## **Revision of the Silurian and Early Devonian Chonetoidean Brachiopods of Southeastern Australia**

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ABSTRACT. Thirty-eight species of ostensibly chonetoid brachiopods (some under open nomenclature) have been described from the Silurian and Lower Devonian rocks of southeastern Australia, although most are neither widely distributed nor abundant. Descriptions of many have been based on inadequate material, and in one significant case (*Johnsonetes australis*) the original material is lost, necessitating selection of a neotype to resolve formally the identity of that species in comparison with the similar species *J. culleni*. In this systematic revision the known species are redescribed and where possible their generic positions and possible synonymy determined; three are rejected from the Chonetoidea.

Silurian taxa include *Strophochonetes melbournensis*, *S. kemezysi* n.sp. and "*Protochonetes*" cf. *minimus*. Early Devonian faunas are much more diverse. Lochkovian species are *S.*? *savagei* n.sp., *S.*? *psiloplia*, "*S*." *cresswelli*, *Parachonetes robustus*, and the poorly known "*Chonetes*" *ruddockensis*. "*Strophochonetes*" *cresswelli* and *P. robustus* are also found in the Pragian, along with *Asymmetrochonetes*? *planata*, *Parachonetes baragwanathi*, *P.*? *bowieae*, *P.*? *suavis*, *Septachonetes micrus*, "*Chonetes*" *taggertyensis* and "*Chonetes*" *foedus*. The youngest species in the region are Emsian: *Johnsonetes australis*, *J. culleni*, *J. latus*, *Septachonetes melanus*, *Parachonetes buchanensis*, *P. spooneri*, *P. konincki* and *P. flemingi*. No species is currently known to be sufficiently widely distributed geographically and sufficiently restricted stratigraphically to be of clear biostratigraphic use.

Several former species are junior synonyms. *Strophochonetes melbournensis* includes *Chonetes infantilis*, and *Johnsonetes australis* includes *Chonetes teicherti*. *Parachonetes robustus*, the namebearer for Gill's "robustus gens", certainly includes both *Chonetes killarensis* and *C. productoida*. It is likely that the two other species of this group, *P. baragwanathi* and *P. buchanensis*, are also synonymous but, for lack of appropriate specimens, this cannot be conclusively established.

The Cambrian *Chonetes concinna*, subsequently (and wrongly) referred to *Eoorthis*, is refigured and confirmed as not being a chonetoidean. *Chonetes gaskini* is shown to be the ventral valve of a spiriferid, and *Chonetes bipartita* has already been assigned to the sowerbyelloid *Plectodonta*.

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The superfamily Chonetoidea is a group of distinctive Palaeozoic spiny brachiopods, in which the spines are restricted to the posterior margin of only one valve. Its representatives are distributed worldwide, and have been shown to be useful environmental and palaeobiogeographic indicators at least in the Silurian and Devonian (Racheboeuf, 1990). Although not a major component of the brachiopod faunas described from the Silurian and Devonian of 246 Records of the Australian Museum (2000) Vol. 52

southeastern Australia, they are common and distinctive enough to have been recognised as long ago as 1876, when McCoy described Chonetes australis from the Devonian of Victoria. About the same time, De Koninck (1877) identified Australian material from several localities, sent to him by W. B. Clarke, as identical with European species. The specimens from Quidong (near Delegate in far southeastern New South Wales) De Koninck unequivocally identified as Chonetes striatella (now Protochonetes). They could be identical with Protochonetes? sp. indet. described from the Silurian of Canberra by Strusz (1982). The specimens from "a dark grey limestone in the Yass District" identified by De Koninck as Chonetes hardrensis are less easy to relate to the species dealt with herein, but could be the Silurian Strophochonetes kemezvsi n.sp. Unfortunately De Koninck figured none of the specimens, which were subsequently lost in the Garden Palace fire of 1882.

Thirty-eight species ascribed to the superfamily have been described from the southeastern Australian Silurian and Devonian, many in a series of papers by E.D. Gill (1942–1951). However, most of the taxa were based on less than adequate material, and have not until now been assessed in the light of modern understanding of the superfamily. The relationships between some long-standing very similar



Figure 1. Map of southeastern Australia providing a key to the location of the chonetoid faunas described in this paper. In the case of geographically close central Victorian localities, the nearest significant town (as noted in the text) is shown.

species have been unclear because of this, and more recently collected specimens have often proved difficult to assign to named species. This study is an attempt to remedy that situation. Opportunity is taken to establish as clearly as possible the stratigraphic and geographic distribution of the species recognised, and to amplify morphological descriptions where appropriate. A synoptic list of the species recognised here is given just before the Systematics section. A map of southeastern Australia (Fig. 1) shows locations referred to in this paper.

#### Materials and methods

Materials. Most of the material used in this study is housed by the Museum of Victoria (Melbourne) and the Australian Museum (Sydney). Published specimens formerly in the collections of the Geological Survey of Victoria, the Universities of Melbourne and Sydney, and University of New England (Armidale) have been transferred to the two State museums. Some specimens are also held by the Geological Survey of New South Wales in Sydney, and the Australian Geological Survey Organisation and Australian National University in Canberra. Additional unpublished material is held by both Canberra organisations and the Museum of Victoria. Registered numbers for fossils now or once held by these various institutions are prefixed by the following acronyms:

- AM Australian Museum.
- Geology Department, Australian National ANU University.
- CPC Commonwealth Palaeontological Collection, Australian Geological Survey Organisation. Geological Survey of Victoria. GSV
- MMF Palaeontological Collection, New South Wales Department of Mineral Resources (Geological Survey of New South Wales).
- MUGD Department of Geology, University of Melbourne.
  - NMV Museum of Victoria.
    - SU Geology Department, University of Sydney.
  - UNE Department of Geology & Geography, University of New England.

Terminology. Morphological terminology and definitions follow those in Racheboeuf (1998), which correspond to those used in the revised Brachiopoda volumes of the Treatise on Invertebrate Paleontology (Williams et al., 1997 et seq.). When referring to hinge spines, position, symmetry and ordering are as in Racheboeuf (1981). Spines are numbered 1, 2, 3... to the right of the ventral umbo, corresponding to 1', 2', 3'... to the left, as viewed with ventral valve uppermost and beak towards top.

Unless otherwise specified, the divergence of bilaterally symmetrical structures, such as anderidia, is quoted as the angle included anteriorly between the structures, not their divergence from the centre-line of the shell. Where possible, the density of radial ribs is specified as the number in a 5 mm sector at a radius of 5 mm.

The following abbreviations (linear measurements in millimetres) are used:

- Ls maximum length of shell excluding hinge spines; coincident with length of ventral valve.
- Ld length of dorsal valve.
- Ws maximum width of shell, measured normal to plane of symmetry.
- Wh width of shell at hinge line.
- Ds depth (or thickness) of shell (= depth of ventral valve in most chonetoids) measured normal to length and width.
- $\alpha$  the angle included between the hinge line and the proximal part of a hinge spine, measured abaxially.

All grid references and map coordinates are based on the Australian Geodetic Datum of 1966. In the descriptive part of this paper, new illustrations are generally not provided for species where no new and informative material is available and the original illustrations are sufficient.

#### **Results**

All but three of the 28 chonetoidean species here recognised can be assigned with varying degrees of confidence to seven genera in two families, Strophochonetidae and Anopliidae, of which the first dominates. Only two species of one endemic genus, *Septachonetes*, are anopliids. Three named species cannot be assigned with any confidence even at the family level.

In Victoria, taxa come from both the Melbourne Trough, and the Early Devonian sequences of East Gippsland (Buchan, Tabberabbera, Tyers). Of two Tasmanian forms, one is probably the same as a species from Buchan, and the other is unusable. In New South Wales most of the species are from the Canberra-Yass Shelf, with a scatter of records from the Molong High farther north, or the ill-exposed Cobar Trough in the west. Unfortunately, in nearly all cases the species are based on specimens from at most only a handful of localities, so biostratigraphic utility is difficult to assess. In the case of taxa from the Emsian of the Taemas region in New South Wales, stratigraphic distribution does seem to be consistent within the basin, but the area concerned is small. The Silurian Melbourne Trough species Strophochonetes melbournensis (Chapman, 1903) is more widely distributed than other taxa, but seems also to have a rather extended stratigraphic range and so is of limited biostratigraphic use. An extended range is also shown by Parachonetes buchanensis (Gill, 1951) in the geographically restricted Emsian sequence at Buchan.

One other consequence of this rather scattered distribution of species both geographically and stratigraphically is the difficulty in establishing phylogenetic lineages. It is possible that the Wenlock-Ludlow Victorian species *Strophochonetes melbournensis* (Chapman, 1903) gave rise to the Ludlow-Přídolí species *S. kemezysi* n.sp. from Yass. A group of species centred around *Parachonetes baragwanathi* (Gill, 1949) was thought by Gill to be a phylogenetic plexus (the "*robustus gens*" of Gill, 1951), but most of these species are incompletely known and most (if not all) will probably eventually be shown to be junior synonyms of *P. robustus* (Chapman, 1903). If that is the case, the range of this taxon will be quite long: mid-Lochkovian to

Emsian-most of the Early Devonian. Its relationship to other Australian species of *Parachonetes* is not clear.

Finally, this study retains as distinct the very similar early to mid-Emsian species *Johnsonetes australis* (McCoy, 1876) from Buchan and *J. culleni* (Dun, 1904) from Taemas. Synonymy of these two species, as proposed by Brock & Talent (1993), could only be established if intermediate forms revealing greater structural variability were to be found. Variability to the extent needed to establish that synonymy would cast doubt on some of the criteria currently used to distinguish a significant number of chonetoid species.

The following synoptic list is of the species recognised herein, arranged systematically, with a summary of their ages and palaeogeographic distribution (the latter abbreviated as: WTT, Western Tasmania Terrane; MT, Melbourne Trough; G, Gippsland "basins"; CYS, Canberra-Yass Shelf; MH, Molong High; CT, Cobar Trough).

Strophochonetes melbournensis (Chapman, 1903); Wenlock to Ludlow, MT.

Strophochonetes kemezysi n.sp.; Late Ludlow to Přídolí, CYS. Strophochonetes sp. Sherwin, 1995; Lochkovian, CT.

Strophochonetes? savagei n.sp.; Early Lochkovian, MH.

- "Strophochonetes" cresswelli (Chapman, 1903); Lochkovian to Pragian, MT.
- Johnsonetes australis (McCoy, 1876); Early to middle Emsian, G.
- Johnsonetes culleni (Dun, 1904); Early Emsian, CYS.
- Johnsonetes latus (Chatterton, 1973); Middle Emsian, CYS. Johnsonetes? sp.; Early Pragian, MH.
- Asymmetrochonetes? planata Lenz & Johnson, 1985; Early Pragian, MH.
- "Protochonetes" sp. cf. minimus (J. de C. Sowerby, 1839); Late Wenlock to Early Ludlow, CYS.
- Protochonetes? sp. indet. Strusz, 1982; Late Wenlock, CYS.
- Parachonetes baragwanathi (Gill, 1949); Early to middle Pragian, MT, G.
- *Parachonetes robustus* (Chapman, 1903); Middle Lochkovian to middle Pragian, MT.
- Parachonetes? sp. cf. robustus (Chapman, 1903); Late Lochkovian, MT.
- Parachonetes buchanensis (Gill, 1951); Emsian, G.
- Parachonetes? sp. cf. buchanensis (Gill, 1951); Early Pragian, WTT.
- Parachonetes konincki Chatterton, 1973; Middle Emsian, CYS.
- Parachonetes flemingi Chatterton, 1973; Middle Emsian, CYS.

Parachonetes? bowieae (Gill, 1945); Early Pragian, MT.

- Parachonetes? suavis (Talent, 1963); Early to middle Pragian, G.
- Parachonetes? spooneri (Talent, 1956); Early Emsian, G. Parachonetes? sp.; Early Pragian, MH.
- Septachonetes melanus Chatterton, 1973; Middle Emsian, CYS.
- Septachonetes micrus (Gill, 1951); Pragian, MT.
- "Chonetes" taggertyensis (Gill, 1945); Early to middle Pragian, G.
- "Chonetes" ruddockensis Gill, 1945; Middle to late Lochkovian, MT.
- "Chonetes" foedus Talent, 1963; Early to middle Pragian, G.

Strophochonetes? psiloplia (Gill, 1945); Lochkovian, MT.

