Silurian athyridide brachiopods from Yass, New South Wales

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Three athyridide taxa from the late Wenlock to Přídolí of the Yass Syncline, belonging to the Superfamilies Nucleospiroidea and Anoplothecoidea, are described, new species being *Nucleospira paula* and *Navispira*? *bicarinata*. The former is also known from the Late Wenlock of Canberra. None of the specimens provide information on the structure of spiralia or jugum. Two further species earlier described by Mitchell, for which no specimens can be found, are discussed. One, *Molongia elegans* (the type species), was based mostly on specimens from Molong, NSW; a lectotype from there is chosen and described.

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Keywords: Silurian, Australia, Brachiopoda, *Nucleospira*, *Navispira*, *Coelospira*, *Molongia*, systematics, new species, biostratigraphy.

ATHRYIDIDE brachiopods were included amongst the fossils listed in early papers describing the geology and stratigraphy of the Yass - Bowning area (Jenkins 1879; Mitchell 1887; Shearsby 1912; Sherrard 1936; Brown 1941). Mitchell (1921) described *Molongia elegans* (based on and illustrated by specimens from Molong, NSW) and *Retzia salteri* (illustrated by one poor specimen from the Hume Limestone Member). Neither of these can be recognised in the material I have studied, including Mitchell's collections now held by the Australian Museum. In the present paper I describe three other athyridide taxa from Yass, of which two are new. In addition, a lectotype for *M. elegans* (genotype) is chosen, briefly described, and illustrated.

Unsurprisingly, *Nucleospira paula* n. sp. is found over an extended stratigraphic range (for an account of the Yass succession see Strusz 2002). At Yass it is known from the *Barrandella* Shale to the lower Cowridge Siltstone, and at nearby Canberra the same species has been reported (in smaller numbers) from the late? Wenlock Walker Volcanics (the age is uncertain, but on stratigraphic grounds is older than the Yass Formation), and is probably also present in the Yarralumla Formation (a lateral equivalent of the Yass Formation). This gives a total range of late? Wenlock to Přídolí. The diminutive *Navispira*? *bicarinata* n. sp. has nearly the same stratigraphic range - Yass Formation or basal Silverdale Formation to lower Cowridge Siltstone. Finally, a few specimens of *Coelospira cavata* Strusz, 1982, are described from the Yass Formation, the basal Black Bog Shale and possibly the *Barrandella* Shale. The distribution of these few taxa is shown in Figure 1.

MATERIAL AND LOCALITIES

Strusz (2002) gave an account of the sources of material used in revising the Yass faunas, including an assessment of their reliability. Details of the localities, including possible Benthic Community assignments for each, were given in the Locality Appendix of Strusz (2002), with additions by Strusz (2003, 2005).

SYSTEMATIC PALAEONTOLOGY

Classification. The classification used here is that given by Alvarez & Copper (2002).

Measurements and symbols. All linear measurements are in millimetres, and unless otherwise specified are as defined by Williams & Brunton (1997); the following symbols are used for these measurements:

Ls, Ws – maximum shell length, width.
Wh – hinge width.
Lv, Ld – ventral valve length (usually coincident with Ls), dorsal valve length.
Ts, Tv, Td – thickness of shell, ventral valve, dorsal valve.
L(Wmax) – length to widest part of shell.

Repositories. The repositories for the specimens studied are shown by the following prefixes to their catalogue numbers: AMF, macrofossil collection, Australian Museum, Sydney; ANU, Department of Earth & Marine Sciences, Australian National

