Type specimens of some Upper Palaeozoic Athyridide brachiopods

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Synopsis

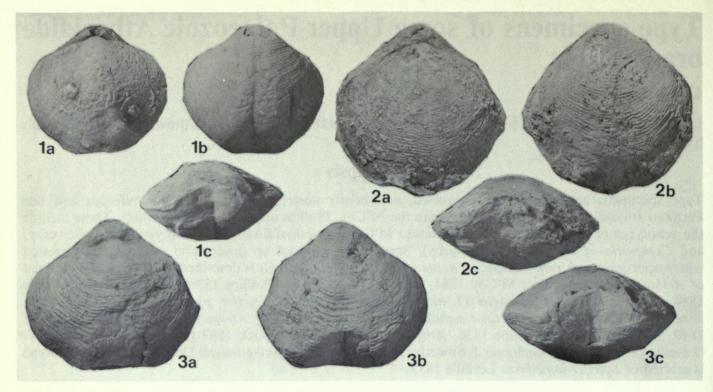
Type specimens are selected or recognized, and briefly described, of eleven Carboniferous and one Permian athyridide species, principally from the M'Coy, Phillips and Sowerby collections. These include the genotypes of Actinoconchus—A. paradoxus M'Coy, Cleiothyridina—C. pectinifera (J. de C. Sowerby) and Composita—C. ambigua (J. Sowerby). Species are assigned to genera and synonymies suggested where appropriate. A new subspecies Actinoconchus expansus patulus is described. Lectotypes are selected of Actinoconchus paradoxus M'Coy 1844, A. expansus expansus (Phillips 1836), Atrypa? obtusa M'Coy 1844 [?= Actinoconchus oblongus (J. de C. Sowerby 1840)], Spirifer planosulcatus Phillips 1836, S. squamosa Phillips 1836 [= Actinoconchus lamellosus (Léveillé 1835)], Atrypa pectinifera J. de C. Sowerby 1840, Spirifer fimbriata Phillips 1836, Athyris squamigera de Koninck 1887 [= Cleiothyridina deroissyi (Léveillé 1835)], Spirifer ambiguus J. Sowerby 1822 and Athyris carringtoniana Davidson 1862. A neotype is erected of Spirifer lamellosus Léveillé 1835.

Introduction

Some years ago, while working on the spire-bearing brachiopods from an Irish Viséan silicified fauna, it became apparent that type specimens had not been selected of several athyridide species in the collections of nineteenth-century authors. More recently correspondence with palaeontologists in Europe and Russia indicates the need for the selection of types in the genera *Actinoconchus*, *Cleiothyridina* and *Composita* without waiting for the publication of the complete Irish fauna. In addition I have already dealt with the case for the type species of *Cleiothyridina* (1972, 1976), and many of the specimens from which types should be chosen are in my care at the British Museum (Natural History).

The subfamily Athyridinae is represented by the following Carboniferous and Permian genera: *Athyris* M'Coy, *Actinoconchus* M'Coy, *Cleiothyridina* Buckman, *Composita* Brown, *Deltachania* Waterhouse, *Nordathyris* Grunt and *Planalvus* Carter. The relationship between M'Coy's two genera is complicated, and briefly discussed below, and the other genus I am concerned with is *Cleiothyridina*. In addition the type species of *Composita*, *Spirifer ambiguus* J. Sowerby, 1822, has its lectotype selected (Figs 26–28), and potential types of *Terebratula concentrica* von Buch 1834 are figured (Figs 1–3).

When distinguishing *Athyris* from *Actinoconchus* M'Coy (1844: 146, 149) stressed that the latter had greatly extended frills 'forming a flat, circular, striated disc', and, on the basis of his single species, he appears to have considered it a non-sulcate and flatter genus than *Athyris*. The type species of *Athyris*, by subsequent designation of King (1850), is *Terebratula concentrica* von Buch 1834, from the mid-Devonian of Gerolstein, Germany. In the Palaeontological Museum of the Humboldt University of Berlin there are six specimens, kindly lent by Dr Jaeger, from the L. von Buch collection, labelled by him as *T. concentrica*, or varieties of the species. Three were given variety names and three were simply called *T. concentrica* and said to be from Bensberg, near Köln. This locality conflicts with that given in the original publication, Gerolstein, which is generally considered to be correct. Von Buch (1834) did not figure his species, and since the Eifel region of Germany is rich in athyrid species it is important to establish a type specimen for *A. concentricus*. In my view this should be done using one of von Buch's original specimens, provided there is no good reason to doubt their validity, even if this results in a change in our concept of the species. However, the selection should be left to those German palaeontologists



Figs 1-3 Athyris concentricus (von Buch). Possible syntypes from the mid-Devonian of the Eifel region, Germany. Von Buch coll., Humboldt University Museum, Berlin, nos 10–12, each viewed dorsally, ventrally and anteriorly. All ×1.5. Fig. 1a-c, no. 10. Fig. 2a-c, no. 11. Fig. 3a-c, no. 12.

most familiar with the athyrid faunas of the region and all possible von Buch material, and for this reason I do no more than figure (Figs 1-3) the three von Buch specimens known to me, which appear to represent his concept of the species, although differing somewhat from his original description.

In 1844 the only species M'Coy described under Actinoconchus was A. paradoxus M'Coy (1844 : 150; pl. 21, figs 6a-c), which is therefore the type species. Davidson (1859) placed A. paradoxus into synonymy with Athyris planosulcata (Phillips, 1836) and most authors have accepted this, with the result that the Treatise (Williams et al. 1965 : H662) states that Phillips' species is the type of Actinoconchus. I agree with Carter (1967) in believing the two species to be distinct and so retain the name A. paradoxus for the type species of Actinoconchus.