## **Systematics**

#### Chonetoidea Bronn, 1862

## Strophochonetidae Muir-Wood, 1962

## Strophochonetinae Muir-Wood, 1962

## Strophochonetes Muir-Wood, 1962

**Type species**. *Chonetes cingulatus* Lindström, 1861, 374. Wenlock, Gotland.

**Diagnosis**. "Shell small, plano- to moderately concavoconvex; well-developed median enlarged costa; long and symmetrically arranged high-angled spines varying from intraverse cyrtomorph proximally to orthomorph vertical distally; cardinal process strongly bilobed internally, anteriorly bounded by a cardinal process pit; no median septum; anderidia long and narrow, anteriorly divergent at 60° and isolated on the valve floor; inner socket ridges short and thin, as two rounded ridges almost parallel to hinge." (Racheboeuf, 1998: 37).

Discussion. It is unfortunate that Muir-Wood (1962) based her genus on a species which had not been effectively redescribed and figured since its erection by Lindström (1861), and which is still not well known. She offered a very brief and incomplete description, and figured only exteriors of both valves. Johnson (1970, pl. 30, figs. 1-5) figured two dorsal interiors and three ventral exteriors from Fröjel, Gotland, and made only brief comments on dorsal internal morphology. Bassett (1977: 160-161) merely reiterated Johnson's limited observations, and Racheboeuf (1981: 36–37, pl. 3, figs. 1–3) again figured only externals supported by a brief description. The ventral interior is thus still little known, as is variability overall. As more genera are erected on the basis of species previously included in Strophochonetes, in the absence of a revision of the type species the concept of what still constitutes Strophochonetes has become less clear.

The original generic diagnosis can be rewritten in the light of changes in terminology as: Shell small, thin, of low convexity, hinge at or close to maximum width. Finely capillate, may be smooth umbonally, ventral median capilla enlarged; increase by intercalation and bifurcation; growth lines often prominent. Hinge spines sparse, fine, long, normal to hinge. Ventral median septum short, enlarged posteriorly; teeth massive, wide, transversely striated; muscle field obscure. Cardinal process bilobate, the lobes posteriorly grooved, fused with cardinal crests; dorsal median septum short or absent, cardinal process pit often absent; anderidia prominent, diverging at about 60°, sometimes curved; sockets small, outer socket ridges extending along cardinal margin.

Johnson (p. 1023 in Boucot & Gauri, 1966) confirmed the variability in the dorsal median septum, stating that it was absent in *S. cingulatus*—certainly the case in the dorsal interiors he figured in 1970. In differentiating *Strophochonetes*, Muir-Wood (1962) quoted smaller size, finer ornament including an enlarged median capilla, fewer but longer spines at a steep angle to the hinge, a narrower, less prominent ventral median

septum which does not develop a median furrow, a shorter dorsal median septum (often absent), and smaller dental sockets. Muir-Wood (1962: 32) also specified that strophochonetines have no cardinal process pit, despite allowing for its occasional presence in her diagnosis of *Strophochonetes*.

Boucot & Harper (1968: 148–149) repeated Muir-Wood's differentiation between *Strophochonetes* and *Protochonetes*, but went on to note the variability shown by the North American *P. novascoticus* (Hall, 1860), concluding that only the angle of the hinge spines appeared to be a reliable difference. This conclusion depended on a study by Harper (1973); however from Harper's description and figures of that species it is clear that there is no single enlarged median ventral capilla but at most a coarsening of the capillae medially, and that the dorsal median septum is long and well developed. That a medial furrow on the ventral median septum may not always be present in *Protochonetes* does not fully negate the taxonomic usefulness of its consistent absence in *Strophochonetes*, and so there is no significant change from the differences set out by Muir-Wood (1962).

Bassett & Cocks (1974: 21) separated Strophochonetes and Protochonetes, at least in the Silurian, especially on the presence of an enlarged ventral median capilla in the former, and consistently bifurcating costellae in the latter. Racheboeuf (1976: 47-49) further discussed the differences between the two genera, and his conclusions (summarised below) were followed by Bassett (1977: 160), who placed most emphasis on internal characters in distinguishing the two genera, and also commented on the considerably greater variability in diagnostic features in Silurian species as opposed to Early Devonian ones (by which time the genera were clearly distinct). Racheboeuf's tabulated differentiation shows Strophochonetes (sensu stricto) differing from Protochonetes in the orientation of the hinge spines ( $\alpha = 90^{\circ}$  as opposed to 40–70°), posteriorly thickened ventral median septum never bifid, anderidia more divergent, inner socket ridges not necessarily straight, dental sockets small, and myophore sometimes quadrilobed. Bassett (1977) also noted that in Strophochonetes, if a dorsal median septum is developed it is short and separate from the cardinal process. This could be construed as indicating the presence of a cardinal process pit, but it is doubtful that the pit is ever truly prominent in either genus.

Racheboeuf (1981: 40–41) characterised *Strophochonetes* as a group of primitive Chonetacea whose external morphology and cardinalia resemble those of the type species. He modified Muir-Wood's definition to some extent:

- -Hinge spines are disposed symmetrically to either side of the beak. The spines, basally oblique, curve progressively towards the plane of symmetry of the shell until they are parallel.
- —The dorsal median septum is absent.
- —The anderidia are long, narrow, and do not fuse posteriorly with the inner socket ridges.
- -The inner socket ridges are short and narrow.
- -No mention was made of the enlarged median ventral capilla or the lack of a cardinal process pit in his diagnosis.

Racheboeuf & Lespérance (1995: 18) provided the formal diagnosis used by Racheboeuf (1998), and quoted above. This differs from Muir-Wood's original definition in specifying the presence of a cardinal process pit, and not allowing the possibility of a dorsal median septum. The only two illustrated dorsal interiors (Johnson, 1970, pl. 30, figs. 1–2) are internal moulds; in one there is clearly no sign of a cardinal process pit, but the other shows a small low protuberance which could be evidence of a weak pit.

From the above, it is clear that until the external and internal variability of *S. cingulatus* is established, and a study made of a wide variety of related Silurian species in the light of that variability, assignment of species (especially Silurian species) to the genera grouped around *Strophochonetes* and *Protochonetes* cannot be achieved with any great confidence.

#### Strophochonetes melbournensis (Chapman, 1903)

#### Figs. 2, 3

Chonetes melbournensis Chapman, 1903: 74–76, pl. XI, fig. 2 only. Chonetes (Chonetes) melbournensis.–Gill, 1945: 132–133. Chonetes infantilis Öpik, 1953: 15, pl. III, figs. 19–22.

**Type material**. Chapman (1903) did not designate a holotype from amongst his listed specimens. Unfortunately many of these, including one of his two figured specimens, are not chonetoideans. I here select a specimen re-figured by Gill (1945) as lectotype. LECTOTYPE. NMV P1419 (Fig. 2a), a ventral external mould from a sewerage tunnel in Flinders Street, Melbourne, near the old fish market, figured Chapman (1903, pl. XI, fig. 2), and described (erroneously) as a dorsal valve by Gill (1945); Melbourne Formation, Ludlow. PARALECTOTYPES *conspecific with lectotype*. NMV P615, 616, 619, 639, 640, 641A,B, 642A, 643A,B from the Swanston Street sewerage tunnel near Collins Street, Melbourne; NMV P623, 625–27 from the same tunnel near the cathedral; NMV P630 + counterpart 638, 631–33, 637A,B from the sewerage tunnel in Domain Road, South Yarra.

**Type material of** *Chonetes infantilis* Öpik. HOLOTYPE CPC 661, PARATYPES CPC 662, 663. Locality 44, Parish of Heathcote (see Talent, 1965).

**Other assigned material**. NMV P874 from GSV locality Bb18 (= NMV PL380, Broadhursts Creek, Wandong-Kilmore East, about 1 km above its confluence with Dry Creek; locality X51 of Williams, 1964), noted by Chapman as a specimen initially identified as a chonetid by McCoy; NMV P30878 from the Domain Road sewerage tunnel; NMV P3097–98 from the Yan Yean Formation at Yan Yean; P52815 collected F. Spry, 1909 from South Yarra (Melbourne); NMV P79767 collected F. Spry, 1922, from an excavation in Melbourne; NMV P142028 from Alexandria Avenue, South Yarra, between the Punt Road bridge and the railway line.

**Syntypes rejected from** *Strophochonetes melbournensis*. NMV P617 + counterpart 621, 618, 620, 622, 624, 642B from the Swanston Street sewerage tunnel; NMV P634A + counterpart 636, 634B, 635 from the Domain Road sewerage tunnel. These are all probably referable to the sowerbyellid *Jonesea thomasi* (Talent, 1965).

**Stratigraphic distribution**. Melbourne Formation (including very dark grey and dark olive-green siltstones of the *Jonesea thomasi* Zone); *Illaenus* Band, Wapentake Formation; Yan Yean Formation (including in part the Kilmore Siltstone of VandenBerg in Douglas & Ferguson, 1988); all in the Melbourne Trough, Victoria.

**Age**. Early Wenlock to Ludlow, Silurian. The *Illaenus* Band was thought by Öpik (1953) to be middle Llandovery, but is now (Strusz, 1996; Rickards & Sandford, 1998) considered more likely to be early Wenlock.

**Diagnosis**. Small, weakly concavo-convex, subquadrate *Strophochonetes* with up to 5 pairs of gently intraverse-cyrtomorph hinge spines, and finely capillate ornament with median capilla on ventral valve usually strongly enlarged. Valve floors heavily papillose, ventral muscle field distinct, anderidia short and diverging at about 80°.

**Description**. Shell small, plano-convex to gently concavoconvex, ventral valve of low convexity (D/L about 0.18). Some ventral valves with broad and very shallow sulcus anteriorly. Outline subquadrate, lateral margins gently sigmoid, with shallow re-entrants in front of small rounded ears; hinge width usually equal to width near midlength, sometimes slightly less. Maximum observed width 12.6 mm, length 7.5 mm; mean Ls/Ws 0.61. Ventral interarea low, apsacline, flat; small apical pseudodeltidium in wide triangular delthyrium; beak very low. Dorsal interarea very low, anacline; possible small apical chilidium; distinct elongate protegular node. Myophore poorly known, probably quadrilobate. Hinge spines fine, relatively long, nearly upright (initial angle with hinge line about 70°), straight to gently cyrtomorph intraverse; up to 5 each side of beak.

Ornament of fine radial capillae, about 27 in 5 mm at 5 mm radius, increase by bifurcation only. Median capilla on ventral valve usually prominent, especially through greater width; enlarged capilla occasionally slightly to one side of plane of symmetry.

Ventral interior with low, narrow median septum, reaching forward to about 25% Ls, and posteriorly widened. Teeth small, widely divergent, barely projecting beyond hinge margin. Muscle field often obscure; where distinct, is flabellate, posterolaterally moderately impressed, and without papillae. Remainder of valve floor, when well preserved, densely papillose; papillae radially arranged beneath capillae, weakest towards cardinal margin and ears. Valve floor posterolateral to muscle field coarsely and less regularly papillose, the papillae generally radially elongate.

Dorsal interior known from only one imperfectly preserved specimen (NMV P639). Cardinal process small, fused to short but strong inner socket ridges which are curved subparallel to hinge margin. Long, low, wide median ridge apparently most pronounced posteriorly and at about midlength. Anderidia short, low, diverging at about 80°. Muscle field obscure. Distal two-thirds of valve floor with numerous small papillae arrayed radially beneath exterior capillae, as in ventral valve.



**Figure 2. a**–**o**: *Strophochonetes melbournensis*; **a**, lectotype NMV P1419, latex from ventral external mould; **b**,**c**, holotype CPC 661 of *Chonetes infantilis*, ventral internal mould; **d**, paralectotype NMV P638, latex from ventral external mould; **e**, paralectotype NMV P639, dorsal internal mould; **f**,**g**, paralectotype NMV P640, dorsal external mould (plus hinge spines on ventral valve) and latex replica; **h**, paralectotype NMV P626, ventral internal mould; **i**, paralectotype NMV P625, ventral internal mould; **j**,**k**, paralectotype NMV P627, ventral internal mould and latex replica; **l**,**m**, paralectotype NMV P641A, ventral internal mould and latex replica; **n**,**o**, paralectotype NMV P641B, dorsal external mould and latex replica. Melbourne Formation; Ludlow (Gorstian?). Scale bars 2 mm.

**Discussion**. With its low convexity, almost universal prominent median ventral capilla, long nearly upright gently cyrtomorph hinge spines, widely divergent anderidia, and dorsal median ridge (not septum), Chapman's species clearly belongs in *Strophochonetes*.