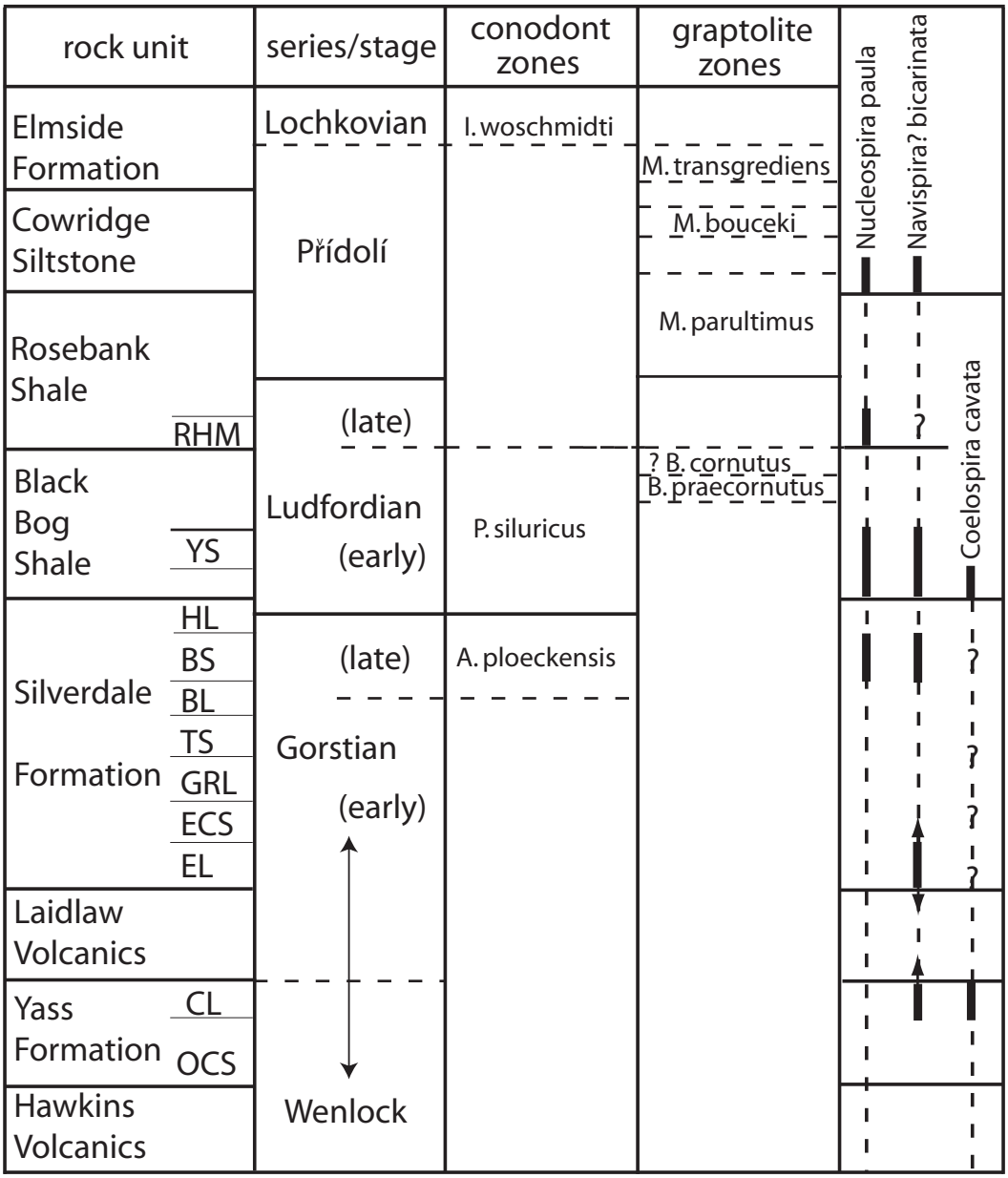

Fig. 1. Horizons of occurrence and overall age range for athyridide species in the Yass Syncline. Dashed lines represent intervals of non-occurrence, and, if extending to the bottom of the chart, indicate earlier occurrence at Canberra - either the Yarralumla Formation, a lateral equivalent of the Yass Formation, or the Walker Volcanics, laterally equivalent to the Hawkins Volcanics. Abbreviations of Member names: RHM - Rainbow Hill Mbr, YS - Yarwood Siltstone Mbr, HL - Hume Limestone Mbr, BS - *Barrandella* Shale Mbr, BL - Bowspring Limestone Mbr, TS - Tullerah Sandstone Mbr, GRL - Gums Road Limestone Mbr, ECS - Excursion Creek Sandstone Mbr, EL - Euralie Limestone Mbr, CL - Cliftonwood Limestone Mbr, OCS - O'Brien's Creek Sandstone Mbr.

University, Canberra; CPC, Commonwealth Palaeontological Collection, Geoscience Australia, Canberra; MMF, Palaeontological collections, Geological Survey of New South Wales, Sydney.

Order ATHYRIDIDA Boucot, Johnson & Staton, 1964

Suborder ATHYRIDIDINA Boucot, Johnson & Staton, 1964

Superfamily NUCLEOSPIROIDEA Davidson, 1881

Family NUCLEOSPIRIDAE Davidson, 1881

Nucleospira Hall in Davidson, 1858.

Type species. *Spirifer ventricosus* Hall, 1857. Lochkovian, New York.

Nucleospira paula n. sp. (Figs 2-4)

1982 *Nucleospira* sp. indet. Strusz, p. 129, fig. 24.
?1985 *Nucleospira* sp. indet. Strusz, p. 115, fig. 10.

Diagnosis. Diminutive *Nucleospira* with subcircular to transversely oval outline, moderately biconvex profile, narrow median sulci on both valves, relatively delicate posteriorly recurved cardinal flange and moderately robust median ridges extending full length of both valves.

Etymology. Latin *paulus*, *-a*, little.

Type material. Holotype ANU9573, paratypes ANU9565-72 (of which 9569 and 9570 are counterparts), 9574, 46513, all from Kemezys' locality KC6 north of 'Silverdale'. Yarwood Siltstone Member, early Ludfordian.

Other Yass Syncline material. *Barrandella* Shale Member, Silverdale Formation: Hattons Corner - MMF17715. Lower Black Bog Shale: KF (= GOU52) - 19 specimens including ANU9579-80, 46506-12, and CPC39419-21. Yarwood Siltstone Member: KC6, 21 - 7 poorly preserved topotypes in addition to type series; KE (= GOU46) - 19 specimens including ANU9576, 46514-5, CPC39422-28; GOU30 - 1 fragment. Rainbow Hill Member, basal Rosebank Shale: KC4 - ANU9710. Basal Cowridge Siltstone: KM - 3 specimens including ANU46516. Horizon uncertain: Bowning - AMF131510.

Stratigraphic distribution. Walker Volcanics, and possibly Yarralumla Formation, Canberra; *Barrandella* Shale Member, Lower Black Bog Shale, Yarwood Siltstone Member, Rainbow Hill Member (rare), and topmost Rosebank Shale to lower Cowridge Siltstone (rare), Yass Syncline.

Age. Late Wenlock to Přídolí.

Description. Shells very small, mostly 3.5-5 mm long, 4-5.5 mm wide; maximum observed Ws 9 mm. Outline subcircular to moderately transversely elliptical (Ls/Ws 0.8-1.0), greatest width about mid-length; profile biconvex, lenticular to moderately swollen. Greatest convexity in posterior third longitudinally, and near mid-line in cross-section, flanks only gently convex. Ventral beak small, low, suberect, apical angle about 120°; dorsal beak very low. When shell closed, space between beaks largely filled by posteriorly directed end of cardinal flange, which is more or less level with ventral umbo (so that Ls≈Ld). Posterior shell margin almost strophic, hinge line wide (Wh/Ws ca 0.6). Ventral area greatly reduced, almost entirely occupied by open delthyrium. No foramen. Narrow, shallow but distinct median sulcus on both valves, extending from umbones to anterior margin. Anterior commissure rectimarginate, straight to slightly emarginate. Larger shells with two or three well-spaced concentric furrows, the inner ones faint, the outermost distinct, in some cases the proximal side almost lamellate. Shell surface covered with closely spaced minute spines. Shell wall thin.

Ventral interior with median ridge extending from delthyrial cavity to anterior margin. Ridge low posteriorly, and narrow where dividing muscle field, rising and widening forwards to beyond mid-length, then decreasing in height towards anterior valve margin. Muscle field elongate oval, diductor scars faint, adductors small, slightly impressed either side of median ridge, with slightly raised outer edges. Teeth elongate parallel to hinge, supported by thickened valve margin and separated from it by narrow grooves. Valve floor may be faintly radially striated, with pair of weak subparallel ridges extending forward from muscle field. Valve floor also finely pitted, probably reflecting the external microspines.

Dental sockets narrow, parallel to hinge line, supported by thickened valve margin. Sockets overhung by inner socket ridges, which extend parallel to posterolateral valve margins from junctions with widely separated, often swollen, moderately divergent ridges extending from beak and probably representing crural bases. These ridges are separated from valve margin by conical grooves continuous with, but at a marked angle to, dental sockets. Ridges joined medially by relatively delicate cardinal flange which curves from antero-ventrally to posteriorly directed, and extends posteriorly beyond dorsal beak. Median ridge strong, widest anterior to mid-length, extends onto cardinal flange. Cardinal process sometimes visible as swelling at posterior end of ridge, on ventral face of cardinal flange; in a few large valves process distinctly trilobed (Fig. 3). Adductor scars narrow, weakly to moderately impressed either side of median ridge. Valve floor as in ventral valve. Brachidium not preserved.