A complication in the differentiation of *Athyris* from *Actinoconchus* stems from M'Coy's own work (1844 : 149, footnote) when he added the information that a specimen he identified as *Athyris squamosa* (Phillips, 1836), which he correctly put in synonymy with *Spirifer lamellosus* Léveillé, 1835, had lamellose extensions forming frills, as in his species *Actinoconchus paradoxus*. He then, surprisingly, concluded that *A. paradoxus* '... may therefore be an *Athyris*'. M'Coy's assignment of *S. lamellosus* to *Athyris* has been followed and the species was figured in the Treatise (Williams *et al.* 1965 : fig. 537, 4b–d) as illustrating the genus. I believe, however, that *S. lamellosus* is more closely related to *A. paradoxus* than to *Athyris concentrica* and that it should be assigned to *Actinoconchus*. This means that *Athyris* remains a genus more typical of Devonian than Carboniferous rocks and contains species lacking the long lamellose shelly extensions typical of *Actinoconchus* and *Cleiothyridina* species.

The case has been presented (Brunton 1972) and accepted (ICZN 1976) for the validation of the generic name *Cleiothyridina* and for the acceptance of *Atrypa pectinifera* J. de C. Sowerby, 1840, as the type species. In the application it was pointed out that the name S. *deroissyi* Léveillé, 1835, had been misinterpreted by Davidson (1861) and confused with *Spirifer fimbriata* Phillips, 1836. Both these names belong to recognizable species assigned to *Cleiothyridina*, but *C. fimbriata* is the commoner species in Viséan rocks of western Europe and was figured by Davidson (1861 : pl. 18, figs 8, 10, 11) as '*Athyris Roysii*'. Léveillé's original spelling *De Roissyi* should now be accepted as *deroissyi*. The name was also used by de Koninck over many years to include several

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species, and by 1887 he had split his concept of the species into Athyris Leveillei and Athyris roissyi, which included not only Léveillé's true species but also C. fimbriata.

M'Coy's (1844) species were based on material in the Griffith Collection, housed in the National Museum of Ireland, Dublin; Phillips' (1836) species were mostly described from the Gilbertson Collection which, with collections of the Sowerbys, is housed in the British Museum (Natural History), London.

Few of the type species described here have ever been refigured since their original publications, and the figures herein are commonly the first photographic illustrations to be presented.

Systematic palaeontology

The notation in the synonymy lists follows Matthews (1973) and outline shape descriptions, where applicable, follow the Systematics Association Committee for Descriptive Biological Terminology (Exell & Lewis 1962).

Family ATHYRIDIDAE Davidson, 1881

Subfamily ATHYRIDINAE Davidson, 1881

Since the work of Boucot, Johnson & Staton (1964), for the brachiopod volume of the Treatise on Invertebrate Paleontology (Williams *et al.* 1965), the family name has usually been assigned to M'Coy, 1844. However, Alvarez, Brime & Brunton (1980) point out that M'Coy's (1844) use of the family name 'Athyridae' does not comply with the rules of the International Code of Zoological Nomenclature (1964) in Article 11, section (e), which states that a family-group name must, when first published, be based on the name of a valid contained genus. Although M'Coy established the new genus *Athyris* in 1844 he placed it in the 'Delthyridae', not the 'Athyridae', a family which remained without the genus name *Athyris* until united by Davidson (1881).

Genus ATHYRIS M'Coy, 1844

TYPE SPECIES. Terebratula concentrica von Buch, 1834 by subsequent designation of King, 1850.

Athyris concentricus (von Buch)

TYPE SPECIMEN. No type specimen has yet been selected. As already indicated, some possible syntypes from von Buch's collection, and named T. concentrica by von Buch, are in the Humboldt University Museum, Berlin (Figs 1–3). However, the situation of Devonian athyrids from the Eifel region of Germany is complex and until palaeontologists there designate a type for the species it is difficult to make a diagnosis of the species or genus.

I think the generic description needs to be emended, from that of Williams *et al.* (1965 : H662), to exclude the very wide and strongly lamellose forms like *A. lamellosus*, which I place in *Actinoconchus*.

Genus ACTINOCONCHUS M'Coy, 1844

DIAGNOSIS. Athyridinae bearing long delicate flanges of shell from rugae or strong growth lines on both valves.

TYPE SPECIES. Actinoconchus paradoxus M'Coy (1844 : 150; pl. 21, figs 6a, b). The only species described by M'Coy in his new genus.

Actinoconchus paradoxus M'Coy

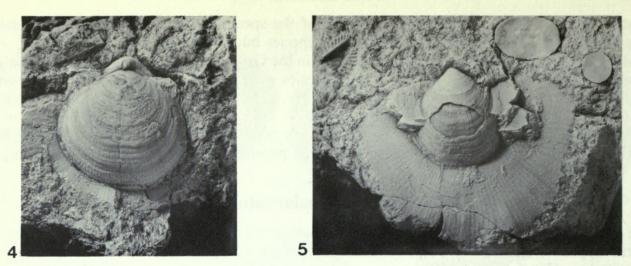
Figs 4-6

v. 1840 Atrypa expansa (Phillips); J. de C. Sowerby (pars) : 14; pl. 617, fig. 1 - lower right only.

v* 1844 Actinoconchus paradoxus M'Coy : 150; pl. 21, figs 6a, b (not 6c).

v. 1859 Athyris planosulcata (Phillips); Davidson (pars): 80; pl. 16, figs 9, 10, 11.

1887 Athyris planosulcata (Phillips); sensu de Koninck (pars) : pl. 21, figs 17, 18, 19.



Figs 4-5 Actinoconchus paradoxus M'Coy. ×1.5. Fig. 4, lectotype (herein selected), from Millicent, Clane, Co. Kildare, Ireland. Griffith coll. in National Museum of Ireland, Dublin. Viewed dorsally, showing part of the radially striated flat shell flange. Fig. 5, from Kildare, Ireland. Davidson coll., BM(NH) B 5392. Viewed ventrally, showing the full extent of one flange and parts of others.

DIAGNOSIS. Subcircular outline, equibiconvex profile, lacking median sulcus or fold. Lamellose flanges flat with fine radiating striations.