*Chonetes infantilis* was based on three rather poorly preserved specimens, of which one (paratype CPC 662) is now missing. The holotype (CPC 661, Fig. 2b,c) is a nearly complete ventral internal mould and counterpart fragmentary external mould, with Ls 3.7 mm, Ws 6.0 mm, Wh 5.8 mm, and Ls/Ws 0.62. Ornament is finely costellate

with the suggestion of an enlarged median capilla; spines are not preserved, but the now lost CPC 662 had one long, fine, straight, upright spine (Öpik, 1953, pl. III, fig. 19). The holotype shows a short, fine median septum which is slightly expanded posteriorly, and small, widely divergent teeth. The remaining paratype (CPC 663) is an incomplete juvenile dorsal external mould which adds little information. The only distinction I can make between Öpik's form and most specimens of *S. melbournensis* is that the one preserved hinge spine on the lost paratype of the former was straight, not gently cyrtomorph. Given the variability in this feature



Figure 3. Scatter diagram of length against width for species assigned to Strophochonetes.

in the type series of *S. melbournensis*, I do not consider it to be of specific value.

**Comparison**. In size and convexity S. melbournensis is close to the type species, S. cingulatus (Lindström, 1861) from the Wenlock of Gotland, and to S. bassetti Racheboeuf, 1981 (Wenlock-Ludlow of Aragon), differing from both in its finer ornament, mode of capillar increase, heavily papillose valve floors, distinct ventral muscle field, less obviously bifid cardinal process, and more divergent anderidia. Strophochonetes cingulatus has more hinge spines, and longer, finer anderidia, whereas S. bassetti has rounded cardinal margins (the hinge line being less than the greatest width), and more robust anderidia. Strophochonetes piptis Bassett, 1979 (Wenlock, Gotland), although generally similar, is somewhat larger, with subovate outline and fewer hinge spines; the ventral median capilla is much less prominent. Internally, the papillae are more subdued, the ventral muscle field is longer but less distinct, and the anderidia are stronger and less divergent, separated by a more obvious median ridge. In S. melbournensis there is a small apical chilidium; Bassett reported chilidial plates, but his figs. 62C,D show quite clearly that these are cardinal crests (see Brunton et al., 1996: 27); it is not clear if there is a chilidium.

Two Russian species are of similar size: *S. minutus* Alekseyeva, 1967 (Emsian?, eastern Siberia) and *S. paucus* Afanas'yeva, 1996 (Emsian to Eifelian, southeastern Siberia), but the descriptions and illustrations are insufficient for detailed comparison, and in both the dorsal interiors are

unknown. Both appear to be more strongly convex than *S. melbournensis*, with coarser ornament.

## Strophochonetes kemezysi n.sp.

#### Figs. 3, 4

**Type material**. HOLOTYPE ANU 9619, an incomplete dorsal internal mould, and PARATYPES ANU 9617, 9620–26, 9629, 9630, 18737 and 49953 from an outcrop of the Rainbow Hill Member (basal Rosebank Shale) in a cutting on the Lachlan Valley Way just north of the Bowning turnoff, 3.5 km north-northwest of the junction with the Hume Highway northwest of Yass, New South Wales (34°44'55"S 148°50'53"E). Locality KD of Kemežys (1967).

Other material. CPC 35008-12 from AGSO locality GOU4 (collected J. Veevers, 1960): slope above limestone scarp, Hatton's Corner, southwest side of Yass River below Booroo Ponds Creek west of Yass, grid reference FB718421 (34°51'31"S 148°52'44"E); lower Black Bog Shale (Yarwood Siltstone Member?). ANU 9589, 9695, 9699, 15618 from Kemežys' locality KC: gully east of the Lachlan Valley Way 1.8 km north of the bridge over the Sydney-Melbourne railway northwest of Yass, grid reference FB697521 (34°45'33"S 148°51'15"E); Yarwood Siltstone Member. CPC 35013-17 from AGSO locality GOU26: low scarp above Yass rifle range, southwest of the Yass-Good Hope road about 800 m from its junction with the Wee Jasper road southwest of Yass, grid reference FB728379 (34°53'13"S 148°53'26"E); Rainbow Hill Member. ANU 9692, 9693, 9698, 9700, 9716, 49947-52 and CPC 35018-20 from Kemežys' locality KE and AGSO locality GOU46 (collected D. Strusz, 1976): small quarry near gate, east side of Lachlan Valley Way due west of "Allview" farmhouse about 500 m southeast of the turnoff to Bowning, northwest of Yass, grid reference FB695528 (34°45'13"S 148°51'9"E); Yarwood Siltstone Member. ANU 9694, 9696, and counterparts 9697 and 9701, and CPC 35021 from Kemežys' locality KF and AGSO locality GOU52 (collected D. Strusz 1982): road cutting, east side of Lachlan Valley Way 650 m north of Bowning turnoff northwest of Yass, grid reference FB689537 (34°44'39"S 148°50'44"E); lower Black Bog Shale (below Yarwood Siltstone Member). Counterparts NMV P79775 and 79776 (collected A. Öpik, 1951), from an old roadmetal quarry at the Derrengullen Creek crossing by the Hume Highway northwest of Yass, in beds with *Monograptus tomczyki* (*M.* sp. aff. *ultimus* of Packham, 1968—see Sherwin, 1979), Rosebank Shale.

Mitchell Collection, all from the Yass Syncline. AM F25987, locality unknown (lithology and accompanying fauna of fenestellids, other bryozoans, and small proetid trilobites are close to those of the Yarwood Siltstone Member at locality GOU46, see above); AM F27218, Bowning, exact locality and horizon unknown, but the specimen also contains cystoid plates; AM F28552, Bowning, exact locality unknown, but from the Rainbow Hill Member since accompanied by Palaeocyathus australis and Gravicalymene? australis; AM F107871, Bowning Township (with F28745, holotype of Stropheodonta striatopunctata Mitchell which, following Brown [1949] and Cocks & Rong [1989], is probably a synonym of Plectodonta davidi Mitchell, and is from Mitchell's "upper trilobite bed", i.e. the Elmside Formation at a level probably of late Přídolí age); AM F28878, Bowning, exact locality and horizon unknown.

**Stratigraphic distribution**. Black Bog Shale (including Yarwood Siltstone Member), Rosebank Shale (including Rainbow Hill Member), Booroo Ponds Group, and lower Elmside Formation, Barambogie Group, Yass Syncline, southeastern New South Wales.

Age. Jonesea thomasi and Notoparmella plentiensis Zones, latest Gorstian? or Ludfordian (Ludlow) to Přídolí (at least parultimus to ultimus Zones and probably younger), Late Silurian (see Garratt & Wright, 1988).

**Etymology**. Named for my friend Dr Kazys Kemežys, whose collections made while undertaking his PhD research at the Australian National University have been of considerable help in this study.

**Diagnosis**. Small, moderately to strongly concavo-convex *Strophochonetes* with up to 4 long, fine hinge spines each side of umbo; well-developed protegulal structures; median capilla high but not significantly widened; ventral median septum short, enlarged posteriorly; inner socket ridges robust, straight; anderidia diverge forward at 40–60°; valve floors finely papillate.

**Description**. Shell small (Ls to 7 mm, Ws to 11 mm), moderately to strongly concavo-convex (Ds/Ls up to 0.48), thin-shelled, so that larger shells often more or less flattened, appearing weakly concavo-convex. Outline semicircular to subovate, maximum width usually at hinge line; cardinal extremities generally flattened, may be extended as small pointed alae. Ls/Ws 0.6–0.8 for small shells, 0.55–0.65 in larger shells. Ventral umbo low, small, projecting slightly posteriorly, formed by distinct protegulum raised slightly above surrounding shell to radius of 0.6–1 mm and

ornamented only by growth lines; umbo with marked median furrow which dies out anteriorly. Ventral interarea low, triangular, apsacline, flat; delthyrium wide, with narrow crescentic pseudodeltidium. Dorsal umbo very low, also without capillae, but with strongly marked protegular structures comprising lanceolate median node up to 1 mm long extending from beak, flanked by pair of shorter, strongly divergent ridges detached from both median node and beak, and becoming low and broad anteriorly. Dorsal interarea very low, hypercline (more or less coplanar with ventral interarea). Notothyrium wide, not completely filled by cardinal process; tiny apical chilidium (often obscure). Myophore protrudes slightly above interarea, with marked median furrow separating two weakly bifid lobes; flanked by small but distinct cardinal crests. Hinge spines long, fine, variable from upright to oblique and from orthomorph to weakly inwards geniculate or cyrtomorph, with strongly oblique bases; up to 4 spines each side.

Ornament of low rounded capillae separated by narrower furrows, about 30 in 5 mm at 5 mm radius in larger shells. Capillae faint at their origin at margin of protegulum, becoming more prominent distally. Ventral median capilla mostly raised slightly above the others, but seldom widened significantly. Capillar increase on both valves usually by both intercalation and bifurcation.

Ventral interior with short, narrow median septum, extending from beak to about 20% of valve length, sometimes continued further forward as faint myophragm. Septum raised and widened posteriorly, where top may be flattened or even bifid. Teeth small, unsupported, more or less parallel to hinge. Muscle field mostly slightly to moderately impressed posteriorly, flabellate; posterolateral margins sometimes marked by fine low ridges. Valve floor weakly to moderately impressed by external ornament, with low, fine papillae radially aligned below intercapillar furrows. A few moderately coarser papillae can occur near hinge line to either side of muscle field. Cardinal extremities generally smooth.

Dorsal interior with raised, proximally bifid cardinal process continuous with robust, straight inner socket ridges diverging from hinge line at c.  $30^{\circ}$ , and often raised on broad ridges. Marked furrows (corresponding to lateral protegulal nodes on umbo) separate inner socket ridges from similarly raised anderidia, which are mostly slightly separate from base of cardinal process, and diverge forward at 40– $60^{\circ}$ , extending to c.  $\frac{1}{3}$  valve length. Weak median ridge extends forward from between ends of anderidia to c.  $\frac{2}{3}$  valve length. Usually small shallow cardinal process pit in front of cardinal process. Valve floor beyond anderidia and socket ridges as in ventral valve. Muscle field obscure.

**Comparison**. *Strophochonetes kemezysi* is very close to *S. melbournensis*; the only difference in size and proportions is that larger shells are relatively a little wider, and *S. melbournensis* is consistently only moderately concavoconvex (Ds/Ls <0.2). Ds/Ls is far more variable in specimens of *S. kemezysi*, even at the one locality, but this is likely to be largely a result of distortion after burial many of the flatter specimens show signs of this, such as cracking or crumpling of the thin shell—so the shell probably was more strongly concavo-convex. There is no sign of the shallow ventral sulcus seen anteriorly in some *S. melbournensis*, in which capillar increase is only by



**Figure 4. a**–**k**: *Strophochonetes kemezysi*; **a**, holotype ANU 9619, latex from incomplete dorsal internal mould; **b**, paratype ANU 9617, latex from incomplete dorsal internal mould; **c**, paratype ANU 9626, latex from dorsal external mould; **d**, paratype ANU 9630, latex from ventral external mould; **e**, paralectotype ANU 9621, latex from ventral internal mould; **f**, paratype ANU 9625, latexes from ventral external and internal moulds; **h**, i, NMV P79776, latex from ventral external mould, and counterpart P79775, latex from ventral internal mould; **j**, paratype ANU 9623, latex from ventral internal mould; **k**, paratype ANU 9622, latex from ventral internal mould. Rainbow Hill Member, Rosebank Shale; Ludfordian. Scale bars 2 mm.

bifurcation. The most obvious external distinction is the greater strength of protegular structures in *S. kemezysi*. The greatest differences are internal: *S. kemezysi* has a shorter ventral median septum, more robust inner socket ridges which do not curve parallel to the hinge, and less divergent anderidia. The papillae are finer, and those posterolateral to the muscle field are not as prominent.

All species of similar size and age in Europe are nearly plano-convex, like *S. melbournensis*, and similarly lack prominent protegular nodes. Internally, *S. kemezysi* is distinctive in having inner socket ridges which, while strongly divergent, do not curve to become parallel to the hinge line; I do not consider this alone to be sufficient to remove it from the genus. The Devonian Siberian species noted in comparison with *S. melbournensis* are apparently as convex as *S. kemezysi*, and also have short ventral median septa, but are much more coarsely ribbed.

## Strophochonetes sp. Sherwin, 1995

Strophochonetes sp. sensu lato Sherwin, 1995: 79, fig. 14.

**Material**. MMF31387, from locality TM 151, "The Meadows" area about 50 km WSW of Cobar; The Meadows 1:100,000 sheet, grid reference 455.995.

**Stratigraphic distribution**. Winduck Group, Cobar Trough, western New South Wales.

Age. Lochkovian, Early Devonian.

