdine Hill, Old Storrige Common, the Malvern Hills, May Hill, and the Tortworth Inlier. The stratigraphy and correlation of rocks of Llandovery age are at the moment under review, and a joint paper on the subject by Dr. A. M. Ziegler, Dr. W. S. McKerrow, and the present writer is in course of preparation. Correlation within the areas and with the type area of Llandovery itself has been effected mainly by the use of evolving brachiopod lineages such as *Stricklandia* (Williams 1951) and *Eocoelia* (Ziegler 1966).

The stropheodontid material falls into six genera, *Leptostrophia*, *Brachyprion*, *Megastrophia*, *Amphistrophia*, *Pholidostrophia*, and *Strophonella*, and they will be described here in that order. As the inter-generic relationships suggested herein are different from previous findings, the present subfamilial arrangement (Williams 1965) is not used.

Acknowledgements. I would like to thank Dr. W. S. McKerrow for supervising my work at the Department of Geology and Mineralogy, Oxford, Dr. A. M. Ziegler for much help and the use of his collections from the southern part of the Borderland, Dr. C. W. Harper for valuable discussion, and the late Professor W. F. Whittard for encouragement and for the loan of his collection from Shropshire. Dr. M. L. K. Curtis kindly supplied some material from the Tortworth Inlier.

The specimens collected by Ziegler and myself are in the University Museum, Oxford (OUM), those described from Professor Whittard's collection are being presented at his request to the Geological Survey (GSM), and use has been made of the material described by Williams in the Sedgwick Museum, Cambridge (SM).

SYSTEMATIC DESCRIPTIONS

Order STROPHOMENIDA Öpik 1934
Superfamily STROPHOMENACEA King 1846
Family STROPHEODONTIDAE Caster 1939

[Palaeontology, Vol. 10, Part 2, 1967, pp. 245-65 .pls. 37-39.]

- 1892 *Leptostrophia* Hall and Clarke, pp. 287-8.
 1939 *Leptostrophia*; Caster, p. 95.
 1939 *Protopleptostrophia* Caster, p. 75.
 1939 *Rhytistrophia* Caster, pp. 86, 87.
 1947 *Leptostrophia*; Allan, p. 438.
 1949 *Eostropheodonta* Bancroft, p. 9.
 1951 *Stropheodonta* (*Eostropheodonta*); Williams, p. 123.
 1953 *Stropheodonta* (*Eostropheodonta*); Williams, p. 35.
 1953 *Leptostrophia*; Williams, p. 40.
 1953 *Protopleptostrophia*; Williams, p. 41.

Type species (by original designation). *Strophomena* (*Strophodonta*) *magnifica* Hall 1857, from the Oriskany Sandstone, Devonian, of New York.

Diagnosis. Plano-convex to gently concavo-convex stropheodontids, with a roughly triangular muscle-field in the ventral valve, bounded laterally by ridges except in some early species, and with socket plates, except in some of the later species. Ornament equally or unequally parvicostellate.

Description. Exterior. Shape semi-circular to subquadrate, usually mucronate. Plano-convex to gently concavo-convex. Ornament medium to fine parvicostellae, sometimes unequal and differentiated. Rugae sporadically developed in all stocks, though usually confined to the alae. Delthyrium open in early stocks, but becoming progressively filled by a pseudodeltidium, which may be entire and even smooth in later stocks.

Pedicle interior. Hinge line not denticulate in early stocks, which carry the denticles on the posterior of a pair of dental plates; later in the phylogeny the plates are lost and the denticles are on a denticular plate fused with the hinge line. This plate is then itself lost and the denticles spread along the hinge line, until in Upper Wenlock stocks and later the denticles occupy nearly all of the hinge line. Diductor muscle field triangular, increasingly impressed; lateral bounding ridges initially obscure except posteriorly but become stronger anteriorly with time. Radial ridges in the muscle field in later stocks only. Adductor scars lanceolate and divided by a small median ridge; becoming increasingly impressed, particularly in gerontic individuals at all stages in the development of the stocks. Pseudopunctae tend to be large near the umbo, becoming finer radially.

Brachial interior. Cardinal process initially small and conjunct, becoming increasingly disjunct. Socket plates strong and present in all except a few of the later stocks, where they become small and are eventually lost completely. Denticles mirror those in the pedicle valve, being in the sockets in the earlier stocks and finally spread along the hinge-line. Adductor muscle scars usually oval and fairly short in relation to the length of the valve, divided by a variably median ridge, often an anterior extension of a short platform. Adductors enclosed by short bounding ridges in some later stocks only.

Range. Ashgill to late Middle Devonian.

Discussion. The type species occurs at some distance both stratigraphically and geographically from the Shropshire Llandovery, but an examination of topotype specimens

of *L. magnifica* in the British Museum leaves no doubt that it is closely related to the common *compressa* of Shropshire and its Silurian allies. The main differences between them, apart from the larger size of the Oriskany specimens, lie in the lack of radial ridges in the muscle field of *compressa* and that its denticles are on a pair of denticular plates near the umbo instead of covering the hinge line.

It has become clear, however, that *Leptostrophia* may be usefully divided into a number of subgenera, in the manner of Williams (1953, etc.), so that one of the most important stocks in the stropheodontids may be better documented and its relationships more clearly shown. The youngest subgenus, *Protoleptostrophia*, is an advanced form without socket plates, and found only in the Devonian. It was first described by Caster (1939, p. 75) and reviewed by Williams (1953, p. 29), who both considered it to be a genus separate from *Leptostrophia*, although Allan (1947, p. 439) considered the type species, *Strophomena blainvillii* Billings, to be congeneric with *L. magnifica*. It is considered here as a representative of the 'talaeo' stage of Williams (1953, p. 31), but further discussion of the form is outside the scope of the present paper. (*Rhytistrophia* Caster 1939 has been correctly considered (Williams 1953, p. 29) to be a synonym of *Leptostrophia*, as it differs only in ornament.)

Eostropheodonta Bancroft 1949 has as its type species *Orthis hirnantensis* M' Coy from the Ashgill. Williams put this as a subgenus of *Strophodonta*, but at the same time (1951, p. 124) remarked on its close relations with the early *Leptostrophia*. *Strophodonta* itself is now known to be restricted to the Devonian, and *Eostropheodonta* may most usefully be considered as the oldest subgenus of *Leptostrophia*, representing the 'eo' stage of Williams. As well as in the Ashgill, the subgenus occurs as the commonest stropheodontid in the Lower Llandovery and includes *L. mullochensis* Reed 1917, *E. whittingtoni* Bancroft 1949 (figured and described as *E. cf. mullochiensis* by Williams 1951), and *E. multiradiata* Bancroft 1949, as well as the recently described *Eostropheodonta* sp. of Boucot and Johnson from Sweden (1964, p. 5, pl. 3, 4), whilst from the Upper Llandovery comes *L. (E.) voraginis* and its subspecies *palustris* described below. The chief difference from *Leptostrophia* (*Leptostrophia*) lies in the presence of dental plates.

The remainder of the genus thus represents the 'meso' stage of Williams, without dental plates, but with socket plates, and may be termed *Leptostrophia* (*Leptostrophia*). The earliest representative of the subgenus is *L. reedi* Bancroft 1949 (= *L. tenuis antecedens* Williams 1951) and occurs in the Lower Llandovery Gasworks mudstone of Pembrokeshire. In fact the early members of the subgenus, exemplified by *L. (L.) compressa*, may be separated from the later members, such as *L. magnifica* itself, by the absence of radial ridges in the muscle field, and by the support of the denticles on denticular plates instead of directly on the hinge line, but these features change imperceptibly with time and are thus not given taxonomic recognition here. For example, the common Wenlock and Ludlow *L. filosa* has radial ridges, but still possesses reduced denticular plates in most cases.

Of course, the fact that the subgenera are descended from one another does not prevent conservative stocks lingering on when others have evolved. At the Bog Mine, Shropshire, *L. (E.) voraginis* sp. nov. and *L. (L.) compressa* occur intimately together, and Dr. C. W. Harper informs me that in Nova Scotia forms with dental plates also occur in the late Llandovery, and possibly into the Wenlock.

Leptostrophia (Leptostrophia) compressa (J. de C. Sowerby 1839)

Plate 37, figs. 1-11

- 1839 *Orthis compressa* J. de C. Sowerby; in Murchison, p. 638, pl. 22, fig. 12.
 1848 *Strophomena compressa* (J. de C. Sowerby); Phillips and Salter, p. 379.
 1852 *Leptaena (Strophomena) compressa* (J. de C. Sowerby); M'Coy, p. 242.
 1871 *Strophomena compressa* (J. de C. Sowerby); Davidson, p. 315, pl. 46, figs. 7-10 (*non* figs. 11-14).
 1912 *Stropheodonta compressa* (J. de C. Sowerby); Reed, p. 136.
 1932 *Leptostrophia compressa* (J. de C. Sowerby); Whittard, list facing p. 896.
 1949 *Stropheodonta compressa* (J. de C. Sowerby) var. *crassa* Bancroft, p. 15.
 1951 *Stropheodonta (Brachyprion) compressa* (J. de C. Sowerby); Williams, p. 130.