TYPE SPECIMEN. In the National Museum of Ireland, Dublin there are five specimens labelled as *A. paradoxus* M'Coy in the Griffith Coll. Two of these are not *A. paradoxus*, and of the other three specimens none is clearly the subject of M'Coy's figs 6a-c. Two specimens, however, are of particular interest. One, from 'Knockagh, Dundalk', is a specimen on black limestone, also containing large fragments of the davidsoniacean brachiopod *Brochocarina* cf. *wexfordensis* (Smyth), one of which underlies the *A. paradoxus* specimen and was probably mistakenly believed to be the lamellose flange. This specimen may have been the origin of M'Coy's fig. 6c, since the illustrated flange extends too far posteriorly and is too strongly ribbed for true *A. paradoxus*, but resembles the combination of *A. paradoxus* with the davidsoniacean¹. Another syntype, from 'Millicent, Clane', Co. Kildare, is well preserved and may have provided information for figure 6a. This specimen is here selected as **lectotype** and figured (Fig. 4). It is probably of early Viséan, Chadian age.

Actinoconchus expansus expansus (Phillips)

Fig. 10

- v* 1836 Spirifera expansa Phillips : 220; pl. 10, fig. 18.
- v. 1840 Atrypa expansa (Phillips) J. de C. Sowerby (pars) : 14; pl. 617, fig. 1 middle two and lower left.
- ? 1859 Athyris planosulcata (Phillips); Davidson (pars) : pl. 16, fig. 4.
- 1859 Athyris expansa (Phillips); Davidson (pars) : pl. 16, figs 14, ? 16.

DIAGNOSIS. Transversely oval in outline, lacking median sulcus. Short delicate flanges from weakly developed growth lines.

TYPE SPECIMEN. Spirifer expansa Phillips (1836 : pl. 10, fig. 18). Gilbertson Coll., Bolland, Yorkshire; probably of late Chadian to early Arundian (early Viséan) age. Here selected lectotype – BM(NH) Pal. Dept. reg. no. B 314.

Actinoconchus expansus patulus subsp. nov.

Figs 7-9

1859 Athyris expansa (Phillips); Davidson (pars) : pl. 16, figs 17-18, ? 16.

¹Flanges as in M'Coy's fig. 6c would not have been possible in life as they would have prevented opening of the valves.

NAME. Latin patulus, meaning spread out or broad.

HOLOTYPE. BM(NH) Pal. Dept. reg. no. 74355. Etheridge Coll. From Viséan limestones of the Kendal region, Cumbria (Fig. 7). It is similar to the specimen illustrated by Davidson (1859 : pl. 16, fig. 17, 17a), also from Kendal.

DIAGNOSIS. Broad, flattened shells, wider than long. Faint external ornamentation of growth lines, rarely preserved, with short delicate lamellae. Exfoliated surfaces display a delicate radial pattern. Valves remain thin-shelled.

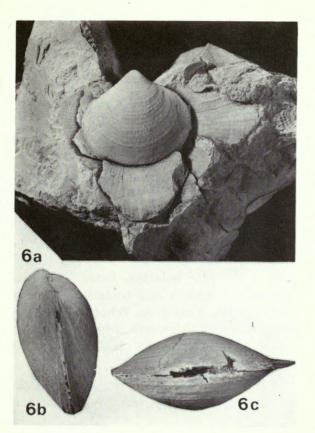
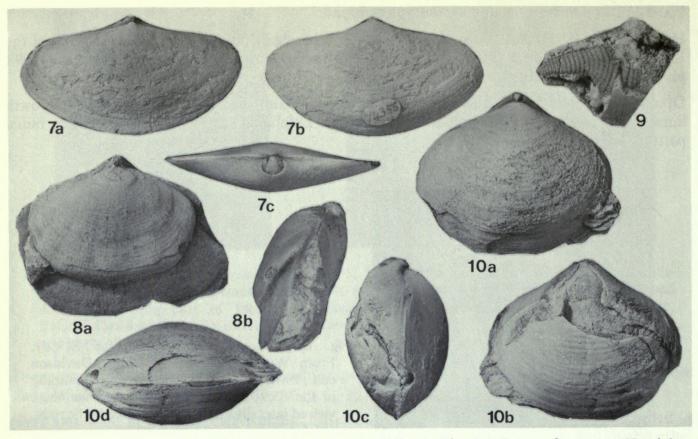


Fig. 6a-c Actinoconchus paradoxus M'Coy. From Wetton Hill, Staffordshire. Davidson coll., BM(NH) B 5396. Fig. 6a viewed ventrally in the rock, with its flanges, $\times 1$. Figs 6b, c viewed laterally and anteriorly, free of the rock, $\times 1.5$.

DISCUSSION. The name Athyris expansa has been used for many years for specimens having a wide variety of shapes. In particular there are low, wide and apparently rather smooth distinctive forms, such as illustrated by Davidson (1859 : pl. 16, figs 17, 18). The specimen for fig. 17 is in the collections of the Institute of Geological Sciences, Leeds, numbered GSL504. The original specimen for fig. 18 is in the Yorkshire Museum, York, YM817. These broad forms, having widths varying from just exceeding their length to almost twice their length, are characterized by having finer growth lamellae than A. expansus expansus and in displaying a fine radial ribbing when the outer shell layers are removed by abrasion (Fig. 8a). Unfortunately locality information accompanying the studied specimens (about 40) is insufficiently precise to tell what geographical or ecological factors controlled the distribution of these specimens. If distinctive distributions could be demonstrated I think these shells should be considered a new species, despite their broadly scattered dimensional plots, which almost include the plot for the lectotype of A. expansus expansus. At present, so as to allow easy reference to the specimens, I propose that they be treated as a sub species. Specimens thought to be conspecific with them are known (D. Mundy, personal communication) from the Asbian limestones of the Craven 'Reef' belt of north Yorkshire. Rocks of a similar late Viséan age also occur in the Kendal region of Cumbria.