**Discussion**. Based on several poorly preserved ventral valves on a single slab of fine sandstone, this is a small moderately convex form with capillae increasing by intercalation, the median capilla slightly enlarged; one specimen has a single spine base preserved. The ventral interior has small teeth, a short low and very thin median

septum, and obscure muscle field. It differs from the older species *S. melbournensis* in the mode of increase of its somewhat coarser and fewer capillae, and in its obscure muscle field. *Strophochonetes? psiloplia* is too poorly known for useful comparison, but is of comparable age. I retain the form in *Strophochonetes* on the presence of a slightly enlarged ventral median capilla and poorly developed ventral median septum, but its known features are not really sufficient for confident identification.

## Strophochonetes? savagei n.sp.

## Figs. 3, 5

Chonetes cresswelli.-Savage, 1974: 29-31, pl. 7, figs. 1-20 (non Chapman, 1903).

**Type material**. HOLOTYPE AM F67255 (Fig. 5; formerly SU P34541), a ventral internal mould figured Savage, 1974, pl. 7, figs. 11–12. PARATYPES AM F67251–54, 67256–61, 67427 (SU P34535–37, 34540, 34542–48); figured specimens SU P34534 and 34538–39 were not transferred to the Australian Museum, and are presumed lost. All from Savage's locality 3, where the Manildra–Canowindra road crosses Mandagery Creek 600 m south of Manildra.

**Stratigraphic distribution**. Manildra Formation, Cowra Trough, central New South Wales

**Age**. *Boucotia janaea* Assemblage Zone (Garratt & Wright, 1988), Early Lochkovian (probably pre-*eurekaensis* Zone—see Mawson *et al.*, 1988), Early Devonian.

**Etymology**. Named for Dr N. Savage, in honour of his pioneering work on Siluro-Devonian brachiopods from central New South Wales.

**Diagnosis**. Small, gently plano-convex, capillate *Stropho-chonetes*? with distinct median ventral capilla, robust variably cyrtomorph hinge spines, short ventral median septum, strongly cleft cardinal process, small cardinal process pit, and strong inner socket ridges almost parallel to hinge line.

**Summary description** (modified after Savage, 1974). Shell very small, semicircular to subquadrate, gently concavoconvex to plano-convex. Ls to 5 mm, Ws to 8 mm; maximum width at hinge line. Ventral interarea low



**Figure 5**. *Strophochonetes? savagei*; holotype AM F67255 (formerly SU P34541), ventral internal mould; photograph courtesy Zhen Yongyi. Manildra Formation; early Lochkovian. Scale bar 2 mm.

apsacline, dorsal interarea almost non-existent. Hinge spines few; bases usually outwards-oblique but variable; spines variably intraverse cyrtomorph to straight and oblique or extraverse cyrtomorph (distally upright).

Ornament capillate; about 40 capillae at 4 mm radius, increasing by intercalation and bifurcation. Ventral median capillae usually prominent.

Ventral interior with narrow median septum extending to about <sup>1</sup>/<sub>6</sub> valve length. Teeth and muscle fields obscure, valve floor papillose, the papillae aligned beneath capillae, and most prominent posterolaterally.

Dorsal interior with strongly bifid cardinal process continuous with robust straight inner socket ridges which are almost parallel to hinge. Anderidia narrow, low, diverging forward at about 40°. Small cardinal process pit. Outer part of valve floor finely and radially papillose.

**Discussion**. The hinge spines are very variable, but apparently mostly cyrtomorph. In one specimen, a prominent spine near the beak is oblique intraverse and almost straight, whereas in another a similarly-placed spine, initially oblique intraverse, curves so that the distal part is straight and upright. A third specimen has one wellpreserved intraverse cyrtomorph spine at the left-hand end of the cardinal margin. Spine bases on others vary from intraverse through upright to extraverse. Only one dorsal interior is known, so the generic position remains a little uncertain. With that slight reservation, the species is referred to *Strophochonetes* on the basis of generally oblique hinge spines, enlarged median capilla, non-bifid ventral median septum, inner socket ridges almost parallel to hinge line, and distinct divergent anderidia.

Strophochonetes? savagei differs from "S." cresswelli because of the prominent median rib on the ventral valve, more variable hinge spines, and relatively longer inner socket ridges. It is also about half the size. It differs from S. *melbournensis* and S. *kemezysi* in being somewhat smaller, with more robust and apparently more strongly cyrtomorph hinge spines. The former has a longer ventral median septum, the latter has less strongly divergent inner socket ridges. The poorly known S.? psiloplia is larger, with nearly upright hinge spines.

## Strophochonetes? psiloplia (Gill, 1945)

## Figs. 3, 6

Chonetes (Chonetes) psiloplia Gill, 1945: 138-139, pl. VIII, fig. 15.

**Type material**. HOLOTYPE NMV P14519, from locality PL1834, Syme's Tunnel, Seville East, east of Lilydale.

**Stratigraphic distribution**. Humevale Formation (in grey siltstone), Melbourne Trough, central Victoria.

Age. Lochkovian, Early Devonian.

**Diagnosis**. Small *Strophochonetes?*, moderately concavoconvex with relatively strongly concave dorsal valve, nearly semicircular outline, long orthomorph nearly upright hinge spines, small ventral median septum and obscure ventral muscle field.



**Figure 6**. *Strophochonetes? psiloplia*; holotype NMV P14519, crushed ventral internal mould (plus mould of dorsal interarea and umbo) and latex replica. Humevale Formation; Lochkovian. Scale bar 5 mm.

**Description**. Shell moderately concavo-convex with little space between valves; Ls 7.3 mm, Ws 13.2 mm (Ls/Ws 0.55), Ds c. 1.5 mm (Ds/Ls 0.2); outline nearly semicircular. Apparently weakly alate, but width at mid-length equals width at hinge line; shallow re-entrants between ears and lateral commissure. Ventral interarea apsacline, low; beak apparently small; dorsal interarea anacline. Delthyrial and notothyrial structures and cardinal process obscure. Indication of fairly prominent dorsal protegular node. One long apparently orthomorph almost upright ( $\alpha$  c. 85°) spine partly preserved. Ornament capillate but not measurable, although seemingly somewhat coarser than in *S. melbournensis*; enlarged median capilla apparently present.

Ventral interior poorly known. Fine median septum reported by Gill not now visible, so cannot have been very long. Ventral muscle field obscure. Valve floor covered with small radially arrayed papillae.

Dorsal interior unknown.

**Discussion**. The holotype is the only specimen. Described by Gill as a ventral valve, it is actually a poorly preserved internal mould in ventral aspect (effectively a ventral internal mould), slightly flattened and damaged near the umbos so that an external mould of both interareas and the proximal part of the dorsal valve is visible. In size and outline it is not greatly dissimilar from *S. melbournensis*, differing most obviously in the almost upright and probably straight hinge spines, and the greater curvature of the dorsal valve; the ribbing seems to be somewhat coarser, and the dorsal valve more strongly concave. Until more detail is available, even the generic position must remain uncertain, but in view of the similarity with *S. melbournensis* assignment to *Strophochonetes* seems most appropriate. It is conceivable that the two are synonymous.

"Strophochonetes" cresswelli (Chapman, 1903)

Figs. 3, 7

Chonetes cresswelli Chapman, 1903: 77–78, pl. XII, fig. 7d; Gill, 1951: 60–61, pl. III, fig. 5.

Chonetes (Chonetes) cresswelli.-Gill, 1945, 134-135, pl. VIII, fig. 5.

Protochonetes? cresswelli.-Boucot & Harper, 1968: 151.

Protochonetes cresswelli.-Chatterton, 1973: 73.

- "Protochonetes" cresswelli.-Garratt, 1983: 88 (in fig. 5 referred to as "Parachonetes").
- non? Chonetes cresswelli.-Philip, 1962: 214-215, pl. XXXII, figs. 7-9.

non Chonetes cresswelli.-Savage, 1974: 29-31, pl. 7, figs. 1-20.

**Type material**. LECTOTYPE NMV P652 (Fig. 7a,b; figured Chapman, 1903, pl. XII, fig. 7), a ventral internal mould, and PARALECTOTYPES NMV P653–55, 1422–23, all from locality PL1803, Hughes Quarry north of Lilydale, Chirnside Park (at the summit of a low hill near the middle of a block bounded by the northern end of Edward Road, Coldstream West Road, and Victoria Road); Christmas Hills 1:25,000 sheet, grid reference 528239. Lectotype selected Gill (1945: 134), by reference to it as "holotype" (ICZN Rule 74b); re-figured Gill (1951, pl. III, fig. 5).

**Other material**. NMV P14712A, B, 15133, 25552, 33117– 19, 33123, 77010, all from locality PL1802—Gill's Locality 2, "Wilson's" near Lilydale (an excavation on Albert Hill Road about 400 m east of its intersection with Victoria Road); Ringwood 1:100,000 sheet, grid reference 535196.

**Stratigraphic distribution**. Humevale Formation, Melbourne Trough, central Victoria.

Age. Lochkovian and Pragian, Early Devonian.

**Diagnosis**. Small, moderately concavo-convex, gently sulcate, finely costellate shells with symmetrically placed hinge spines, usually proximally intraverse cyrtomorph becoming upright distally, no enlarged ventral median costa; ventral median septum short, high and thickened but not bifid posteriorly; no dorsal median septum, but sometimes a low, narrow breviseptum; straight anderidia diverge anteriorly at 30–50°.

Description. Shell small (Ls to 10 mm, Ws to 15 mm), ovate, length about <sup>2</sup>/<sub>3</sub> width, hinge line less than maximum width (which is at about 40% of length); cardinal angles obtuse. Ventral valve moderately to strongly convex (depth 0.2–0.4 length), dorsal valve gently to moderately concave (depth up to <sup>1</sup>/<sub>3</sub> length), body cavity shallow. Broad, shallow, commonly gently V-shaped ventral sulcus often present. Ventral beak small; interarea low, flat, orthocline to apsacline; delthyrium triangular, with narrow arcuate pseudodeltidium. Dorsal interarea very low, flat, anacline; myophore with median furrow deeper than lateral furrows, and flanked by narrow chilidial plates; small, narrow protegular node. Hinge spines long and fairly thin; attitude variable, but generally proximally steeply oblique and intraverse cyrtomorph, becoming upright distally; up to 3 seen on each side of umbo, symmetrically placed.



**Figure 7**. **a**–**l**: "*Strophochonetes*" cresswelli; **a,b**, lectotype NMV P652, ventral internal mould and latex replica; **c**, paralectotype NMV P1422, latex from ventral internal mould; **d**, NMV P15133, ventral internal mould; **e**, paralectotype NMV P654, latex from ventral internal mould; **f**, NMV P33117, latex from dorsal external mould—note marginal zone of subdued ornament; **g,h**, paralectotype NMV P1423, ventral internal mould and anterodorsal view of latex replica; **i,j**; NMV P14712A, dorsal internal mould and latex replica; **k**, paralectotype NMV P653, latex from dorsal external mould; **l**, paralectotype NMV P655, latex from dorsal external mould; **k** paralectotype NMV P655, latex from dorsal external mould. Humevale Formation; Lochkovian to Pragian. Scale bars 2 mm.

Radial ornament costellate; ribs fine, rounded, lowest near cardinal angles and slightly more crowded medially than laterally. Ribs on dorsal valve opposed to furrows on ventral valve (clearly visible on NMV P1422); increase on the latter by bifurcation and consequently by intercalation on the former; about 20–22 costae increase to about 50–60 ribs marginally. At 5 mm radius generally 11–12 ribs in 5 mm medially. Ribs weaker near margin in some specimens, almost absent in distinct submarginal zone in a dorsal external mould. Fine growth lines noticeable mainly near hinge margin. Ventral interior with well-developed strongly divergent teeth supported by very short divergent dental plates. Median septum thin, reaches to about <sup>1</sup>/<sub>4</sub> valve length, posteriorly high and thickened, anteriorly very low. Ventral muscle field subtriangular, moderately impressed posteriorly, obscure anteriorly, its floor only slightly less corrugated by external ribs than remainder of valve floor. Outer half of valve floor finely papillose.

Dorsal interior with distinct anderidia diverging at about  $30-50^{\circ}$  from base of small elevated cardinal process, and reaching to about <sup>1</sup>/<sub>4</sub> valve length; distal ends of anderidia

swollen. Of two known dorsal interiors, NMV P14712A (Ld = 8.3 mm.) has very low median breviseptum extending from  $\frac{1}{3}$  to  $\frac{2}{3}$  Ld, NMV P25552 (Ld = 5.5 mm) shows no sign of a median septum. No cardinal process pit or accessory septa. Inner socket ridges narrow, high, fused to cardinal process, straight and strongly divergent. Outer parts of valve floor very finely papillose.

