BRACHIOPODS FROM THE LOWER DEVONIAN MANDAGERY PARK FORMATION, NEW SOUTH WALES

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ABSTRACT. The basal limestone of the Mandagery Park Formation, New South Wales, thought to be of early Siegenian age, has yielded a rich fauna of brachiopods. Almost all previous work on Lower Devonian brachiopods in eastern Australia has been concerned with faunas preserved in shale horizons and relatively little is known about faunas from Lower Devonian limestones. The brachiopods from the Mandagery Park Formation basal limestone described herein differ considerably from the assemblages previously described from eastern Australian Lower Devonian shale localities and show a marked resemblance to brachiopod faunas from Lower Devonian limestones in central and eastern Europe, the Urals, Siberia, and western North America. The evidence of these fossils supports the views of earlier authors who have suggested that frequent migrations of benthonic invertebrates occurred between Eurasia and eastern Australia during Lower Devonian time. The fossils described herein are *Dolerorthis packhami* sp. nov., *Isorthis festiva* Philip, *Platyorthis*, sp., *Gypidula* cf. *victoriae* Chapman, *Anastrophia magnifica australis* subsp. nov., *Leptaena* cf. *goldfussiana* Barrande, *Drahanostrophia burrenensis* sp. nov., *Machaeraria* cf. *formosa* (Hall), *Zlichorhynchus*? sp., *Linguopugnoides carens* (Barrande), *Cryptatrypa* cf. *philomela* (Barrande), *Meristella subovata* sp. nov., *Nucleospira* cf. *inelegans* (Barrande), and *Sturtella mandageriensis* gen. et sp. nov.

DURING Lower Palaeozoic times the Lachlan Geosyncline of south east Australia consisted of several parallel troughs separated by relatively stable blocks or geanticlines. Thick deposits of greywacke and shale accumulated in the troughs while limestones were often deposited in the marginal areas. Periodic extrusions of acid and intermediate lavas are represented in the troughs by frequent horizons of volcanic detritus which often forms a major component of the greywacke beds. The thickest deposits occurring in the troughs are greywacke-shale sequences of Silurian and Devonian age, and these are particularly well developed in the Hill End Trough (Packham 1968) and the Cowra Trough (Pakham 1960, Ryall 1965, Savage 1968*a*). Much of the trough sediment has yielded only a sparse graptolitic fauna and in parts of the Hill End Trough great thicknesses of sediment have yielded no fossils at all (Packham 1968). However, towards the margins of the troughs, and where the more stable areas have been subject to periodic transgressions, rich shelly faunas are common and mixed graptolitic-shelly faunas also occasionally occur.

The brachiopods described in this paper are from an area towards the western margin of the Cowra Trough where several small limestone lenses were deposited during the early Devonian. At about this time the trough was narrowing and shallowing after a major expansion during the late Silurian. Along the eastern margin of the Cowra Trough a much thicker accumulation of limestone was beginning to develop at about the same time (Strusz 1965, 1967).

Stratigraphy. The Mandagery Park Formation is exposed in the vicinity of Manildra, New South Wales (text-fig. 1) and is the second of three dominantly calcareous formations deposited in the Cowra Trough during early Devonian times which together comprise the Gregra Group (Savage 1968*a*). Near Manildra it is underlain by the richly

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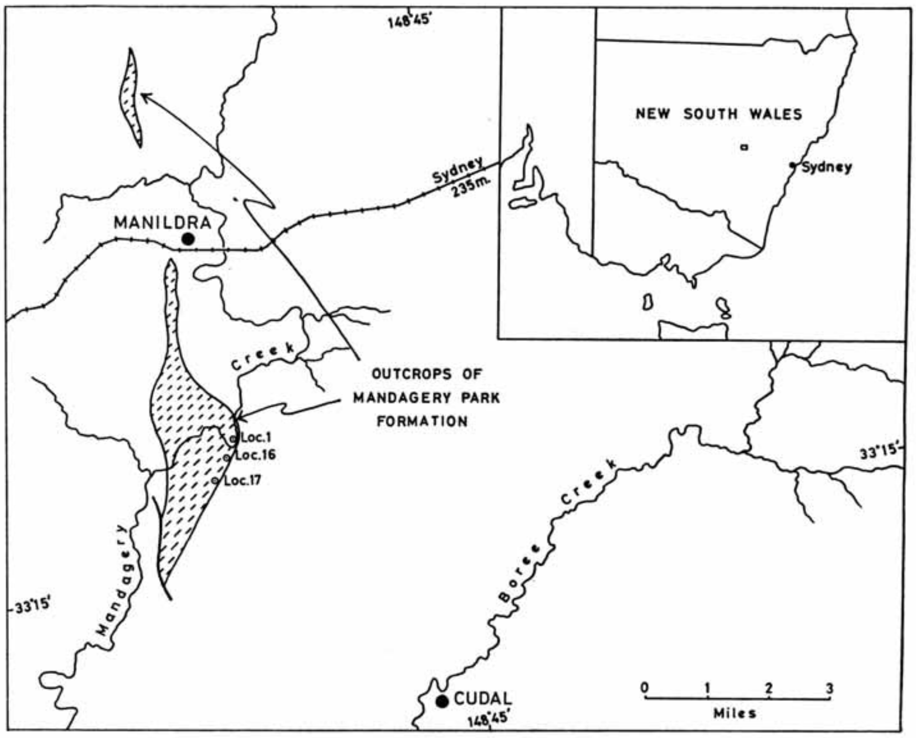
fossiliferous olive-green Maradana Shale and 5 miles to the south-east, near Cudal, it is overlain by the limestones and calcareous shales of the highly calcareous Garra Formation. Its precise relationship to the latter formation is uncertain and possibly the upper part of the Mandagery Park Formation near the western margin of the Cowra Trough is equivalent in age to the lowest part of the Garra Formation further east.



TEXT-FIG. 1. Location of the Mandagery Park Formation at the type area.

During most of the Silurian the Cowra Trough appears to have been downwarping steadily and at least 6000 ft of greywackes, shales, and siltstones were deposited in the region immediately to the east and south of Manildra (Savage 1968*a*). In the early Devonian, conditions appear to have more nearly approached equilibrium and the Gregra Group sediments were deposited in a shallowing neritic environment. The greywacke facies of the Silurian pass upwards into the calcareous facies of the Lower Devonian.

The maximum preserved thickness of the Mandagery Park Formation is about 1600 ft. The richly fossiliferous basal limestone, which is about 350 ft thick at its maximum development, grades upwards into poorly fossiliferous tuffaceous sandstone and unfossiliferous arkosic sandstone with occasional cross-bedding. In the lowest horizon of the formation silicification makes possible the extraction of large numbers of well-preserved fossils. These are mainly brachiopods, but corals, gastropods, and conodonts are also present. From this horizon the genera *Anastrophia*, *Quadrithyris*, *Proreticularia*, *Eoglossinotoechia*, *Linguopugnoides*, *Cryptatrypa*, *Ogilviella*, and *Atrypina* have all been recorded from Australia for the first time. Elsewhere these genera are most commonly found in assemblages from limestones, particularly in central and eastern Europe, the Urals, and other areas forming part of the Bohemian–Uralian–western North American early Siegenian faunal province. It seems likely that these forms will be found eventually in other Australian limestones at about this horizon.

The stratigraphy and structure of the Manildra area have been described in more detail elsewhere (Savage 1968*a*) together with faunal lists and a discussion of possible local correlations. This present paper is primarily concerned with the silicified brachiopods from the Mandagery Park Formation. All the material described here is from that formation at Locality 1, 3 miles south of Manildra (text-fig. 1). Similar assemblages have been collected from Localities 16 and 17, at the same horizon. Parts of the fauna have been described already (Savage 1968 *b*, *c*, 1969, 1970). The remaining brachiopods are described in the systematic treatment below.

Faunal affinities. Although papers have been written on brachiopods from Lower Devonian shales in Victoria and Tasmania (Gill 1942, 1948, 1950; Talent 1963, 1965; Philip 1962), little is known about brachiopods from Lower Devonian limestones in these areas. The assemblages described are generally similar to the shale faunas at Manildra but very different from the limestone faunas. Lower Devonian brachiopods have also been described from New Zealand by Allan (1935, 1947) and Shirley (1938) but here again the material is from shale horizons and the faunas have very little in common with the Manildra limestone faunas on account of differences in both facies and horizon.

It is with the assemblages from some of the classical Lower Devonian areas of central and eastern Europe that the Mandagery Park Formation brachiopods have the closest affinities. It has often been observed that there is a fundamental difference between the faunas associated with the predominantly psammitic facies of the Rhinelands and those of the calcareous facies of Bohemia (Shirley 1938; Erben 1962, 1964; Bouček, Horný, and Chlupáč 1966). As Boucot, Johnson, and Talent (1969, p. 5) have recently noted, these faunal differences are not determined solely by environmental-lithological factors, for alterations in lithology in a single area do not result in alterations of Bohemian and Rhenish biofacies. There is presumably a lithological control within each faunal province, but the generic composition of assemblages from different rock types has a strong provincial flavour and is apparently determined by palaeogeographical factors. Pre-continental drift relationships were undoubtedly of great importance in the delimitation of these Lower Devonian provinces. In Bohemia, where the Lower Devonian calcareous facies is so well developed, a tripartite stratigraphic division into the Lochkovian, Praguian, and Zlíchovian stages is usually accepted. The Lochkovian, which is correlated here with the Gedinnian and part of the Siegenian, consists chiefly of limestone with some interbedded shales and cherts. It includes the Kotýs Limestone and the Lower Koněprusy Limestone, both highly fossiliferous. The Praguian is correlated with the middle and upper Siegenian together with the lower Emsian. This includes the Radotín Limestone, Kosoř Limestone, Upper Koněprusy Limestone, and the Dvorce-Prokop Beds. Many of the brachiopods collected from these two stages show a striking resemblance to the Manildra brachiopods and most of the forms from the limestone horizon of the Mandagery Park Formation have a close equivalent in the Kotýs and Koněprusy Limestones. The similarity between the atrypids and the spiriferids in the two areas is very marked and this similarity is of particular interest as close equivalents of the Manildra species are rare elsewhere. The forms *Quadrithyris robusta molongensis* Savage, *Howellella nucula australis* Savage, *Ambocoelia praecox dorsiplicata* Savage, *Proreticularia beddiei* Savage, *Linguopugnoides carens* (Barrande), *Gypidula* cf. *victoriae* Chapman, and *Reticulatrypa fairhillensis* Savage are represented in Bohemia by *Quadrithyris robusta* (Barrande), *Howellella nucula* (Barrande), *Ambocoelia operculifera* Havlíček, *Proreticularia carens* (Barrande), *Linguopugnoides carens* (Barrande), *Gypidula caduca* (Barrande), and the non 'punctate' forms commonly included within the '*granulifera*' group of atrypids (Barrande 1879; Havlíček 1951, 1959; Savage 1969, 1970).

The faunas from the Borszczow Stage of the classic sections of Podolia are chiefly of Bohemian facies but there is less limestone and more calcareous shale than at most of the Bohemian localities (Kozlowski 1929, p. 7; Boucot and Pankiwskyj 1962, p. 8). This increase in the argillaceous nature of the substratum can be expected to have affected the composition of the fauna. Furthermore, the Pridolian age Borszczow assemblages are considerably older than the early Siegenian assemblages from the Manildra limestone. Despite these factors, a remarkable number of species from Manildra are conspecific, or almost conspecific, with forms from Podolia. *Anastrophia magnifica australis* subsp. nov., *Ambocoelia praecox dorsiplicata* Savage, *Howellella nucula australis* Savage, *Cyrtina praecedens* Kozlowski, *Machaeraria* cf. *formosa* (Hall), *Reticulatrypa fairhillensis* Savage, *Linguopugnoides carens* (Barrande), and *Nucleospira* cf. *inelegans* (Barrande) from the Manildra limestone closely resemble the Podolia species *Anastrophia magnifica* Kozlowski, *Ambocoelia praecox* Kozlowski, *Howellella laeviplicata* (Kozlowski), *Cyrtina praecedens* Kozlowski, *Machaeraria althi* (Kozlowski), *Reticulatrypa nieczlaviensis* (Kozlowski), *Linguopugnoides carens* (Barrande), and *Nucleospira robusta* Kozlowski (Kozlowski 1929; Savage 1969, 1970).

The presence of *Anastrophia magnifica australis* in the Manildra fauna is particularly significant. *Anastrophia* is a relatively rare genus and forms with a transverse outline appear to comprise a distinct group characteristic of the Bohemian–Uralian–Tasman–Nevadan early Siegenian faunal province (cf. Old World Province Bohemian Community of Boucot, Johnson, and Talent 1969).

As might be expected from the discussion above, the Mandagery Park Formation fauna is very different from the Appalachian Lower Devonian faunas. The Appalachian assemblages do not include many of the genera which are present in Bohemia and other Old World Province areas. These include *Quadrithyris*, *Proreticularia*, *Eoglossinotoechia*, *Linguopugnoides*, *Reticulatrypa*, *Zlichorhynchus*, *Carinatina*, *Ogilviella*, *Falsatrypa*, *Septatrypa*, and *Cryptatrypa*. Also absent from the Appalachian Lower Devonian deposits is the transverse form of *Anastrophia* mentioned above.

The western North American early Siegenian brachiopod faunas, reported from central Nevada and the Yukon (Johnson 1965; Lenz 1967, 1968) are quite distinct from the early Siegenian Appalachian faunas and have very clear Bohemian–Uralian affinities.

Illustrations of most of these early Siegenian forms from Nevada and the Yukon have yet to be published but it is clear from the faunal lists of Johnson (1965) and Lenz (1967), and from material and photographs sent to me by these workers, that the Manildra limestone brachiopods have close affinities with early Siegenian species from the Great Basin, Nevada and from Royal Creek in the Yukon. This is indicated by the occurrence in western North America of the eastern European forms *Anastrophia* cf. *magnifica* Kozlowski, *Gypidula* cf. *pelagica* (Barrande), *Quadrithyris* cf. *minuens* (Barrande), *Howellella* cf. *nucula* (Barrande), *Ambocoelia* cf. *praecox* Kozlowski, *Reticulatrypa nieczlaviensis* (Kozlowski), *Linguopugnoides* cf. *praecox* (Barrande), *Spirigerina* cf. *supramarginalis* (Khalfin), and *Cymostrophia* cf. *stephani* (Barrande) (see Johnson 1965, Lenz 1967). During late Gedinnian and early Siegenian times the eastern and western parts of North America were apparently covered by two distinct epicontinental seas with western North America part of a faunal province stretching from central Europe, through Asia, to the Yukon and Nevada. An offshoot of this great Eurasian–Western North American migration route appears to have passed into eastern Australia.