> Actinoconchus oblongus (J. de C. Sowerby) Figs 11, 12

v* 1840 Atrypa oblonga J. de C. Sowerby : 16; pl. 617, fig. 3.



- Figs 7-9 Actinoconchus expansus patulus subsp. nov. All $\times 1$. Fig. 7, holotype, from near Kendal, Cumbria. Etheridge coll., BM(NH) 74355, viewed dorsally, ventrally and posteriorly. The shell material is broken from the ventral umbo. Fig. 8, from Settle, Yorkshire. Wheelton Hind coll., BM(NH) B 52835, viewed dorsally and laterally. Showing a step in growth, which affected both valves; this is not a marginal flange. Fig. 9, from Parkhouse Hill, Derbyshire. Wheelton Hind coll., BM(NH) B 52840. Ventral view showing part of the spiralia.
- Fig. 10 Actinoconchus expansus expansus (Phillips), $\times 1$. Lectotype (herein selected), from Bolland, Yorkshire. Gilbertson coll., BM(NH) B 314, viewed dorsally, ventrally, laterally and anteriorly.

v? 1844 Atrypa? obtusa M'Coy : 155; pl. 22, fig. 20².

1859 Athyris planosulcata var. oblonga (J. de C. Sowerby) Davidson : pl. 16, figs 13, 13a (copied from Sowerby 1840).

DIAGNOSIS. Elongate oval in outline with slight anterior sulcation in both valves forming marginal ligation. Thickness about three-quarters maximum width. Weakly lamellose exterior with? short delicate flanges.

TYPE SPECIMEN. Atrypa oblonga J. de C. Sowerby (1840 : pl. 617, fig. 3). BM(NH) Pal. Dept. reg. no. B 61035. Sowerby Coll., Queen's County (Co. Laois), Ireland. Here recognized as holotype, as being the only specimen available to Sowerby in 1840 (p. 16). Fig. 11.

Actinoconchus planosulcatus (Phillips)

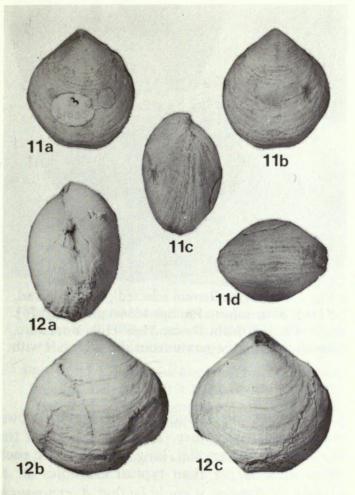
Figs 13, 14

- v* 1836 Spirifera planosulcata Phillips : 220; pl. 10, fig. 15.
- v. 1840 Atrypa planosulcata (Phillips) J. de C. Sowerby : pl. 617, fig. 2, left side and bottom right.
 - 1859 Athyris planosulcata (Phillips); Davidson : pl. 16, fig. 2 (redrawn from Phillips, 1836).

²In the National Museum of Ireland, Dublin (Griffith Collection) there are two specimens of *Atrypa obtusa* M'Coy. The larger specimen, from 'Skerries, Milverton', about 18 miles north of Dublin, is very similar to this figure and is here selected **lectotype** (Fig. 12). The smaller specimen is also marked as coming from 'Milverton', and is conspecific. These specimens lack the slight anterior sulcation and are relatively slightly wider than the type specimen of *A. oblonga*.

DIAGNOSIS. Irregular pentagonal outline, slightly wider than long with thickness approximately half of width. Both valves with persistent shallow median sulci forming ligate anterior. Ornament of weakly developed shell lamellae and rarely preserved broad delicate flanges.

TYPE SPECIMEN. Spirifer planosulcata Phillips (1836 : 220; pl. 10, fig. 15). BM(NH) Pal. Dept. reg. no. B 317. Gilbertson Coll., Bolland, Yorkshire. Here selected lectotype. Conspecific specimens from the Craven 'Reef' belt, north Yorkshire, are of late Viséan, Asbian age.



- Fig. 11 Actinoconchus oblongus (J. de C. Sowerby), $\times 1$. Holotype from Queen's County [Laois], Ireland. Sowerby coll., BM(NH) B 61035, viewed dorsally, ventrally, laterally and anteriorly. [= Atrypa oblonga J. de C. Sowerby 1840 : pl. 617, fig. 3.]
- Fig. 12 Actinoconchus obtusus (M'Coy), $\times 1$. Lectotype (herein selected), from Skerries, Milverton, Ireland. Griffith coll., National Museum of Ireland, Dublin; viewed laterally, ventrally and dorsally. [Here placed provisionally in synonymy with A. oblongus].

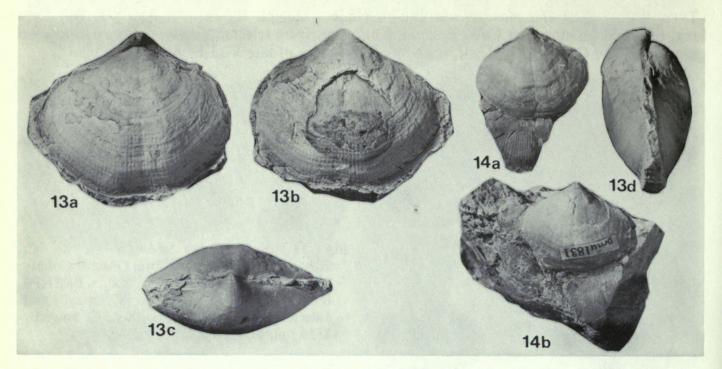
Actinoconchus lamellosus (Léveillé) Figs 15–17

- 1835 Spirifer lamellosus Léveillé : 39; pl. 2, figs 21-23.
- v* 1836 Spirifer squamosa Phillips : 220; pl. 10, fig. 21.
- v. 1859 Athyris lamellosa (Léveillé); Davidson : pl. 16, figs 1, 1a, b.
- v. 1863 Athyris lamellosa (Léveillé); Davidson : pl. 51, fig. 14.
 - 1887 Athyris lamellosa (Léveillé); de Koninck; pl. 21, figs 1-3, ? 4, 5 (? 6-8) 11, 12.
 - 1965 Athyris lamellosa (Léveillé); Boucot, Johnson & Staton in Williams et al. : fig. 535, 4a, b, c.