Description. Exterior. Plano-convex to concavo-convex with the curvature gentle, making specimens appear fairly flat. Ornament variable but always parvicostellate, variably impressed, but slightly larger costellae at irregular intervals. New ribs originate by intercalation. Shape approximately semicircular, but with a variable length/width ratio within a population. Small ears, often not preserved. Fine growth lines are rarely seen. Medium-sized area. Umbo not very prominent.

Pedicle interior. No dental plates, but the hinge line projects slightly anteriorly on either side of the umbo in two flanges termed denticular plates, on the dorsal side of which are located the denticles. These flanges rarely extend more than a quarter of the distance from the umbo to the ears. The diductor muscle field is flabellate and roughly triangular in outline, with lateral bounding ridges which are strong towards the umbo and weaken anteriorly. The angle of divergence of the muscle field is variable, but systematically so (see discussion). The adductor scars are often seen as lanceolate and separated by a median ridge which is more pronounced near the umbo. Pseudopunctae occur over the whole shell, but are much coarser medio-posteriorly.

Brachial interior. Straight hinge. Cardinal process lobes directed ventrally. Socket plates widely divergent with denticles posterior to them in the socket into which the denticular plate fits. Notothyrial platform usually visible, but variable in height, triangular in shape with the apex elongated anteriorly. Adductor scars variably impressed, but tend to be oval and slightly flabellate anteriorly. As in the pedicle valve, the pseudopunctae coarsen towards the umbo.

EXPLANATION OF PLATE 37

All specimens treated with ammonium chloride. Grid references are given in the text.

- Figs. 1-7. *Leptostrophia compressa* (J. de C. Sowerby). 1, Pedicle internal mould, OUM C9142, $\times 2.2$; 2, Brachial internal mould, OUM C9144, $\times 1.7$, both from Hope Quarry. 3, Pedicle internal mould, GSM 102722, $\times 1.4$, from Josey's Wood B. 4, Pedicle internal mould, OUM C6279, $\times 1.1$, from H-L-C. 5, Pedicle internal mould, OUM C10829, $\times 2.2$, from Josey's Wood B. 6, Pedicle internal mould, OUM C2668, $\times 1.0$, from M-S-B. 7, Brachial internal mould, OUM C2658, $\times 2.0$, from M-S-B.
 Figs. 8, 11. *Leptostrophia compressa crassa* (Bancroft). 8, Pedicle internal mould, OUM C3482, $\times 1.3$. 11, Pedicle internal mould, lectotype, OUM C3489, $\times 1.4$. Both from T-M-A (fig. 11 shows a boring, presumably made by a gastropod, close to the umbo).
 Fig. 9. *Leptostrophia tenuis* Williams. Pedicle internal mould, holotype, SMA 30044, $\times 1.8$, from River Sefin, Llandoverly.
 Fig. 10. *Mclearnites* sp. Pedicle internal mould, BMNH BB31278, $\times 1.5$, from reservoir near Winsle, Pembrokeshire.
 Figs. 12-14. *Leptostrophia ostrina* sp. nov. 12, External view, brachial valve, holotype, OUM C14014, $\times 1.0$. 13, 14, Internal and external moulds of pedicle valve, OUM C14019, $\times 1.8$. All from Hughley.

Dimensions (in cm.).

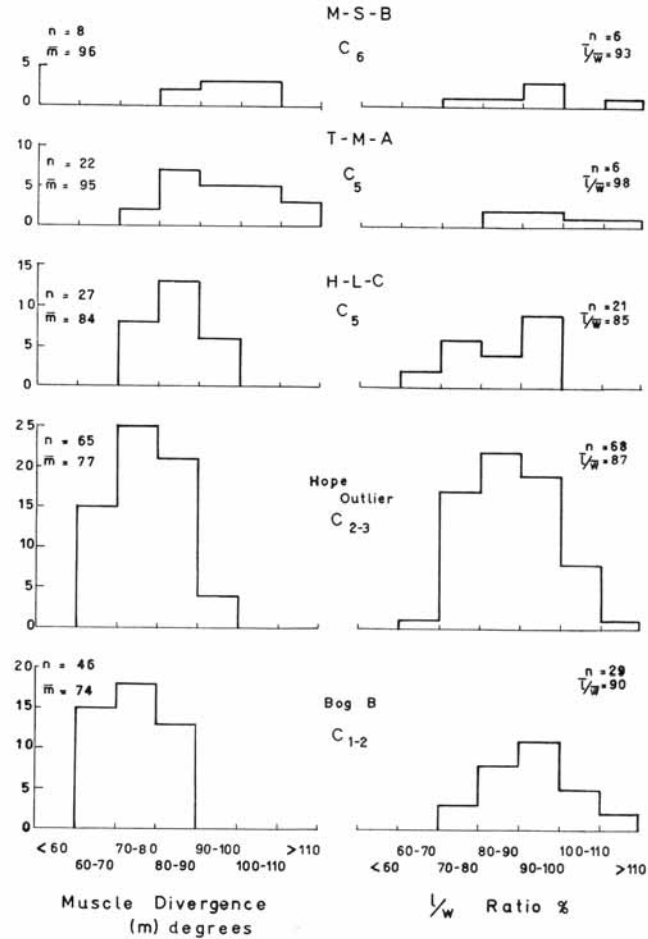
			<i>Length</i>	<i>Width</i>
Holotype	GSM R6879	Pedicle valve	broken	2.71
Hope Quarry	OUM C9141	„ „	0.59	0.82
„ „	OUM C9142	„ „	0.99	1.40
„ „	OUM C9146	„ „	0.70	1.08
„ „	OUM C9144	Brachial valve	broken	2.67

Discussion. The species was named and figured in 'The Silurian System', and the original specimen is still in existence (GSM Geol. Soc. Coll. R6879). The type locality, Hope Quarry, Shropshire, is within the area, but although two collections were made from the locality, the species is not common there and only four pedicle valves and three brachial valves were obtained. These were enough, however, to be sure that the common stropheodontid of other localities such as Hope Outlier [Grid Ref. SJ/3482 0140] and Josey's Wood B [Grid Ref. SJ/3653 0221] (very close geographically and stratigraphically to Hope Quarry [Grid Ref. SJ/3551 0208]) could be identified as *compressa*.

The species, though very numerous at certain localities, has a restricted distribution in Shropshire, being confined to the Bog Quartzite and Venusbank Formation, although related species of *Leptostrophia* occur rarely in the Pentamerus Beds and Purple Shales, and *Brachyprion arenacea*, which is considered to be a derivative of *compressa*, occurs in the Pentamerus Beds of Norbury and elsewhere. Thus in Shropshire it occurs only in beds of C₁ to C₃ in age.

In the southern part of the Welsh Borderland, however, in large collections made by Dr. A. M. Ziegler and available to the writer, *compressa* occurs in the Damery and Tortworth Beds of Tortworth (C₅ and C₆), in the Yartleton Beds (C₅ and C₆) and sandstone lenses of the Woolhope (Lower Wenlock) of May Hill, in the Wyche Beds (C₅ and C₆) of the Malvern Hills, and at one locality in the Cowleigh Park Beds (C₁) of Ankerdine Hill. (The Yartleton beds include locality M-S-B [Grid Ref. SO/6932 2270].) *L. compressa* has not yet been identified from any shales.

Thus, apart from beds of C₄ age, we have continuous collections of *compressa* ranging in age from C₁ to Lower Wenlock. Measurements were made of the length, width, and angle of divergence of the diductor muscle scars in moulds of the pedicle valve, and the results plotted in the form of histograms of length/width ratios and muscle scar divergences. When a stratigraphical sequence is chosen from the larger collections and placed above one another (text-fig. 1), it is seen that the mean muscle divergence increased with time. The associated length/width ratios, however, show a variety of means with no apparent pattern. If the length/width ratio had decreased with the increase of muscle divergence, this would not have been surprising, because as the shell grew broader the widening of its musculature would have kept pace with it; but as the length/width ratio does not follow the divergence, then the latter's widening is suspected as being a genetic trend rather than an ecological one. This is further supported by the plot (text-fig. 2) of two collections from the same stratigraphical horizon and less than a mile apart geographically. This shows the length/width ratios to be markedly different, whilst the muscle divergence is extremely similar. It is also relevant that the only two *compressa*-bearing localities which are approximately the same age in the two halves of the Welsh Borderland, Bog Mine and the Cowleigh Park Beds of Ankerdine Hill [Grid Ref. SO/7376 5696], which are both C₁ on other brachiopod evidence, should have extremely