Remarks. Several authors have commented on the

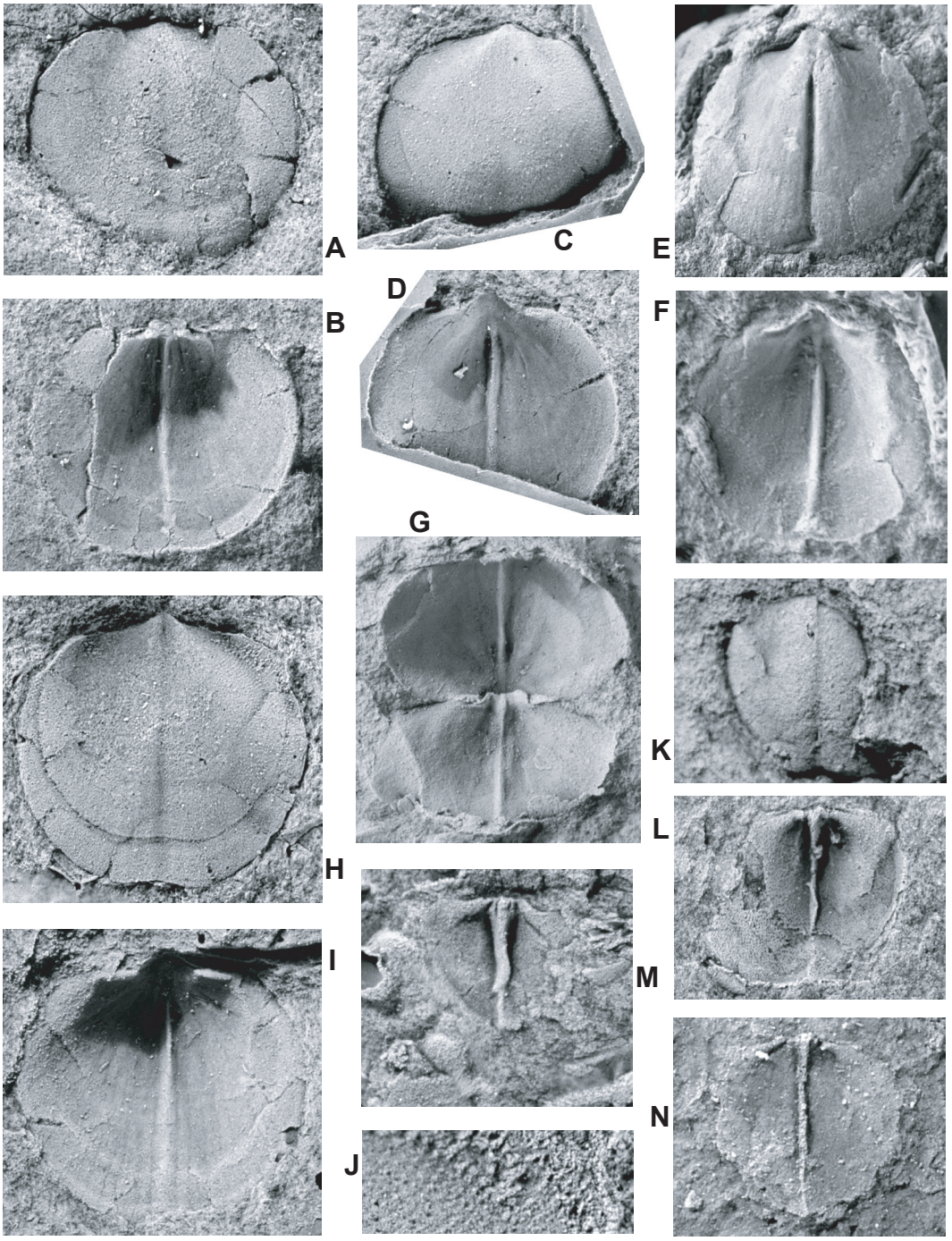

Fig. 2. Nucleospira paula n. sp. A-B, holotype ANU9573, dorsal valve exterior and interior. C-D, paratype ANU9568, incomplete ventral valve exterior and interior. E-F, AMF131510, ventral internal mould and latex replica. G, ANU9710, interior of gaping shell (ventral valve at top). H-J, paratype counterparts ANU9569, 9570; H-I, ventral valve exterior and interior, J, portion of ventral valve exterior showing microspines. K-L, ANU9579, dorsal valve exterior and interior. M, ANU9580, incomplete dorsal valve interior showing details of cardinal process. N, ANU46515, incomplete dorsal valve interior. All except E are latex replicas; all except J are x8; J is x30. Lower Black Bog Shale: K-M (locality KF); Yarwood Siltstone Member: A-D, H-J (loc. KC6), N (loc. KE); Rainbow Hill Member: G (loc. KC4); unknown horizon: E-F (Bowning).

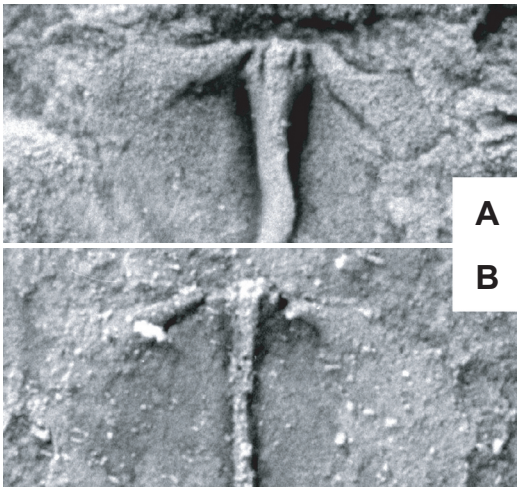

Fig. 3. Nucleospira paula n. sp. A, ANU9579 (see Fig. 2M). B, ANU46515 (see Fig. 2N). Posterior ends of dorsal valve interiors, showing trifid cardinal processes. Latex replicas, x16.