The Mandagery Park Formation faunas have little in common with the 'Austral' Lower Devonian faunas of South Africa, South America, the Falkland Islands, and Antarctica. Faunas from these areas described by Reed (1903, 1904, 1906, 1908, 1925), Knod (1908), Clarke (1913), Kozlowski (1923), Boucot and Gill (1956), Boucot, Caster, Ives, and Talent (1963), and Boucot, Johnson, and Doumani (1965) contain a preponderance of terebratulids, leptocoeliids, and chonetids. The composition of these assemblages probably reflects the combined effects of geographical isolation and the brackish, shallow water conditions which are thought to have prevailed in the Gondwanaland basins at that time. However, as we have seen, the Mandagery Park Formation brachiopods are decidedly 'Boreal' in character and strikingly close to the Bohemian brachiopod assemblages. Terebratulids, leptocoeliids, and chonetids are conspicuously absent and there is no evidence of 'Austral' affinities in the Cowra Trough, or indeed in any part of the Australian mainland, during Lower Devonian time.

In the systematic treatment below, specimen numbers are those of the Palaeontology Collection, Department of Geology and Geophysics, University of Sydney.

SYSTEMATIC PALAEONTOLOGY

Phylum BRACHIOPODA
Order ORTHIDA Schuchert and Cooper 1932
Superfamily ORTHACAEA Woodward 1852
Family HESPERORTHIDAE Schuchert and Cooper 1931
Subfamily DOLERORTHINAE Öpik 1934
Genus DOLERORTHIS Schuchert and Cooper 1931

Type species. Orthis interplicata Foerste 1909, by original designation.

Dolerorthis packhami sp. nov.

Plate 69, figs. 1–32; text-fig. 2

Diagnosis. A *Dolerorthis* with a sulcate dorsal valve, a high ventral interarea, subparallel delthyrial margins, and only a small number of secondary costae.

Material. Of about 200 specimens only 12 are complete shells with the valves conjoined, the remainder consisting of isolated dorsal and ventral valves with the latter predominating. Specimen SU 19522 is the holotype and other illustrated specimens are paratypes.

Description. Exterior. The shell is subquadrate to semi-elliptical in outline with the greatest width between mid-length and the anterior margin. The lateral profile is convex-plane to biconvex. Five mature ventral valves with lengths from 9·5 to 12·1 mm have width/length ratios ranging from 1·09 to 1·38 with a mean of 1·23. The sole mature conjoined specimen, which has a length of 8·7 mm, has a width/length ratio of 1·20 and a thickness/length ratio of 0·49. The ventral valve is deeper than the dorsal valve because of the long, flat, apsacline interarea (Pl. 69, figs. 25, 31). A high, open delthyrium is slit-like with subparallel margins. The dorsal valve is gently convex and has a short, concave, anacline interarea (Pl. 69, figs. 25, 31) and an open notothyrium which includes an angle of 55–65°.

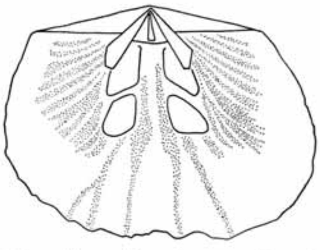
A distinct sulcus is present in the dorsal valve but there is little or no fold in the ventral valve and the anterior commissure is straight. The ornament is of strong angular costae which multiply by lateral branching from 10 to 12 primaries, the secondaries arising at varying distances from the beak, giving a fascicostate ornament marginally. In 7 mature ventral valves with a length exceeding 10 mm the number of costae at 5 mm from the beak varies from 14 to 18 with a mean of 16, and at 10 mm from the beak the number varies from 27 to 30 with a mean of 29.

Ventral interior. Short, receding dental lamellae diverge anteriorly and merge with a thickened muscle area which extends anteriorly for one-quarter of the valve length (Pl. 69, fig. 32). Strong triangular teeth have their outer edges almost perpendicular to the hinge line (Pl. 69, fig. 13). The short, triangular muscle area consists of deeply impressed diductor scars situated either side of a more elevated adductor field. The diductor scars extend well up onto the dental lamellae.

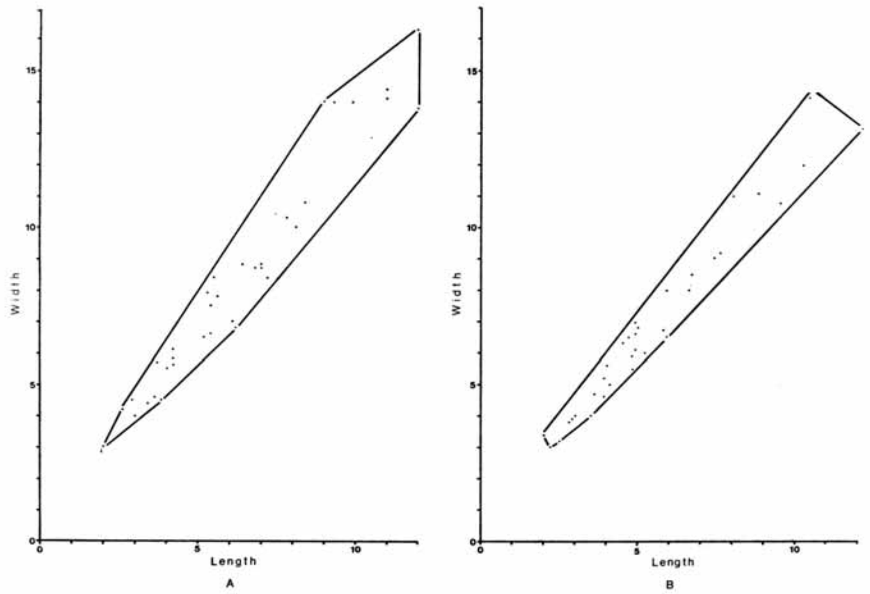
EXPLANATION OF PLATE 69

Figs. 1–32. *Dolerorthis packhami* sp. nov. 1–5, Ventral, dorsal, posterior, anterior, and lateral views of SU 19524 showing the long apsacline ventral interarea and short anacline dorsal interarea. 6–10, Ventral, dorsal, posterior, anterior, and lateral views of ventral valve SU 19529. 11–15, Ventral, dorsal, posterior, anterior, and lateral views of ventral valve SU 19530 showing the typically subparallel delthyrial margins and strong triangular teeth. 16–20, Dorsal, ventral, posterior, anterior, and lateral views of dorsal valve SU 19521. 21–25, Dorsal, ventral, posterior, anterior, and lateral views of SU 19522 (holotype) showing the linear cardinal process and straight blade-like brachiophores. 26–30, Ventral, dorsal, posterior, lateral, and anterior views of SU 19527, a young valve showing a wide hinge line and a V-shaped delthyrium. 31, Ventral view of dorsal valve SU 19526 showing the cardinalia and the adductor muscle field. 32, Antero-dorsal view of ventral valve SU 19533 showing the thickened muscle field and the strong, receding dental lamellae. (Figs. 1–30 × 3; figs. 31, 32 × 6.)

Figs. 33–48. *Isorthis festiva* Philip. 33, Interior of dorsal valve SU 19539 showing the large quadripartite muscle field and cardinalia. 34–35, Exterior and interior of relatively large ventral valve SU 19535 showing the shape of the muscle field with distinct boundaries to the adductor scar on the low median ridge. 36–38, Dorsal, ventral, and posterior views of dorsal valve SU 19536 showing the large muscle field. 39–43, Ventral, dorsal, anterior, lateral, and posterior views of ventral valve SU 19537 showing the deeply impressed muscle field, distinct lateral umbonal cavities, and shallow crural fossettes. 44–48, Dorsal, ventral, posterior, anterior, and lateral views of complete shell SU 19534. (All figures × 2.)



TEXT-FIG. 2. *Dolerorthis packhami* sp. nov. Dorsal mantle canal system drawn from gerontic specimen SU 22674.



TEXT-FIG. 3. *Dolerorthis packhami* sp. nov. Scatter diagrams and limiting polygons of dimensions plotted in millimetres. A. Width and length of 35 dorsal valves. B. Width and length of 35 ventral valves.

Dorsal interior. The cardinal process is a linear ridge, long and high, and slightly thickened anteriorly (Pl. 69, fig. 22, 23). Long, blade-like brachiophores thin distally and diverge at 55–65° with the inner edges continuous with the notothyrial margins. Small shallow sockets deepen and expand laterally. The large adductor muscle field extends half the distance to the anterior margin and is divided by a broad median ridge. Subtriangular anterior adductors are separated from slightly smaller, oval, posterior adductors by low, anteriorly directed ridges (Pl. 69, fig. 31). Distinct diductor scars are visible on the notothyrial platform each side of the cardinal process. In gerontic specimens a digitate to pinnate mantle canal system is sometimes visible (text-fig. 2).

Measurements (in mm)

		Length	*Width*	*Thickness*
SU 19522	Dorsal valve (Holotype)	8·4	10·8	—
SU 19523	Dorsal valve	9·3	14·0	—
SU 19524	Complete shell	4·2	6·0	2·7
SU 19525	Complete shell	4·0	4·9	2·9
SU 19530	Ventral valve	8·8	11·1	—

Ontogeny. In young individuals the hinge line is at least as wide as the more anterior parts of the shell (Pl. 69, fig. 26). This relationship is not maintained during growth and in mature specimens the cardinal angles are distinctly obtuse with the hinge line only about four-fifths the width at mid-length (Pl. 69, fig. 11, 21). Another change is in the form of the delthyrium which has divergent lateral margins in the young specimens but is more parallel-sided and slit-like in mature specimens (Pl. 69, fig. 28, 13). The internal features do not alter with growth apart from a gradual thickening of most structural details, the appearance of a distinctly impressed dorsal muscle field and mantle canal system (Pl. 69, fig. 31; text-fig. 2), and the progressive elevation of the ventral muscle field (Pl. 69, fig. 32). Although the position of maximum width of the valves may change, the relationship of overall width to length varies very little during growth and a linear width–length plot results (text-fig. 3).

Discussion. This Manildra form resembles the Wenlock Limestone species *Dolerorthis rigida* (Davidson) but differs in possessing a distinct dorsal sulcus. Several other late Silurian orthids appear to be closely related to the Manildra material but have been referred by most workers to the genus *Schizonema* (senior objective synonym of *Schizoramma*; see Bassett 1970) on the basis that they possess accessory ridges flanking the cardinal process. Boucot (1960, p. 294), Williams (1965, p. H318), Amsden (1968, p. 28), and Bassett (1970, p. 18) all accept this distinction. In the absence of knowledge concerning the functional and genetic significance of these notothyrial platform ridges it is difficult to see why they should be afforded generic importance. In most other respects the two genera are much alike and it is an indication of the confusion associated with the *Dolerorthis-Schizonema* relationship that *Schizoramma* (= *Schizonema*) has been illustrated in the brachiopod treatise (Williams 1965, pp. H317–H318, *in* Moore) with photographs of the species *Schizoramma hami* Amsden, now referred to *Dolerorthis* by Amsden (1968, p. 28). A distinction between the dorsal mantle canal systems of the two genera is made in the treatise. The Manildra species has a system more nearly digitate than apocopate (text-fig. 2) and this is suggestive of *Schizonema*. However, if the form is a *Schizonema* it is notable in completely lacking notothyrial ridges and an apical plate in the delthyrium.

The North American Upper Silurian species *Dolerorthis hami* is close to the Manildra *Dolerorthis*. Externally there is a difference only in the height of the ventral interarea, the Manildra species being considerably higher. Internally *Dolerorthis packhami* can be distinguished by its much longer brachiophores.

Dolerorthis was recorded by Schuchert and Cooper (1932, p. 89) as ranging only from the Lower to Middle Silurian, and by Williams (1965, p. H316) as ranging from the Middle Ordovician to Upper Silurian. Although Boucot (1960) suggests a range extending into the late Gedinnian, this would still appear to be too restrictive. Several forms have been recorded from the middle or late Lower Devonian and early Middle Devonian which are *Dolerorthis* as presently defined. *Dolerorthis persculpta* Philip 1962 is from the Boola Beds, Victoria, now thought to be of Siegenian age, Johnson (1965) has a *Dolerorthis* from the early Siegenian of Nevada, and Wright (1967) has recorded *Dolerorthis* from Eifelian age deposits in New South Wales.

Dolerorthis persculpta is the only species of *Dolerorthis* hitherto described from Australia. The external ornamentation and cardinalia are similar to those of *Dolerorthis packhami* but the Victorian species possesses a distinctly convex ventral umbo, a shorter ventral interarea, and a wider delthyrium (Philip 1962, p. 194, fig. 8*a*, *b*).

Superfamily DALMANELLACEA Schuchert 1913
Family DALMANELLIDAE Schuchert 1913
Subfamily ISORTHINAE Schuchert and Cooper 1931
Genus ISORTHIS Kozlowski 1929

Type species. Isorthis szajnochai Kozlowski 1929, by original designation.

Isorthis festiva Philip 1962

Plate 69, figs. 33–48

1962 *Isorthis festiva* Philip, p. 201, pl. 31, figs. 3–6, text-fig. 12.

Material. The collection totals 33 silicified specimens of which only 4 are complete shells with conjoined valves. Of the remainder 8 are dorsal valves and 21 are ventral valves.

Description. Exterior. The shell is subcircular in outline with the maximum width at about mid-length. The lateral profile is unequally biconvex with the ventral valve deeper than the dorsal valve (Pl. 69, fig. 48). A mature conjoined specimen with a length of 10·5 mm has a width/length ratio of 1·02 and a thickness/length ratio of 0·64. A low broad sulcus in the dorsal valve extends from the beak to the gently sulcate anterior commissure but there is no distinct fold on the ventral valve (Pl. 69, figs. 46, 47). Both valves are multicostellate with the costellae multiplying by bifurcation and intercalation to number, in the case of 3 dorsal valves, 32, 34, and 38 at 3 mm from the dorsal beak, spaced at 6 per mm medially, and 56, 58, and 58 at 6 mm from the beak, spaced at 4 per mm medially.

Ventral interior. Anteriorly divergent dental lamellae advance one-quarter to one-third of the distance to the anterior margin and enclose narrow but distinct lateral umbonal cavities (Pl. 69, fig. 40). Strong triangular teeth have shallow crural fossettes on their antero-medial surfaces (Pl. 69, fig. 40). The muscle field, which extends one-third of the distance to the anterior margin, consists of two deeply impressed elongate diductor scars bounded laterally by the dental lamellae, and by low ridges extending anteriorly from the lamellae (Pl. 69, figs. 35, 40). The diductor scars are separated medially by a low adductor ridge.

Dorsal interior. A narrow cardinal process has a bilobed or irregularly multilobed myophore. Deep antero-laterally expanding sockets are supported on distinct fulcral pads and high brachiophores diverge anteriorly at about 90° (Pl. 69, figs. 37, 38). The large muscle field is oval to subquadrate in outline and extends at least half the distance to the anterior margin (Pl. 69, figs. 33, 37). It is usually elevated rather than depressed and is bounded by prominent lateral ridges. The rounded posterior adductors are separated from the larger oval anterior adductors by transverse ridges and the entire muscle field is divided by a low median ridge.