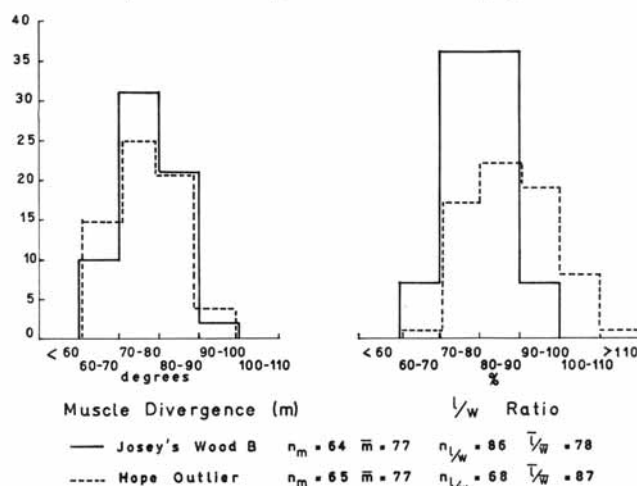


TEXT-FIG. 1. Histograms of pedicle valve muscle divergence and length/width ratios of five different populations of *Leptostrophia compressa* (J. de C. Sowerby) at successive periods of Upper Llandovery time. For localities see text.

similar mean muscle divergencies, 74 and 76 degrees respectively. The two localities are, moreover, in quite different lithologies, one a coarse quartzitic sandstone and the other a fine-grained micaceous silt. Thus the mean muscle divergence appears to be of potential use in determining the degree of evolution of this species, and hence the age of the rock in which it occurs.

Text-fig 1 had been drawn up before it was realized that collection T-M-A from the Damery Beds of Tortworth [Grid Ref. ST/7268 9212] was particularly interesting in two

respects: firstly, that although it is correctly dated as C_5 , it is in fact probably older than collection H-L-C (from the Wyche Beds of the Malvern Hills [Grid Ref. SO/7464 5108] because the latter 'definitely overlies beds containing *Pentameroides* whereas T-M-A surely underlies beds containing *Pentamerus/Pentameroides* transients' (Dr. A. M. Ziegler, personal communication, October 1964); and, secondly, that the muscle bounding ridges in the T-M-A specimens are, in many cases, much more curved than in any other collection of *compressa* from higher or lower stratigraphical horizons. In other



TEXT-FIG. 2. Histograms of pedicle valve muscle divergence and length/width ratios of two populations of *Leptostrophia compressa* of the same age and from less than a mile apart. For localities see text.

words, the T-M-A population shows all intergrades between individuals with a muscle field as in typical *Leptostrophia* (Pl. 37, fig. 8) and individuals with a muscle field (Pl. 37, fig. 11) like that found in the genus *Mclearnites*. If this is not the effect of homoeomorphy, which it shows no signs of being, then this collection may be treated as representative of the progenitors of *Mclearnites* and hence of the whole douvillinid stock. No British record of *Mclearnites* has so far been made (its earliest North American record is *M. newsomensis* from the Upper Wenlock) but in a small collection from the Coralliferous Series (Wenlock), near St. Ishmael's, Winsle, Pembrokeshire, there occur crushed but unmistakable specimens of a brachiopod (Pl. 37, fig. 10) seemingly intermediate between the T-M-A specimens and the type of *Mclearnites*, *M. mertoni*, from the Lower Devonian of Arisaig, Nova Scotia (for illustration of this species, see McLearn 1924, pl. 4, figs. 16-18).

[Dr. C. W. Harper has shown (*in Boucot et al.* 1966, p. 41, and paper in preparation on the Arisaig Series) that *Mclearnites* Caster 1945 is not synonymous with *Shaleria* (as thought by Williams 1953), but is in fact a primitive mesodouvillinid which differs from *Mesodouvillina* s.s. in being plano- to gently concavo-convex, in contrast to *Mesodouvillina* which is strongly concavo-convex. There are also ornamental differences.]

Assuming this theory to have some validity, it would explain the otherwise anomalous position of the T-M-A specimens in the muscle divergence sequence of *compressa*, by an earlier and as yet unrecorded split in the *compressa* line just prior to C₅ which resulted in the ancestry of the douvillinids from the leptostrophid stock. Bancroft (1949, p. 15) has 'suggested' that the Charfield Green form of *compressa* (from which locality the T-M-A collection comes) should be distinguished under the varietal name *crassa*, though without figuring the variety or designating any particular specimens. This will prove a convenient term for labelling the *Mcleanites* ancestors, although they are still considered here as a subspecies of *compressa*. The situation illustrates the difficulty of applying Linnaean nomenclature to intermediate members of an evolving lineage, especially where a change of genus is involved. *Leptostrophia* and *Mcleanites* are definitely distinct genera higher in the stratigraphical sequence, so it would obviously be unwise to consider them as synonyms on information from the present horizon.

It is useful to compare *compressa* with other contemporary forms of *Leptostrophia* without dental plates; these consist of *Leptostrophia tenuis* Williams 1951 from C₁ at Llandovery, and *Leptostrophia ostrina* sp. nov. from the Purple Shales. *L. tenuis* (the holotype of which, SMA 30044, is figured here, Pl. 37, fig. 9, for comparison) comes from the badly sorted black shales of the Sefin footbridge, and differs from *compressa* mainly in details of ornamentation. Some of the central costellae are not straight on *tenuis*, and they are to be seen more on the muscle-fields than on any *compressa* of comparable size (this is not due entirely to the different modes of preservation, but because of less secondary calcite being deposited near the umbo in the shale form due, no doubt, to different metabolism in different surroundings). The inequality of the parvicostellae is much more apparent and regular on *tenuis* than on *compressa*. The dentition, musculature and cardinalia are, however, virtually identical in the two species, and they are obviously very closely related. Indeed, there is a case that can be made out that the ornamental differences are subspecific or geographical, and that the two species are in fact conspecific, but until larger collections of *tenuis* are made, and length/width ratios and muscle divergences measured, it seems better to treat the two species as separate.

Leptostrophia ostrina, which occurs rarely in the Purple Shales, has also a dissimilar ornament, but in addition it has a markedly different growth pattern, as it is very mucronate in the smaller growth stages, but then grows much faster in an anterior direction. It is described in more detail below.

Leptostrophia (Leptostrophia) ostrina sp. nov.

Plate 37, figs. 12-14; Plate 38, fig. 1

Diagnosis. Early form of *Leptostrophia* without dental plates but with denticular plates, allometric growth, and differentiated ornament.

Description. Exterior. Shell nearly flat, but slightly concavo-convex. Very mucronate in young stages, but elongating anteriorly faster than laterally during growth. Fine rugae often present at the ears. Parvicostellate ornament, but unequal. The larger costellae, although superficially very regular and pronounced, are in detail irregularly spaced, both in distance and in the number of smaller costellae between them, which varies from one to six. New costellae arise by intercalation. Very thin shells (except where some secondary

deposition has taken place near the umbo), and the talaeolae are often seen exteriorly arranged in lines down the costellae. Medium-sized area.

Pedicle interior. No dental plates, but a pair of denticular plates occupying approximately one-third of the hinge line in adult specimens. Triangular diductor muscles only faintly impressed, and often invisible except postero-laterally where low muscle-bounding ridges may be seen leading to the hinge line. Adductor scars not seen, except as two very faint impressions between the diductors separated by an extremely short median ridge close to the umbo only.

Brachial interior. Stout cardinal process and socket plates. Very weakly impressed platform of roughly triangular shape immediately anterior of the cardinal process, and extending for only a very short distance. Adductor scars very weakly impressed, and in the few specimens available their exact shape remains uncertain.

Type locality. Purple Shales of Hughley brook [Grid Ref. SO/5605 9747].

Holotype. Brachial valve, OUM C14014.

Dimensions (in cm.) (all specimens from Hughley).

		<i>Length</i>	<i>Width</i>
Brachial valve	OUM C14006	0.26	0.66
" "	OUM C14017	0.79	1.46
" "	OUM C14014	3.24	3.68
Pedicle valve	OUM C14003	0.17	0.32
" "	OUM C14021	0.74	1.39
" "	OUM C14020	0.91	1.50
" "	OUM C14019	2.08	2.56

Discussion. This species is very closely related to *L. compressa*, but differs from it by the thinness of its valves (no doubt because of its muddy habitat; it has only been found so far in the Purple Shales of Shropshire), the differentiation of its ornament (which is approached, but never reached, by *L. compressa*), and by its allometric growth. It is a rare fossil, and a large sample could not be obtained, but of the twelve specimens in the collection from Hughley seven gave measurements of both length and width which demonstrate that the younger shells have a much lower length/width ratio than the adults. This may also be seen in the growth lines of the adult specimens.

Leptostrophia (Eostropheodonta) voraginis sp. nov.

Plate 38, figs. 2-8

Diagnosis. An *Eostropheodonta* with regular parvicostellate ornament and wide muscle divergence angle.