difficulty of distinguishing species of *Nucleospira*. However, as noted by Strusz (1982), the present species is distinctive in its combination of very small size, narrow but distinct sulci on both valves, long and moderately robust median ridges in both valves, and relatively delicate cardinal flange. Closest are *Nucleospira raritas* Amsden, 1958b, and *N. lentilca* Havlíček in Havlíček & Štorch, 1990. The former, from Wenlock and Ludlow strata in the USA, is similar in size, and in having narrow median sulci and long, well developed median ridges in both valves. It differs in its subcircular outline (Ls/Ws 0.9-1.1), more even convexity in both longitudinal and transverse profiles, a somewhat larger ventral beak, more swollen cardinalia, and little or no sign of the median ridge on the face of the rather shorter cardinal flange. *Nucleospira lentilca*, from the Wenlock of Bohemia, was separated from the Devonian *N. inelegans* (Barrande, 1879) by Havlíček (in Havlíček & Štorch 1990); it is only certainly known from the Wenlock of Bohemia and Arctic Canada (Jin & Chatterton 1997). Silurian records of *N. inelegans* which could be *N. lentilca* are Kulkov (1967: Wenlock, Gorno Altai), Kulkov (in Ivanovskiy & Kulkov 1974: Přídolí, Altai-Sayan Mts) and Biernat (1981: Ludlow, Poland). *Nucleospira lentilca* is larger than the Yass species (Jin & Chatterton recorded shells up to 11 mm long, 12.9 mm wide), but very similar in shape except for a more prominent ventral beak. The sulci are fainter, the median ridges in both valves tend to be narrower, and the muscle fields are fainter. The delthyrium in *N. lentilca* is completely closed by a deltidium (this could be simply a factor of size), and more significantly the

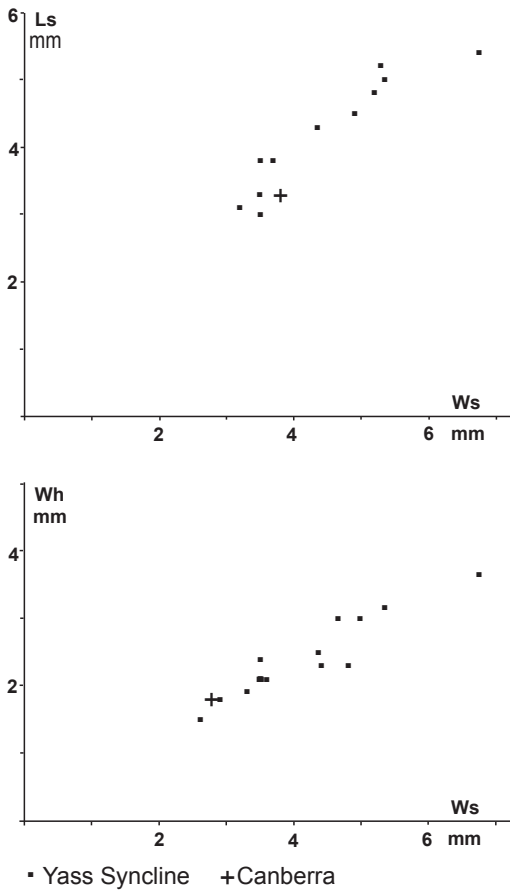

Fig. 4. Nucleospira paula n. sp. Plots of shell length Ls and hinge width Wh against shell width Ws for specimens from the Yass Syncline, and CPC21039 from the Walker Volcanics, Canberra.

cardinal flange (also curved to emerge posteriorly beyond the dorsal umbo) is more swollen, longer, and distinctly bilobed.

Nucleospira sp. indet. Strusz, 1985, from the Wenlock? Canberra Formation, is known from only a few poorly preserved and distorted dorsal valves. The maximum width is at about 1/3 the length of the shell, and the median ridge is obscure posteriorly, but reaches the anterior margin. It could be the same species as at Coppins Crossing and Yass, but better and more abundant material from the Canberra Formation is needed before that can be established. In shape it resembles the specimen from Cadia in central New South Wales figured by Rickards *et al*. (2001, fig. 3f) as *Nucleospira*? sp. That specimen, however, appears to have a much more subdued ventral median ridge. The Cadia locality is of late Wenlock (*lundgreni-testis* Zone) age (Rickards & Wright 2004).

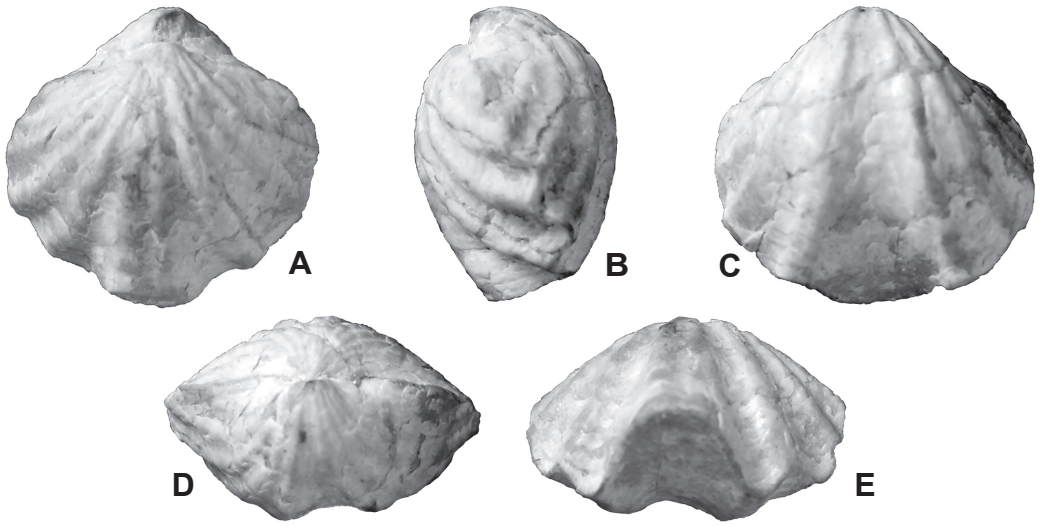

Fig. 5. Molongia elegans Mitchell, 1921. Lectotype AM F29454 in A, dorsal; B, lateral; C, ventral; D, posterior and E, anterior aspects; all x3.

Superfamily RETZIELLOIDEA Rzhonsnitskaya, 1974
Family RETZIELLIDAE Rzhonsnitskaya, 1974

Molongia Mitchell, 1921

Type species. Molongia elegans Mitchell, 1921.

Molongia elegans Mitchell, 1921 (Figs 5-6)

1921 *Molongia elegans* Mitchell, p. 547, pl. 31 figs 6-8, 12.

Type material. Not specified by Mitchell, but is amongst the large brachiopod collection purchased from Mitchell's widow in 1930. The syntypes are AM F29451 (Mitchell 1921, pl. 31, fig. 8; refigured Rong *et al*. 1994, pl. 2, figs 6-8, 10-11, and Rong *et al*. 1994, fig. 1R-U), AM F29452 (Mitchell 1921, pl. 31, fig. 6; refigured Rong *et al*. 1994, pl. 2, figs 1-5), and AM F29454 (Mitchell 1921, pl. 31, fig. 7). All are from the Molong district (for comments on the source of Mitchell's Molong material, see Rong *et al*. 1994, p. 567; Strusz 2005, p. 222-3; and the discussion on *Atrypoidea* by Strusz 2007). Rong *et al*. (1994) did not re-examine all of Mitchell's specimens, being principally concerned with investigating the internal structure using topotypes, and therefore did not designate a lectotype. In view of the close relationship between *Retziella* and *Molongia* shown by Rong *et al*. (1994), the occurrence of *Retziella* in nearby Canberra, and Mitchell's report of *Molongia* at Yass, I consider this to be necessary. I therefore designate AM F29454, the best preserved syntype, as lectotype. AM F29451 and 29452 thus become paralectotypes.