Measurements (in mm)

		Length	*Width*	*Thickness*
SU 19534	Complete shell	10·5	10·9	6·7
SU 19535	Ventral valve	14·5*	15·7	—
SU 19537	Ventral valve	7·5	8·7	—
SU 19539	Dorsal valve	7·5	6·5	—

* Estimated

Discussion. This Manildra material differs from the type species, *Isorthis szajnochai* Koslowski, and from most other eastern European species, in having a very pronounced dorsal sulcus. There is, however, a marked resemblance to Barrande's illustrations of his species *Orthis pinguissima* Barrande (Barrande 1879, pl. 62, fig. I, 1*a*, *b*, 2*a–f*) and it is possible that the material described herein should be referred to that species. Another species of *Isorthis* with a pronounced dorsal sulcus is the Silurian form from Tennessee, *Isorthis arcuaria*, but that species is easily distinguished from the Australian form by its strongly incurved ventral beak (Hall and Clarke 1892, pl. 5*c*, fig. 21; Amsden 1949, pl. 1, fig. 14) and less broad dorsal muscle field (Amsden 1949, pl. 1, fig. 16).

The type specimens of *Isorthis festiva* were collected from probable Siegenian age deposits in Victoria. They are preserved as moulds and have suffered distortion but it is clear that they are markedly ventribiconvex with a distinct dorsal sulcus and possess a large dorsal muscle field. The Manildra specimens cannot be distinguished from them in any significant feature.

Another Victorian isorthid is *Reeftonia alpha* (Gill) from the Emsian age Tabberabbera Formation. In the past this species has been referred most often to *Isorthis* (see Philip 1962, Talent 1963) and undoubtedly many of the specimens from the type locality have distinct *Isorthis* characteristics. The species, however, appears to be highly variable (Talent 1963) and the specimen figured by Johnson and Talent (1967, pl. 22, fig. 9), which Dr. Johnson has assured me is undistorted, has a dorsal muscle field quite unlike *Isorthis*.

Family RHIPIDOMELLIDAE Schuchert 1913
Subfamily PLATYORTHINAE Harper, Boucot, and Walmsley 1969
Genus PLATYORTHIS Schuchert and Cooper 1931

Type species. *Orthis planoconvexa* Hall 1859, by original designation.

Platyorthis sp.

Plate 74, figs. 16–21

Material. Only two specimens have been found, both dorsal valves.

Description. *Exterior*. In outline the dorsal valve is transversely elliptical with the anterolateral and postero-lateral margins evenly rounded (Pl. 74, fig. 16). The width/length ratio of the larger valve is 1·30 and that of the smaller valve 1·43. In profile both dorsal valves are weakly convex with a slight sulcus (Pl. 74, figs. 18, 20). The valve surface is costellate with the costellae multiplying mainly by bifurcation to number, in the case of the larger specimen, 28 at the 3 mm growth stage, spaced at 4 per mm medially, and 48 at the 6 mm growth stage, spaced at 3 per mm medially. Away from the central part of the valve the costellae curve outwards so that the most posterior costellae curve to intersect the postero-lateral margin (Pl. 74, fig. 16).

Dorsal interior. The posteriorly directed cardinal process is supported on a long, inclined shaft lying between the thick, erect brachiophores (Pl. 74, figs. 17, 18, 20). The sockets are not well preserved in this material. The quadripartite muscle field extends just anterior to mid-length and consists of a pair of elliptical posterior impressions separated by the anterior part of the cardinal process shaft, and a pair of larger, more widely separated anterior adductor impressions. The valve margins bear flattened crenulations, the raised parts having a distinctive double barrelled appearance (Pl. 74, fig. 17).

Measurements (in mm)

		Length	*Width*
SU 20676	Dorsal valve	6·4	8·3
SU 20677	Dorsal valve	3·7	5·3

Discussion. The transversely elliptical outline with evenly rounded lateral margins, the short hinge line, the almost flat profile, and the long inclined cardinal process, are all characteristic features of the genus *Platyorthis*.

The Manildra material appears to differ from the type species, *Platyorthis planoconvexa* from the Deerparkian of Maryland, in not possessing a clearly bilobed cardinal process, but this may be only a preservation feature of the two valves available. *Platyorthis* has not been recorded from Australia previously.

Order PENTAMERIDA Schuchert and Cooper 1931
Superfamily PENTERAMACEA M'Coy 1844
Family PENTAMERIDAE M'Coy 1844
Subfamily GYPIDULINAE Schuchert and LeVene 1929
Genus GYPIDULA Hall 1867

Type species. *Gypidula typicalis* Amsden 1953, by subsequent designation of Amsden, 1953.

Gypidula cf. *victoriae* Chapman 1913

Plate 72, figs. 1–11

1913 *Gypidula victoriae* Chapman, p. 106, pl. 11, fig. 12.

Material. All 59 specimens are isolated valves and they are mostly broken. There are only 2 whole dorsal valves in a total of 22, and only 1 whole ventral valve in a total of 37.

Description. *Exterior*. In outline the shell is transversely elliptical with the greatest width at about mid-length. The hinge-line is short and has a width only about one-quarter that of the shell (Pl. 72, fig. 1). The ventral valve is strongly convex with an inflated umbo and a small, erect beak (Pl. 72, fig. 6). An apsacline, concave interarea has an apical angle of about 100° and is bordered by low distinct beak ridges (Pl. 72, fig. 10). The wide, triangular delthyrium includes an angle of 60–70° (Pl. 72, fig. 10). The dorsal valve is convex but much less so than the ventral valve. It has a beak which is erect to sub-erect (Pl. 72, fig. 9) and a low poorly defined interarea which is divided by a wide notothyrium (Pl. 72, fig. 1). A prominent fold and sulcus are developed anteriorly. Four angular plications are present on the fold and three in the sulcus (Pl. 72, figs. 5, 6).

Ventral interior. The dental lamellae converge downwards and anteriorly to form a V-shaped spondylium supported by a median septum (Pl. 72, figs. 4, 10, 11). The median septum is variable in length and is shorter than the spondylium in some specimens but advances up to one third the distance to the anterior margin in others. Long, narrow tooth ridges border the delthyrial margins and project as short, strong teeth, subtriangular in section (Pl. 72, figs. 10, 11). The musculature within the spondylium is indistinct.

Dorsal interior. Short hinge plates extend about one-quarter the width of the valve and are separated by a moderately deep notothyrial cavity (Pl. 72, figs. 1, 8). This is divided by a deep, narrow pit under the beak (Pl. 72, fig. 1). The sockets form triangular notches between the lateral edges of the hinge plates and the valve wall. Converging downwards from the hinge plates are large, triangular inner lamellae. These unite along their lower, dorsal edges with long, subvertical brachial processes which diverge slightly anteriorly (Pl. 72, figs. 1, 3). Supporting the latter are a pair of thin, outer lamellae which converge dorsally and almost meet before uniting with the valve floor. Anteriorly the edges of the outer lamellae extend almost to the valve mid-length.

Measurements (in mm)

		Length	*Width*	*Thickness*
SU 20677	Ventral valve	13·3	10·1	6·3
SU 20680	Dorsal valve	15·0*	20·0*	—
SU 19557	Dorsal valve	9·3	11·6	3·3

* Estimated

Discussion. The Manildra material appears to be conspecific with *Gypidula victoriae* Chapman 1913, from Victoria, although further collecting from Chapman's locality may show differences not apparent from the single specimen he described. A considerable variation in the depth of the dorsal valves occurs in the Manildra specimens and it is possible there would also be some variation in the form of the specimens at the Victorian locality. *G. vultura* Talent 1963, also from Victoria, differs from *G. victoriae* in being completely smooth.

A form from Europe close to the Manildra specimens is *Gypidula caduca* (Barrande 1879). This is gently plicate and has a wide, angular ventral fold limited each side by a distinct plication as in the Australian material. The posterior half of the shell is also smooth (see Barrande 1879, pl. 22, fig. 1*a–h*). When more is known of *G. caduca* it will be possible to compare the forms more constructively and it would not be surprising if they prove to be conspecific, with *G. caduca* the senior synonym. As Chapman observed (1913, p. 107) *G. victoriae* also resembles *G. galeata* (Dalman), a species from the Upper Silurian of Gotland which is common in the Wenlock and Ludlow of Britain (Davidson 1871, p. 145; Alexander 1947, p. 154) and which has also been recorded from eastern Europe (Kozlowski 1929, p. 135). The Manildra form is similar in general shape to *G. galeata* but has plications which are larger and more angular.

Superfamily PORAMBONITACEA Davidson 1853
Family PARASTROPHINIDAE Ulrich and Cooper 1938
Genus ANASTROPHIA Hall 1867

Type species. Pentamerus verneuili Hall 1857, by original designation.

Anastrophia magnifica australis subsp. nov.

Plate 70, figs. 1–34

Diagnosis. A form of *Anastrophia* close to *Anastrophia magnifica* Kozlowski 1929 but with less prominent cardinal extremities, fewer costae, and a less swollen dorsal umbo.

Material. In a collection of over 300 silicified specimens 72 are complete shells with the valves conjoined. The remainder consists of isolated dorsal and ventral valves about equally represented. Specimen SU 19554 is the holotype and other illustrated specimens are paratypes.

Description. Exterior. The shell is transversely sub-elliptical in outline with the greatest width usually at mid-length but sometimes at the wide, straight hinge line. The cardinal extremities are auriculate (Pl. 70, fig. 10). In lateral profile the shell is strongly biconvex (Pl. 70, fig. 5). Ten mature shells with lengths from 5·6 to 8·0 mm have width/length ratios ranging from 1·06 to 1·49, with a mean of 1·33, and thickness ratios ranging from 0·63 to 1·02, with a mean of 0·84. A wide, apsacline ventral interarea is bounded by low but distinct beak ridges. The apical angle is difficult to measure with accuracy but is estimated to vary from 125 to 135°. The open delthyrium, which includes an angle of 70–80°, is obscured by the dorsal beak. A dorsal fold and ventral sulcus become well defined in the anterior half of the shell and the anterior commissure is strongly uniplicate (Pl. 70, fig. 28). Both valves are costate with 4 or 5 costae on the dorsal fold, 3–4 in the ventral sulcus, and 5–6 either side on the lateral slopes. The costae are high and angular and occasionally increase by bifurcation (Pl. 70, figs. 25, 30). The shells are often asymmetrical with one of the subcentral costae strongly overdeveloped on one side (Pl. 70, figs. 4, 10, 33).

Ventral interior. The dental lamellae converge to form a spondylium supported by a short median septum. The spondylium extends approximately one-third the distance to the anterior margin and the median septum extends slightly further (Pl. 70, figs. 11, 13, 14). The prominent teeth diverge as a continuation of stout tooth ridges along the delthyrial margins (Pl. 70, figs. 10, 11). Shallow crural fossettes face antero-medially (Pl. 70, figs. 11, 12).

Dorsal interior. Sub-parallel crural lamellae rise directly from the valve floor and extend anteriorly one-quarter of the valve length. Projecting laterally from them are small flange-like alate plates with their free ends directed dorso-laterally (Pl. 70, fig. 8). The crural lamellae support brachial processes consisting of subvertical curved ridges with the convex sides directed inwards (Pl. 70, figs. 7, 8). At the posterior ends of the brachial processes the hinge plates curve laterally to form concave socket plates united with the valve wall (Pl. 70, fig. 7). The sockets are small but deep. No muscle scars are evident in the material available.

Measurements (in mm) (see also text-fig. 4)

		Length	*Width*	*Thickness*
SU 19547	Complete shell	4·1	5·4	3·1
SU 19548	Complete shell	5·6	8·0	4·5
SU 19549	Complete shell	7·2	8·9	5·5
SU 19550	Ventral valve	6·4	10·0	—
SU 19552	Dorsal valve	5·2	7·6	—
SU 19554	Broken shell (Holotype)	7·2	8·3	—

Ontogeny. A sufficient range of immature specimens is available (Pl. 70, figs. 15–30) to show that the auriculate cardinal extremities, characteristic of the mature shells, are not present in the younger shells. In addition to possessing rounded cardinal margins the young forms also differ from the mature forms in lacking an incurved dorsal beak and a prominent fold and sulcus (Pl. 70, figs. 18, 24, 28, 29). The disproportionately greater width of older specimens is evident from the width and length dimensions plotted in text-fig. 4. The allometric increase in thickness is less marked.

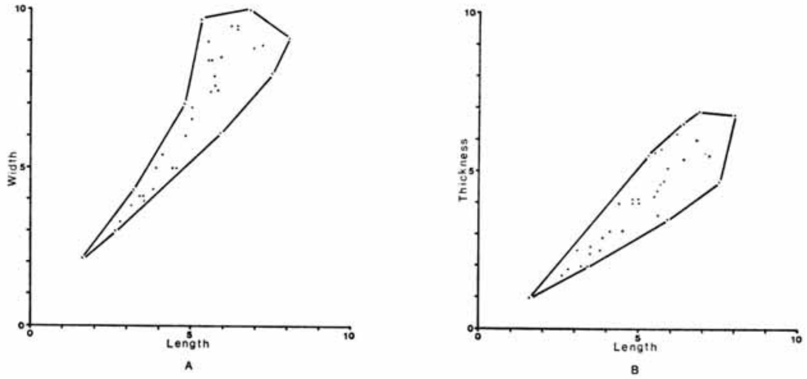
Discussion. The Manildra material is characterized by a wide hinge line with sharp cardinal extremities. In outline it is similar to *Anastrophia magnifica* Kozlowski from the Borszczow Stage of Podolia but the specimens from Podolia have more costae and a more swollen dorsal umbo. Johnson (1965) has recorded *A.* cf. *magnifica* from the Windmill Limestone in Nevada and Lenz (1967) has recorded *A.* cf. *magnifica* from his *Monograptus yukonensis* zone in the Yukon. Both workers assign an early Siegenian age to their horizons (Lenz 1967, p. 595; Johnson, Boucot, and Murphy 1967). Johnson has also recorded *A. magnifica* from a Gedinnian age horizon in the Roberts Mountain Formation, Nevada (pers. comm.).

EXPLANATION OF PLATE 70

Figs. 1–34. *Anastrophia magnifica australis* subsp. nov. 1–5, Dorsal ventral, posterior, anterior, and lateral views of complete shell SU 19548. 6, Antero-ventral view of dorsal valve SU 19553 showing the crural lamellae, brachial processes, and alae. 7–8, Ventro-lateral and ventro-anterior views of dorsal valve SU 19552 showing the sub-parallel crural lamellae, the brachial processes, and the small alae. 9, Conjoined specimen SU 19554 (holotype) with the dorsal valve partly broken away to show the internal features and the articulation. 10–12, Posterior, dorso-lateral, and dorsal views of ventral valve SU 19550 showing the auriculate cardinal extremities, small prominent teeth, shallow crural fossettes, and spondylium supported on the median septum. 13–14, Dorso-lateral and dorso-anterior views of broken ventral valve SU 19551 showing the spondylium and the median septum. 15–19, Dorsal, ventral, posterior, anterior, and lateral views of a very young immature specimen SU 19545 showing the short, non-auriculate hinge line, the distinct notothyrium, and the absence of a fold and sulcus. 20–24, Dorsal, ventral, posterior, anterior, and lateral views of an immature specimen SU 19546 showing many of the features present in SU 19545 but having grown sufficiently to develop a bifurcation of the central costa of the ventral valve. 25–29, Mature specimen SU 19549 showing a long auriculate hinge line, an incurved dorsal beak, a distinct ventral interarea, and a prominent fold and sulcus. 30–34, Dorsal, ventral, posterior, anterior, and lateral views of an immature specimen SU 19547. (All figures × 3·5.)