Description. Exterior. Shape approximately semicircular but slightly mucronate, though with the ears seldom preserved. Rugae occasionally seen near the ears only. Ornament subequally parvicostellate with new ribs arising by intercalation. The costellae are approximately straight down the median axis, but curve smoothly laterally. Medium-sized area.

Pedicle interior. Prominent dental plates which diverge at approximately 90 degrees. In larger specimens the plates are non-uniform, changing direction dorsally with one or

more ridges running along the plate. The plates are fused posteriorly to the hinge line, which protrudes slightly anteriorly as a small denticular plate bearing the denticles. Diductor scars usually faintly impressed, bounded postero-laterally by weak ridges which diverge at a greater angle than the dental plates. Occasionally the scars are seen to be rounded anteriorly, e.g. OUM C7064 (Pl. 38, fig. 6), and very occasionally a slight median ridge is seen in the anterior part of the muscle field. Adductor scars are normally very faintly impressed or invisible, but from occasional specimens appear lanceolate. Pseudopunctae tend to coarsen near the umbo where secondary deposition has taken place in adults, apart from the smooth areas of muscle attachment.

Brachial interior. Thick socket plates with denticles on the posterior edge. Smaller cardinal process lobes. Slight raised ridge on the hinge line near the umbo to fix the posterior end of the dental plates. Small platform about 2 mm. wide and extending about 3 mm. anteriorly from the cardinal process in adult specimens, separating very weakly impressed oval adductor scars. Pseudopunctae coarsen towards the umbo, but not so markedly as in most species of *Leptostrophia*.

Type locality. Cowleigh Park Beds of Ankerdine Hill [Grid Ref. SO/7352 5625].

Holotype. Pedicle valve, OUM C6676.

Dimensions (in cm.).

			<i>Length</i>	<i>Width</i>
Pedicle valve	OUM C6676	(holotype)	1.97	2.28
" "	OUM C1280		1.18	1.34
" "	OUM C1257		1.46	1.86
" "	OUM C1248		2.01	2.66

The other measured specimens come from the Huntley Hill Beds of May Hill [Grid Ref. SO/7014 2104].

Discussion. In the Huntley Hill Beds of May Hill, the Cowleigh Park Beds of Ankerdine Hill, the Bog Quartzite, and very rarely in the Venusbank Formation of Shropshire, there occurs a *Leptostrophia* which appears at first sight very similar to *L. compressa*, except for a pair of well-developed dental plates. Fortunately at two localities (Bog, Shropshire, and at another locality on Ankerdine Hill [Grid Ref. SO/7376 5696]), this

EXPLANATION OF PLATE 38

All specimens treated with ammonium chloride. Grid references not given below are in text.

Fig. 1. *Leptostrophia ostrina* sp. nov. Pedicle external mould OUM C14021, $\times 3.4$, Hughley.

Figs. 2-8. *Leptostrophia (Eostropheodonta) voraginis* sp. nov. 2, 3, Internal and external moulds of pedicle valve, holotype, OUM C6676, $\times 1.4$, Ankerdine Hill. 4, Pedicle internal mould, OUM C10488, $\times 1.7$, from Bog. 5, Pedicle internal mould, OUM C1280, $\times 1.6$, from Huntley Hill Beds, May Hill [Grid Ref. SO/7014 2104]. 6, 7, Pedicle internal moulds, OUM C7064 and 7074, $\times 1.3$ and $\times 2.4$, both from Ankerdine Hill. 8, Brachial internal mould, OUM C6652, $\times 2.6$, from Ankerdine Hill.

Figs. 9-11. *Leptostrophia (Eostropheodonta) voraginis palustris* subsp. nov. 9, Two pedicle internal moulds, OUM C15825-6, $\times 3.0$. 10, Pedicle internal mould, holotype, OUM C15824, $\times 3.1$. 11, Brachial internal mould, OUM C15837, $\times 6.7$. All specimens from Marshbrook.

Figs. 12-15. *Brachyprion arenacea* (Davidson). 12, Pedicle internal mould, OUM C8814, $\times 2.0$, from Norbury. 13, 14, Two views of strongly convex pedicle internal mould, OUM C6311, $\times 1.7$, from locality H-L-C. 15, Pedicle internal mould, GSM 102721, $\times 1.2$, from Norbury.

species occurs in small numbers in collections also containing much larger numbers of *L. compressa*. It was thought at first that these might represent single populations with a few members retaining the plates of the early stropheodontids but with the majority having lost them. (This would have meant a polyphyletic loss of dental plates for *Leptostrophia*, as *L. reedi* had already lost them by Lower Llandovery times.) However, an analysis of the Bog collection revealed a difference in the angle of divergence of the ventral muscle field. All the specimens of *compressa* lay between 60 and 90 degrees (see also text-fig. 1), whereas all those of *voraginis* lay between 90 and 115 degrees. Thus the ranges do not overlap. This fact, taken together with the presence of dental plates, indicates that two different species are involved. In the other locality, Ankerdine Hill, *voraginis* shows a much more striking ornament when compared with *compressa*, the latter being smoother at this locality than is typical for the species, and also having a much more impressed musculature than *voraginis*, although the two species occur up to the same size there (up to 3.9 cm. wide).

The species is comparable with *L. mullochensis* Reed 1917, *Eostropheodonta whittingtoni* Bancroft 1949, and *E. multiradiata* Bancroft 1949, all from the Lower Llandovery. The argument for separating these forms, all with dental plates, as a separate subgenus within *Leptostrophia* has been put forward above.

The species differs from *mullochensis* and *whittingtoni* (which may prove to be subspecies of each other) by the different style of ornamentation; the costellae of these species meander and are differentiated into groups, and the muscles are not visible at all in the type specimens in the British Museum and Sedgwick Museum. *E. multiradiata* is a poorly known form, but the low length/width ratio of the holotype (SMA 30113) and the prominent pseudopunctae distributed in lines down the costellae, both combine to give an impression of specific difference from *voraginis*, although the species are probably closely related, but until more material is recovered from the type locality of *multiradiata* (the Frolic, Haverfordwest) it seems preferable at the moment to keep the two forms distinct.

Leptostrophia (Eostropheodonta) voraginis palustris subsp. nov.

Plate 38, figs. 9-11

Diagnosis. Thin-shelled *Eostropheodonta* with rather irregular parvicostellae.

Type locality. Mudstones in Pentamerus Beds, Shropshire, in stream bank near Marshbrook [Grid Ref. SO/4341 8982].

Holotype. Pedicle valve, OUM C15824.

Dimensions (in cm.). All specimens from the type locality.

			<i>Length</i>	<i>Width</i>
Pedicle valve	OUM C15824	(holotype)	0.86	broken
" "	OUM C15825		0.67	0.85
" "	OUM C15828		0.42	0.59
" "	OUM C15827		0.95	1.42
" "	OUM C15829		1.29	1.62

Discussion. In the Pentamerus Beds of Shropshire, which are mainly blue mudstones, there occurs a rare *Leptostrophia* with dental plates which is closely similar to *L. (E.) voraginis* (already described), which has only been found in sandstones or siltstones.

The shell is thinner, and, in addition, the ornament is less strongly developed, and of variable height along the ribs (Pl. 38, fig. 10). Whilst these differences could be due solely to the different environment, there is a case for creating a subspecies within *voraginis* to cover these forms. This subspecies is interesting also in that quite small specimens have been recovered from Marshbrook. In a brachial valve (Pl. 38, fig. 11) the two socket plates are extremely large in comparison with the embryo cardinal process. The presence of only two large talaeolae on one side and three on the other, just anterior of the socket plates, indicates that the size of a talaeola remained constant throughout the life of the animal, with an increase solely in the number present. In rather larger pedicle valves (e.g. Pl. 38, fig. 9), the dental plates are also large in relation to the shell size, and there are no signs of denticles on the hinge, indicating that at this period of stropheodontid evolution the relative positions of the valves were delimited solely by teeth and sockets at this early growth stage.

BRACHYPRION Shaler 1865

- 1865 *Brachyprion* Shaler, p. 63.
 1892 *Brachyprion* Hall and Clarke, p. 288.
 ? 1939 *Brachyprion* Caster 1939, p. 33.
 non 1951 *Stropheodonta* (*Brachyprion*) Williams, p. 124.
 1953 *Stropheodonta* (*Brachyprion*) Williams, p. 35 (non pl. 7, figs. 5–7).

Type species. *Strophomena leda* Billings 1862, from the Silurian of Anticosti Island, Canada.

Discussion. The types of Billings's species are lost, but a lectotype was designated by Twenhofel (1928, p. 188). This came from the Jupiter Formation, which is equivalent to high Llandovery. The British species which may be assigned to the genus are *B. arenacea* (Davidson 1871) and *B. sp.*, both from the Upper Llandovery and described below, and *B. waltoni* (Davidson 1847). The genus occurs in the Ludlow, but no species have yet been described from that horizon.