Topotypes. Topotypes available to assess variability (see scatter diagrams, Fig. 6) are AM F28538, 28539, 29210, and MMF11300, 19623 (the last two are bulk specimens also containing *Atrypoidea australis* and a spiriferid).

Description of Lectotype. The lectotype is a partially decorticated biconvex shell 13.4 mm long, 14.0 mm wide, 8.9 mm thick. Outline suboval, with large erect ventral beak truncated by circular permesothyrid foramen. Dorsal fold prominent anterior to mid-length, with weak median furrow not matched by median ridge in ventral sulcus. Five rounded ribs on each dorsal flank. Anterior commissure uniplicate, tongue rounded-trapezoid. Surface sculpture uncertain, but appears to be smooth apart from sparse and very weak growth lines.

Remarks. Rong *et al*. (1994) have shown that *Molongia elegans* is a probable local derivative from *Retziella*, the most likely ancestral species being *Retziella capricornae* (McKellar, 1969). The latter has been described by Strusz (1984) (as *Molongia elegans capricornae*) from the Yarralumla Formation of Canberra, which can be correlated with the Yass Formation. Mitchell (1921) gave two localities for his species, the type locality and "Bowning, Parish of Bowning", in both instances "associated with *Atrypoidea australis*". There are abundant (mostly incomplete) specimens from Molong in

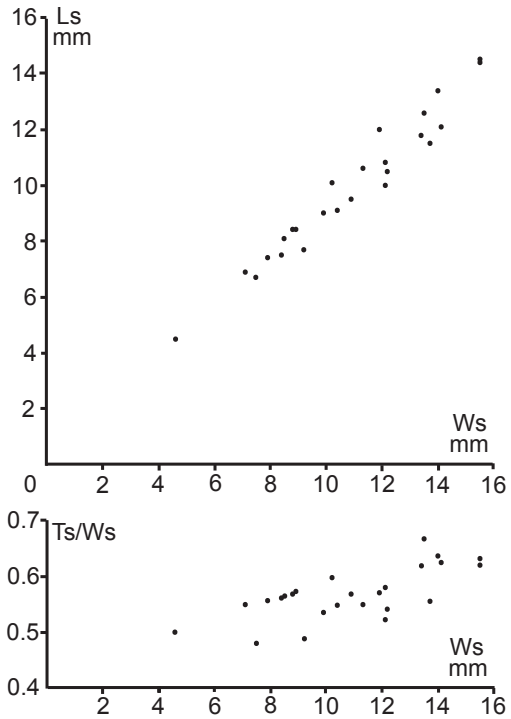

Fig. 6. Molongia elegans Mitchell, 1921. Plots of Ls and Ts/Ws against Ws for 25 specimens from the type locality.

the Australian Museum collections, but none from the Yass Syncline. Nor are there specimens from the Yass Syncline in the other material available to me. While the presence of one or other of these retziellid species in the Yass sequence would not be surprising, it cannot at present be established.

Twenty-five measured specimens show that Ls/Ws varies from 0.83 to 1.01 (mean 0.91), Ts/Ws varies from 0.48 to 0.67 (mean 0.57), the ratio increasing with increasing shell size (see Fig. 6).

Suborder RETZIIDINA Boucot, Johnson & Staton, 1964
?Superfamily RHYNCHOSPIRINOIDEA Schuchert, 1929
?Family RHYNCHOSPIRINIDAE Schuchert, 1929

"**Retzia salteri** (Davidson, 1848)"

Remarks. Mitchell (1921, pp. 547-548, pl. 31, figs 4-5) described a single small ribbed shell from "..limestone bed of Limestone Creek, beneath the Lower Trilobite Beds.." - probably the Hume Limestone Member, certainly the Silverwood Formation. He ascribed it to *Retzia salteri* (Davidson, 1848), which was considered a synonym of *Homoeospira baylei* (Davidson, 1848) by Cocks (1978, p. 161). Mitchell's specimen cannot now be found in the Australian Museum collections. The quoted size (Ls 11.1 mm, Ws 12.7 mm) is somewhat larger than that of the anoplothecid *Coelospira cavata*, known from both Canberra and (now) Yass. The described exterior certainly conforms to that of *Homoeospira* - ribbed, weakly bisulcate with median ribs weaker than those on the flanks, apical foramen - and so differs significantly from *Coelospira*. No mention was made of endopunctae, however. The size is also comparable with the retziellids *Molongia elegans* Mitchell, 1921 (based on material from Molong, NSW, but which Mitchell also reported from Bowning) and *Retziella capricornae* (McKellar, 1969) (recorded - as *Molongia* - by Strusz 1984, from the Yarralumla Formation of Canberra) but the bisulcate profile is quite different. Unless the original specimen or new material is found, the occurrence of retziidine-like species at Yass cannot be established.

Suborder Uncertain
Superfamily ANOPLOTHECOIDEA Schuchert, 1894
Family ANOPLOTHECIDAE Schuchert, 1894
Subfamily COELOSPIRINAE Hall & Clarke, 1895

Navispira Amsden, 1983

Type species. *Anoplotheca* (*Coelospira*) *saffordi* Foerste, 1903.

Navispira? bicarinata n. sp. (Figs 7-9)

Type material. Holotype ANU9738, paratypes ANU46521-46528 from Kemezys' collections KC6, 20, 47 and 48, north of 'Silverdale'. Yarwood Siltstone Member, Black Bog Shale; Ludfordian.