Figs. 35–43. *Machaeraria* cf. *formosa* (Hall). 35–39, Ventral, dorsal, posterior, lateral, and anterior views of conjoined specimen SU 19569 showing well the typically rounded contours. 40–41, Antero-ventral and ventral views of dorsal valve fragment SU 19573 showing the form of the hinge plates, the crura, and the cardinal process. 42–43, Antero-dorsal and dorsal views of broken ventral valve SU 19571 showing the slender dental lamellae, the shallow crural fossettes, and the long muscle scars. (Figs. 35–39, 42, 43, × 3; figs. 40, 41, × 6.)

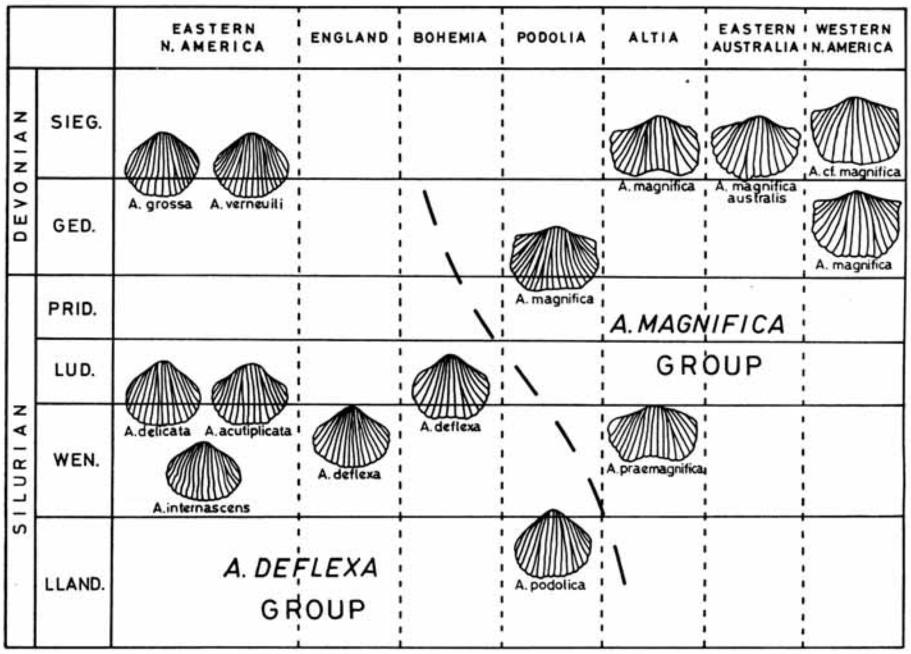
The type species from New York, *Anastrophia verneuili*, is less transverse than the Manildra form and does not possess the long hinge line. It also has more costae and a more swollen umbo. *A. acutiplicata* Amsden, from the late Silurian Brownsport Formation of Tennessee has a narrow hinge line like *A. verneuili* but possesses fewer costae. The two other North American species are *A. grossa* Amsden, from the Lower Devonian of Oklahoma, and *A. internascens* Hall, from the middle Silurian of New York. Both are more rounded in outline than the Australian material and have more swollen umbones. *A. deflexa* (Sowerby), from the Wenlock Limestone of England, and *A. podolica* (Wenjukow), from the Lower Silurian Kitaygorod Formation of Podolia, are also rounded species with swollen umbones.



TEXT-FIG. 4. *Anastrophia magnifica australis* subsp. nov. Scatter diagrams and limiting polygons of 35 specimens plotted in millimetres. A. Plot of width to length. B. Plot of thickness to length.

Species of *Anastrophia* appear to be divisible into two general groups on the basis of external shape. One group comprises species characterized by a short hinge line and a subcircular outline. Species included in this group are *A. deflexa* from the Upper Silurian of Britain, Gotland, and Bohemia, *A. podolica* from the Lower Silurian of Podolia, *A. acutiplicata*, *A. internascens*, and *A. delicata* from the Upper Silurian of eastern North America, and *A. verneuili* and *A. grossa* from the Lower Devonian of eastern North America. The second group comprises forms with a long hinge line and a transversely elongate outline. Forms referred to this group are *A. magnifica* from the Lower Devonian of Podolia, *A. praemagnifica* and *A. magnifica* from the Upper Silurian and Lower Devonian of the Altai Mountains, *A. magnifica australis* from the Lower Devonian of eastern Australia, and *A. magnifica* from the Lower Devonian of western North America. The distribution of these species is shown in text-figures 5–7. It is appreciated, however, that there are considerable differences in size between average specimens of the various species included within these two groups and that further distinctions can be drawn based on variations of the internal lamellae, the prominence of the umbones, the inclination of the beaks, and the arrangement of the costae.

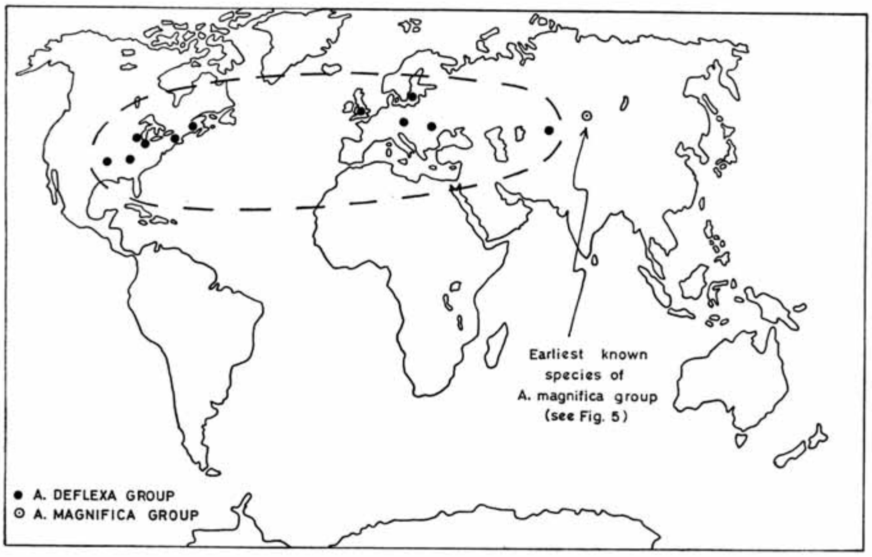
The transversely elongate species of *Anastrophia* are first recorded from the Altia Mountains of Siberia in Upper Silurian times and later occur westwards in eastern and central Europe and eastwards in eastern Australia and western North America (text-fig. 6). By Lower Devonian times their occurrence gives a reliable indication of the extent of the Bohemian–Uralian–Tasman–Nevadan faunal province (text-fig. 7). The rounded species of *Anastrophia* are widely distributed in eastern North America and across Europe at intervals during the Silurian but they appear to have become restricted to the Appalachian and Midcontinent areas of North America by the early Devonian (text-fig. 7). This withdrawal to the North American continent east of the Rocky Mountains coincides with the isolation of a distinctive Appalachian fauna in these areas during late Gedinnian and early Siegenian times.



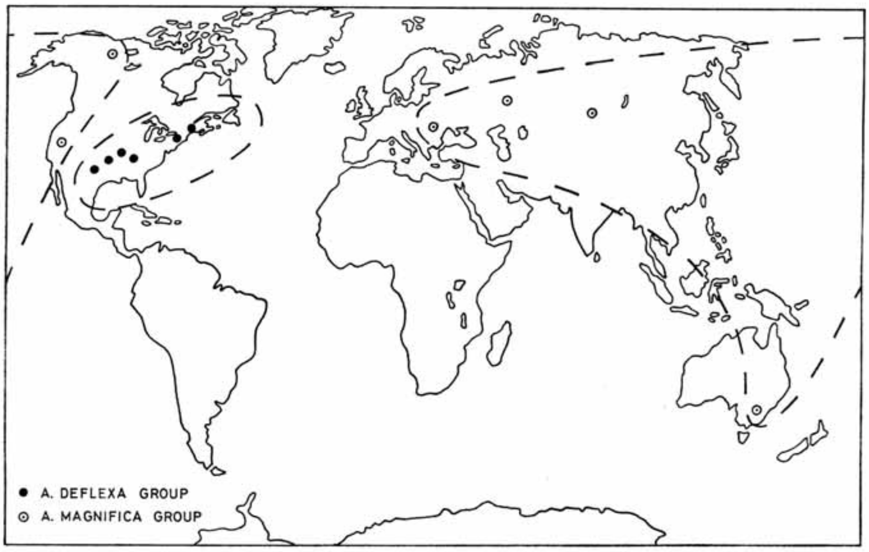
TEXT-FIG. 5. Geographical and stratigraphical distribution of rounded and transverse forms of *Anastrophia*.

Order STROPHOMENIDA Öpik 1934
Superfamily STROPHOMENACEA King 1846
Family LEPTAENIDAE Hall and Clarke 1895 (1894)
Genus LEPTAENA Dalman 1828

Type species. Leptaena rugosa Dalman 1828, by subsequent designation of King, 1846.



TEXT-FIG. 6. Known Silurian occurrences of *Anastrophia*.



TEXT-FIG. 7. Known Lower Devonian occurrences of *Anastrophia*.

Leptaena cf. *goldfussiana* Barrande 1848

Plate 74, figs. 1–8

1848 *Leptaena depressa* var. *goldfussiana* Barrande, p. 235, pl. 22, fig. 4.
1879 *Strophomena rhomboidalis* Wilck. sp. = *Leptaena depressa* Dalm.; Barrande, pl. 41, figs. 11–13.
1967 *Leptagonia goldfussiana* (Barrande 1848); Havlíček, p. 103, pl. 17, figs. 10–18.

Material. Of a total of 6 specimens, 1 is almost complete with the valves conjoined, 2 are broken ventral valves, and 3 are fragments of dorsal valves.

Description. Exterior. The shell is subrectangular in outline with the greatest width along the hinge line. A concavo–convex lateral profile is accentuated by the pronounced geniculate anterior trail. The ventral valve is flat to gently convex over the non-geniculate part, but with a slightly swollen umbo and a swollen geniculate rim. The angle of geniculation is about 100°. Anteriorly the trail descends steeply but is less steep along the sides. A short, apsacline interarea includes an apical angle of about 140° (Pl. 74, figs. 2, 3). The delthyrium is largely closed by a gently convex pseudodeltidium leaving a small foramen which appears to encroach on the umbo in old age (Pl. 74, figs. 2, 8). The dorsal valve is planar or gently concave away from the lateral and anterior margins which are sharply reflexed to correspond with the ventral trail. The interarea is very short, almost linear, and the notothyrium is filled by an inflated cardinal process (Pl. 74, figs. 2).

The surface of both valves is covered by coarse concentric corrugations which progressively increase in size away from the umbones up to the line of geniculation, after which they cease (Pl. 74, fig. 1). From the few specimens available it appears that 10–14 corrugations are typical in a mature specimen. Fine radiating ridges cover the whole of the exterior, including the geniculate rim.

Ventral interior. A prominent muscle field extends one-quarter to one-third the valve length (Pl. 74, fig. 8). The raised rims of the flabellate diductor scars join rudimentary dental lamellae which diverge anteriorly at about 110°. The diductors are separated by a broad median adductor area which is strongly elevated and continuous from the pedicle foramen to the anterior limit of the muscle field (Pl. 74, fig. 4, 8). A narrow myophragm separates the adductor scars medially (Pl. 74, fig. 4). Prominent teeth are strongly divergent at 70–80° as continuations of the tooth ridges along the delthyrial margins (Pl. 74, fig. 3).

Dorsal interior. A large bipartite cardinal process extends just posterior of the hinge line. Continuous with the cardinal process lobes are massive socket ridges (Pl. 74, fig. 7). These extend antero-laterally around moderately deep sockets which are open posterolaterally. Ill-defined muscle scars are excavated into a raised muscle platform which extends half the valve length. The rounded posterior adductors are larger and more widely spaced than the elongate-oval anterior adductors. At the anterior and lateral margins of the dorsal disc is a distinct diaphragm which has no equivalent furrow on the external surface of the valve.

Measurements (in mm)

		Length	*Width*	*Thickness*
SU 20688	Ventral valve	10·4	19·0*	—
SU 20689	Complete shell	8·8	14·0*	8·4

* Estimated

Discussion. Although only a few specimens of this Manildra form are available, several important features are sufficiently well preserved to demonstrate a close relationship with the Bohemian species *Leptaena goldfussiana* Barrande. The ventral valve of the Manildra form has a very well-developed pedicle collar and a large foramen (Pl. 74, fig. 1), both features given by Havlíček (1967, p. 103) to distinguish this species. The sharp geniculation of the trail and complete absence of a ventrally directed ridge at the periphery of the ventral disc are further diagnostic features (Havlíček 1967, p. 103). The irregular nature of the corrugations and widely flaring lateral geniculation of the Manildra form (Pl. 74, fig. 8) are also very apparent in the material illustrated by Barrande (Barrande 1879, pl. 41, fig. 12*a*). The same features can also be seen in specimens of this species from the Koněprusy Limestones, kindly sent to the writer by Dr. Havlíček.

Superfamily DAVIDSONIACEA King 1850
Family SCHUCHERTELLIDAE Williams 1953
Genus DRAHANOSTROPHIA Havlíček 1967

Type species. Drahanostrophia ficneri Havlíček 1967, by original designation.

Drahanostrophia burrenensis sp. nov.

Plate 73, figs. 1–21

Diagnosis. A planoconvex *Drahanostrophia* with posteriorly recurved socket plates.

Material. Of 32 silicified specimens only 1 is complete with the valves in contact. The remaining 19 dorsal valves and 12 ventral valves are mostly broken or fragmentary. SU 19558 is the holotype and other figured specimens are paratypes.

Description. Exterior. The shell is semicircular to transversely oval in outline with a wide, straight hinge line (Pl. 73, figs. 1, 2). The lateral profile ranges from unequally biconvex in younger specimens, to planoconvex, convexoplanar, or resupinate in mature forms (Pl. 73, figs. 3, 15, 19). The ventral valve is slightly convex over the costellate part of the valve but has considerable depth because of the high interarea. The height of the interarea is commonly about one-third of the width, and it is planar and apsacline, making an angle of about 50° with the umbo. The delthyrium is almost closed by a convex pseudodeltidium, with a slight opening at the base (Pl. 73, figs. 3). A low notothyrium is completely filled by a large cardinal process ankylosed to posterior extensions of the strongly recurved inner socket plates (Pl. 73, figs. 20, 21). A small hood-like chilidium forms a narrow arch over the cardinal process.

Neither valve has a fold or sulcus and the anterior commissure is rectimarginate. The surface ornament is multicostellate with costellae which increase repeatedly by intercalation to number, in the case of the holotype, 40 at 3 mm from the dorsal beak, 64 at 6 mm from the beak, and 116 at 12 mm from the beak. The primary costellae are the most strongly developed and they are distinct to the valve margin (Pl. 73, fig. 2). Numerous irregular growth-lines cross the radial ornament (Pl. 73, fig. 10).