Brachyprion arenacea [Salter MS.] (Davidson 1871)

Plate 38, figs. 12–15; Plate 39, fig. 1

- 1865 *Strophomena arenacea* Salter, Catalogue Mus. Pract. Geol., p. 36, *nomen nudum*.
 1871 *Strophomena arenacea* [Salter MS.]; Davidson, p. 296, pl. xlii, fig. 6 (non figs. 7, 8).
 non 1883 *Strophomena arenacea* Salter; Davidson, p. 197, pl. xvi, figs. 2–5.
 1945 *Brachyprion arenaceus* [Salter MS.]; Lamont and Gilbert, p. 664, *pars*, pl. 5, figs. 1–4, 8–9; pl. 7, figs. 1, 4.
 non 1945 *Brachyprion arenaceus* [Salter MS.] var. *lobatus* Lamont and Gilbert, p. 667.
 non 1945 *Brachyprion arenaceus* [Salter MS.] var. *geniculatus* Lamont and Gilbert, p. 669.

Diagnosis. An early *Brachyprion*, with internal configuration close to early *Leptostrophia*, but with variable convexity, and weak parvicostellate ornament.

Description. Exterior. Shape semicircular, with small ears. Pedicle valve varies in profile from gently convex to very convex, sometimes with an increase of convexity near the valve margin. Brachial valve usually gently concave, but occasionally the concavity increases near the anterior margin. Weak ornament of unequal parvicostellae, sometimes irregularly differentiated. Beak small and scarcely projecting. Large area, with open delthyrium and a chilidium.

Pedicle interior. Denticles on a pair of denticular plates fused with the hinge line and extending for not more than one-third of the way along it. No dental plates. Diductor muscle scars well impressed posteriorly, where they are enclosed by short bounding ridges, but weaken as they diverge anteriorly. Their shape varies from triangular and flabellate to a rather more oval shape, with all intergrades. Adductor scars rarely seen, but are lanceolate and situated between the diductors, and are separated by a variably developed, but sometimes quite prominent, median ridge. Fine pseudopunctae, coarsening slightly towards the umbo, may be seen except on the muscle field.

Brachial interior. Denticles on the hinge line corresponding with those in the pedicle valve. Strong disjunct cardinal process lobes, in the hollow between which occurs a very fine chilidial ridge. Widely divergent socket plates, which define the posterior limits of the muscle-field. Weakly developed Y-shaped platform. Adductor scars poorly impressed and approximately oval, separated by a variably developed median ridge which is an extension of the platform. Fine pseudopunctae cover the surface, apart from the muscle field.

Dimensions. Lectotype (GSM 11692) from Norbury, Shropshire: width 4.2 cm., length 2.4 cm. Dimensions of a collection from Norbury are shown in text-fig. 3.

Discussion. *Arenacea*, as used up to the present, harbours two quite distinct species, as suspected by Davidson (1871, p. 297):

- (a) a stropheodontid, referable to *Brachyprion* (Davidson 1871, pl. xlii, fig. 6);
- (b) a leptaenid with very elongate muscle bounding ridges (Davidson 1871, pl. xlii, figs. 7, 8).

The question arises as to which is the true *arenacea*. Salter never figured or described his species, and so the first description falls to Davidson in his monograph. He figured three specimens, fig. 6 (from Norbury), which is the *Brachyprion*, and figs. 7 and 8 (from Gunwick Mill and Huntley Hill), which are leptaenids. As the original specimens are still in existence in the Geological Survey Museum, any lectotype should be designated from amongst them. In the supplement to his monograph (1883) Davidson figured more specimens as *arenacea*, this time from Girvan, but these have dental plates and are yet another species.

Lamont and Gilbert (1945) realized that all three shells figured by Davidson in 1871 were not identical and accordingly put them into three subspecies, *arenaceus* forma typica, *arenaceus lobatus*, and *arenaceus geniculatus*. The types they designated were as follows:

- forma typica: SMA 16219 and 16220 *a* and *b* (as lectosyntypes);
- lobatus*: BU 397, GSM 11461 (Davidson's fig. 7) (as syntypes);
- geniculatus*: GSM 11460 (Davidson's fig. 8), BU 394-6 (as syntypes).

The original of Davidson's fig. 6 they figured as 'probably a *forma typica*' (GSM 11692). Thus as it is the only one of Davidson's three specimens which they designate as *arenacea* s.s., this must in fact be the lectotype. This is the first specimen figured by Davidson and is the *Brachyprion*. The three Cambridge specimens from Presteigne

which Lamont and Gilbert designated as the lectosyntypes of *forma typica* are also *Brachyprion*, but they are referred here to *Brachyprion sp.*, described below.

The type locality of *B. arenacea* is thus Norbury, Shropshire. This is not in fact one locality, but a group of quarries round the village of that name, worked and collected during the last century, and the precise locality of the lectotype is not known. However, specimens may today be collected at several localities in the area, and a large collection was made from a single band near the top of the most extensive quarry [Grid Ref. SO/3587 9284]. One of the most striking features of the sample was its great variability, particularly in the convexity of the pedicle valve. A plot of length against height for the collection (text-fig. 3) demonstrates this well. Thus this species is somewhat difficult to place within the stropheodontids, as the population shows all intermediates between a contemporary *Leptostrophia* (the flatter part of the population) and *Brachyprion*. The internal resemblance to contemporary *Leptostrophia* (e.g. *L. compressa*) is striking in every qualitative particular, except perhaps for a tendency for the ventral muscle field to be more oval in some specimens than is usual in *Leptostrophia*. This contributes to the mean muscle divergence of 74 degrees ($n = 80$), which is less than one would expect of an *L. compressa* of similar age. The Norbury collection is late C₃ or early C₄ on the evidence of associated *Eocoelia* (Ziegler 1966).

Thus, although on balance the species is referred to *Brachyprion*, the fact that it is the earliest species of the genus indicates that it may represent the genus just after an evolutionary divergence from *Leptostrophia*. Earlier species previously attributed to the genus, such as *B. matutinum* Lamont 1935 and *S. (B.) sefinensis* Williams 1951, are considered here to be pholidostrophids.

Norbury is the only locality in Shropshire from which *B. arenacea* has been obtained, but it occurs in the Wyche Beds of the Malverns and the Damery Beds of Tortworth. It is known so far only from sandy facies and thus seems to have been aptly named.

Brachyprion sp.

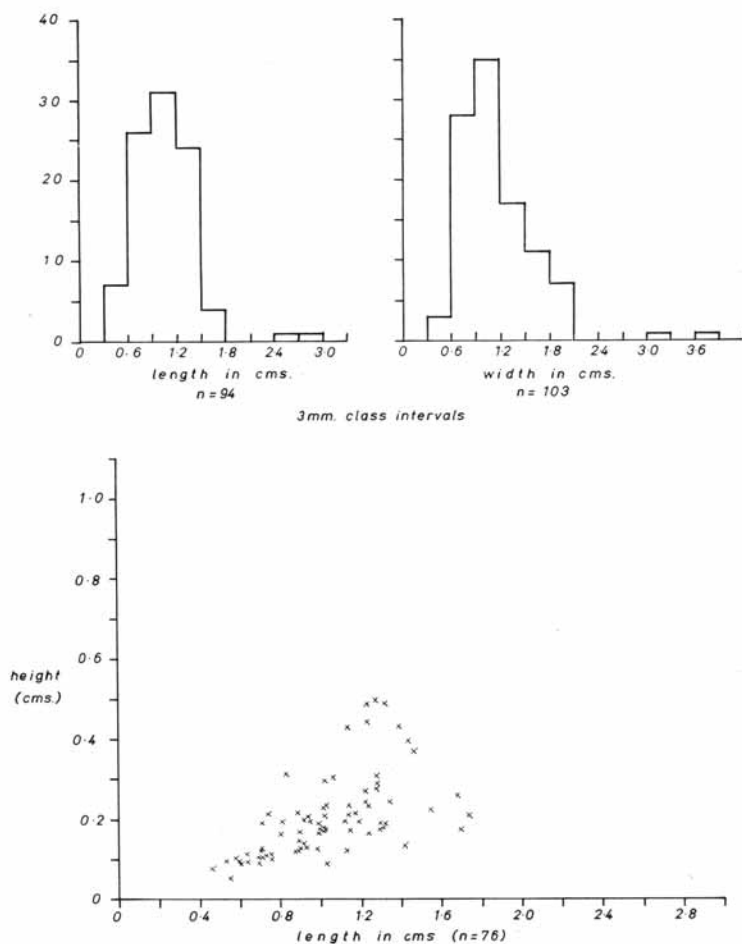
Plate 39, fig. 2

1945 *Brachyprion arenacea* [Salter MS.]; Lamont and Gilbert, p. 664, *pars*, pl. 5, figs. 5-7, ?10.