**Discussion**. The position of this species is still uncertain, partly because of relatively poor preservation of much of the available material. Earlier (Strusz, 1984: 133) I remarked that Chatterton's (1973) assignment to *Protochonetes* was incorrect and Savage's (1974) to *Chonetes* correct, in the belief that there were upright spines and a cardinal process pit, but subsequent examination shows this to be incorrect. In shell shape, ornament (except the lack of an enlarged median costa), distally parallel cyrtomorph hinge spines, and internal structures this species is similar to a number of Early Devonian strophochonetines, but the particular combination of structures is shared by none of them. The undifferentiated median costa suggests the Protochonetinae, but all protochonetines have orthomorph oblique hinge spines and weakly divergent anderidia.

"Strophochonetes" cresswelli differs from typical Strophochonetes in having no cardinal process pit, a weakly developed dorsal breviseptum, and anderidia attached to the cardinal process. Ctenochonetes Racheboeuf, 1976, has orthomorph spines, the first two present on only one side of the umbo; although its cardinal process is supported by well-developed anderidia as in "S." cresswelli, it also has a well-developed median septum; moreover, the sockets are partly covered ventrally by flaps developed from the inner socket ridges. In Johnsonetes the median costa is not prominent, being enlarged only umbonally, and the cardinal process is supported by the anderidia, but in it too the first two hinge spines are inserted only to one side of the umbo, and the dorsal median septum is much better developed.

Similar in size, ornament, shallow ventral sulcus and ventral internal structures is "*Strophochonetes*" longispina (Mansuy, 1912) as revised by Racheboeuf & Thanh (in press). That species, however, has more closely spaced upright hinge spines, and a distinct posteriorly widened median septum supporting the cardinal process.

It is likely that "*S*." *cresswelli* is a generically distinct strophochonetine, but erection of a new genus requires better material than is currently available.

The three ventral internal moulds from the Lochkovian Boola Formation of the Tyers area, East Gippsland, ascribed to this species by Philip (1962: 214–215, pl. 32, figs. 7–9) are less convex, with the external ornament only weakly reflected on the coarsely papillose valve floors. They differ most markedly in the hinge spines, which are inwardsoblique, and on this account alone are considered unlikely to be conspecific with "*S*." *cresswelli*. In the absence of dorsal valves the identity of Philip's species remains unknown, but the hinge spines suggest possible comparison with the Vietnamese Early Devonian *Bacbonetes janvieri* Racheboeuf & Thanh (in press).

The specimens described by Savage (1974) from the Lochkovian Maradana Shale of central New South Wales are rejected from *P.? cresswelli* because there is a prominent

median rib on the ventral valve, and the inner socket ridges are significantly longer. They form the basis of the new species *Strophochonetes? savagei*, described herein.

## Johnsonetes Racheboeuf, 1987

**Type species**. *Chonetes filistriata* Walcott, 1884. Emsian, Nevada.

**Diagnosis**. "Shell small to medium, markedly concavoconvex and transverse in outline; when present, median enlarged costa developed on beak only; spines orthomorph vertical, asymmetrically arranged with more spines on one side; homologous spines appearing first on the opposite side; long and thin dorsal median septum supporting a stout, short and wide cardinal process; inner socket ridges low, rounded, anteriorly divergent at 130–140°; anderidia short, anteriorly divergent at 45–50° and posteriorly fused with cardinal process." (Racheboeuf, 1998: 41).

Remarks. Racheboeuf (1987) assigned four species to Johnsonetes: the type species from Nevada, two new Emsian species from the Canadian Arctic Archipelago, and Protochonetes latus Chatterton, 1973, from the Emsian (not Pragian) of Australia. In the quoted diagnosis one of the characteristics is that the hinge spines are vertical to the hinge. The specimens of J. filistriata figured by Johnson (1970, pl. 31, figs. 1–17) suggest this to be the case, though few of the figured ventral valves show much more than spine bases. As recorded below, it is not the case with Chatterton's species. In J. ellesmerensis Racheboeuf, 1987, the spines are proximally upright or very steeply oblique extraverse, but then bend inwards to become orthomorph intraverse. The holotype of J. arcticus Racheboeuf, 1987 (his pl. 1, figs. 19-21) suggests steeply oblique spines, possibly cyrtomorph intraverse. In all other respects these species appear to be congeneric. If the genus is to be redefined to include species with oblique spines, then I would also include in it the Australian species Chonetes australis McCoy, 1876, and Chonetes culleni Dun, 1904. With *Protochonetes latus* these form a group of very similar species. To that group I would tentatively add Devonochonetes? sp. 2 Lenz & Johnson, 1985, from the Pragian of New South Wales, in agreement with Racheboeuf (1998: 41). I disagree with Racheboeuf in also assigning Devonochonetes? sp. 1 Lenz & Johnson, 1985, to Johnsonetes. In view of these changes, I have provided redescriptions of all the species concerned.

#### Johnsonetes australis (McCoy, 1876)

## Figs. 8, 9

- Chonetes australis McCoy, 1876: 141–142, pl. XXXV, figs. 3–5; Gill: 1951, 64–68, pl. III, figs. 18, 19, 21; Talent, 1956: 41–43, pl. III, figs. 10, 11.
- Chonetes (Chonetes) australis.-Gill, 1945: 136.
- Chonetes teicherti Gill, 1951: 70-71, pl. III, figs. 12-15.
- Protochonetes australis.-Chatterton, 1973: 71.
- "Chonetes" teicherti.-Chatterton, 1973: 77.

**Type material**. The two ventral valves figured by McCoy have been missing for many years (see Gill, 1945: 136);



**Figure 8. a**–**p**: *Johnsonetes australis*; **a,b**, neotype NMV P134773, ventral valve with well-preserved protegulal structures; **c**–**e**, holotype NMV P123136 of *Chonetes teicherti*, latex from ventral external mould (c,d) and partially decorticated ventral valve (e) showing very distinct protegulal structures; **f**, NMV P1222, calcined and partly decorticated ventral valve; **g**, NMV P127638A/1, ventral valve on paratype slab of *Chonetes teicherti*; **h**, NMV P79717, ventral valve showing distinct protegulal structures; **i**, NMV P127952, dorsal valve with distinct protegulal structures; **j,k**, NMV P127638B/2, ventral valve on paratype slab of *Chonetes teicherti*; **l–n**, NMV P127544, isolated shell in dorsal, ventral and posterior aspects (showing chilidial plates); **o**, NMV P127543/3, dorsal valve on slab, showing anderidia on crests of low ridges; **p**, NMV P34619, posterior part of ventral valve. Buchan Group; Emsian. Scale bars 2 mm (d,e) and 5 mm.

the last reference to their being available is by Dun (1904, p. 322), who noted that Chapman "compared a specimen of *C. culleni* with McCoy's type". Searches in 1984 and 1997 have been unsuccessful, and both specimens must be considered lost. To permit comparison of McCoy's species with *Protochonetes culleni* (Dun) I here select a neotype. NEOTYPE NMV P134773 (Fig. 8a,b; formerly GSV 47639), a ventral valve collected by Curt Teichert from just below

the top of the Buchan Caves Limestone in Slocombe's Creek, 800 m north of East Buchan Road, Buchan, East Gippsland, figured by Gill (1951, pl. III, fig. 19).

**Type material of** *Chonetes teicherti* **Gill**. HOLOTYPE NMV P123136A+B (Fig. 8c–e; formerly MUGD 1979, 1980), a ventral valve and counterpart external mould from Moon Rd, Buchan (Gill, 1951, pl. III, figs. 12, 13). PARATYPES NMV P127638A+B (formerly MUGD 1982, 1983), counterpart slabs with crowded dissociated valves from McLarty's Gully, near Murrindal, Buchan; the one valve figured by Gill (1951, pl. III, figs. 14, 15) cannot be recognised.

**Other material**. *Previously figured specimens*. NMV P1222, a calcined worn ventral valve from Buchan (Gill, 1951, text-fig. 7); P15134, a badly corroded silicified ventral valve from Buchan (Gill, 1951, text-fig. 6); P34619 (formerly GSV 47556), posterior part of a ventral valve from just south of Buchan Caves Reserve (Gill, 1951, text-fig. 4); P127544 (formerly MUGD 2183), a free shell from Davidson's Cliff, Jackson's Crossing, Buchan District (Talent, 1956, pl. III, figs. 10, 11); P127952 (formerly MUGD 1984), a dorsal valve from north of the north end of Moon's Road, Buchan (Gill, 1951, pl. III, figs. 18, 21).

*Unfigured specimens*. NMV P1264 (Buchan), P79710 (Slocombe's Creek, Buchan), P79714–15, P79717–20 (Buchan), P79723–25 (about 800 m northwest of the top of Moon's Rd, East Buchan), P79726 (ex GSV 47556, from south of Fairy Cave, Buchan), P80094–98 (Buchan), P127543 (Buchan?, ex MUGD 2185; cited Talent, 1956, p. 43).

**Stratigraphic distribution**. Buchan Caves Limestone and Taravale Mudstone, Buchan Group, Buchan Rift, eastern Victoria.

Age. Emsian, Early Devonian.

**Diagnosis**. Medium-sized moderately convex species of *Johnsonetes* with convexity increasing with size; all except median rib arising outside pronounced ventral protegulum; ribs steadily increase in size with growth, median costa becoming undifferentiated beyond adult midlength; 4–7 hinge spines each side of beak, spine 1 very fine and upright, spine 1' absent, remainder orthomorph oblique, robust, asymmetric; ventral interarea flat; inner socket ridges relatively long; prominent notothyrial platform; anderidia raised on broad ridges.

Description. Shell medium-sized (Ls to 16 mm, Ws to 28 mm), subovate (Ls/Ws mostly 0.6–0.8), with greatest width either at hinge line (where small alae are often developed) or towards midlength (when alae are absent). Small shells only moderately convex (Ds/Ls c. 0.15 for Ls <5 mm), but as shell size increases so does convexity, Ds/Ls reaching 0.3 or more for Ls about 12-14 mm (equivalent to Ws of 17-22 mm). Weak anterior ventral sulcus in some larger shells. Shell in large specimens relatively thick. Ventral umbo comprises slightly raised protegular region of about 0.8–1 mm radius, ornamented only by strong growth lines and median costa. Ventral interarea low, triangular, apsacline to orthocline, and flat; delthyrium wide, pseudodeltidium crescentic, distinctly raised. Dorsal umbo flat, with prominent elliptical protegular lobe and lateral nodes (terminology of Kemežys, 1965), ornamented only by strong growth lines; interarea very low, flat, anacline, with wide notothyrium flanked by narrow, triangular chilidial plates; myophore quadrilobate, central lobes larger than outer ones.

Hinge spines developed in alternating manner described by Chatterton (1973) and Garcia-Alcalde & Racheboeuf (1975); innermost (spine 1) very fine and upright or steeply intraverse, 1' absent, remainder oblique orthomorph and fairly robust,  $\alpha$  usually 75–80° but can be as low as 50°; spine bases more strongly oblique than spines.

Ornament costellate, ribs increasing steadily in size distally, and occasionally in number by bifurcation; at 5 mm radius usually 11–16 (mostly 12–14) ribs in 5 mm; a shell 9.8 mm long has about 54 ribs at margin, spaced only 9 in 5 mm medially. Median costa arises at beak, remainder radiate from margin of protegulal area. Ventral median costa somewhat enlarged proximally, but does not increase in size at same rate as others, so by about midlength in larger shells is no longer distinctive.

Ventral interior with robust triangular teeth without supporting plates. Median septum short, thickened posteriorly. Muscle field smooth-floored, flabellate, moderately impressed and with sharp margins posterolaterally.

Dorsal interior with prominent, moderately curved inner socket ridges which are distally flared and subparallel to hinge line. Sockets deep, conical; outer socket ridges fine, slightly raised. Cardinal process short, wide, deeply bifid, raised on prominent notothyrial platform which is fused to inner socket ridges and is often axially furrowed; no cardinal process pit. Anderidia fine, detached from cardinal process but rest on very prominent broad ridges extending from notothyrial platform; anderidia diverge at about 30-50°. Prominent depressions separate these ridges from inner socket ridges and median septum. Anderidia reach up to one third valve length, their supporting ridges may extend almost to midlength. Median septum proximally low, narrows and rises forward to midlength or beyond; distal end low but distinct, may reach 80% Ld. Adductor muscle scars small, triangular, confined by anderidia and median septum, gently impressed. Beyond median septum, anderidial ridges and inner socket ridges, valve floor bears coarse, elongate, radially arranged papillae; shallow furrow, continuous with depressions anteromedian to inner socket ridges may define inner margin of this papillose zone (Fig. 7o).