Ventral interior. Prominent tooth ridges project anteriorly from the delthyrial margins and support short teeth. Dental lamellae appear to be totally absent (Pl. 73, figs. 6, 8, 18). No muscle field is visible in the material examined.

Dorsal interior. The cardinalia occupy only one-sixth of the hinge line. The cardinal process is bilobed with each lobe deeply grooved and posteriorly directed (Pl. 73, figs. 4, 21). An angular cleft divides the lobes which are divergent ventrally at about 25° (Pl. 73, fig. 21). The socket plates arise from the valve floor but are strongly recurved posteriorly and medially to overhang the sockets and to fuse with the notothyrial margins (Pl. 73, figs. 20, 21). The sockets are widely expanding and open laterally (Pl. 73, figs. 3, 5). A weakly impressed muscle field is large and subcircular, extending two-fifths of the distance to the anterior margin and laterally just beyond the socket ridges (Pl. 73, fig. 1). It is bounded by barely perceptible elevations.

Measurements (in mm)

		Length	*Width*	*Thickness*
SU 19558	Dorsal valve (Holotype)	16·0*	25·0*	—
SU 19564	Complete shell	5·2	6·7	2·8
SU 19566	Ventral valve	4·3	6·8	—

* Estimated

Ontogeny. Young and mature stages of both valves have been collected. The young dorsal valves show the posteriorly directed cardinal process and postero-laterally opening sockets present in the mature specimens but differ in having a relatively longer hinge line and no sign of a muscle field. In a gerontic dorsal fragment a deposit of callus has formed between the socket plates where it obscures the posterior part of the earlier formed muscle striations (Pl. 73, fig. 20). The young ventral valves have a less acute angle between the interarea and the valve floor than in the large mature specimens but even at a very young stage there seems to be some distortion of the ventral umbo, indicating an early apical attachment. Also present at this stage is a convex pseudodeltidium which completely closes the delthyrium.

Discussion. The only occurrence of *Drahanostrophia* described previously is that of the type species, *D. ficneri*, from the Middle Devonian of Moravia. The Manildra material differs from the younger species in having posteriorly recurved socket plates instead of simple, non-concave plates (see Havlíček 1967, p. 202).

Order RHYNCHONELLIDA Kuhn 1949
Superfamily RHYNCHONELLACEA Gray 1848
Family RHYNCHOTREMATIDAE Schuchert 1913
Subfamily ORTHORHYNCHULINAE Cooper 1956
Genus MACHAERARIA Cooper 1955

Type species. *Rhynchonella formosa* Hall 1857, by original designation.

Machaeraria cf. *formosa* (Hall 1857)

Plate 70, figs. 35–43

1859 *Rhynchonella formosa* Hall, p. 236, pl. 35, figs. 6*o*, 6*p*, 6*r*.
1893 *Stenoschisma formosa* (Hall); Hall and Clarke, p. 187, pl. 56, figs. 41–45.
1955 *Machaeraria formosa* (Hall); Cooper, p. 55, pl. 13B, figs. 13–29.
1963 *Machaeraria formosa* (Hall); Kulkov, p. 44, pl. 3, figs. 17–19.
1967 *Machaeraria formosa* (Hall); Gratsianova, p. 74, pl. 7, fig. 3.

Material. Of 12 silicified specimens 3 are complete shells with the valves conjoined and the remainder are isolated valves and posterior fragments showing the articulation.

Description. Exterior. The shell is transversely ovate to subtriangular in outline with rounded contours and with the greatest width anterior to midlength (Pl. 70, figs. 35, 36). In lateral profile the shell is subequally biconvex with the greatest thickness at about mid-length. Two conjoined specimens, with lengths of 9·0 mm and 8·1 mm have width/length ratios of 1·13 and 1·18 and thickness/length ratios of 0·63 and 0·71. The ventral valve is gently convex with a strongly curved umbo terminating in a small sub-erect beak (Pl. 70, fig. 38). The delthyrium is partly closed by disjunct deltidial plates which leave a narrow foramen extending to the posterior extremity of the valve. The dorsal valve is more convex than the ventral valve with a broad, prominent umbo incurved beneath the ventral interarea (Pl. 70, figs. 37, 38). A pronounced dorsal fold and ventral sulcus arise at about one-third of the shell length and extend to the strongly uniplicate anterior commissure (Pl. 70, fig. 39). In specimen SU 19569, 21 angular costae are present on each valve with 3 on the fold and 2 in the sulcus. In specimen SU 22676, 15 costae are present on each valve with 4 on the fold and 3 in the sulcus. In both of these specimens the costae on the fold bifurcate very close to the beak and the central costa of the sulcus arises by intercalation.

Ventral interior. Slender dental lamellae are slightly convex inwards and bound narrow umbonal cavities (Pl. 70, fig. 42). The teeth diverge anteriorly and have shallow crural fossettes on their antero-medial surfaces (Pl. 70, fig. 42). A narrow ventral muscle field extends half the distance to the anterior margin. It is restricted to the sulcus and has an elongate, subtriangular outline with a relatively straight anterior margin (Pl. 70, figs. 42, 43). Only diductor scars have been observed.

Dorsal interior. The hinge plates are deeply divided by a narrow notothyrial cavity containing a long, septate cardinal process (Pl. 70, figs. 40, 41). The deep, triangular sockets are bounded by the valve margin posteriorly and by large subtriangular outer hinge plates antero-medially (Pl. 70, fig. 41). From the inner edges of the hinge plates, and with their bases bounding the notothyrial cavity, arise long ventrally curved crura which are crescentic in cross-section with convex outer surfaces. (Pl. 70, figs. 40, 41). No median septum is present. In the few specimens available the dorsal muscle field has not been preserved.

Measurements (in mm)

		Length	*Width*	*Thickness*
SU 19569	Complete shell	9·0	10·1	5·7
SU 22671	Complete shell	8·1	9·6	5·8

Discussion. This Manildra form closely resembles the type material from the Helderbergian of New York (Cooper 1955, pl. 13B), the only difference of note being the greater prominence of the parietal slopes of the fold and sulcus of the North American form.

Australian material has been assigned to *Machaeraria* previously by Talent (1963). His specimens from the Emsian Tabberabbera Formation of Victoria are not sufficiently well preserved to permit a detailed comparison but as they possess a dorsal median septum they are far removed from *M. formosa.*

The species described by Kozlowski (1929) as *Stenochisma althi* is very probably a *Machaeraria* but differs from the type material in having more evenly sized costae. The costae in the sulcus of *M. formosa* are spread much more widely than those of *M. althi* (cf. Cooper 1955, Pl. 13B; Kozlowski 1929, pl. 5) and the parietal slopes of the fold and sulcus are more strongly developed.

Machaeraria has been described from several areas of Siberia. The form from the Altai Mountains, described as *M. formosa* by Kulkov (1963, p. 44, pl. 3, figs. 17–19) is close to the Manildra and New York material externally but the serial sections of Kulkov (p. 45) show relatively long dental lamellae and large lateral umbonal cavities. Also from the Altai Mountains is *M. kurjensis* Gratsianova 1967. This Lower Devonian species is more rounded than *M. formosa* and has a lenticular lateral profile (Gratsianova 1967, pl. 6, fig. 9). A further Asiatic form is *M. pygmaea* Alekseeva 1967, recently described from the Lower Devonian of the Cherskogo Mountains in north-east Siberia. This is a small form of the genus with a maximum width more posteriorly placed than in the type species (Alekseeva 1967, pl. 6, fig. 2, 3).

Genus ZLICHORHYNCHUS Havlíček 1963

Type species. Zlichorhynchus hiatus Havlíček 1963, by original designation.

Zlichorhynchus? sp.

Plate 71, figs. 30–34

Material. Only a single specimen has been found. This shows the external details very well but nothing is known of the internal features.

Description. The shell is subovate in outline with the greatest width anteriorly. The

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EXPLANATION OF PLATE 71

Figs. 1–29. *Meristella subovata* sp. nov. 1–5, Dorsal, ventral, posterior, anterior, and lateral views of conjoined specimen SU 16678 (holotype). 6–10, Dorsal, ventral, posterior, anterior, and lateral views of smaller conjoined specimen SU 16676. 11–12, Ventral and ventro-lateral views of broken dorsal valve SU 16680 showing the small concave cardinal plate supported by the high median septum. 13–14, Dorsal and antero-dorsal views of broken ventral valve SU 16686 showing the advancing dental lamellae and the absence of a distinct muscle field. 15, Dorsal view of broken ventral valve SU 16684 showing the deltidial plates and advancing dental lamellae. 16, Lateral view of broken specimen SU 16682 showing a complete spire and one of the primary lamellae attached to a crus. 17, Anterior view of broken specimen SU 16679 showing the articulation of the valves. 18, Antero-lateral view of fragment SU 16681 showing the broad jugal saddle resting on the median septum (but slightly displaced posteriorly), the primary lamellae resting on the valve floor and no longer attached to the crura, and the broken remains of one of the jugal loops. 19–23, Dorsal, ventral, posterior, anterior, and lateral views of an immature specimen SU 22673 showing the narrower outline, more rounded anterior margin, and rectimarginate anterior commissure which occur in the earlier growth stages. 24–28, Dorsal, ventral, posterior, anterior, and lateral views of SU 16677. 29, Antero-dorsal view of broken ventral valve SU 16683 showing the prominent dental lamellae and absence of an impressed muscle field. (All figures × 4.)

Figs. 30–34. *Zlichorhynchus*? sp. Dorsal, ventral, posterior, lateral, and anterior views of SU 20684 showing the rounded features, the low fold and sulcus, and the large hypothyridid foramen. (All figures × 4.)

Figs. 35–38. *Nucleospira* cf. *inelegans* (Barrande). Lateral, posterior, and two anterior views of SU 20687 showing the profiles and the strong hinge plate with its distally pointed lobes. (All figures × 4.)

posterior margin is bluntly rounded, the lateral and anterior margins gently rounded, and the antero-lateral margins strongly rounded (Pl. 71, fig. 30). In lateral profile the shell is subequally biconvex with the ventral valve the deeper and with the greatest thickness just posterior to midlength (Pl. 71, fig. 33). The width/length ratio of the sole specimen is 0·94 and the thickness/length ratio 0·58. The ventral valve curvature increases strongly towards the umbo and the beak is prominent and erect (Pl. 71, fig. 33). The delthyrium is large with an apical angle of about 75°. Along the delthyrial margins small deltidial plates are present (Pl. 71, fig. 32). A broad, poorly defined dorsal umbo is incurved beneath the ventral interarea. A low dorsal fold and ventral sulcus become discernible at about two-thirds the shell length and extend to the weakly uniplicate anterior commissure (Pl. 71, fig. 34). The shell surface is costate with 20 angular costae on each valve. No bifurcation or intercalation of the costae occurs and increase is by further growth of weak costae on the postero-lateral margins (Pl. 71, fig. 30). There are 4 costae on the fold and 3 in the sulcus. Towards the antero-lateral margins the costae curve outwards slightly at about three-quarters the shell length.

Measurements (in mm)

		Length	*Width*	*Thickness*
SU 20684	Complete shell	7·0	6·6	4·1

Discussion. Without a knowledge of the internal features this species cannot be unquestionably referred to *Zlichorhynchus* but the external features strongly suggest that genus. The differences between this specimen and *Z. hiatus* are the presence in the Manildra form of a low fold and sulcus together with lateral costae which curve gently outwards near the anterior margin. Further material may show that this is a new species of *Zlichorhynchus* or even of *Machaeraria*. However, the type species of the latter differs from this Manildra specimen in possessing a strong fold and sulcus, more pointed umbones, and a delthyrium largely closed by disjunct deltidial plates.

Family PUGNACIDAE Rzhonsnitskaya 1956

Genus LINGUOPUGNOIDES Havlíček 1961

Type species. Rhynchonella carens Barrande 1879, by original designation.

Linguopugnoides carens (Barrande 1879)

Plate 72, figs. 12–19

1879 *Rhynchonella nympha* var. *carens* Barrande, pl. 122, fig. 4, 5.
1906 *Rhynchonella nympha* Barrande; Siemiradzki, p. 170, pl. 7, fig. 2.
1929 *Camarotoechia carens* (Barrande); Kozlowski, p. 155, pl. 9, figs. 5–17.
1937 *Camarotoechia carens* (Barrande); Nikiforova, p. 37, pl. 6, fig. 11.
1954 *Camarotoechia carens* (Barrande); Nikiforova, p. 101, pl. 10, figs. 6–9.
1961 *Linguopugnoides carens* (Barrande); Havlíček, p. 94, pl. 11, figs. 1, 2.

Material. Of 9 silicified specimens, 2 are sufficiently complete to show the general form of the shell. The others are posterior and anterior fragments which show the important internal features and the nature of the articulation.

Description. Exterior. The shell is transversely ovate to subtriangular in outline with the greatest width anterior to mid-length. The lateral profile is unequally biconvex, the dorsal valve being much deeper than the ventral valve (Pl. 72, fig. 15). The ventral valve is weakly convex but with a strong flexure at the anterior margin to form a prominent tongue (Pl. 72, fig. 12). The umbo is narrow and gently curved, and the beak is small and erect to incurved. The interarea is very short and narrow with a small, mesothyrid foramen (Pl. 72, fig. 16). The dorsal valve is very strongly convex with a broad, inflated umbo, which is incurved beneath the ventral beak. A broad ventral sulcus extends most of the valve length to the anterior margin where it is very pronounced and forms a conspicuous vertical tongue within the dorsal fold (Pl. 72, fig. 12). The posterior parts of both valves are smooth but strong plications develop anteriorly. The sulcus bears 2 or 3 plications and the fold 3 or 4, with a further 2 or 3 on the anterior parts of the lateral slopes (Pl. 72, fig. 14).

Ventral interior. Short, slender dental lamellae are widely divergent anteriorly and are placed close to the valve walls. The lateral umbonal cavities are narrow but distinct (Pl. 73, fig. 18). Small, anteriorly thickened teeth project from the dorsal edges of the dental lamellae. The muscle field has not been observed.

Dorsal interior. The hinge plates are divided by a narrow cleft (Pl. 72, fig. 19). The outer plates are triangular and slightly concave upwards. Their inner edges support the crural bases and define the sides of the septalium, and their outer edges form low socket bounding ridges (Pl. 72, figs. 17, 18). The sockets diverge at about 110° and are elevated well above the valve margins. Long, ventrally curved crura are crescentic in cross-section with the convex faces directed ventro-laterally (Pl. 72, fig. 17). The septalium is very short but the median septum is long and slender, extending about one-third of the distance to the anterior margin (Pl. 72, fig. 17). The muscle field cannot be seen in this material.