Discussion. There occurs in some places near the top of the Upper Llandovery a form of *Brachyprion* which differs from *B. arenacea* in the following ways, apart from always having a convex pedicle valve:

- (a) the muscles are much more impressed, particularly the adductor scars;
- (b) immediately laterally of the diductor scars there is a zone where the pseudopunctae are much larger than those normally seen on *B. arenacea*;
- (c) there is a ridge, superficially similar to that seen on most species of *Leptaena*, but not so well developed, which is subcircular in outline and merging with the hinge line at the lateral ends of the denticular plates. This ridge confines the area of large pseudopunctae.

The species might be a gerontic form of *arenacea*, but if so has produced a remarkable change in the general aspect of the pedicle interior. Unfortunately the species is not



TEXT-FIG. 3. *Above*, Histograms of length and width of a population of *Brachyprion arenacea* (Davidson) from a single rock band at Norbury, Shropshire. *Below*, A plot of length against height for the same population, illustrating the wide variation in convexity.

represented in the collections of Ziegler or myself, but specimens in Bristol University Museum (12131, etc.) are from 'Damery Beds, Avening Green, Tortworth' and in the Sedgwick Museum (SMA 16219-21) from 'close under limestone, Presteigne'. Thus, until more material is recovered, and in particular the brachial valve known, it would be premature to give this form a name, as it could prove to be a subspecies of *B. arenacea*.

Megastrophia (Eomegastrophia) subgen. nov.

Type species. *M. (E.) ethica* sp. nov.

Diagnosis. *Megastrophia* with dental plates.

Discussion. In the Pentamerus Beds of Shropshire there is a large stropheodontid which is convex and carries dental plates. This is an ancestor, direct or indirect, of *Megastrophia (Protomegastrophia)* Caster 1939, which has as its type species *Leptaena profunda* Hall 1852 and has been refigured by Williams (1953, pl. 9, figs. 1-3) from the Middle Silurian of North America. The brachial valves of the two subgenera are very similar, and the pedicle valves differ only in the presence or absence of dental plates. Thus the new subgenus represents the 'eo' stage of Williams (1953).

Megastrophia (Eomegastrophia) ethica sp. nov.

Plate 39, figs. 7, 9, 10

Diagnosis. *Megastrophia* with dental plates.

Description. Exterior. Convex pedicle valve, concave brachial valve. Ornament of fine parvicostellae, which are irregular both in strength and differentiation. New ribs arise by intercalation. Rugae sometimes present near the ears. Shell thin and often irregular. Umbo not prominent. A small area, considering the size of the shell.

Pedicle interior. Dental plates fused to small denticular plates bearing the denticles. The muscle field is not too well defined owing to the thin shell, but is roughly triangular

EXPLANATION OF PLATE 39

All specimens treated with ammonium chloride. Grid references not given below are in text.

Fig. 1. *Brachyprion arenacea* (Davidson). Brachial internal mould, OUM C8888, $\times 1.7$, from Norbury, Shropshire.

Fig. 2. *Brachyprion* sp. Pedicle internal mould, Bristol University 12131, $\times 1.4$, from 'Damery Beds, Avening Green, Tortworth', Gloucestershire.

Figs. 3, 5, 8. *Amphistrophia whittardi* sp. nov. 3, Pedicle internal mould, OUM C13514, $\times 2.6$. 5, Pedicle valves, mainly exfoliated, holotype top left, OUM C13527-8, $\times 2.0$. 8, Brachial internal mould, OUM C13536, $\times 2.5$. All specimens from Domas, Shropshire.

Figs. 4, 6. *Megastrophia (Eomegastrophia)* sp. 4, Pedicle internal mould, GSM 102719, $\times 1.1$, from '150 yards SW of New House, Marshbrook', Shropshire. 6, Oblique view of same valve, showing musculature and vestigial dental plates.

Figs. 7, 9, 10. *Megastrophia (Eomegastrophia) ethica* sp. nov. 7, 9, Two brachial internal moulds on the same slab, GSM 102717, $\times 1.0$. 10, Pedicle internal mould, holotype, GSM 102715, $\times 1.0$. All specimens from Morrellswood.

Fig. 11. *Pholidostrophia (Eopholidostrophia) sefinensis* (Williams). Pedicle internal mould, holotype, SMA 30051, $\times 2.0$, from River Sefin, Llandovery.

Figs. 12-17. *Pholidostrophia (Eopholidostrophia) salopiensis* sp. nov. 12, 13, Pedicle internal mould, OUM C2756, $\times 2.5$, from Yartleton Beds, May Hill [Grid Ref. SO/6936 2271]. 14, Brachial internal mould, OUM C5650, $\times 1.5$, from Wyche Beds, Malvern Hills [Grid Ref. SO/7430 5152]. 15, Pedicle internal mould, holotype, GSM 102720, $\times 2.5$, from Domas. 16, Partly exfoliated pedicle valve showing dentition, OUM C12668, $\times 3.0$, from Purple Shales of Boathouse Coppice, Shropshire [Grid Ref. SJ/6205 0398]. 17, External view of brachial valve, showing cardinal process, OUM C13996, $\times 3.0$, from Hughley.

and flabellate anteriorly. Adductor scars lanceolate and separated by a small median ridge. Pseudopunctae prominent except on the muscle field, coarsening towards the umbo.

Brachial interior. Strong cardinal process lobes directed ventrally, between which is a small undifferentiated process. Rather weak socket plates diverging at a wide angle, on the posterior part of which are the denticles. Weak notothyrial platform, extending anteriorly into a slight but positive median ridge. Adductor scars oval and flabellate. No mantle canal systems visible.

Type locality. Pentamerus Beds exposed in brook near Morrellswood, Shropshire [Grid Ref. SJ/6284 0637].

Holotype. Pedicle valve, GSM 102715.

Dimensions (in cm.). All specimens from Morrellswood.

			<i>Length</i>	<i>Width</i>
Pedicle valve	GSM 102715	(holotype)	3.02	3.90
" "	GSM 102716		1.61	2.01
Brachial valve	GSM 102717		2.44	2.83
" "	GSM 102718		broken	4.9 approx.

Discussion. This is the only species of *Megastrophia* so far recorded with dental plates, and as it is also the earliest, an ancestral form for the stock may be postulated. Apart from the convexity it is very similar to *Leptostrophia* (*Eostropheodonta*) and it is from this stock that its origins seem most likely. In fact the species might have been put down as an aberrant convex form of *Eostropheodonta* had it not been for the discovery of some more *Eomegastrophia* material (here figured in Pl. 39, figs. 4 and 6 as *Eomegastrophia* sp.) in the Whittard Collection from 'near New House, Marshbrook', a locality not now exposed. This clearly shows the dental plates, but in a much more vestigial form than in *M. (E.) ethica*, and it also shows very well the characteristic megastrophid musculature as well as being rather more convex than the Morrellswood specimens, which occur in a shale.

AMPHISTROPHIA Hall and Clarke 1892

- 1892 *Amphistrophia* Hall and Clarke, p. 292.
 1914 *Strophoprion* Twenhofel, p. 25.
 1939 *Amphistrophia* Caster, p. 100.
 1953 *Amphistrophia* Williams, p. 45.

Discussion. This distinctive convexo-concave stock, so far known only from the Wenlock and Ludlow, has as its type species *Strophomena striata* Hall 1843 from the Waldron Shale of North America. The only ascribed British species is *Orthis funiculata* M' Coy 1846 (Williams 1953, p. 63). A new species is described below, which extends the range of the genus.

Amphistrophia whittardi sp. nov.

Plate 39, figs. 3, 5, 8

- 1932 *Stropheodonta funiculata* (M' Coy); Whittard, list facing p. 896.

Diagnosis. *Amphistrophia* with no muscle bounding ridges and a differentiated ornament.

Description. Exterior. Shape semicircular and slightly mucronate, with umbones not prominent. Convexo-concave with the two valves fairly flat except for the smooth geniculation near the anterior margin, which consists of an increase of convexity rather than a division into disc and trail. Ornament parvicostellate and differentiated to give an impression of uniform segments, which are in detail not uniform either in their size or in the number of smaller costellae between the larger ones. A large costella occurs at approximately 20 degree intervals near the umbo, but other large costellae arise anteriorly so as to keep the distance between them roughly constant. New ribs arise by intercalation. Fairly small area.

Pedicle interior. No dental plates. Small denticular plates with small denticles, which also occur as regularly spaced nodes on up to one-third of the hinge line. Muscles faintly impressed, often invisible, although in a few specimens faint straight bounding ridges diverging at approximately 90 degrees may be seen close to the umbo. Pseudopunctae distributed evenly over the shell.

Brachial interior. Very divergent, rather weak, socket plates. Strong cardinal process lobes which are directed ventrally in the 'disjunct 1' phase (Williams 1953, p. 12). No sign of adductor muscle scars, except as areas of fewer pseudopunctae near the umbo which are separated by an extremely faint platform hardly worthy of the name, consisting of a slight swell immediately anterior to the cardinal process.

Type locality. Purple Shales in the brook near Domas, Shropshire [Grid Ref. SJ/5936 0062].