DIAGNOSIS. Depressed obovate in outline. Persistent ventral sulcus, with or without shallow dorsal sulcus, and strong rounded uniplicate anterior commissure. Long, radially corrugated shell flanges extending from rugae displaying growth lines.

TYPE SPECIMENS. Léveillé's types appear to be lost (Gaetani 1968 : 711). M'Coy (1844 : 148) synonymized S. squamosa Phillips 1836 (Lectotype B 309, Fig. 15, in the Gilbertson Coll., BM(NH), herein selected) with S. lamellosus Léveillé, 1835, and this has been accepted by most subsequent authors. Léveillé described the species from the shales in the Tournai region, Belgium. A neotype (Fig. 16), closely corresponding to Léveillé's figs 21 and 23, and coming from the

well-known silicified fossiliferous shales of that region, is here erected. It is from the Piret Coll., BM(NH) Pal. Dept. reg. no. B 20138, and most probably was collected from late Tournaisian (Tn3b) strata.



Figs 13-14 Actinoconchus planosulcatus (Phillips). Fig. 13, lectotype (herein selected), from Bolland, Yorkshire. Gilbertson coll., BM(NH) B 317, $\times 1.5$ [= S. planosulcata Phillips 1836 : pl. 10, fig. 15]. Viewed dorsally, ventrally, posteriorly and laterally. Fig. 14, from Butter Haw Hill, Yorkshire. Mundy coll. 1831, BM(NH) BB 62974, $\times 0.9$. Viewed dorsally, separate from the rock but with part of its flange, and ventrally, as in the rock.

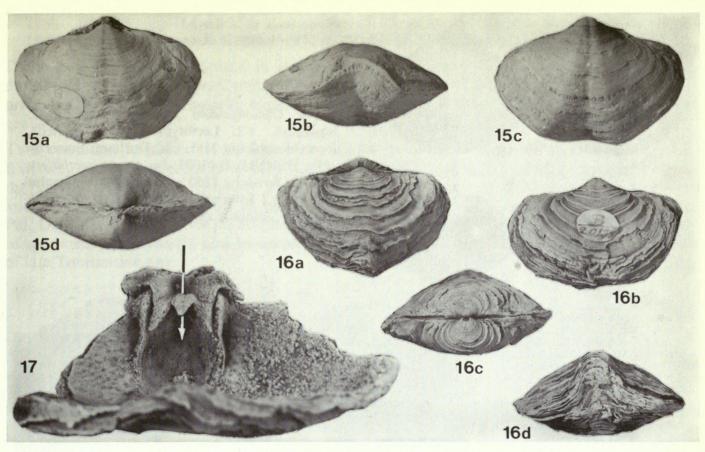
DISCUSSION. The five species assigned above to Actinoconchus include all the better known specific names used in nineteenth century western European literature. The type species of the genus, A. paradoxus, is distinctive in its subcircular outline and very flat, long shelly flanges, each having radial ornamentation. A. expansus expansus grew larger than typical examples of A. paradoxus, is broader than long, but had similar lamellose flanges; it could be that A. expansus is simply a large form of A. paradoxus, and if this proves to be so the name predates that of M'Coy. A. oblongus is an unusual species, the like of which, other than Sowerby's type, I have not seen. The length is greater than the width and at the opposed anterior margin the commissure is slightly ligate. In other respects the known features are similar to A. paradoxus, and since both came from southern Ireland it may be that A. oblongus is an unusually elongate form of A. paradoxus is characterized by its pentagonal outline and ligate anterior. The name has been much confused and misused, largely because Davidson (1859) applied it to specimens as distinctive as A. lamellosus and A. paradoxus.

Actinoconchus species are known throughout the Lower Carboniferous of North America, Europe and the Middle East, but seem to be absent from north-eastern USSR and Australia. It does not extend into the Permian.

Genus CLEIOTHYRIDINA Buckman, 1906

DIAGNOSIS. Athyridinae with lamellose growth bands bearing flattened spine-like frills.

TYPE SPECIES. Atrypa pectinifera J. de C. Sowerby (1840 : 14; pl. 616). Validated by the I.C.Z.N. (1976).



- **Fig. 15** Actinoconchus squamosus (Phillips), ×1.0. Lectotype (herein selected), from near Kendal, Cumbria. Gilbertson coll., BM(NH) B 309. Viewed dorsally, anteriorly, ventrally and posteriorly. [Here placed in synonymy with A. lamellosus].
- Figs 16–17 Actinoconchus lamellosus (Léveillé). Fig. 16, neotype (herein erected), from the Tournai region, Belgium. Piret coll., BM(NH) B 20138, $\times 1$. Viewed dorsally, ventrally, posteriorly and anteriorly. The well-preserved strongly lamellose ornamentation results from the specimen being silicified. Fig. 17, from the same collection as Fig. 16, BM(NH) BB 62961, $\times 3$. The interior of the umbonal regions of a silicified specimen showing the articulation, dental plates, cardinal plate (perforated at arrow) and pedicle cavity.