Other material. Yass Formation or basal Silverdale Formation: GOU51U - 2 specimens including CPC39429. *Barrandella* Shale Member, Silverdale Formation: GOU2a - 6 specimens including CPC39430-34, MMF17702, 17314. Lower Black Bog Shale: KF (= GOU52) - 25 specimens including ANU46517-20, CPC39447-53; GOU4 - about 30 specimens including CPC39435-46. Yarwood Siltstone Member, Black Bog Shale: KE (= GOU46) - 8 specimens including ANU46529-33, CPC39454; GOU30 - 1 poor specimen; unknown locality but lithology and associated "*Nikiforovaena*" *bowningensis* (Mitchell, 1921) indicate this level

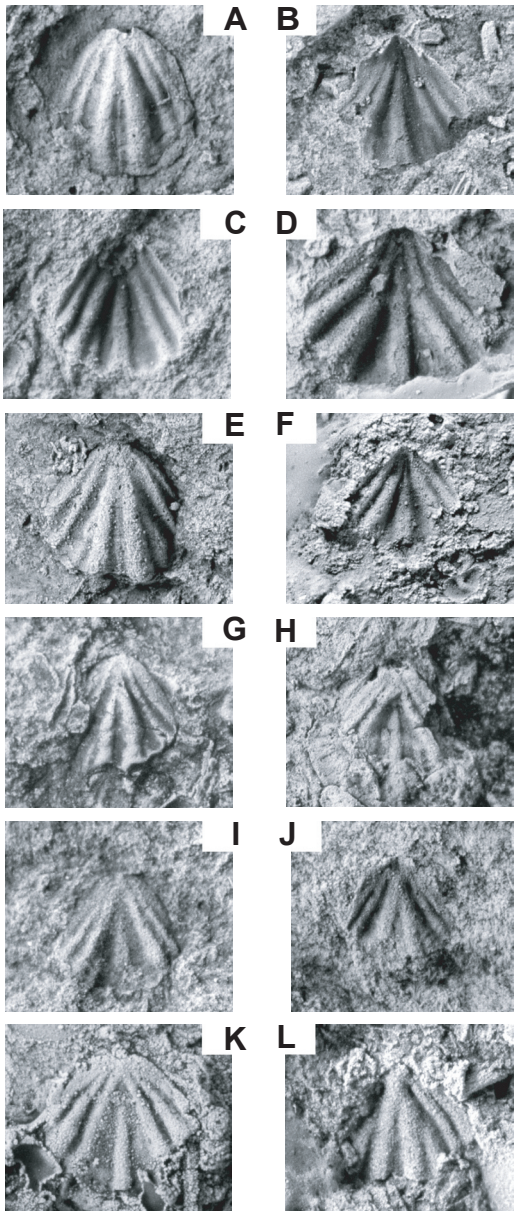

Fig. 7. Navispira? *bicarinata* n. sp. A, holotype ANU9738, ventral exterior. B, paratype ANU46521, ventral interior. C, paratype ANU46527, ventral interior. D, ANU46533, ventral interior. E, ANU46518, ventral exterior. F, ANU46519, ventral interior. G-H, paratype ANU46522, ventral exterior and dorsal interior. I-J, ANU46532, dorsal exterior and interior. K, paratype ANU46523, dorsal exterior. L, ANU46531, dorsal interior. All latex replicas, x10. Lower Black Bog Shale: E-F (locality KF); Yarwood Siltstone Member: A-C, G-H, K (loc. KC6), D, I-J, L (loc. KE).

- AMF131512. Basal Cowridge Siltstone: KM - more than 12 poor or fragmentary specimens, including ANU46534. Mitchell Collection: AMF131511 (locality and horizon unknown; with *Mesopholidostrophia bendeninensis* [Mitchell, 1923] so probably Black Bog Shale), AMF131513 (Bowning, horizon unknown; with *Spirigerina mitchelli* Strusz 2007, so Rainbow Hill Member or below).

Stratigraphic distribution. Yass Formation or basal Silverdale Formation, *Barrandella* Shale Member, Black Bog Shale including the Yarwood Siltstone Member, topmost Rosebank Shale or basal Cowridge Siltstone.

Age. Late Wenlock or Gorstian to Přídolí (pre-*bouceki* Zone).

Etymology. Latin *bi*-, double + *carinatus*, keeled, referring to the very prominent twin ribs forming the ventral fold.

Diagnosis. Small naviculate shell with ventral keel of two prominent ribs fused on umbo, separated anteriorly by fine mid-rib; dorsal sulcus wide, with well developed inserted mid-rib; ventral muscle field weakly impressed, not raised anteriorly above valve floor to form cella; dorsal adductor scars small, weakly impressed, without myophragm.

Description. Shell small for *Navispira* species, generally about 2 mm wide (maximum seen 3.6 mm - CPC39429). Outline highly variable from elongate to transversely oval, greatest width slightly forward of mid-length. Profile ventribiconvex; ventral valve broadly naviculate, with relatively wide fold (about ⅓Ws); dorsal valve moderately convex, with wide (>½Ws) fairly shallow sulcus; anterior commissure plicosulcate. Ventral beak short, dorsal beak very low, both wide; ventral area low, delthyrium open; no foramen seen. Cardinal margin relatively wide (up to ⅓Ws), gently curved. Fold formed by two very prominent rounded radial ribs diverging from beak, furrow dividing them being equally prominent beyond umbo, and divided anteriorly by fine, inserted mid-rib. Smaller but rapidly widening secondary ribs split off from outer sides of median rib-pair anteriorly. Fold flanked by two pairs of rounded, laterally curved primary ribs diverging from cardinal margin, to bring total to nine in larger shells. Dorsal sulcus defined by prominent pair of widely divergent primary ribs (fused at beak), from inner sides of which diverge less prominent secondary ribs at or in front of mid-length. Prominent mid-rib inserted at length

Fig. 8. Navispira? *bicarinata* n.sp. A, ANU46520 (lower Black Bog Shale, locality KF), ventral interior with distinct myophragm dividing narrow impressed diductor scars. B, paratype ANU46521 (Yarwood Siltstone Member, loc. KC6), ventral interior with weak myophragm and diductor scars, showing divergent teeth supported by valve walls. C, ANU46532 (Yarwood Siltstone Member, loc. KE), dorsal interior showing prominent inner socket ridges, small shallow adductor field at apex of notothyrial cavity. All latex replicas x20.

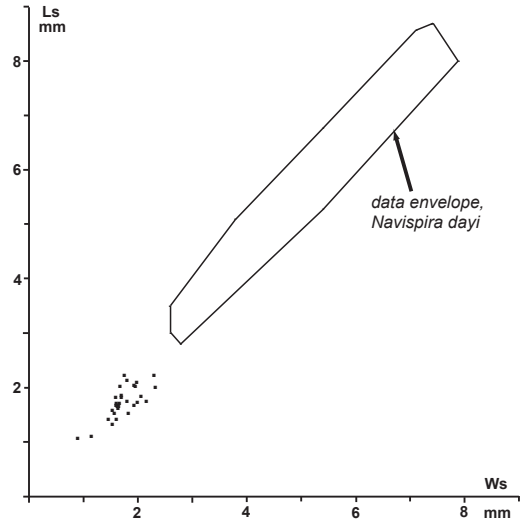

Fig. 9. Scatter diagram of shell length Ls against width Ws for *Navispira*? *bicarinata*, and the data envelope of the same plot for *Navispira dayi* (Chatterton, 1973).

of about 0.5 mm. Two pairs of ribs, diverging from cardinal margin, flank sulcus, inner pair strong, outer pair short and low. Growth lines very faint or absent, never lamellose. Shell walls thin.