Holotype. Pedicle valve, OUM C13527. The species is named in honour of the late Professor W. F. Whittard.

Dimensions (in cm.). All pedicle valves from Domas.

		<i>Length</i>	<i>Width</i>
OUM C13527	(holotype)	0.92	1.66
OUM C13522		1.07	1.86
OUM C13528		1.07	1.83
OUM C13526		0.41	0.57

Discussion. Although this is the earliest species of *Amphistrophia* yet described, its morphogeny has proceeded some way along the general trends of stropheodontid phylogeny; for example, it lacks dental plates, has cardinal process lobes in the 'disjunct 1' phase, and even possesses faint denticular nodes on the hinge line itself. Thus even earlier forms of the genus may be expected. There are some specimens very similar to the present species in the Sedgwick Museum (SMA 32569 and SMA 32597) from 'Locality K, below the path SW of Uzmaston, the Frolic, Haverfordwest'. This locality is in the Uzmaston Beds of the Millin Stage (Jones *in* Strahan *et al.* 1914, p. 105), which may be in part slightly older than the Purple Shales, but further work remains to be done on the correlation of the Pembrokeshire succession.

The species differs from *A. funiculata* (M' Coy) from beds of Wenlock or Ludlow age in County Kerry, in not having the high muscle bounding ridges enclosing the oval diductor scars of the latter, and in having differentiated ornament as opposed to approximately equal parvicostellae. It is a rather rare fossil, except at the type locality, where 18 pedicle and 9 brachial valves were recovered (5 per cent. of the total population). The

species is, however, distributed throughout the Purple Shales, but has been found in no other formation in the Welsh Borderland.

PHOLIDOSTROPHIA Hall and Clarke 1892

Discussion. The stropheodontids of the *Pholidostrophia* group have recently been revised by Harper, Johnson, and Boucot (1967, in press). In their paper they divide the early members into two subgenera, a new subgenus with *Stropheodonta (Brachyprion) sefnensis* Williams 1951 as type species, and *Mesopholidostrophia* Williams 1950, on the basis of general evolutionary development. The species described below seems to be intermediate between these subgenera. There is no doubt, however, that its shell is not nacreous, and it is thus ascribed to the earlier subgenus.

Pholidostrophia salopiensis sp. nov.

Plate 39, figs. 12-17

Diagnosis. Early *Pholidostrophia* with very weak ornament and variably developed ridges in the ventral muscle field.

Description. Exterior. Concavo-convex, with the pedicle valve often hemispherical apart from the ears, and the brachial valve with a gentler curve, though the shell convexity varies within a population. Small umbo. Large area with open delthyrium and strong chilidium. The ornament varies from almost non-existent to extremely fine irregular parvicostellae, best developed at the anterior margin. New costellae arise by intercalation. Rugae occur very rarely near the ears. The shell is thick for the size of the species, and secondary calcite deposition has occurred over much of the interior in many specimens.

Pedicle interior. Denticles for about one-third of the hinge line, which are carried on a pair of long denticular plates fused with the hinge line. Diductor muscle field broad, open anteriorly and surrounded at the posterior end by bounding ridges which are straight near the umbo, but may curve inwards slightly before dying out. There are several, usually three (one of which may be median), ridges of an irregular nature running antero-laterally in the muscle field. Lanceolate adductor muscle scars often well-impressed posteriorly, but fading anteriorly into the ridge pattern. No internal trace of ornament, but coarse pseudopunctae cover most of the valve except close to the anterior commissure.

Brachial interior. Prominent disjunct cardinal process, with the two lobes supported at the base by a shell thickening, which often produces a small knob on the exterior (Pl. 39, fig. 17), probably an exaggeration of the original protegular node. Widely divergent and slightly curving socket plates. Denticles on the hinge line. Small oval adductor muscle scars close to the umbo, separated by a slight ridge forming a platform which goes back to the base of the cardinal process. As with the pedicle valve there is no internal sign of the ornament, and coarse pseudopunctae cover most of the shell.

Type locality. Domas, Shropshire (same as *Amphistrophia whittardi*).

Holotype. Pedicle valve, GSM 102720.

Dimensions (in cm.).

				<i>Length</i>	<i>Width</i>
Domas	Pedicle valve	GSM 102720	(holotype)	0.60	0.92
Hughley	„ „	OUM C13983		0.61	1.10
„	„ „	OUM C13991		0.37	0.61
„	Brachial valve	OUM C13996		0.42	0.74

Discussion. The pholidostrophid which occurs commonly over the whole Welsh Borderland in beds of C₄ to C₆ age differs from the earlier *P. sefinensis* (Williams 1951) in the much weaker ribbing and in the development of variable ridges in the ventral muscle field, which replace the well-developed parvicostellate ornament and the fine straight solitary median ridge of the latter species. *P. salopiensis* occurs in all types of sediment from sandstone to fine shale and was much more successful in terms of numbers than *sefinensis* (whose holotype is refigured here (Pl. 39, fig. 11) for comparison). The two species are undoubtedly very closely related, and it is tempting to think that the first may be the ancestor of the second, although there is no detailed statistical information at the moment on populations of successive ages; but several features of the present species, such as the cardinal process lobes (which have proceeded further on the 'disjunct' line of Williams 1953, p. 12), suggest that it may well be a phylogenetic descendant of *sefinensis*. Despite the fact that pholidostrophids occur commonly at many if not most localities, no species has been figured or described from anywhere in the British Llandovery apart from the original description of *sefinensis* (Williams 1951, p. 124).

STROPHONELLA Hall 1879

Discussion. A few large resupinate brachiopods belonging to the genus *Strophonella* have been found at various Llandovery localities in the Welsh Borderland. They are all in poor condition and form such an insignificant part of the fauna that full description is withheld until better material has been found. Until then they may be compared with *S. (Eostrophonella) davidsoni* (Holtedahl 1916), which is a C₁ form from Llandovery described by Williams (1951, p. 128). They certainly do not have the prominent musculature of the Wenlock *S. (Strophonella) euglyphya* (Hisinger 1819). Unfortunately no complete pedicle valve has been found, and so it is not known whether the specimens possess dental plates, which prevents them from being positively assigned to their correct subgenus within *Strophonella*.

Material. Wyche Beds, Malvern Hills [Grid Ref. SO/7672 4442], 1 pedicle valve. Bog Mine, Shropshire [Grid Ref. SO/3510 9815], 1 brachial valve. There is also one specimen in the Geological Survey Museum from Hope Quarry, a brachial valve (GSM 11703).