Measurements (in mm)

		Length	*Width*	*Thickness*
SU 20681	Conjoined valves	10·9	12·4*	9·1*

* Estimated

Discussion. This Manildra material is closely related to the eastern European type species, *Linguopugnoides carens* (Barrande). The figured type specimen (Barrande 1879,

EXPLANATION OF PLATE 72

Figs. 1–11. *Gypidula* cf. *victoriae* Chapman. 1–2, Ventral and dorsal views of large broken dorsal valve SU 20679. The outer crural lamellae rise from the valve floor to join the anteriorly divergent brachial processes which then join the inner lamellae posteriorly. The small ridges on the inner lamellae possibly mark the posterior limit of the adductor muscle field. 3, Ventral view of dorsal valve SU 20680 showing most of the features visible in SU 20679. 4–7, Dorsal, anterior, lateral, and posterior views of ventral valve SU 20677 showing the galeate form and the anteriorly developed angular plications. 8–9, Ventral and lateral views of dorsal valve SU 19557. (All figures × 3.)

Figs. 12–19. *Linguopugnoides carens* (Barrande). 12–16, Anterior, dorsal, ventral, lateral, and posterior views of broken conjoined specimen SU 20681 showing the acuminate antero-dorsal margin and the strongly inflated dorsal valve. 17, Anterior view of conjoined fragment SU 20699 showing the long median septum, the short septalium, the strongly upcurved crura, and the ventrally converging dental lamellae. 18, Anterior view of conjoined fragment SU 20683 showing the articulation. 19, Ventral view of dorsal posterior fragment SU 20682 showing the hinge plates and crural bases. (All figures × 4.)

pl. 122, fig. IV–4; Havlíček 1961, pl. XI, fig. 1) is less deep than the Manildra material and has 4 plications on the fold compared with three on the Australian specimen with this part preserved. However, these differences appear to have no specific significance. The specimen sectioned by Havlíček (1961, fig. 34) is quite as deep as the Manildra material and the studies of Kozlowski on *Linguopugnoides carens* from Podolia showed that over 80% of his measured specimens had a thickness 0·7 of the shell length or greater (Kozlowski 1929, p. 157). From these observations it would appear that the majority of specimens of *L. carens* are much deeper than the type specimen chosen by Havlíček. The statistical studies of Kozlowski also show that about 10% of his measured specimens had 3 plications on the fold or less (Kozlowski 1929, p. 157). Internally, the Manildra material is very like the specimen from Bohemia figured by Havlíček (1961, fig. 34) and the specimen from Podolia figured by Kozlowski (1929, fig. 48).

Linguopugnoides has been described from the Altai Mountains of Siberia by Gratsianova (1967). Internally the species *L. strigata* (Khodalevich) and *L. remissus* Gratsianova do not appear to differ significantly from the type species (Gratsianova 1967, fig. 30, 31). Externally the greater width and more plicate flanks of *L. strigata* are distinctive whilst *L. remissus* appears to be more like the type material in shape apart from possessing only 2 plications on the fold. Both of these Altai forms appear to fall within the range of variation demonstrated by Kozlowski for the Podolia material.

Order SPIRIFERIDA Waagen 1883
Superfamily ATRYPACEA Gill 1871
Family LISSATRYPIDAE Twenhofel 1914
Subfamily SEPTATRYPINAE Kozlowski 1929
Genus CRYPTATRYPA Siehl 1962

Type species. Terebratula philomela Barrande 1847, by original designation.

Cryptatrypa cf. *philomela* (Barrande 1847)

Plate 73, figs. 22–27

1847 *Terebratula philomela* Barrande, p. 387, pl. 15, fig. 7.
1879 *Atrypa philomela* (Barrande); Barrande, pl. 84, fig. II, pl. 134, fig. I, pl. 145, figs. I, II.
1962 *Cryptatrypa philomela* (Barrande); Siehl, p. 196, pl. 26, fig. 6, pl. 27, figs. 1, 2, pl. 37, figs. 7, 8.

Material. Only 2 specimens are present in a collection from this locality totalling several thousand shells. One of these was split to expose the interior.

Description. Exterior. The shell is circular in outline and has a biconvex, lenticular profile (Pl. 73, figs. 25, 26). The width/length ratio of a specimen 3·2 mm in length is 1·06 and the thickness/length ratio is 0·47. The ventral valve is evenly convex with a narrow umbo and a straight beak projecting well beyond the short hinge line (Pl. 73, figs. 22, 26). No interarea is evident. The delthyrium has a width about one-tenth the maximum valve width and includes an angle of about 80°. It is flanked by narrow deltidial plates which reduce the size of the triangular foramen only slightly (Pl. 73, fig. 22). The dorsal valve is also evenly convex apart from a small umbo which projects slightly into the foramen (Pl. 73, fig. 25). There is no sign of a fold or sulcus and the shell surface is without ornament. The anterior commissure is rectimarginate (Pl. 73, fig. 24).

Ventral interior. A narrow delthyrial cavity is bordered by subparallel dental lamellae which extend about one-fifth of the valve length (Pl. 73, fig. 27). The anterior edges of these lamellae rise almost vertically from the valve floor to terminate in simple, robust teeth. No muscle field has been observed.

Dorsal interior. Small hinge plates diverge at about 90° and are well separated by a wide notothyrial cavity. Downwards the hinge plates are curved to meet the posterior wall of the valve, forming the floor of the widely divergent sockets. From the distal ends of the hinge plates prominent pointed crura project antero-ventrally (Pl. 73, fig. 27). In the only internal valve available the teeth have broken off during separation of the valves and nothing of the articulating surface of teeth or sockets is visible. The muscle field, which extends about one-fifth of the distance to the anterior margin, consists of two weakly impressed lanceolate scars separated by a very low median ridge.

Measurements (in mm)

		Length	*Width*	*Thickness*
SU 20680	Conjoined valves	3·2	3·4	1·5

Discussion. Cryptatrypa is a poorly known genus. The interior features were described by Siehl (1962) but little is known of the form of the crura or the musclature. Characterized by a simple lenticular form and a smooth surface, *Cryptatrypa* appears to provide little of diagnostic value below the generic level.

Barrande's figures of *Cryptatrypa philomela* (Barrande 1879, pl. 84, fig. II, pl. 134, fig. I, pl. 145, figs. I, II) show that some of the larger Bohemian specimens are longitudinally oval and develop a gentle dorsal fold. This is also evident in Siehl's specimens from the Greifensteiner Kalk (Siehl 1962, pl. 37, figs. 7, 8). However, the smaller specimens have a circular outline and a rectimarginate commissure. The Manildra material is here tentatively referred to the European type species as no significant differences are evident in the small number of specimens available.

EXPLANATION OF PLATE 73

Figs. 1–21. *Drahanostrophia burrenensis* sp. nov. 1–5, Ventral, dorsal, lateral, posterior, and ventro-lateral views of large dorsal valve SU 19558 (holotype) showing the external ornamentation with the distinct primary costellae and the posteriorly directed cardinal process fused to the short socket plates. 6–7, Anterior and posterior views of ventral fragment SU 19563 showing the prominent tooth ridges, the short teeth, and the delicately ornamented deltidium. 8, Antero-dorsal view of ventral valve SU 19567 showing the tooth ridges and the absence of dental lamellae. 9–10, Posterior and ventral views of large broken ventral valve SU 19562 showing the planar, apsacline interarea, the convex deltidium, and the distorted umbo. 11–15, Antero-ventral, ventral, anterior, dorsal, and lateral views of conjoined specimen SU 19564 showing the unequally biconvex form of this young specimen and the attachment distortion of the ventral umbo. 16–19, Ventral, anterior, antero-dorsal, and lateral views of young ventral valve SU 19566. 20–21, Ventral and posterior views of dorsal fragment SU 19559 showing the cardinal process, sockets, and socket plates of a large gerontic specimen. (All figures ×3.)

Figs. 22–27. *Cryptatrypa* cf. *philomela* (Barrande). 22–26, Dorsal, ventral, anterior, posterior, and lateral views of conjoined specimen SU 20680. 27, The same specimen after breakage to reveal the widely separated hinge plates and the antero-ventrally directed, pointed crura. (Figs. 22–26 ×6; fig. 27 ×14.)

Superfamily ATHYRIDACEA M'Coy 1844
Family MERISTELLIDAE Waagen 1883
Subfamily MERISTELLINAE Waagen 1883
Genus MERISTELLA Hall 1859

Type species. Atrypa laevis Vanuxem 1842, by subsequent designation of Miller 1889.

Meristella subovata sp. nov.

Plate 71, figs. 1–29

Diagnosis. An equally biconvex *Meristella* with an erect beak and a rectimarginate commissure. Internally a broad jugal saddle bifurcates to form accessory loops. The dental lamellae are short and the ventral muscle field is not distinctly impressed.

Material. Of over 150 silicified specimens 41 are complete shells with the valves conjoined. The remainder are separate dorsal and ventral valves or fragments of valves. Specimen SU 16678 is the holotype and other illustrated specimens are paratypes.

Description. Exterior. The shell is longitudinally pyriform to subpentagonal in outline with the maximum width just anterior of midlength (Pl. 71, figs. 1, 6, 24). The lateral profile is equally biconvex. Ten mature conjoined specimens with lengths from 5·5 to 8·0 mm have width/length ratios ranging from 0·71 to 0·97, with a mean of 0·83, and thickness/length ratios ranging from 0·53 to 0·71, with a mean of 0·58. The ventral valve has a narrow, erect beak terminating in a small, rounded foramen (Pl. 71, figs. 5, 6, 13). No interarea is evident. The delthyrium is wide with an apical angle estimated to vary from 85 to 95° and the deltidial plates meet medially to form the anterior margin of the foramen (Pl. 71, figs. 1, 13). The dorsal valve is equally convex and possesses a distinct umbo. A broad shallow sulcus is developed in the anterior part of the ventral valve but the dorsal valve is without a corresponding fold and often bears a slight sulcus. The anterior commissure is rectimarginate or gently uniplicate (Pl. 71, figs. 4, 27).

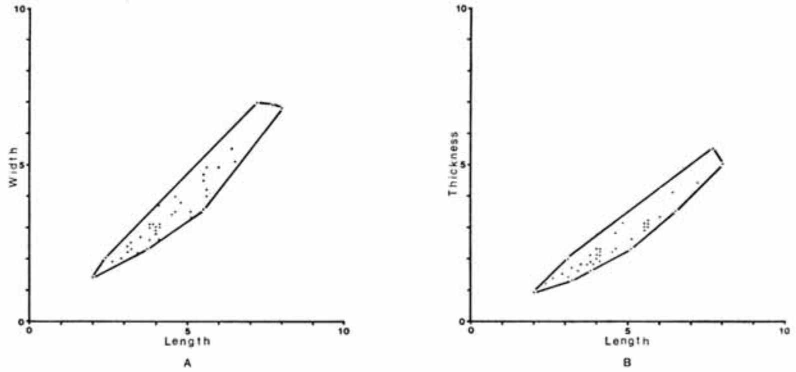
Ventral interior. Short dental lamellae enclose narrow umbonal cavities laterally (Pl. 71, fig. 29). Small, rather flattened teeth project antero-medially from the valve margin (Pl. 71, fig. 13). No muscle impressions have been preserved.

Dorsal interior. A small concave cardinal plate is present (Pl. 71, fig. 11). The deep, narrow sockets are bounded laterally by the up-curved posterior edges of the short, pointed crural lamellae (Pl. 71, figs. 11, 12). A high median septum supports the cardinal plate and projects slightly up through it (Pl. 71, fig. 11). The septum extends almost half the valve length. Laterally directed spiralia each make 6 or 7 volutions (Pl. 71, fig. 16). Primary lamellae are attached to the crura at a sharp angle. They turn downward and anteriorly along the valve floor and, at about one-third the valve length, they become very deep and are joined together by a broad, anteriorly projecting jugal saddle supported on the high median septum (Pl. 71, fig. 18). The jugum bifurcates posteriorly forming two accessory lamellae which then curve back anteriorly as loops to rejoin the jugum. No muscle impressions are preserved.

Measurements (in mm)

		Length	*Width*	*Thickness*
SU 16676	Complete shell	4·6	4·0	2·8
SU 16677	Complete shell	5·6	4·9	3·0
SU 16678	Complete shell (Holotype)	7·2	7·0	4·4

Ontogeny. The youngest stages of this species have the maximum width at about mid-length and have a rectimarginate anterior commissure. Later stages have the maximum width well towards the anterior of the shell and a very gentle ventral sulcus, without a corresponding dorsal fold, resulting in a slightly emarginate anterior margin (Pl. 71, fig. 2). The ventral beak is almost straight in the younger forms but later becomes increasingly erect (Pl. 71, figs. 5, 23). Throughout growth the relationship of width and thickness to length is almost linear (text-fig. 8).



TEXT-FIG. 8. *Meristella subovata* sp. nov. Scatter diagrams and limiting polygons of 40 specimens plotted in millimetres. A. Plot of width to length. B. Plot of thickness to length.

Discussion. For many years meristellids possessing jugal loops but lacking the 'shoe-lifter' structure of *Merista* have been commonly placed in the genus *Meristella.* Boucot, Johnson, and Staton (1964) state that in the subfamily Meristellinae they 'will give primary consideration to the presence or absence of dental lamellae together with the nature of the muscle field configuration' and they have included within the genus *Meristina* species traditionally considered as *Meristella* but which possess dental lamellae and have sub-parallel ventral muscle bounding ridges. They restrict to *Meristella* species with obsolescent dental lamellae and a widely flaring ventral muscle field. The Manildra species differs from both these genera as defined above in that it has distinct dental lamellae but no visibly impressed muscle field. Furthermore, it is equally biconvex and has an erect beak, features normally observed only in young forms of *Meristella* and *Meristina.*

Several other meristellid genera possess dental lamellae and a slightly impressed ventral muscle field but differ from the Manildra species in other very significant details. *Whitfieldella* has similar ventral internal features and, in addition, usually has an erect beak and an equally biconvex form. However, the structure of the jugum in *Whitfieldella,* as described for the type species (Hall and Clarke 1893, p. 59), is quite different from that of the Manildra species and although jugal structures seem to be very variable and are far from being fully understood, they remain a key factor in generic and familial classification within the Athyridacea.

Meristella sp. has been recorded from Yass, New South Wales, (Brown, 1941) but has not been described. The form described as *Meristina* (?) *australis* by Dun (1904) from Molong, New South Wales, was later redescribed by Mitchell and Dun (1920) and assigned to a new atrypid genus, *Atrypoidea*. *Meristella* sp. has been recorded at Tyers and at Heathcote, Victoria. The Tyers specimen is considered by Talent (1965, p. 37) to be a lissatrypid but this is not evident from the illustration of Philip (1962, pl. 35, fig. 3). The Heathcote specimens figured by Talent (1965) are known only from ventral internal moulds. From the photographs they appear to be costate (pl. 15, figs. 4, 6, 8) and may be incorrectly assigned. They are distinct from the Manildra specimens both in the form of the muscle field and in the shell outline.

Of the eastern European species, *Meristella upsilon* Barrande, from the Upper Silurian of Bohemia, is externally very like *M. subovata* but the internal features of Barrande's species have not been described and a detailed comparison is not possible. In Podolia only *M. wisnioskii* is known from the late Silurian and early Devonian and this species is far removed from the Manildra material, being less elongate and having a tightly incurved ventral beak (Nikiforova 1954, pl. 17, figs. 3*a*–4*e*).