Cleiothyridina pectinifera (J. de C. Sowerby) Fig. 18

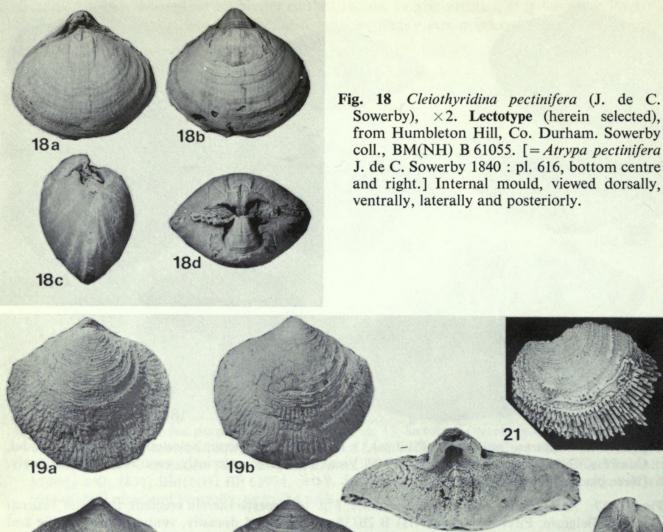
- v* 1840 Atrypa pectinifera J. de C. Sowerby : 14; pl. 616.
 - 1850 Cleiothyris pectinifera (J. de C. Sowerby) King : 138; pl. 10, figs 1-10.
 - 1858 Athyris pectinifera (J. de C. Sowerby) Davidson : 21; pl. 1, figs 50-56; pl. 2, figs 1-5.

DIAGNOSIS. Small (up to about 15 mm wide), broadly ovate in outline and strongly biconvex in profile. Concentric shell lamellae with spinose frills.

TYPE SPECIMEN. Atrypa pectinifera J. de C. Sowerby (1840 : pl. 616, specimen illustrated at the bottom right and centre). BM(NH) Pal. Dept. reg. no. B 61055. Sowerby Coll., from Humbleton Hill, Co. Durham; of Upper Permian age. Here selected **lectotype.**

Cleiothyridina fimbriata (Phillips) Figs 19–22

- 1836 Spirifer fimbriata Phillips : 220 (no figs).
- 1843 Terebratula plano-sulcata (Phillips); de Koninck : 301 (pars); pl. 21, figs 1e, f.
- ? 1844 Athyris depressa M'Coy : 147; pl. 18, fig. 7.
- v. 1861 Athyris Royssii (Léveillé); Davidson : 84 (pars); pl. 18, figs 8-11 (fig. 11 from Phillips' specimen).



22 20a 20b 20 Figs 19–22 Cleiothyridina fimbriata (Phillips). Fig. 19, lectotype (herein selected), from Florence

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Court, Co. Fermanagh, Ireland. Phillips coll., Oxford University Museum, E 1093, $\times 2$. Viewed dorsally and ventrally. Fig. 20, from Lesmahago, Lanarkshire, Scotland. Davidson coll., BM(NH) BB 62973, $\times 1.5$. Viewed dorsally, ventrally, anteriorly and laterally. Figs 21–22, silicified specimens from near Derrygonnelly, Co. Fermanagh, Ireland. Fig. 21, BM(NH) BB 62975, ×2.5; part of a dorsal valve, showing well-preserved ornamentation. Fig. 22, BM(NH) BB 62976, ×3; dorsal valve interior showing the inner socket ridges and perforated cardinal plate.

DIAGNOSIS. Subcircular to very broadly obovate in outline, with plain, rectimarginate anterior commissure. Thin concentric shell lamellae separate into long spinose frills.

TYPE SPECIMEN. Spirifer fimbriata Phillips (1836: 220). Oxford University Museum, E 1093. Phillips Coll., from Florence Court, near Enniskillen, Co. Fermanagh, Ireland; probably of early D₁ Asbian age. Here selected lectotype; replica in BM(NH), Pal. Dept. reg. no. BB 58678.

Cleiothyridina deroissyi (Léveillé)

Figs 23-24

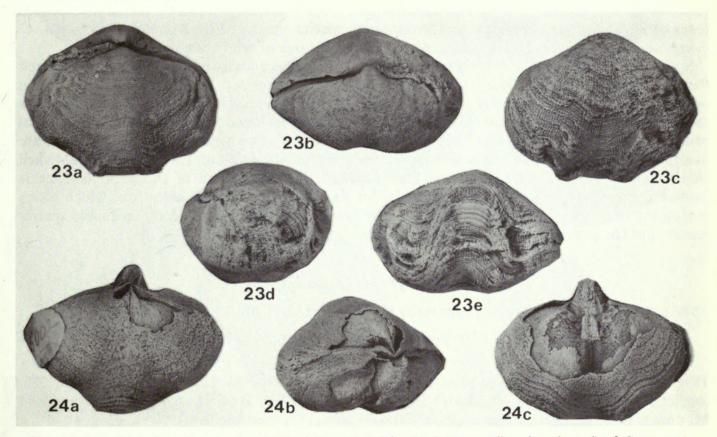
1835 Spirifer De Roissyi Léveillé : 39; pl. 2, figs 18-20.

Terebratula Royssii (Léveillé) de Koninck (pars) : 300; pl. 21, figs 1a?, 1b-d. 1843

1887 Athyris Roissyi (Léveillé); de Koninck (pars) : 82; pl. 19, figs 28, 29.
1887 Athyris squamigera de Koninck : 82; pl. 20, figs 16–22.

DIAGNOSIS. Transversely elliptical in outline, strongly biconvex in profile, and with persistent dorsal fold and ventral sulcus forming strongly parasulcate anterior commissure. Pedicle aperture present. Closely spaced, radially aligned, concentric spinose frills. Cardinal process small for genus.

TYPE SPECIMEN. Léveillé's (1835) specimens appear to be lost. In the de Koninck collection, BM(NH), there are specimens with de Koninck's manuscript labels, called *A. squamigera* from the 'carb. sup. Tournay', Belgium. This is the area from which Léveillé described his species, and the specimen here selected as **lectotype** of *C. squamigera* de Koninck (Fig. 23; BM(NH) Pal. Dept. reg. no. BB 62968) is similar to Léveillé's illustrations of *S. De Roissyi*, and is typical of specimens which should now be called *C. deroissyi* (Léveillé) from the Tournai area, probably of late Tournaisian age.



Figs 23-24 Cleiothyridina deroissyi (Léveillé), ×1.5. Fig. 23, lectotype (herein selected) of C. squamigera (de Koninck), from the Tournai region of Belgium. De Koninck coll., BM(NH) BB 62968, viewed dorsally, posteriorly, ventrally, laterally and anteriorly. Fig. 24, from the same collection as Fig. 23, BM(NH) 65002, viewed dorsally, posterolaterally and ventrally showing the internal mould of the umbonal region.