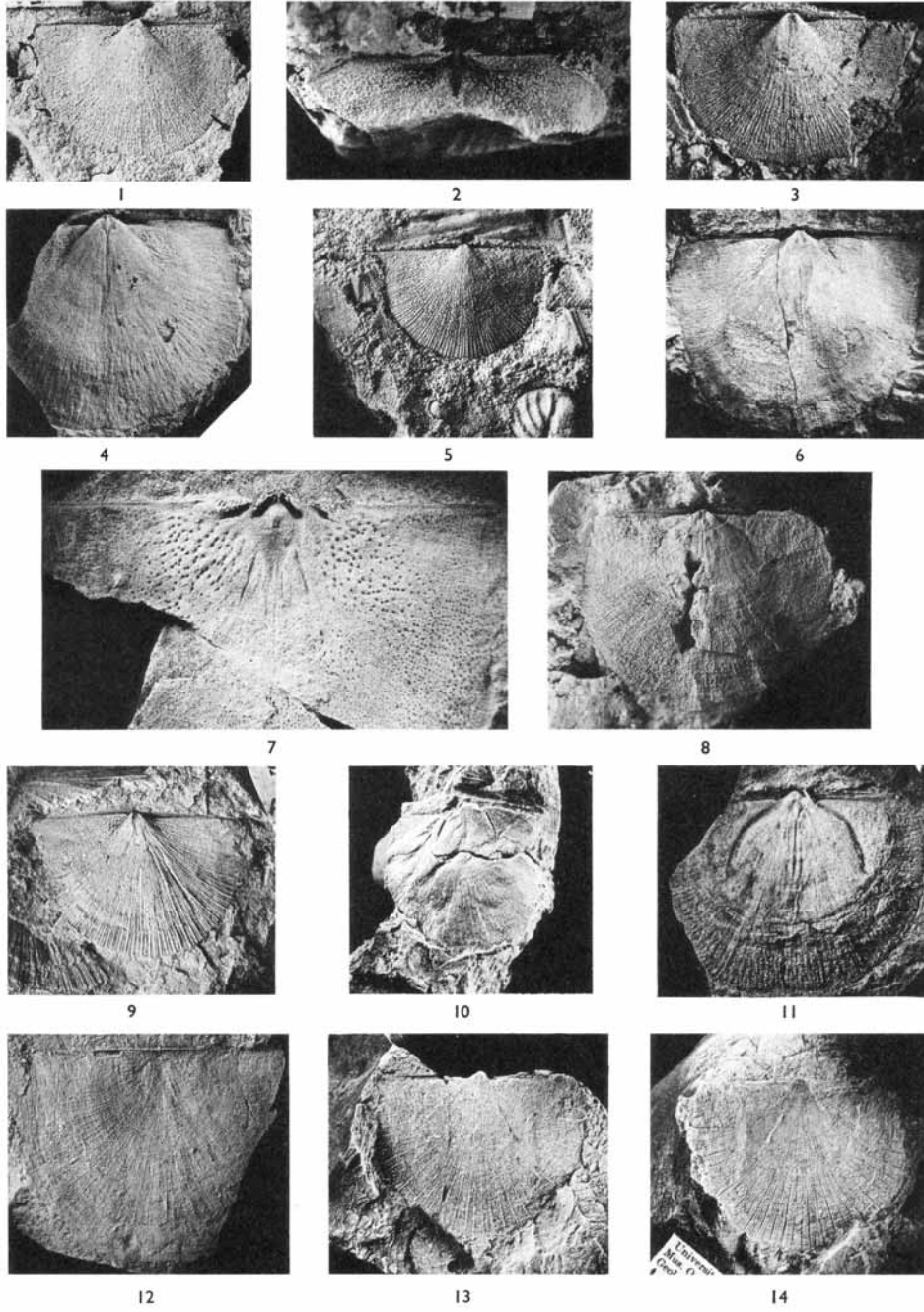
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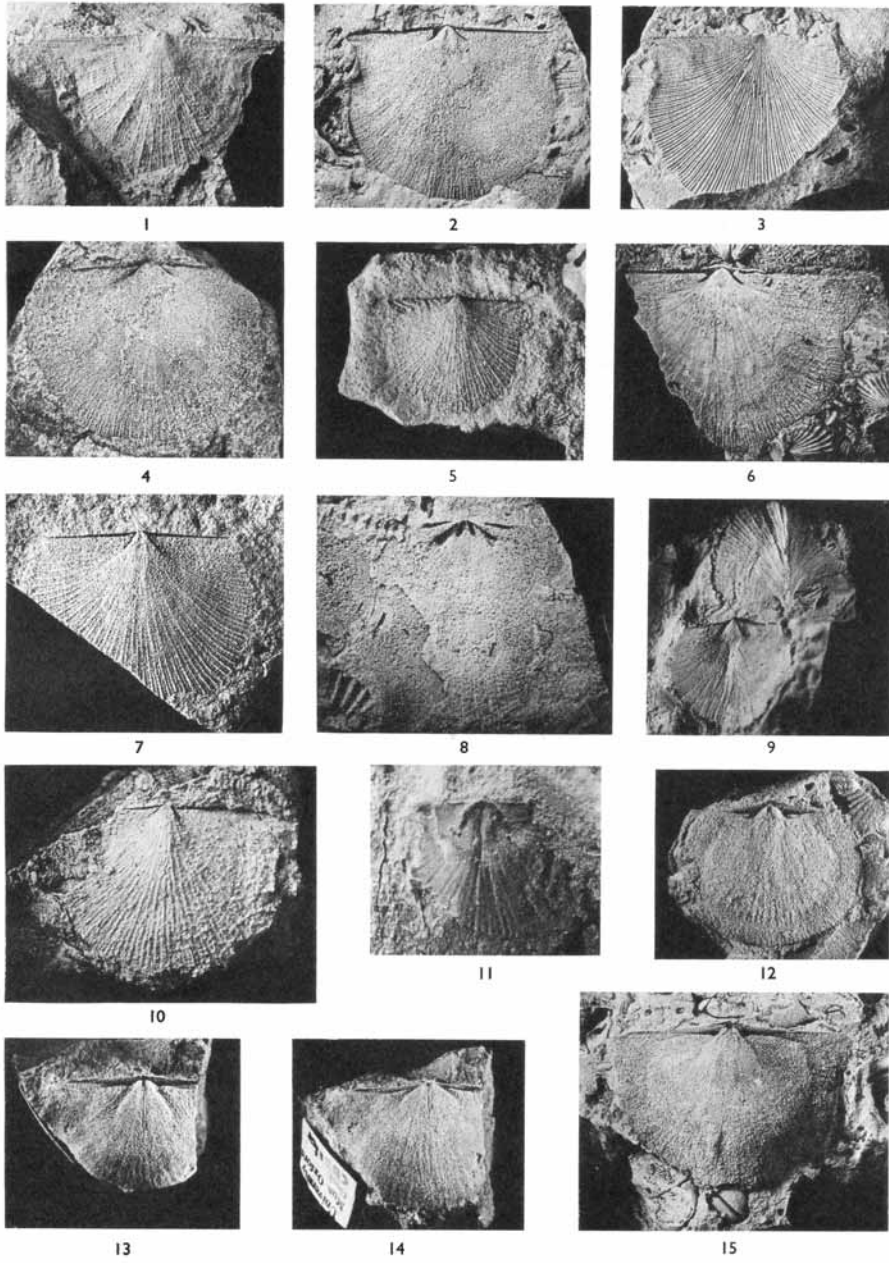
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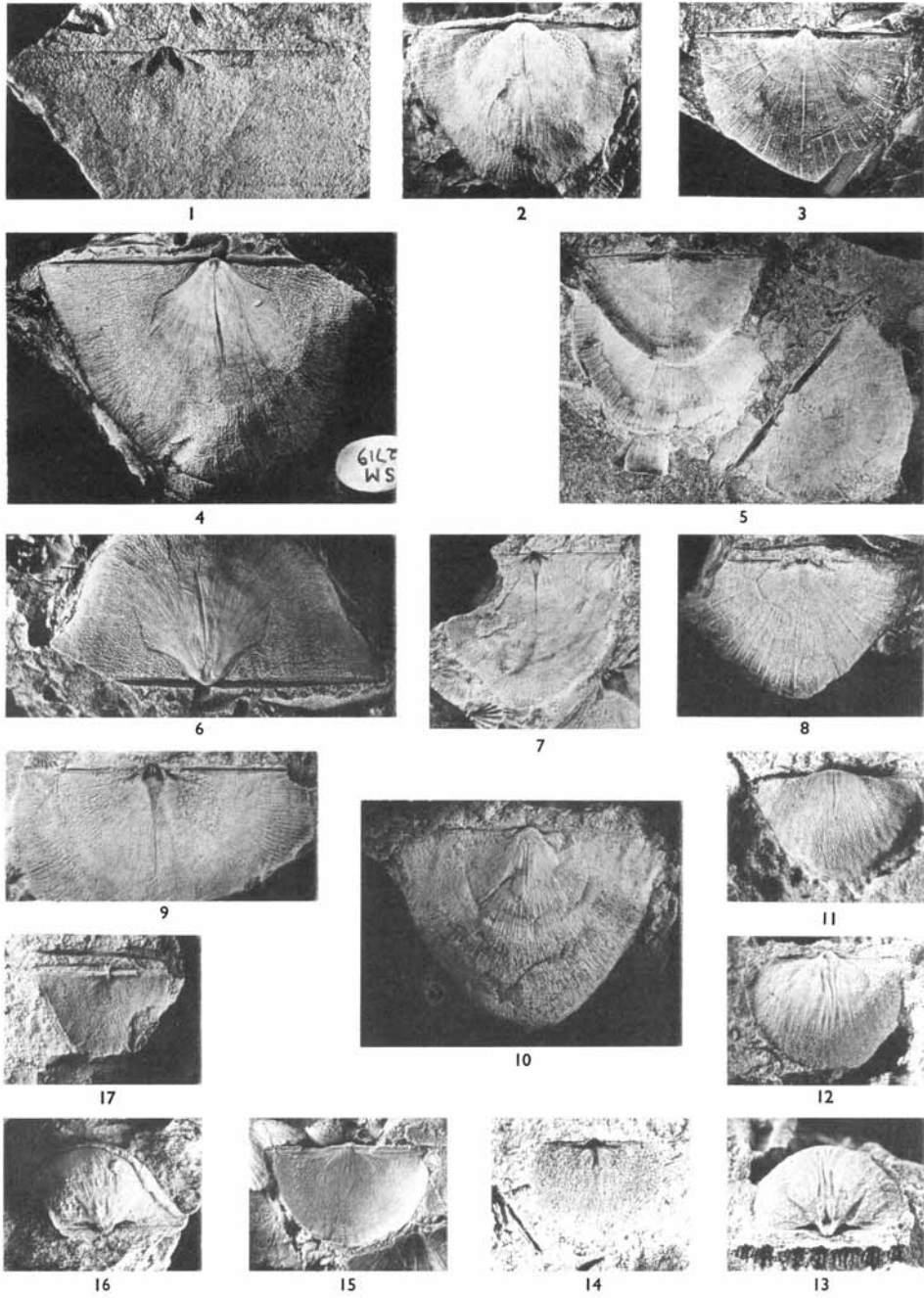
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