**Discussion**. McCoy's species is assigned to *Johnsonetes* because of the asymmetric insertion of hinge spines and absence of spine 1', and its short, wide cardinal process supported by divergent rounded inner socket ridges, and median costa only enlarged posteriorly. In common with J. latus Chatterton, 1973, which was unequivocally assigned to Johnsonetes by Racheboeuf (1987), it differs from the type species by its oblique hinge spines. In that feature and the only weakly enlarged median costa it also recalls Novellinetes Havlíček & Racheboeuf, 1979, from the Emsian of Bohemia. However that genus has only three spines, very fine ornament, a strongly impressed ventral muscle field, very small anderidia, a deep cardinal process pit but no dorsal median septum, and long, narrow inner socket ridges which are almost parallel to the hinge line. Ctenochonetes Racheboeuf, 1976, a widespread Old World Province Early Devonian genus, is similar in overall appearance, but has perpendicular spines of which the first two are absent to one (usually the left) side of the umbo, and dental sockets overhung by flap-like extensions of the inner socket ridges.

Gill (1951) based *Chonetes teicherti* on specimens on two slabs of black limestone from different localities in the

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Buchan district of Victoria, specifying amongst the distinguishing characters small size (Ws to 6 mm), prominent protegulal structures, and only two spines on the right side of the ventral valve. He also noted that the species occurred "on the same slabs" as specimens assigned to C. *australis*, being readily distinguished by its smaller size. The figured paratypes NMV P127638A+B are unrecognisable on a slab crowded with other valves, mostly small but including several larger than 6 mm. However, all show the same pronounced ventral protegulum crossed only by the median costa. Plots of Ls and Ds against Ws for all Buchan specimens previously ascribed to C. australis and C. teicherti show no differentiation. Comparison of the types of the two forms (neotype NMV P134773, Fig. 8b, and holotype NMV P123136, Fig. 8c) shows no distinguishing features. Gill's type, moreover, does show traces of spine 2', so spine insertion is the same as found in Johnsonetes australis. I consider that C. teicherti is the juvenile form of J. australis.

**Comparison**. Johnsonetes australis is very similar to J. culleni, to the extent that Brock & Talent (1993: 236) considered them synonymous. Their relationship is discussed following the description of J. culleni.

*Protochonetes* sp. Brock & Talent, 1993, from the Emsian of Queensland, is similar in size and proportions to *J. australis*, and their fig. 11D suggests the same tendency to develop a sulcus. The dorsal internal structures and type of hinge spine are unknown; the ventral muscle field seems to be somewhat less distinct, and the median septum finer and longer than in *J. australis*. Better material is needed before its generic relationships can be determined.

## Johnsonetes culleni (Dun, 1904)

#### Figs. 9, 10

Chonetes Culleni Dun, 1904: 321–323, pl. 61, figs. 1, 1a. Protochonetes culleni.–Chatterton, 1973: 69–73, pl. 16, figs. 1–22.

**Type material**. Dun's syntypes comprise MMF4002, a number of disarticulated valves on a slab of yellowish-grey buff-weathering argillaceous limestone, associated with *Spinella yassensis* (De Koninck, 1877). Dun figured one ventral valve exterior (fig. 1) and one partly obscured dorsal valve interior (fig. 1a). The type locality is portion 65, Parish of Taemas, southwest of Yass, N.S.W. As noted by Chatterton (1973), this is about 1.5 km south of "Taemas" homestead on the now abandoned road from Mountain Creek to the old Taemas Bridge, at (or close to) a locality long known as "Shearsby's Wallpaper"—see also Strusz *et al.* (1970). LECTOTYPE (here chosen) MMF4002A, the original of Dun's fig. 1 (Fig. 10a). PARALECTOTYPEs are all the remaining valves on the slab, numbered MMF4002B–I; F4002B is the original of Dun's fig. 1a (Fig. 10b,c).

**Other material**. Topotypes ANU 18947a–c and CPC 10558, figured by Chatterton (1973, pl. 16, figs. 15–22). Figured specimens ANU 18945a–f, CPC 10559–62 from the *Receptaculites* Member, Taemas Formation (Chatterton, 1973, pl. 16, figs. 1–14).

**Stratigraphic distribution**. Spirifer yassensis and basal Receptaculites Limestone Members, basal and middle

Taemas Formation, Canberra-Yass Shelf, southeastern New South Wales.

Age. Polygnathus dehiscens Zone, Early Emsian, Early Devonian (Mawson et al., 1992).

**Diagnosis**. Medium-sized costellate species of *Johnsonetes* with all costae radiating from beak, the median costa little differentiated even umbonally; up to seven asymmetrically arranged robust orthomorph oblique hinge spines either side of umbo, spine 1' absent; ventral interarea concave; prominent notothyrial platform, posteriorly widened dorsal median septum; prominent geniculate anderidia not raised on ridges.

Description. Shell medium-sized (Ls to 15 mm, Ws to 20 mm), concavo-convex, subovate (Ls/Ws mostly 0.6-0.8); small alae common. Greatest width mostly towards midlength, but may be at hinge when alae more extended than usual-in which case cardinal extremities generally less convex than remainder of ventral valve. Adult shells moderately to strongly convex, Ds/Ls 0.35-0.5. Ventral valve thicker than dorsal valve. Faint ventral sulcus in silicified specimens from basal Receptaculites Limestone Member. Ventral umbo low, protegulum not differentiated; interarea low and weakly concave, apsacline to orthocline. Delthyrium broad, triangular (apical angle 80–100°), constricted laterally by bases of hinge teeth and apically by small but often high pseudodeltidium whose distal margin reflects shape of myophore. Dorsal umbo flat, protegular node insignificant, lateral nodes absent; interarea almost linear, anacline. Notothyrium wide, myophore triangular, quadrilobed and flanked proximally by narrow cardinal crests; chilidial plates narrow, triangular, only developed in apical half of notothyrium.

Hinge spines robust, orthomorph to very weakly cyrtomorph intraverse, oblique. Lectotype shows six spines on each side, those on left being best preserved, the spines uniformly oblique,  $\alpha = 50-60^{\circ}$ . Paralectotypes less well preserved but show same spine form,  $\alpha$  up to 75°. Spine insertion alternate, as in *J. australis*, spine 1 very fine (often not preserved), 1' absent. Chatterton reported up to seven spines on each side, and noted that  $\alpha$  decreases outwards to as little as 40°, with some tendency for outermost spines to be cyrtomorph intraverse.

Ornament fine, costellate, with 11–16 ribs in 5 mm at 5 mm from umbo. Both bifurcation and intercalation uncommon, so that ribs increase steadily in size distally; about 56 at margin in lectotype. Costae arise at beak; median costa not enlarged.

Ventral interior with triangular teeth extending only moderately beyond corners of delthyrium, and without supporting plates. Median septum short; proximally broad and flat-topped but only occasionally furrowed, narrowing and at first rising forward, then rapidly becoming lower and finer; length generally about a fifth and does not exceed a quarter of valve length. Muscle field flabellate, moderately impressed posterolaterally; adductor scars, where clearly differentiated, small, ovate, enclose anterior part of median septum, and are surrounded by diductor scars. Low ridges bounding posterolateral parts of muscle field in some specimens. External ornament strongly impressed on valve floor; coarse elongate papillae outside muscle field aligned beneath inter-rib furrows.



**Figure 9**. Scatter diagrams of shell length against width, and depth against length, for species of *Johnsonetes*. Points for shells originally assigned to *Chonetes teicherti*, and for topotypic and non-topotypic *J. culleni*, are given distinct symbols.

Dorsal interior with strong, rounded inner socket ridges diverging from hinge line at about 25–30°, and prolonged beyond sockets as broad low ridges. Socket ridges fused proximally to low notothyrial platform, from which arises short, wide cardinal process. Platform either smooth-topped or with shallow median groove continuous with furrow between process lobes; no cardinal process pit. Median septum extends from front of platform; initially low and broad, it becomes narrower and higher forward before dropping relatively abruptly, finally dying out a little beyond midlength. Prominent anderidia diverge from base of

septum, generally at  $25-30^{\circ}$  ( $40^{\circ}$  in the one paralectotype dorsal interior). Anderidia more strongly divergent anteriorly than posteriorly, changing divergence at point of greatest height (at about 30% of valve length); low anterior sections can extend almost to midlength. Forward ends of posterior sections often swollen, and bear co-linear low-angle spinose protuberances ending just behind junctions with anterior sections. Valve floor strongly corrugated by reflection of inter-rib furrows, with coarse papillae aligned on them distally, as in ventral valve.



**Figure 10. a**-**d**: *Johnsonetes culleni*—syntype slab MMF4002. Note that the letter suffixes for individual valves have been scratched into adjacent rock, and can be seen on the photos. **a**, lectotype ventral valve MMF4002A at right, paralectotype dorsal valve MMF4002F (left) and ventral valve MMF4002G (bottom); **b**, paralectotype dorsal valve MMF4002B (bottom left) and ventral valves MMF4002D, E; **c**, paralectotype dorsal valve MMF4002B; compare Fig. 70; **d**, paralectotype ventral valve MMF4002H. *Spirifer yassensis* Limestone Member, Taemas Formation; Emsian. Scale bars 5 mm.

**Discussion**. Johnsonetes culleni and J. australis are very similar. Apart from their similar size and shape, they share a tendency to develop a weak ventral sulcus, robust oblique hinge spines, and a prominent sometimes posteromedially furrowed notothyrial platform. These similarities, and similar age, have led some authors (e.g., Brock & Talent, 1993: 236) to consider them synonymous.

When erecting Johnsonetes culleni, Dun (1904) separated it from J. australis on three features: its more convex ventral valve, coarser and fewer ribs, and less marked flattening towards the cardinal angles. My observations tend to support the first, but not strongly—Ds/Ls is  $\geq 0.3$  in J. australis, 0.35–0.5 in J. culleni. The third difference also is apparent, but not reliable, as it depends on the size of the alae in J. culleni. However, the size and number of ribs is very similar in the two forms.

Chapman (in Dun, 1904) compared specimens of *J. culleni* with McCoy's types of *J. australis*, and considered the former were relatively longer (not supported herein), with a ventral valve more convex umbonally but less convex distally (not clearly demonstrable), with a tendency towards bifurcation of the ribs (uncommon in both, a little more frequent in *J. culleni*), with longer hinge spines (not clearly demonstrable), and were of greater size (incorrect).

Gill (1950) and Talent (1956) briefly re-described *J. australis* on the basis of non-type specimens from Buchan, but made no comparisons. Chatterton (1973) assigned both species to *Protochonetes*, recognised their similarity, and suggested the possibility of synonymy. He considered that *J. australis* differed from *J. culleni* in having anderidia raised on ridges, and having longer and more prominent continuations of the inner socket ridges. I can confirm both of these differences.

To all the above, I would add two things. The ventral interarea is flat in *J. australis*, weakly concave in *J. culleni*. Secondly, there is a significant difference in protegular development, which also most clearly established the junior synonymy of *Chonetes teicherti* with *J. australis* (see above). In *J. australis* both dorsal and ventral protegular structures are prominent, the ventral protegulum bearing only growth lines and the median costa (the other costae arising at its margin); in *J. culleni* the protegular structures are obscure, and all the costae radiate from the beaks.

Johnsonetes latus (Chatterton, 1973) is almost indistinguishable from J. culleni internally; it differs only in its smaller maximum size, more transverse outline with the greatest width always at the hinge line, and fewer more widely spaced hinge spines. Chatterton thought the two formed an evolutionary sequence within *Protochonetes*. I can confirm, from traces of spine bases preserved on a few of his generally coarsely silicified specimens, his comment (p. 75) that (using Racheboeuf's terminology) the absence of spine 1' is shared by Johnsonetes latus and J. culleni one of the factors leading to Chatterton's suggested phylogenetic relationship between the two. ?Devonochonetes sp. 2 Lenz & Johnson, 1985, herein tentatively assigned to Johnsonetes, is even smaller than J. latus, and significantly more finely ornamented.

#### Johnsonetes latus (Chatterton, 1973)

Protochonetes latus Chatterton, 1973: 73–76, pl. 17, figs. 3–24. Johnsonetes latus.–Racheboeuf, 1987: 7–9.

**Type material**. HOLOTYPE ANU 18948, a silicified shell from Chatterton's locality A, on the east side of a creek flowing south into Burrinjuck Reservoir about 3 km south of Good Hope, west of Yass, NSW (34°57'14"S 148°48'55"E); figured Chatterton (1973), pl. 17, figs. 18–20. PARATYPES ANU 18949a–k, CPC 10563–65; it is not clear whether these specimens (from the Warroo Limestone Member) are from the vicinity of the type locality only, or include specimens from Chatterton's locality Cyrillic-D, a little to the north.