Although this species name is common in the literature, from Davidson's (1861) misuse of the name for *C. fimbriata*, the species is uncommon in Europe, other than at the type area in Belgium. In Britain it forms only a minor constituent of some Viséan faunas. In the United States a closely similar species, *C. prouti* (Swallow), occurs near the Tournaisian/Viséan boundary.

Cleiothyridina glabristria (Phillips)

Fig. 25

- 1861 Athyris Royssii (Léveillé); Davidson (pars) : pl. 18, figs 1 (repeating Phillips 1836), 2, 4.
 - 1887 Athyris ingens de Koninck : 83; pl. 20, figs 1-10.

v* 1836 Spirifera glabristria Phillips : 220; pl. 10, fig. 19.

DIAGNOSIS. Large (c. 60 mm wide), depressed obovate in outline with strong uniplicate commissure developed from persistent ventral sulcus. Rugose anteriorly with? short spinose frills.

TYPE SPECIMEN. Spirifer glabristria Phillips (1836 : 220; pl. 10, fig. 19). BM(NH) Pal. Dept. reg. no. B 316. Gilbertson Coll., Bolland. Here recognized as holotype.

DISCUSSION. The four *Cleiothyridina* species dealt with here are distinctive in shape. The Permian type species, *C. pectinifera*, is the smallest, reaching about 15 mm in width, the most circular in outline, and remains unfolded. *C. fimbriata* is larger, reaching 20 mm or more in width, and although rounded anteriorly has an unusually transverse posterior margin. The commissure remains rectimarginate. *C. deroissyi* is strongly transverse in outline and strongly uniplicate anteriorly. The spinose frills, so characteristic of the genus, are composed of needle-like 'spines' finer than the flattened ones of the other two species.

Other species names which should be included in *Cleiothyridina* are *C. depressa* (M'Coy, 1844) [?=C. fimbriata (Phillips, 1836)] (p. 227); *C. squamigera* (de Koninck, 1851) [=C. deroissyi (Léveillé, 1835)] (p. 228); *C. ingens* (de Koninck, 1887), which is probably the non-exfoliated form of *C. glabristria* (Phillips); and three other species names of de Koninck (1887), viz. *C. membranacea*, *C. ornata* and *C. waageni*, the true identities of which are questionable.

Species assigned to *Cleiothyridina* extend from Tournaisian through Carboniferous and Permian strata. Recently Grunt (*in* Sarytcheva 1977) has pointed out that about ten species occur in the Permian, especially late Permian, of the Russian platform. The assignment of the species herein to either *Actinoconchus* or *Cleiothyridina* is based principally on the external ornamentation of the shell. Unfortunately, the interiors of some species are unknown and are likely to remain so through a lack of suitable material for preparation. The use of different shell characteristics would lead to different classifications, but the nature of the shell lamellae is probably a more significant character than, for example, folding and sulcation, which alters during the ontogeny of the individual. The aim here is to provide data on the available species names, not the provision of a tight classification.

Genus COMPOSITA Brown, 1849

TYPE SPECIES. Spirifer ambiguus J. Sowerby (1822 : 105; pl. 376).

Composita ambigua (J. Sowerby) Figs 26–28

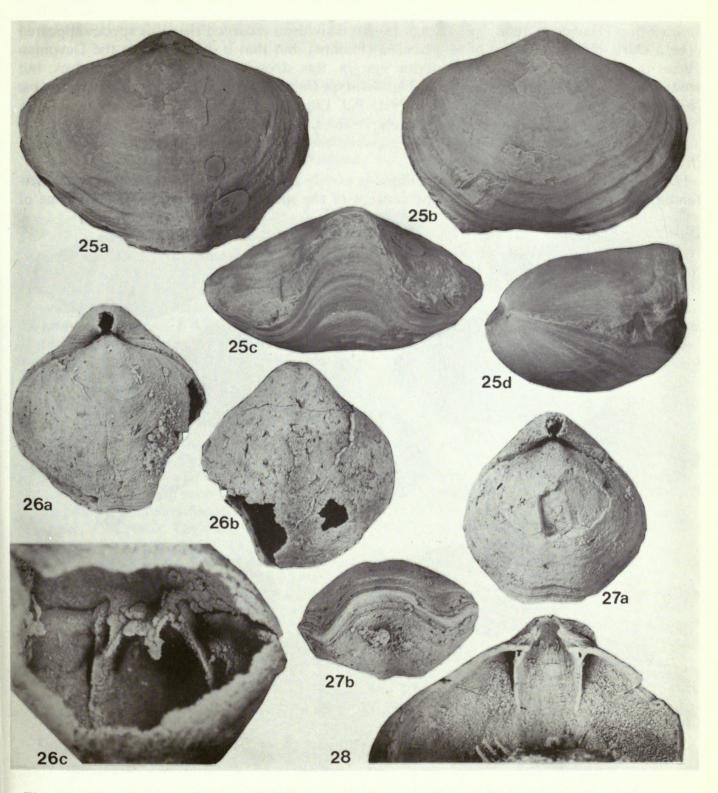
TYPE SPECIMEN. Lectotype, here selected, the specimen, figured by J. Sowerby (1822 : pl. 376, top left) in the Sowerby Coll., BM(NH) Pal. Dept. reg. no. B 61041, from '... decomposed Mountain Limestone, near Bakewell ...', Derbyshire. This, and the other two specimens in the Sowerby Coll., are silicified and partially broken revealing some of the interior (Figs 26, 28). The other two specimens are B 61042 (pl. 376, top right) and B 61043 (pl. 376, middle and bottom). The age of the strata yielding these specimens is probably uppermost Viséan, Brigantian, P_2 .