Teeth well developed, somewhat elongate anterolaterally and vertically, attached to locally thickened valve walls, moderately divergent forward. There may be shallow depressions between front edges of teeth and valve wall, but distinct dental plates not developed. Delthyrial cavity entirely occupied by oval, indistinct, weakly impressed muscle field; narrow, elongate, parallel diductor scars weakly to moderately impressed, separated by narrow myophragm which dies out before mid-length; front of field not raised above valve floor.

Dorsal interior poorly known. Sockets widely divergent, inner socket ridges strong, curved over sockets. Crura appear to arise from sides of socket ridges as short upright rods. Cardinal process obscure, adductor field small, weakly impressed, apical, without myophragm. Broad bifid ridge in front of muscle field reflects form of dorsal sulcus.

Remarks. Externally, this species is a typical *Navispira*, distinguished from other small species of that genus in details of the rib pattern - the strongly flared secondaries diverging from the very prominent median rib-pair on the ventral valve, such that the lateral ribs are distinctly curved, and the relatively widely divergent ribs defining a fairly shallow dorsal sulcus. It is assigned only tentatively to that genus because the ventral muscle field is not raised anteriorly above a distinct cella, and there is a short, narrow ventral median ridge rather than a well developed median septum. In this respect it is closer to *Coelospira*, although it should be noted that other *Navispira* species lack a high platform: *N. dayi* (Chatterton, 1973), *N. planorostra* (Johnson, Boucot & Murphy, 1976), *N. septata* (Lenz & Johnson, 1985), *N. virginia* (Amsden, 1958a).

There is close external resemblance, at least ventrally, to small (juvenile?) specimens of *Navispira dayi* from the Emsian of the Taemas area, west of Yass - compare ANU9738 (Fig. 7A) with ANU18955a (Chatterton 1973, pl. 19, fig. 15). The dorsal valves in *N. dayi* have a well developed myophragm, and the ribs in and defining the sulcus are less differentiated than in *N.*? *bisulcata*. It is conceivable that *N. dayi* is derived from *N.*? *bicarinata*.

Also similar externally is *N. virginia* from the Lochkovian of Tennessee, Oklahoma and Nevada (Amsden 1958a; Boucot & Johnson 1967; Johnson 1973), a species also reported from the Lochkovian and Emsian of western Siberia (Kulkov & Peregoedov 1990). Apart from being

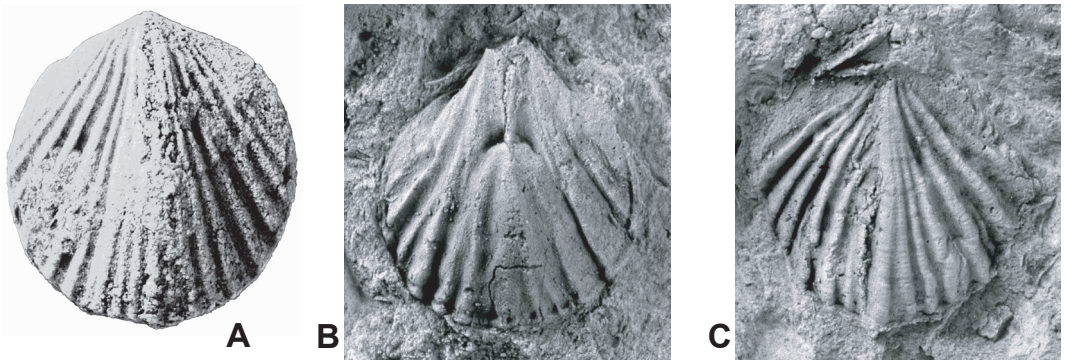

Fig. 10. Coelospira cavata Strusz, 1982. A, CPC39455, complete shell in ventral aspect; Yass Formation, locality GOU48. B, AMF131515, ventral internal mould, Yass or Silverdale Formations near Bowning. C, AMF131516, dorsal external mould plus ventral interarea; on same piece as B. All x6.

somewhat larger, it differs in having a shallower but more posteriorly beginning median furrow on the ventral fold, mostly lacking a fine mid-rib (Boucot & Johnson report a thread-like rib in some), radial ribs which do not split on the ventral valve, distinct growth lines and a deeper dorsal sulcus. The interior, as described by Johnson (1973) is also closely comparable, the ventral muscle field not raised in either species.

Of Silurian species, all except *N. planorostra* are significantly larger, with more ribs, the ventral median rib-pair being less prominent, and a stronger median ventral rib. *Navispira planorostra* (from the Ludlow of Nevada) is more like *N.*? *bicarinata*, but the ribs on the flanks of both valves are radial, and narrower and sharper, separated by wider furrows; the dorsal sulcus is deeper and narrower, the dorsal mid-rib lower; internally, the socket ridges are larger and more strongly curved, there is a well developed dorsal myophragm, and a small but distinct cardinal process.

Coelospira Hall, 1863

Type species. *Leptocoelia concava* Hall, 1857. Lochkovian, New York.

Coelospira cavata Strusz, 1982 (Figs 10-11)

1982 *Coelospira cavata* Strusz, p. 126-129, fig. 23A-K.

Type material. See Strusz (1982, p. 126).

Yass Syncline specimens. Cliftonwood Limestone Member, Yass Formation: GOU48 - CPC39455-73 plus numerous other poorly preserved specimens. Lower Black Bog Shale: GOU52 - CPC39474. Unknown horizon, Bowning: AMF131515-6 (an associated fragmentary *Epelidoaegiria minuta chilidifera*? suggests Yass or Silverdale Formations - see Strusz 2003).

Stratigraphic distribution. Walker Volcanics, Canberra; Yass Formation, Silverdale Formation? (rare), lower Black Bog Shale (rare), Yass Syncline.

Age. Late Wenlock or early Gorstian to early Ludfordian.