Family NUCLEOSPIRIDAE Davidson 1881
Genus NUCLEOSPIRA Hall 1859

Type species. *Spirifer ventricosa* Hall 1857, by original designation.

Nucleospira cf. *inelegans* (Barrande 1847)

Plate 71, fig. 35–38

1848 *Terebratula inelegans* Barrande, p. 52, pl. 17, fig. 1.
1879 *Atrypa inelegans* (Barrande); Barrande, pl. 83, fig. I, pl. 84, fig. IV.
? 1929 *Nucleospira robusta* Kozlowski, p. 216, pl. 11, figs. 24–35.
? 1954 *Nucleospira robusta* Kozlowski; Nikiforova, p. 155, pl. 18, fig. 9.
1963 *Nucleospira inelegans* (Barrande); Kulkov, p. 108, pl. 9, fig. 2.
1967 *Nucleospira inelegans* (Barrande); Kulkov, p. 131, pl. 21, fig. 6.

Material. Of a total of 9 silicified specimens, 7 are complete with the valves conjunct, 1 is largely complete but has been opened antero-laterally, and the remaining specimen consists of part of a dorsal valve showing the hinge plate.

Description. Exterior. The shell is almost circular in outline with the greatest thickness just posterior to mid-length (Pl. 71, fig. 35). The lateral profile is equally biconvex and almost globular in one specimen. Two specimens, 7·5 and 7·4 mm in length, have width/length ratios of 1·06 and 0·95 and thickness/length ratios of 0·67 and 0·51, respectively. The ventral beak is small, pointed, and erect to incurved (Pl. 71, fig. 35). The interarea is very short, apsacline to orthocline, and gently concave with a width about one third of the shell width. A very faint sulcus is present on the ventral valve but there is no fold on the dorsal valve. No spines or pustulae are preserved in this silicified material. A few faint growth-lines are present anteriorly.

Ventral interior. Prominent rounded teeth are supported by strong bases but without dental lamellae (Pl. 71, figs. 37, 38). A low median septum extends from the umbonal area for about three-quarters of the valve length (Pl. 71, fig. 37). The muscle field has not been observed.

Dorsal interior. A strongly upcurved hinge plate divides at about half its length and forms two stout lobes (Pl. 71, figs. 37, 38). These diverge gently and terminate in ventro-laterally directed points. The crural bases are not distinct. Between the hinge plate lobes, and posterior to them is a prominent recurved cardinal process. A narrow, elongate muscle area extends about half the valve length (Pl. 71, fig. 38). The posterior adductors are enclosed by the longer anterior adductors.

Measurements (in mm)

		Length	*Width*	*Thickness*
SU 20687	Broken conjoined valves	7·5	8·0*	5·0

* Estimated

Discussion. The genus *Nucleospira* has been recorded several times from localities in Victoria and also in New Zealand. In each case, however, the material was poorly preserved and the features used in making determinations have not been sufficiently distinctive to clearly delineate the species. Shirley (1938) has identified his Baton River material as *N.* cf. *marginata* Maurer, and Gill (1942) has given the same name to his Victorian material. Talent (1963) has erected the new species *N. bellornata* for his specimens from the Tabberabbera Formation of Victoria and distinguishes this by the very fine nature of the spinules on the surface and the absence of a dorsal sinus.

This Manildra form is more gibbous than the type species, *Nucleospira ventricosa* (Hall), the specimen figured herein being one of the less convex of those collected. In other external features it is in no way unusual and as no spinules are visible in this silicified material it is impossible to compare it in this respect with *N. bellornata.* Internally the Manildra form differs from both *N. ventricosa* (Hall) and *N. concinna* (Hall) in the tapering ventro-laterally directed hinge plate lobes.

The Manildra material closely resembles *Nucleospira inelegans* (Barrande) from the Upper Silurian and Lower Devonian of Bohemia (Barrande 1879, pl. 83, fig. I, pl. 84, fig. IV) and it seems likely that the two forms are conspecific. There is also a marked similarity to *N. robusta* Kozlowski from the Lower Devonian of Podolia which appears to differ from the Bohemian material in size only, a questionable specific characteristic in view of the influence on size of environment.

EXPLANATION OF PLATE 74

Figs. 1–8. *Leptaena* cf. *goldfussiana* (Barrande). 1–2, Ventral and dorsal views of conjoined specimen SU 20689. 3–5, Posterior, dorsal, and ventral views of broken ventral valve SU 20691 showing the apsacline interarea and the broad median adductor area separating the diductor scars. 6–7, Dorsal and ventral views of posterior dorsal fragment SU 20690 showing the dorsal muscle field. 8, Dorsal view of broken ventral valve SU 20688 showing the short muscle field, the well-developed pedicle collar, and the absence of a ridge between the ventral disc and trail. (All figures ×4.)

Figs. 9–15. *Sturtella mandageriensis* gen. et. sp. nov. 9–13, Posterior, lateral, anterior, ventral, and dorsal views of conjoined specimen SU 20678 (holotype) showing the longitudinally elliptical outline, the straight costae with rounded profile, the prominent ventral beak, and the hypothyridid foramen. 14–15, Lateral views of SU 20678 after splitting to show the imperforate hinge plate resting on the dorsal valve floor, the absence of a cardinal process, and the well developed vertical dental lamellae. (Figs. 9–13 ×8; figs. 14, 15 ×14.)

Figs. 16–21. *Platyorthis* sp. 16–18, Dorsal, ventral, and posterior views of dorsal valve SU 20677 showing the transversely ovate outline, the well impressed adductor field, and the long inclined cardinal process shaft. 19–21, Dorsal, posterior, and ventral views of dorsal valve SU 20676 showing the erect brachiophores and the flattened crenulations at the valve margin. (All figures ×6.)

In Siberia, material from the Upper Silurian and the Lower Devonian of the Altai Mountains has been assigned also to *Nucleospira inelegans* (Kulkov 1963, 1967). These Siberian specimens are very like the Manildra specimens.

Order TEREBRATULIDA Waagen 1883
Superfamily STRINGOCEPHALACEA King 1850
Family RHIPIDOTHYRIDIDAE Cloud 1942
Subfamily RHIPIDOTHYRIDINAE Cloud 1942
Genus STURTELLA nov.

Type species. Sturtella mandageriensis sp. nov.

Diagnosis. A small, costate rhipidothyrid with a hypothyridid foramen. Internally the hinge plates are united to form an imperforate cardinal plate resting on the floor of the dorsal valve. In the ventral valve dental lamellae are well developed.

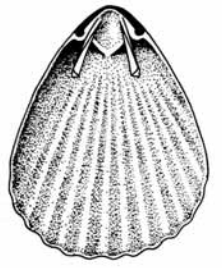
Discussion. The hypothyridid foramen, imperforate cardinal plate, and well developed dental lamellae place *Sturtella* in the Rhipidothyrididae. It most closely resembles *Rhipidothyris* Cooper and Williams, from the Middle Devonian of North America, but lacks the dorsal median septum present in that genus and is considerably more elongate and more delicately costate than the type species, *Rhipidothyris plicata* from the Tully Formation of New York (Cooper and Williams 1935, pl. 60, figs. 8–10).

Sturtella mandageriensis sp. nov.

Plate 74, figs. 9–15; text-fig. 9

Material. Only 2 specimens have been found and the genus is clearly rare at this horizon. The holotype SU 20678 has been split to expose the internal features.

Description. Exterior. The shell is longitudinally elliptical in outline with the greatest width just anterior to mid-length (Pl. 74, fig. 1). The hinge line is short with a width about one-third the maximum shell width and the anterior margin is evenly rounded. The lateral profile is equally biconvex with both valves of low convexity (Pl. 74, fig. 10). The width/length ratio of the holotype, which has a length of 4·3 mm, is 0·81 and the thickness/length ratio is 0·37. The ventral valve has a straight beak terminating in a conspicuous hypothyridid foramen. The delthyrium has an apical angle estimated as 50°. No deltidial plates are preserved. The dorsal valve has a less prominent umbo and has no interarea visible in the conjoined shell. A very gentle sulcus is developed on the dorsal valve but there is no perceptible fold on the ventral valve (Pl. 74, fig. 9). The anterior commissure is rectimarginate (Pl. 74, fig. 11). Both valves are ornamented with straight costae which arise at the posterior margin and do not increase in number anteriorly. At the 4 mm growth stage about 18 costae are present on each valve (Pl. 74, figs. 12, 13). In cross-section both costae and interspaces are rounded (Pl. 74, fig. 11).



TEXT-FIG. 9. *Sturtella mandageriensis* gen. et sp. nov. Drawing of dorsal valve interior based on specimen SU 20678.

Ventral interior. A deep delthyrial cavity is bounded by high, vertical dental lamellae which extend about one-quarter the distance to the anterior margin with the anterior edges advancing along the valve floor (Pl. 74, fig. 14). The lamellae are sub-parallel and enclose large lateral umbonal cavities. No muscle field is visible in the material available.

Dorsal interior. The hinge plates, which extend anteriorly about one-sixth of the valve length, are united along the valve floor to form a concave imperforate cardinal plate (Pl. 74, fig. 15; text-fig. 9). Running along the lateral margins of the hinge plates are crural bases, triangular in cross-section. From the crural bases crura project anteriorly about one-quarter the valve length (Pl. 74, figs. 14, 15). The sockets are placed well below the hinge plates on the valve floor so that the edge of the hinge plates form the outer edges of the sockets (text-fig. 9). No muscle field is preserved.

Measurements (in mm)		*Length*	*Width*	*Thickness*
SU 20678	Conjoined valves (Holotype)	4·3	3·5	1·6

REFERENCES TO OCCURRENCES OF *ANASTROPHIA* IN TEXT FIGURES 5–7

Text-fig. 5. Tracings of dorsal valves are based on the following photographs.

Anastrophia delicata Amsden; Amsden 1951, pl. 16, fig. 2.
A. verneuili (Hall); Cooper 1944 (*in* Shimer & Shrock), pl. 114, fig. 48.
A. grossa Amsden; Amsden 1958, pl. 2, fig. 27.
A. acutiplicata Amsden; Amsden 1949, pl. 2, fig. 5.
A. internascens Hall; Cooper 1944 (*in* Shimer & Shrock), pl. 114, fig. 53.
A. deflexa (J. de C. Sowerby), from England; *British Palaeozoic Fossils*, 2nd edn., 1966, pl. 18, fig. 3.
A. deflexa (J. de C. Sowerby), from Bohemia; Barrande 1897, pl. 34, fig. 15*c*.
A. podolica (Wenjukow); Nikiforova 1954, pl. 3, fig. 13*b*.
A. magnifica Kozlowski, from Podolia; Nikiforova 1954, pl. 4, fig. 1*b*.
A. magnifica Kozlowski, from Altai; Kulkov 1963, pl. 1, fig. 3*c*.
A. magnifica Kozlowski, from Nevada; unpublished photograph sent by J. G. Johnson.
A. praemagnifica Kulkov; Kulkov 1967, pl. 6, fig. 6*b*.
A. magnifica australis Savage; herein, pl. 70, fig. 1.
A. cf. *magnifica* Kozlowski, from Nevada; unpublished photograph sent by J. G. Johnson.

Text-fig. 6. The following Silurian occurrences of *Anastrophia* are shown.

Anastrophia deflexa (J. de C. Sowerby); Wenlock Limestone, England, J. de C. Sowerby 1839, p. 625; Eke-margelsten, Gotland, Hede 1921, p. 93; Dlauha Hora, Bohemia, Barrande 1879, pl. 34, figs. 15–17; *A. podolica* (Wenjukow), Kitaygorod Formation, Podolia, Nikiforova 1954, p. 63; *A.* aff. *internascens* Hall, Upper Silurian, Northern Pribalkasch, Rukavischnikova 1961, p. 45; *Anastrophia* sp., Back Bay, New Brunswick, Boucot *et al.* 1966, p. 21; *A. internascens* Hall, Niagaran Series, Wisconsin, Hall & Clarke 1893, p. 224; Indiana, Cooper 1944 (in Shimer & Shrock), p. 303; New York, Cooper 1944 (in Shimer & Shrock), p. 303; *A. acutiplicata* Amsden, Brownsport Formation, Tennessee, Amsden 1949, p. 50; *A. delicata* Amsden, Henryhouse Formation, Oklahoma, Amsden 1951, p. 79; *A. praemagnifica* Kulkov, Chagirskay Formation, Altai, Kulkov 1967, p. 41.

Text-fig. 7. The following Lower Devonian occurrences of *Anastrophia* are shown.

Anastrophia cf. *verneuili* (Hall), Hedgehog Formation, Maine, Boucot & Johnson 1967, table 1; *A. verneuili* (Hall), Helderberg Group, New York, Hall & Clarke 1893, p. 224; Birdsong

Shale, Tennessee, Boucot & Johnson, 1967, table 1; Bailey Limestone, Missouri, Boucot & Johnson, 1967; Pillar Bluff Limestone, central Texas, Boucot & Johnson 1967, table 1; *A. grossa* Amsden, Haragan Formation, Oklahoma, Amsden 1958, p. 65; *A. magnifica* Kozlowski, Borszczow Stage, Podolia, Kozlowski 1929, p. 140; Petropavlovsk Formation, eastern Urals, Khodalevich 1951, p. 18; Solovikha Limestone, Altai, Kulkov 1963, p. 18; *A. magnifica australis* Savage, Mandagery Park Formation, New South Wales, herein; *A.* cf. *magnifica* Kozlowski, Windmill Limestone, Nevada, Johnson 1965, p. 371; *Monograptus yukonensis* zone, Yukon, Lenz 1967, p. 592.