DISCUSSION. In general, European species of *Composita* are most prolific in late Devonian and Carboniferous rocks, especially if some Permian species are transferred to *Spirigerella* Waagen (1883). *Actinoconchus* species are confined to Carboniferous rocks found at low palaeolatitudes while *Cleiothyridina*, with its greatest European diversity in Lower Carboniferous rocks, extends through to the Permian of many areas, and especially the north-eastern U.S.S.R.

Other poorly-known species

Another athyridide species named in the nineteenth century is *Spirifer phalaena* Phillips (1841: 71; pl. 28, fig. 123), described from Hope, near Torquay in south Devon, England. The name was repeated, as *Martinia phalaena* (Phillips), by M'Coy (1844 : 140), but applied to a species distinct from Phillips', as is seen from Davidson's figure (1861 : pl. 18, figs 13, 13a, b) of the Griffith Collection specimen described by M'Coy. Davidson called this brachiopod *Athyris*

squamigera de Koninck, but it should now be included in the species Athyris hibernica Douglas (1909 : 573; pl. 26, fig. 5). Spirifera phalaena Phillips is the type species of the Devonian genus Anathyris von Peets, 1901, and the type specimen is in the collections of The Institute of Geological Sciences, London, GSM 6866. The Devonian athyridide species related to Anathyris are being studied by F. Alvarez of Oviedo, Spain.



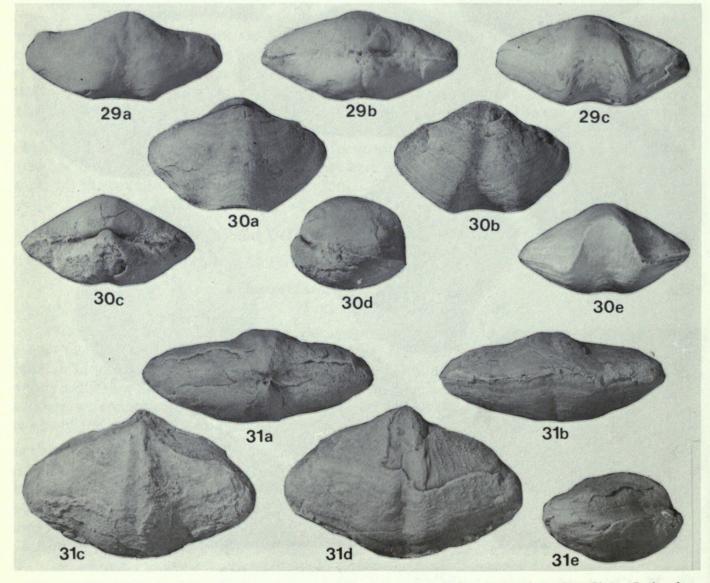
- **Fig. 25** Cleiothyridina glabristria (Phillips), ×1. Holotype from Bolland, Yorkshire. Gilbertson coll., BM(NH) B 316, viewed dorsally, ventrally, anteriorly and laterally.
- **Figs 26–28** Composita ambigua (J. Sowerby). Syntypes from Bakewell, Derbyshire. Sowerby coll., BM(NH) B 61041–43. Fig. 26a, b, lectotype (herein selected), B 61041, viewed dorsally and ventrally, $\times 2.5$. Fig. 26c the same specimen, umbonal region interior showing the articulation, dental plates, cardinal plate and crura, $\times 5$. Fig. 27, B 61042, viewed dorsally and anteriorly, $\times 2.5$. Fig. 28, B 61043a, ventral valve interior showing the posterior region, $\times 3$.

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The type specimen of *A. hibernica* Douglas is in the Oxford University Museum, E 148, with a replica in the BM(NH), Pal. Dept. reg. no. BB 61822 (Fig. 29). The assignment of the species to a more modern genus is uncertain, but it is probably closer to *Actinoconchus* than to *Athyris* or *Cleiothyridina*.

Yet another species name in the literature is *Athyris carringtoniana* Davidson, 1862, known from only three specimens from the Lower Carboniferous (probably mid-Viséan) of Wetton, Staffordshire (Davidson 1862 : pl. 52, figs 18–20). Davidson recorded that this species appeared to be a Carboniferous variety of *A. phalaena* (Phillips), but that it differed from the Devonian species in having a less straight posterior margin, less strongly or widely folded valves, but stronger ribs bordering the median sulci. The **lectotype** (here selected, Fig. 31) of *A. carringtoniana* Davidson is in the Davidson Coll., BM(NH) Pal. Dept. reg. no. B 7882, and was figured by Davidson (1862 : pl. 52, fig. 19). Interestingly, in the United States of America a closely similar and rare species is described as *Athyris papilioniformis* McChesney, from the Mississippian Chester series of Illinois.

The type specimen of A. phalaena (Phillips) is poorly preserved and provides no clear understanding of the species. If, however, the concept of the species is extended to include some of



Figs 29-30 'Athyris' hibernica Douglas, ×1. Fig. 29, holotype from Cratloe, Co. Clare, Ireland. Douglas coll., Oxford University Museum E 148, viewed ventrally, posteriorly and anteriorly. Fig. 30, from Killmallock, Co. Wexford, Ireland. J. Wright coll., BM(NH) B 40302, viewed dorsally, ventrally, posteriorly, laterally and anteriorly.

Fig. 31 'Athyris' carringtoniana Davidson, $\times 2$. Lectotype (herein selected) from Wetton, Staffordshire. Davidson coll., BM(NH) B 7882, viewed posteriorly, anteriorly, dorsally, ventrally and laterally.

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the abundant Devonian material from north Spain, it becomes clear that there is much variation in its external shape, and some of these forms resemble *A. carringtoniana* externally. Once the Spanish species have been fully described, and if more specimens of *A. carringtoniana* allow the morphology of the cardinalia and jugum to be discovered, it should be possible to decide whether or not Davidson's species should be included in *Anathyris*. If it does belong here it means that the range of the genus must be extended into the Dinantian; if it does not belong to *Anathyris* the external shape is more suggestive of assignment to *Cleiothyridina* than to other genera.

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