**Stratigraphic distribution**. Upper *Receptaculites* Limestone Member and lower Warroo Limestone Member, Taemas Formation, Canberra-Yass Shelf, southeastern New South Wales.

## Age. Emsian (perbonus-gronbergi Zone), Early Devonian.

**Diagnosis**. Small, transverse, moderately convex, costellate species of *Johnsonetes* with distinct triangular alae, few hinge spines, deep inter-rib furrows, distinct notothyrial platform fused to strong anderidia and prominent median septum.

**Description**. Shell small (Ls to 10 mm, Ws to16 mm), transverse (Ls/Ws about 0.6) with greatest width at hinge line, strongly concavo-convex (Ds/Ls about 0.6), slightly less convex posterolaterally. Outline subtriangular to subtrapeziform, cardinal angles acute, slightly extended as ears. Ventral umbo broad, beak low; interarea gently concave, low, weakly apsacline to orthocline, divided by wide delthyrium with narrow arcuate pseudodeltidium. Dorsal umbo almost flat, protegular and lateral nodes distinct only in early growth stages; interarea very low, anacline; notothyrium almost filled by chilidial plates and low, wide, quadrilobed myophore. Ornament finely costellate (about 10-13 in 5 mm at 5 mm radius), increase mainly by bifurcation on ventral valve, intercalation on dorsal. Ribs rounded, separated by deep, narrow furrows. Valve interiors strongly corrugated by external ribs.

Hinge spines widely separated, asymmetrically developed, spine 1' absent, with up to three each side of umbo. Spine 1 very close to axis, gently cyrtomorph intraverse; remainder steeply oblique, obliquity increasing outwards ( $\alpha$  apparently no less than 75°).

Ventral interior with broad triangular teeth extending only moderately beyond corners of delthyrium, and without supporting plates. Median septum short, initially thickened, tapering forward, and highest a short distance in front of beak, generally dying out by Ls/4. Muscle field flabellate, impressed posterolaterally; adductor scars sometimes clearly differentiated, and then small, ovate, separated by median septum, and surrounded by diductor scars. Valve floor papillose, the papillae elongate and aligned beneath inter-rib furrows.

Notothyrial platform prominent. Cardinal process large, wide, projecting posteriorly, bilobed, supported by robust, straight inner socket ridges overhanging deep sockets; ridges diverge forward at about 120–130°, lateral to sockets becoming lower and broadening rearwards. Ridges form straight posterior margins to distinct visceral cavity. Prominent, tapering, median septum extends forward from notothyrial platform to about three quarters of valve length. Anderidia also prominent, straight, fused to junction of inner socket ridges and notothyrial platform, diverge forward at about 50°, extend to about valve midlength. Vascula media occur as narrow grooves flanking median septum beyond midlength. Valve floor with large elongate papillae radially aligned below inter-rib furrows, and only prominent outside visceral cavity.

**Comparison**. The type species J. filistriata (Walcott) is of similar size, but is less convex, can have a shallow ventral sulcus, and is subquadrate in outline; the hinge spines are upright, and on the ventral valve the ribs, which are finer than in J. latus, appear to radiate from a distinct protegular area on which there is often only the median capilla. Internally, J. latus differs in its stronger anderidia, prominent dorsal median septum continuous with a distinct notothyrial platform, and less strongly bilobed cardinal process. Of the two species from the Emsian of the Canadian Arctic described by Racheboeuf (1987), J. arcticus is larger and less transverse with a more rounded outline, somewhat more finely costellate ornament, smaller cardinal process, narrower dorsal median septum, and less divergent anderidia. The other, J. ellesmerensis, is significantly smaller and less convex, may develop a weak ventral sulcus, and has less robust dorsal internal structures. For comparison with the other Australian species, see under J. culleni.

#### Johnsonetes? sp.

2Devonochonetes sp. 2 Lenz & Johnson, 1985: 59, pl. 16, figs. 5, 9–12, 14.

**Material**. AM F64788–92, from 549 m above the base of the Garra Formation in the composite section of Lenz & Johnson (1985: 38–39) south of Wellington Caves, near Wellington, NSW. Recorded by the authors from between 512 and 830 m above the base of the formation.

**Stratigraphic distribution**. Garra Formation, Molong High, central New South Wales.

Age. Probably *Eognathus sulcatus* Zone (see Lenz & Johnson, 1985, text-fig. 4), early Pragian, Early Devonian.

**Description**. Shell small (Ls to 6 mm, Ws to 10 mm), moderately concavo-convex, subovate to semicircular with maximum width towards midlength. Surface finely costellate (28 in 5 mm at 5 mm radius in F64791); ribs rounded, increasing by bifurcation and intercalation. Median rib not enlarged. Ventral umbo low; interarea low, apsacline; delthyrium small, with narrow pseudodeltidium apically arched over top of median septum. Dorsal interarea linear.

Hinge spines few, robust, apparently upright, probably orthomorph; insertion asymmetric. Ventral interior with short, strong, proximally high median septum; teeth short but wide, unsupported. Ventral muscle field weakly impressed posteriorly, otherwise obscure. Valve floor densely papillose, papillae radially aligned below inter-rib furrows. 264 Records of the Australian Museum (2000) Vol. 52

Dorsal interior with low, wide, posteriorly directed cardinal process arising from distinct notothyrial platform. Platform fused to strong, widely divergent inner socket ridges whose distal ends are low and broad; outer socket ridges narrow. Median septum medium to long (*contra* Lenz & Johnson—see their pl. 16, fig. 5), low, extending forward from notothyrial platform, can extend beyond midlength. Anderidia low, arise at junction of inner socket ridges and notothyrial platform, diverge at about 50°, reach about a quarter of valve length

**Discussion**. Lenz & Johnson gave a very brief description of this form. That above is based on their illustrated specimens. I disagree with the authors that this species could possibly be one end-member of a variable species also including their *?Devonochonetes* sp. 1. The ornament is significantly finer, the bases of the hinge spines are upright rather than oblique, there is an arched pseudodeltidium, a bilobed rather than trilobed myophore, better developed dorsal median septum, and more widely divergent anderidia.

The overall morphology is strophochonetine. The asymmetrical positioning of the hinge spines, clearly visible in all the figured ventral valves, suggests either *Johnsonetes* or the similarly finely costellate *Novellinetes* Havlíček & Racheboeuf, 1979. The prominent notothyrial platform, wide cardinal process, well-developed dorsal median septum and poorly impressed ventral muscle field preclude the latter, and strongly resemble the same structures in *J. australis* and *J. culleni*. This is a smaller and more finely ornamented species than those, but I think it probable that it is an early representative of the group. Racheboeuf (1998: 41) assigned the species to *Johnsonetes*, but as it is not yet possible to demonstrate that spine 1' is consistently absent (although it does look likely), that assignment is here considered as tentative.

#### Asymmetrochonetes Smith, 1980

**Type species**. *Asymmetrochonetes spinalonga* Smith, 1980: 49. Lochkovian, Canadian Arctic Archipelago.

**Diagnosis**. "Shell small with variably developed median enlarged costa; orthomorph perpendicular spines on right side of pedicle valve only, very rarely on left side only; inner socket ridges, median septum and anderidia faintly developed but present." (Racheboeuf, 1998: 39).

**Remarks**. Lenz & Johnson (1985: 59) considered *Philippotia* Racheboeuf, 1982 (= *Chlupacina* Havlíček & Racheboeuf, 1979), to be a junior synonym of *Asymmetrochonetes* Smith, 1980, both of which have hinge spines to one side only, on the basis (*contra* Smith, 1980) that the median costa is enlarged in both. Racheboeuf (1990: 167) disagreed with that synonymy, because *Asymmetrochonetes* has a faint dorsal median septum in place of the cardinal process pit developed in *Chlupacina*. From the diagnoses in Racheboeuf (1998), the two also differ in the development of the anderidia (weakly developed in *Asymmetrochonetes*, distinct but short, and widely divergent, in *Chlupacina*) and inner socket ridges (only weakly developed in *Asymmetrochonetes*).

## Asymmetrochonetes? planata Lenz & Johnson, 1985

Asymmetrochonetes planata Lenz & Johnson, 1985: 59–60, pl. 16, figs. 13, 15–24.

**Type material**. HOLOTYPE AM F64796 (Lenz & Johnson, pl. 16, figs. 17, 21) and PARATYPES AM F64793–95, 64797–99, from 610, 553, 608 and 717 m above the base of the Garra Formation in the composite section of Lenz & Johnson (1985: 38–39) south of Wellington Caves near Wellington, New South Wales.

**Stratigraphic distribution**. Between 514 and 717 m (616 m in Lenz & Johnson's text-fig. 4) above the base of the Garra Formation, Molong High, central New South Wales.

Age. Probably *Eognathus sulcatus* Zone, early Pragian, Early Devonian.

**Diagnosis**. Small weakly biconvex to plano-convex strophochonetine with only two spines on left side of hinge, none on right; ornament finely costellate, median costa little to slightly enlarged; ventral valve with arched pseudodeltidium, short median septum; dorsal valve with short, straight inner socket ridges, short detached anderidia and median septum, small cardinal process pit.

**Description**. Shell small (Ls to 7 mm, Ws to 11 mm for figured specimens), gently biconvex through planoconvex to occasionally slightly resupinate, subovate to semicircular, greatest width at hinge. Surface finely costellate (about 25 capillae in 5 mm at 5 mm radius), median capilla often slightly enlarged; capillae rounded, radiating from umbo; increase by bifurcation. Ventral umbo very low, interarea low, apsacline; pseudodeltidium strongly arched, arcuate. Dorsal umbo flat, interarea linear, notothyrium filled by small quadrilobed myophore. Two sinuous, upright to intraverse hinge spines on left side of valve only.

Ventral interior with small triangular teeth, short (Ls/5) but strong median septum, obscure muscle field. Valve floor with low papillae aligned beneath intercapillar furrows.

Cardinal process wide, short, posteriorly directed, the lobes separated by deep but narrow furrow, and supported by short, strong, straight, widely divergent inner socket ridges. Cardinal process pit small to distinct, shallow, somewhat elongate. Anderidia short, narrow, isolated, diverge forward at 45–50°. Median septum short, low, rounded, detached from cardinal process. Adductor muscle scars small, narrow, triangular, strongly impressed between anderidia and median septum; valve floor in front of scars coarsely papillose, remainder of valve floor as in ventral valve.

**Remarks**. Lenz & Johnson gave only a brief description, enlarged here to allow discussion of the generic position of their species, which displays characteristics of both *Asymmetrochonetes* and *Chlupacina*. There is a short but distinct dorsal median septum (as in *Asymmetrochonetes* but not *Chlupacina*) but also a variably developed, sometimes elongate, cardinal process pit (one of the characteristics of *Chlupacina*). *Asymmetrochonetes*? *planata* also resembles *Chlupacina* more than *Asymmetrochonetes* in that its anderidia are distinct, short and thin, and diverge at 45– 50°, but unlike in *Chlupacina* the front margins of cardinal process and inner socket ridges do not rise nearly vertically from the valve floor. In view of this mixture of characteristics, the species is only tentatively retained in *Asymmetrochonetes*.

## Protochonetinae Racheboeuf, 1998

## Protochonetes Muir-Wood, 1962

**Type species**. *Protochonetes ludloviensis* Muir-Wood, 1962, 51. Ludlow, Welsh Borderlands.

**Diagnosis**. "Small to medium, plano- to concavo-convex shell; pseudodeltidium and chilidium, or chilidial plates present; median enlarged costa usually absent or weakly developed; spines symmetrically arranged, orthomorph oblique, low to high-angled; dorsal interior with median septum and weakly divergent anderidia; inner socket ridges varying from short and curved to long, narrow, parallel to hinge line." (Racheboeuf, 1998: 44).

# *Protochonetes* sp. cf. *minimus* (J. de C. Sowerby, 1839)

## Fig. 11

Protochonetes sp. cf. minimus.-Strusz, 1982: 122-123, fig. 16, cum syn.-Strusz, 1984: 132-133, fig. 10.

**Material**. CPC 20420–33, 20995–21000, 21073 from three localities near Coppins Crossing on the Molonglo River, Canberra, and CPC 23781–90 from one locality west of Yarralumla, Canberra.

**Stratigraphic distribution**. Siltstone within the Walker Volcanics, and Yarralumla Formation, Canberra-Yass Shelf, Australian Capital Territory.