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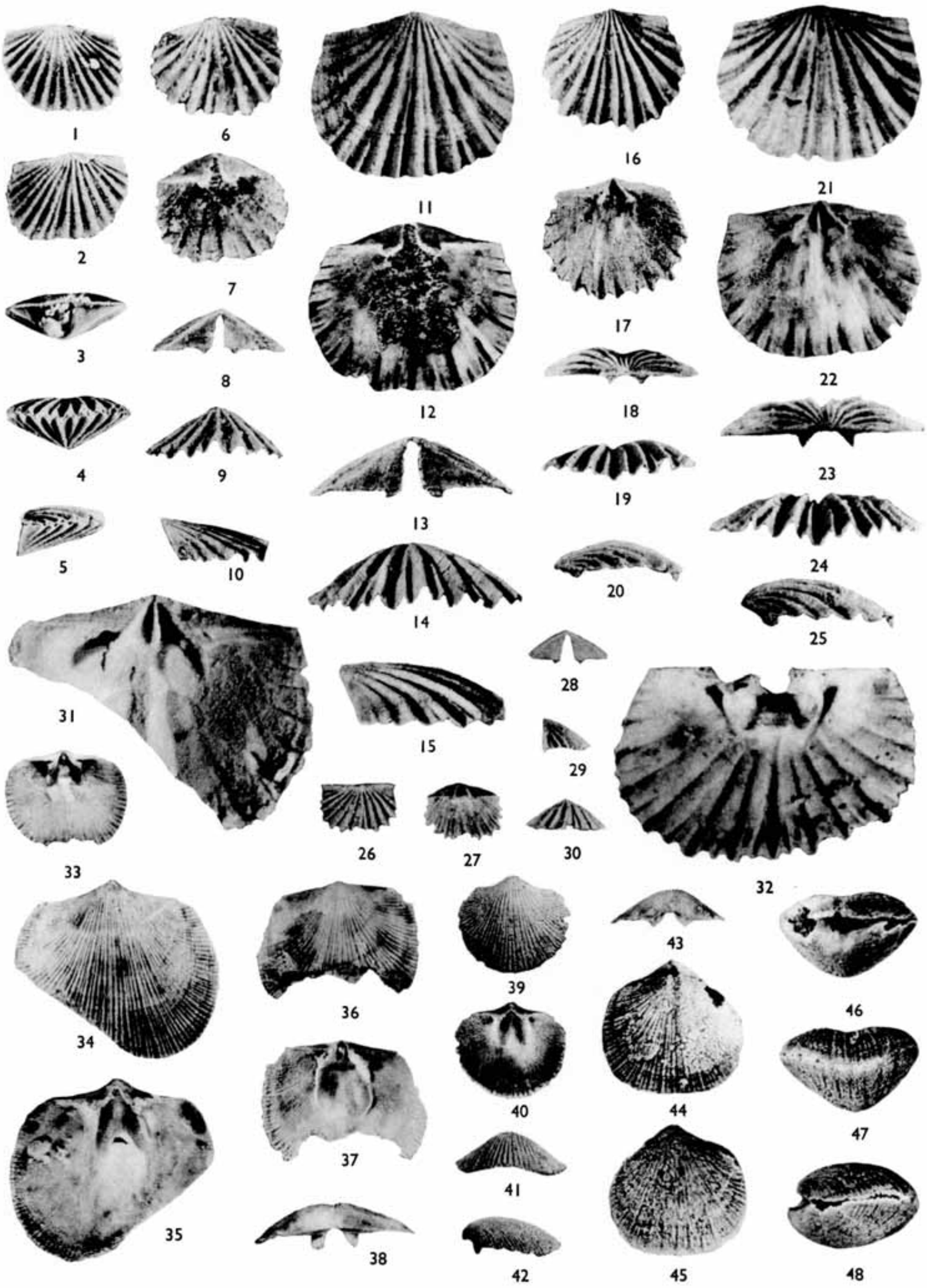
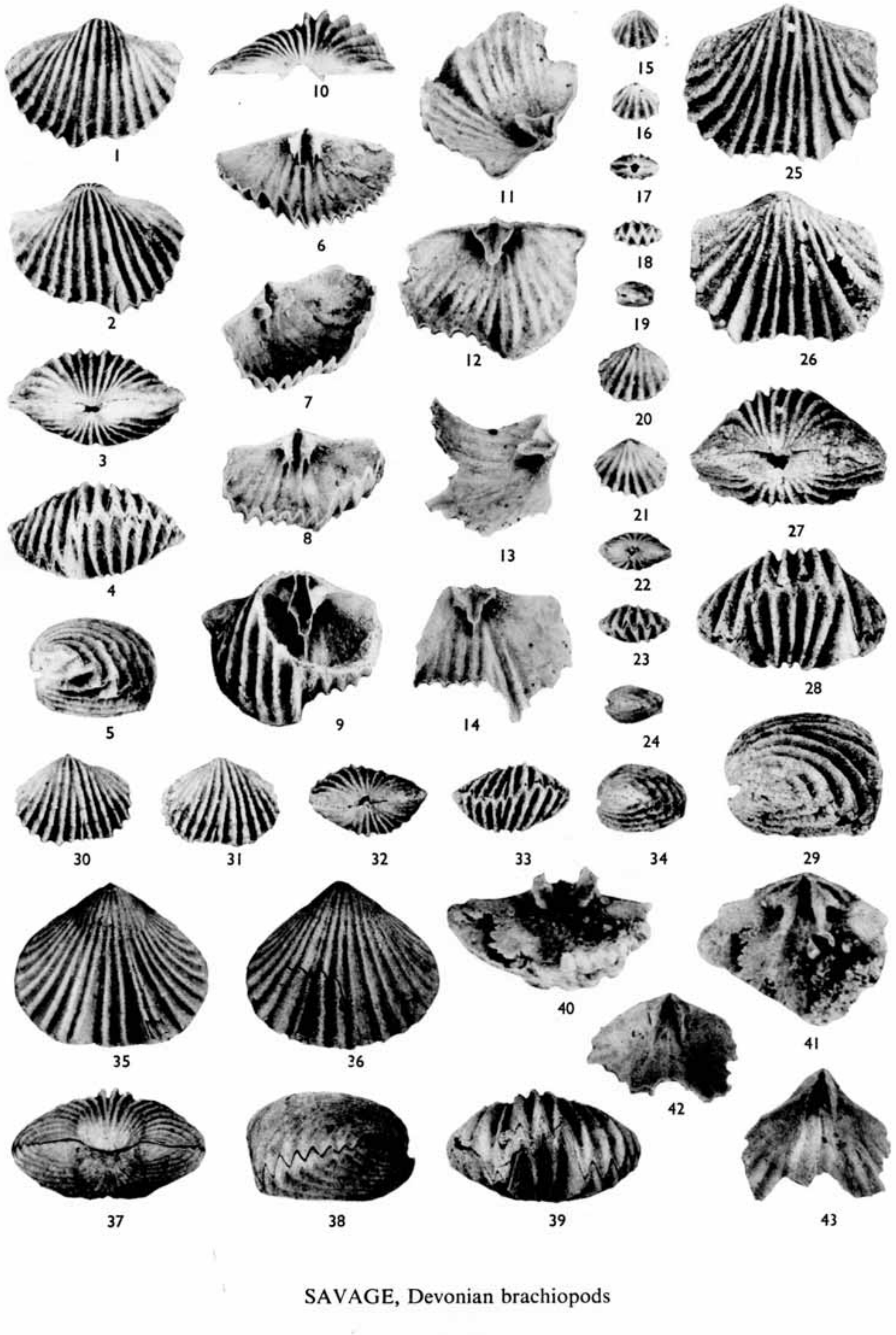
PLATE 69



SAVAGE, Devonian brachiopods



SAVAGE, Devonian brachiopods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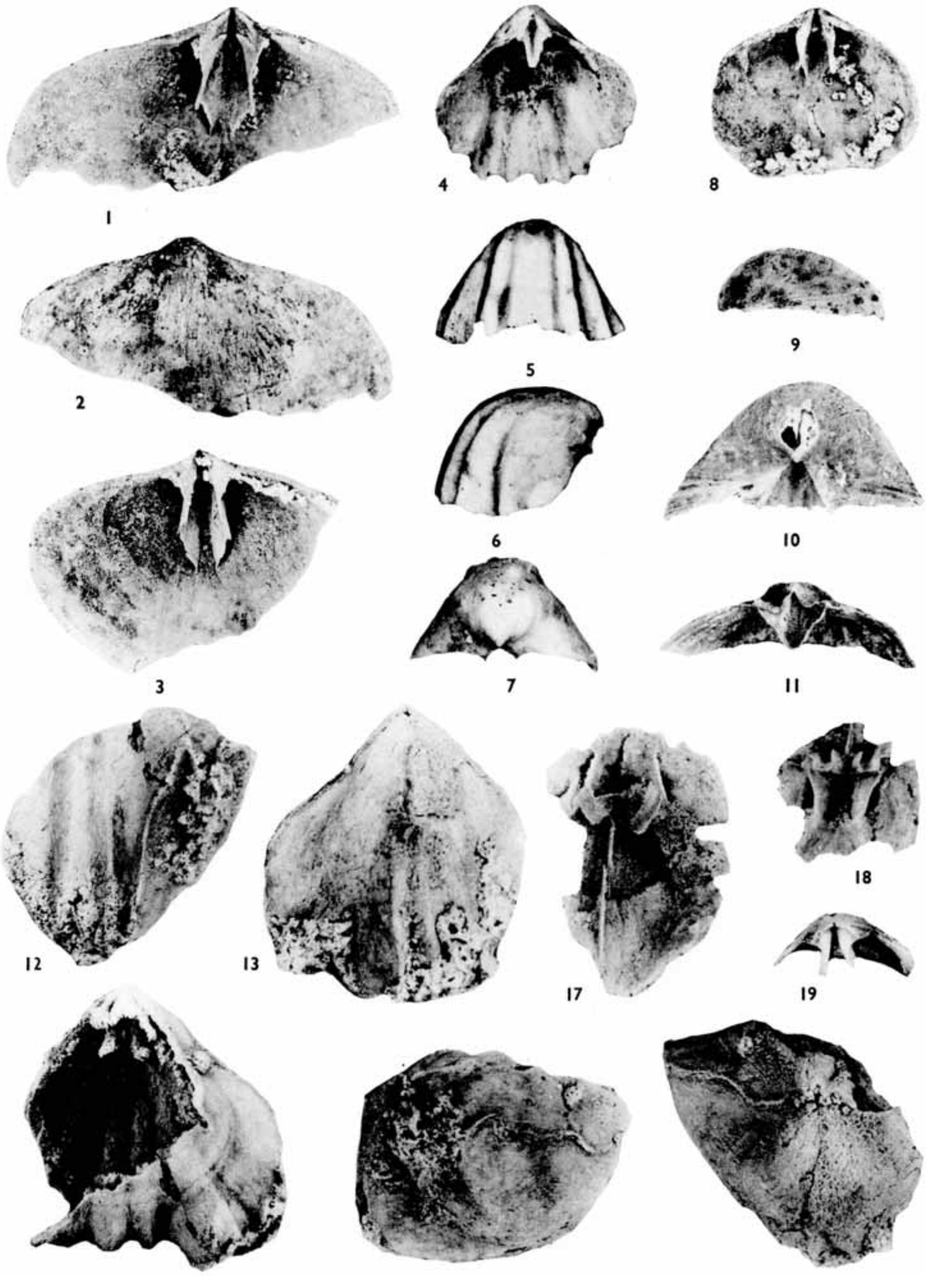
SAVAGE, Devonian brachiopods



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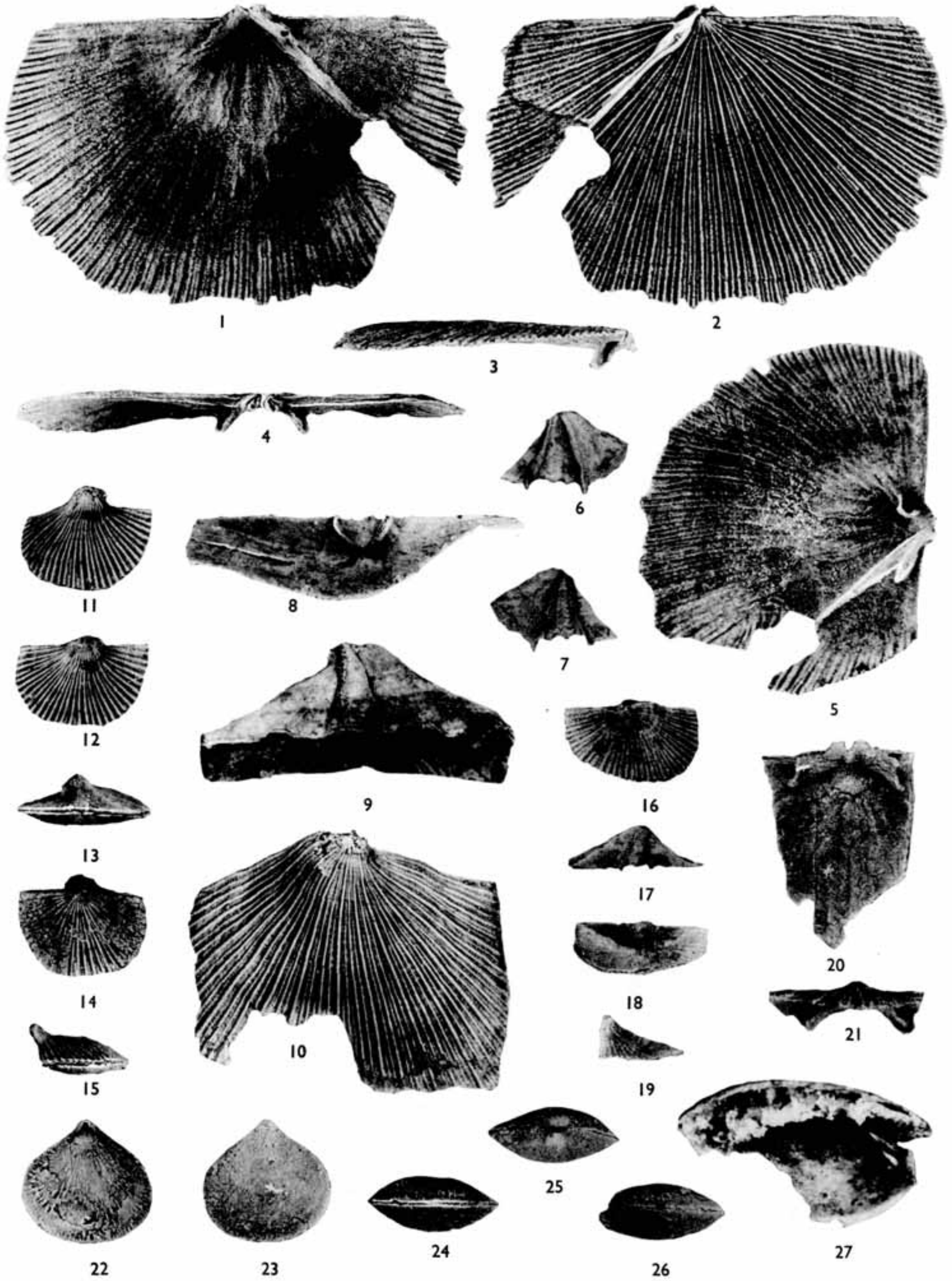

SAVAGE, Devonian brachiopods


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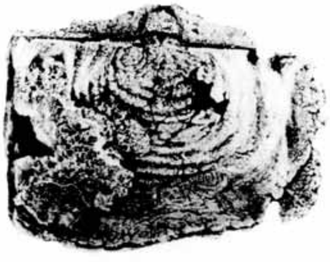
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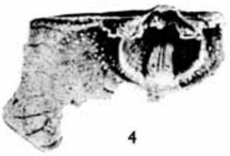
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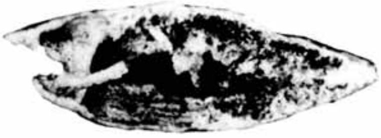
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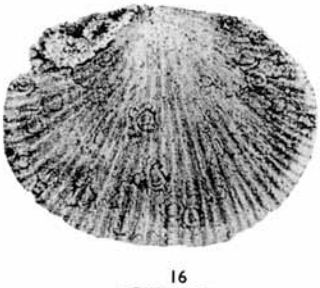
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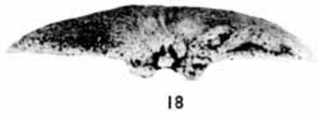
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SAVAGE, Devonian brachiopods