Remarks. The specimens from the Yass Syncline, relatively abundant only in the Yass Formation, differ very little externally from the original Walker Volcanics population. They are larger (the largest Canberra specimen is the holotype, with Ls 4.0 mm, Ws 4.3 mm - see Fig. 11). The largest Yass specimen is CPC39455 from the Yass Formation (Ls 6.65 mm, Ws 6.10 mm), while most are more than 4.5 mm wide and long. Length and width are about equal in smaller specimens (the Canberra mean Ls/Ws is 1.0), but the larger ones are somewhat elongate (for Ws > 4.5 mm, mean Ls/Ws is 1.05). This is of no great significance, however, given the wide scatter about the mean shown in plots for the Canberra material. The outline and profile, the flat orthocline ventral area, and the number and arrangement of the ribs on both dorsal and ventral valves are the same.

There is only one good ventral internal mould (AMF131515, Fig. 10B). In it, the anteriorly elevated muscle field extends a little farther forward than in Canberra specimens, and is medially damaged so that the nature of the myophragm is obscure; the number of ribs visible on the valve floor is somewhat less than usual (about 16 instead of 20-22), and the beak appears rather more prominent than in most (but this is a variable feature). There are no significant

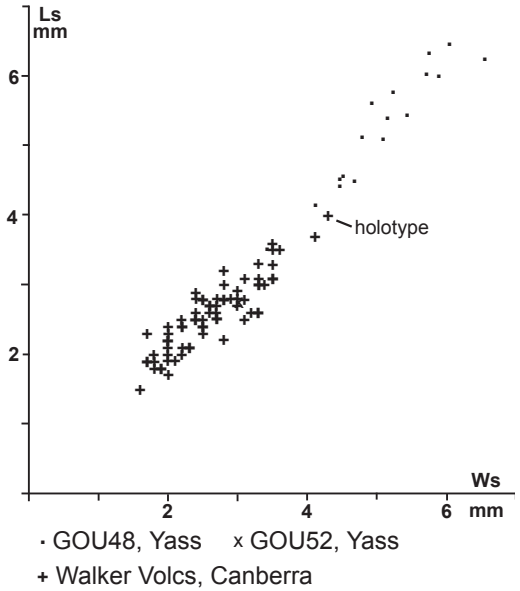

Fig. 11. Coelospira cavata Strusz, 1982. Scatter diagram of shell length Ls against width Ws for specimens from Yass localities GOU48 (Yass Formation) and GOU52 (lower Black Bog Shale), and the Walker Volcanics in Canberra.

differences between the Canberra and Yass specimens.

Coelospira cavata, both at Yass and Canberra, displays all the external features of typical *Coelospira*, but the ventral interior is more like that of *Navispira*, with the ventral muscle field raised anteriorly above a deep cella. As described by Boucot & Johnson (1967), it is the Silurian species since placed in *Navispira* which have this characteristic internal structure (the dorsal interiors are much the same in both genera). However, it is combined with a strongly naviculate shape characterised by a pair of prominent raised ribs (often separated anteriorly by a very fine mid-rib) forming the keel-like ventral fold. Devonian species they regarded as being characterised by a more rounded multi-ribbed fold with ribs smaller than on the flanks, and a less clearly raised ventral muscle field - features considered to define *Coelospira*. Two naviculate Devonian species have already been placed in *Navispira* (*Coelospira dayi* Chatterton, 1973, assigned to *Navispira* by Alvarez & Copper 2002, p. 1612; *N. trepida* Havlíček, 1999). Further Australian and Canadian Devonian species which can be assigned to that genus are *C. exilicosta* Smith, 1980, *sensu lato*; *C. pusilla arctica* Lenz, 1977; *C. septata* Lenz & Johnson, 1985; probably *C. praedayi* Lenz & Johnson, 1985. *Navispira dayi* and *C. septata* have impressed ventral muscle scars which are not raised anteriorly, whereas the interiors of *C. exilicosta* and *C. pusilla arctica* are what Boucot & Johnson (1967) thought typically Silurian.

Clearly, as noted by Alvarez & Copper (2002), *Navispira* extends from the mid-Silurian into the Early Devonian, but the morphological differences from *Coelospira* are not as clear-cut as envisaged by Boucot & Johnson (as can indeed be deduced from the diagnoses of the genera given by Alvarez & Copper 2002, p. 1609, 1612). Only two Silurian species have been described which are not clearly *Navispira*. One is *C. cavata*, which combines features of both genera. The other is *C. expansa* Benedetto & Toro, 1989, from the Ludlow of Argentina. In juvenile specimens of the latter (e.g., pl. 1, fig. 1) the fold has a pair of prominent raised ribs (keel-like posteriorly), but these are separated over most of the valve length by a lesser but still well developed mid-rib. Moreover, in most specimens the median paired ribs are not accentuated anteriorly, the ribs on the fold being as variable in size as those on the flanks. These specimens are thus externally far closer to typical *Coelospira*. The ventral interior shows large triangular diductor scars moderately impressed into an anteriorly weakly raised field, but no distinct cella.

It is clear that there is considerable morphological overlap between the two genera. Based on the above discussion, I am inclined to place more weight than I did in 1982 (when most comparisons were drawn with species now placed in *Navispira*) on the difference in the form of the ventral fold rather than on the more variable details of the interior. *Coelospira* has a multi-ribbed, rounded ventral fold on which the ribs are of the same size or smaller than those on the flanks (except close to the beak, where the pair of median ribs characteristic of the subfamily is initially prominent), and there is often a well developed mid-rib, while in *Navispira* the fold is keel-like, the keel being formed by a very prominent pair of ribs between which is often developed a very fine mid-rib arising anterior to the ventral umbo. Despite its well developed cella and anteriorly raised ventral muscle field, on this basis *C. cavata* is a *Coelospira*, and is the oldest species so far described.

Coelospira cavata, especially relative to its size, is more finely ribbed than the other species. It differs from the type species, *C. concava*, in its somewhat narrower and shallower sulcus which tends to flare anteriorly. Internally, the ventral muscle field is smaller, and there is no dorsal myophragm. It is much more finely ribbed than *C. camilla* Hall, 1867, in which the initial median rib-pair remains moderately prominent anteriorly,

but the fold is subdued in transverse profile. Internally, *C. camilla* has impressed ventral muscle scars which are not raised anteriorly above a cella, and very strong cardinalia. *Coelospira dichotoma* (Hall 1859) is much larger but externally is otherwise much like *C. cavata*; the ventral muscle field is relatively larger, not raised anteriorly, and the cardinalia, especially the cardinal process, are much stronger. The single valve from the late Wenlock of Cadia tentatively referred to *Coelospira* by Rickards *et al*. (2001, fig. 3k) is smaller, and with significantly coarser ribs. The only other Silurian species, *C. expansa*, is similar in size, but the ribs are coarser and bifurcate less often, and as noted above the ventral muscle field is larger and there is no cella.

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