**Age**. Wenlock (probably Homerian) to earliest Ludlow (early Gorstian), Early to Late Silurian.

**Description** (summary after Strusz, 1982 and 1984). Shell small (Ws to 9 mm), thin, moderately concavo-convex, transverse, subovate to subquadrate, greatest width about midlength, cardinal angles obtuse or weakly alate. Umbones and dorsal interarea obscure; ventral interarea narrow, apsacline; delthyrium apparently open. Up to four straight or gently curved strongly oblique hinge spines on each side ( $\alpha c. 40-50^\circ$ ). Capillate, ventral median capilla not accentuated; increase by both bifurcation and intercalation. Myophore small, quadrilobed, median groove much stronger than other two; no chilidial plates have been seen.

Teeth small, subparallel to hinge. Ventral muscle field flabellate, weakly impressed. Ventral median septum short (c. 10% Ls), fine, expanded and in some shells bifid posteriorly. Valve floor strongly reflects external ornament, but lacks obvious papillae.

Dorsal interior unknown.

**Comparison**. The summary description given above is included to facilitate comparisons. The generic position of Sowerby's species remains uncertain, as the dorsal interiors are still unknown; as noted elsewhere (Racheboeuf, 1976;



**Figure 11. a**–**d**: "*Protochonetes*" sp. cf. *minimus*; **a**, CPC 23781, ventral valve; **b**, CPC 23785, dorsal external mould (and hinge spines); **c**, CPC 23787, ventral internal mould; **d**, latex from ventral external mould. Yarralumla Formation (a–c) and Walker Volcanics (d); Homerian to early Gorstian. Scale bars 2 mm.

Strusz, 1982) the greatest similarity is with *Protochonetes*. Racheboeuf (1998: 45) unequivocally refers it to that genus. There are several other small species of *Protochonetes*, but only three bear close comparison with *P*. sp. cf. *minimus*. *Protochonetes tenuistriatus* (Hall, 1860) from the late Llandovery of Nova Scotia, as re-described by Harper (1973), is a little larger, more transverse, with the greatest width forward of the hinge line, and has a longer, better developed ventral median septum. Somewhat larger again are *P. elyensis* Sheehan, 1982 (Wenlock, Nevada) and *P. harricanensis* Jin *et al.*, 1993 (late Llandovery, Arctic Canada); the former differs from *P*. sp. cf. *minimus* in being markedly elongate, strongly concavo-convex, and more finely capillate, whereas the latter is only gently concavo-convex, coarsely capillate, and has relatively robust close-set hinge spines.

Two Australian Silurian chonetoideans which could be mistaken for *P.* sp. cf. *minimus* are *Strophochonetes melbournensis* (Chapman) and *S. kemezysi* n.sp. The former is much less convex and can have a broad sulcus anteriorly; the outline is subquadrate and gently alate, there is a prominent ventral median capilla, and the long hinge spines are usually nearly upright, mostly gently cyrtomorph. *Strophochonetes kemezysi* is closer in size and convexity, but is widest at the hinge line and has finer, generally upright or steeply oblique hinge spines; it normally has an accentuated ventral median capilla. Reasonably preserved specimens can be easily distinguished from *P.* sp. cf. *minimus* by the distinctive strophochonetine median capilla.

#### Protochonetes? sp. indet. Strusz, 1982

## Fig. 12

Protochonetes? sp. indet. Strusz, 1982: 123, fig. 17.

Material. CPC 20434; locality 101, near Coppins Crossing, Molonglo River west of Canberra.

Stratigraphic distribution. Shale within the Walker



Figure 12. *Protochonetes*? sp. indet. Strusz, 1982; CPC 20434, ventral valve. Walker Volcanics; Homerian. Scale bar 5 mm.

Volcanics, Canberra-Yass Shelf, Australian Capital Territory.

Age. Homerian, late Wenlock, Early Silurian.

**Discussion**. The single rather poorly preserved small ventral valve tentatively assigned to *Protochanetes* by Strusz (1982), is of low convexity and semi-ovate outline, with subdued fine ribs (without accentuated median costa) which appear to be parvicostellate. There are four very oblique spine bases, but the course of the spines away from the cardinal margin is unknown. The valve is partly decorticated, revealing that the valve floor is densely papillose, with the papillae radially arranged. No other details are known.

The apparently parvicostellate ornament recalls the Chonostrophiidae, but the shell is definitely not resupinate. Overall appearance, size and proportions are close to those of *Strophochonetes kemezysi* and *S. melbournensis*. In particular, NMV P626–27 (ventral internal moulds, paralectotypes of *S. melbournensis*) show the same papillose valve floor, and the internal reflection of similarly fine ornament. Of the two, P626 has a prominent median capilla but P627 does not, which means its absence in the Canberra specimen is not by itself significant. However, the shallow angle at which the spine bases in that specimen leave the cardinal margin makes it highly unlikely that the two are synonymous, and the original assignment is left unchanged.

#### Parachonetinae Johnson, 1970

#### Parachonetes Johnson, 1966

**Type species**. *Chonetes macrostriata* Walcott, 1884: 126, pl. 2, fig. 13?, pl. 13, figs. 14, 14c; subsequent designation Johnson, 1966: 367. Emsian, Nevada.

**Diagnosis**. "Shell medium to large, strongly concavoconvex; radial rounded, irregular costae; spines orthomorph, high-angled to perpendicular and symmetrically arranged; dorsal valve interior with a wide, more or less deep cardinal process pit between the bases of the two lobes of the cardinal process; long anderidia anteriorly divergent at 35°. Posteriorly fused with the cardinal process lobes; well-developed median septum; low, ill-defined inner socket ridges anteriorly divergent at 100–130°." (Racheboeuf, 1998: 47).

**Discussion**. When erecting his new genus, Johnson unequivocally included only four species: the type species *Chonetes macrostriata* Walcott, 1884 from the Emsian of Nevada; *C. verneuili* Barrande, 1879 from the Early

Devonian of Eurasia; and from the Early Devonian of Victoria, *C. baragwanathi* Gill, 1949, and *C.? suavis* Talent, 1963 (with the comment that these two species might be synonymous). Chatterton (1973) described two new species from the Emsian of New South Wales. Johnson (1966) suggested there were two species groups: one centred around *P. macrostriatus* and including the Victorian species, and the other comprising *P. verneuili* (Barrande).

In 1951, Gill formally recognised "... a rich gens of apparently indigenous species related to *C. robustus*, and it is proposed that in future this group is known as the *C. robustus gens*." He included in this species-group *Chonetes buchanensis, killarensis, productoidus, baragwanathi, robustus* and *cresswelli*. It was characterised as "... a group of larger, rather coarsely costellate species, with short ventral median septum, and spines set at right angles to the hingeline. Where known, the dorsal valve has a comparatively long median septum and two accessory septa [i.e. anderidia]."

The present study has shown that only C. cresswelli does not belong in this "gens" (group), that the first three in the above list are subjective synonyms, and that the remaining two could well be so. All are strongly concavo-convex; coarsely and somewhat irregularly ribbed, the ribs radiating not only from the beak, but from the inner part of the cardinal margin, with which they make a large angle; have orthomorph hinge spines on either side of the beak; and the shell floor is finely and densely papillose at least marginally. Shells closest to P. baragwanathi and P. robustus are large, with a tendency to develop rounded alae, and can develop shallow ventral sulci; the ventral interarea is orthocline to anacline and sometimes twisted (as in the type species, P. macrostriatus), and the hinge spines are oblique (contra Gill). Only the absence of dorsal interiors in some species prevents final resolution of the relationships within the group, but otherwise the similarities are so great that I have no doubt all are Parachonetes.

I tentatively suggest adding two other species to the *robustus* group: *C. bowieae* Gill, 1945, and *C.? suavis* Talent, 1963. These species differ from those unequivocally placed in the group in being a little smaller, with little if any tendency to form alae, and no sulcus; the spines are upright in the former, unknown in the latter. Another significant difference (enough to leave some uncertainty even on generic position) is that the ribs radiate from very near the beak, so making a shallow angle with the hinge. Nevertheless the overall morphological similarities between *P.? bowieae*, *P.? suavis* and the *robustus* species-group are considerable.

Congeneric but not so close morphologically are *P. konincki* and *P. flemingi* Chatterton, 1973, and possibly *P.? spooneri* (Talent, 1956). All are large and coarsely ribbed, but have consistently anacline ventral interareas, alae absent or small and angular, no sulci, more oblique hinge spines (at least in Chatterton's species), and lower ventral median septum.

Table 1 compares ventral valve structures in all these species, while the relationship between length and width is plotted for most of them in Figs. 14 and 17. Of those most likely to be conspecific (i.e. "*Chonetes*" baragwanathi, "*C*." killarensis, "*C*." productoida, "*C*." robusta and "*C*." buchanensis), the generic position is firmly established only in *P. baragwanathi*, in which both valves are known. The incompletely known taxa which I nevertheless consider to be very probably conspecific are questionably included in its synonymy list to highlight that situation, but are then treated separately because none has been adequately described to current standards. Should additional specimens be found which firmly establish that only one species is involved, then for that species the earliest name, that of *"Chonetes" robusta* Chapman, 1903, will take priority.

## Parachonetes baragwanathi (Gill, 1949)

## Figs. 13, 14

- ? Chonetes robusta Chapman, 1903: 76–77, pl. 12, fig. 8; Gill, 1945: 134; Gill, 1949: 109, pl. 3, figs. 15, 17; Boucot & Harper, 1968: 151.
- ? Chonetes (Chonetes) killarensis Gill, 1945: 140–141, pl. 8, fig. 14; Boucot & Harper, 1968: 151.
- ? Chonetes (Chonetes) productoida Gill, 1945: 141–142, pl. 8, figs. 3, 7, 12.
- Chonetes baragwanathi Gill, 1949: 107–109, pl. 3, figs. 10, 14, 16, 20, 23.
- Chonetes? baragwanathi.-Talent, 1963: 68, pl. 36, figs. 1-21, pl. 37, figs. 1-7.
- ? Chonetes? sp. B Talent, 1963: 69, pl. 41, fig. 7.
- Parachonetes baragwanathi.-Johnson, 1966: 366.
- ? Chonetes buchanensis Gill, 1951: 68–70, pl. 3, figs. 17, 20; Talent, 1956: 45.

**Type material**. HOLOTYPE NMV P52367 (Fig. 13a; formerly GSV 27219), a posteriorly damaged distorted ventral internal mould from NMV PL565 (Gill's locality

23), Sandy's Creek, Tabberabbera area; this is on a slope 250 m southeast of Warrigal Bend, Parish of Nungatta, East Gippsland; figured Gill (1949, pl. 3, figs. 7, 14, 16); Kilgower Member, Tabberabbera Formation. PARATYPE NMV P31927 (GSV 27214A, B), a distorted dorsal internal mould from locality NMV PL564 (= G22), Sandy's Creek; figured Gill (1949, pl. 3, fig. 10).

**Other material**. *Figured or cited by Gill (1949)*. NMV P31930 (GSV 27180, 27183; Gill, 1949, pl. 3, fig. 23) + counterpart 52382 (locality NMV PL564 = G22), and topotype P52380 (GSV 27200).

*Figured by Talent, 1963.* NMV P47585–92 (ex GSV 56587, 56505, 56259, 56379, 56625, 56380a, 56380b, 56053b), 60863–70 (ex GSV 56565a, 56353, 56598, 56274, 56368, 56612, 56056c, 56606), 60938 (GSV 55882), 60939 (GSV 55878), 74166 (GSV 56325), 74167 (GSV 56251) from several Tabberabbera localities. Also possibly NMV P60908 (formerly GSV 57150), from Talent's locality 46, hillside southwest of left branch, Dead Bull Creek, Parish of Nungatta, Gippsland, figured Talent (1963, pl. 41, fig. 7).

**Stratigraphic distribution**. Kilgower and possibly Dead Bull Members, Tabberabbera Formation, Mitchell Syncline, eastern Victoria.

Age. Pragian, Early Devonian.

**Diagnosis**. Large coarsely and irregularly costellate species of *Parachonetes*, the lateral costae radiating from the hinge

**Table 1**. Comparison of ventral valve structures for Australian species of *Parachonetes*. The table is arranged with members of the *"robustus"* group in columns 1–3, possible members of the group in columns 4–5, and species distant from that group in the remainder. Structures common to all and so not shown in the table are: profile strongly concavo-convex; ornament coarsely costellate; ribs rather wavy and radiating from beak and nearby cardinal margin; valve floor finely and densely papillose marginally; teeth triangular, small but prominent, slightly to moderately elongate parallel to hinge.

	baragwanathi	robustus	buchanensis	bowieae	suavis <sup>1</sup>	spooneri	konincki	flemingi
size alae	large absent, or large, rounded	medium absent, or moderate, rounded	large large, rounded	medium none? or weak	medium absent or weak	large absent	very large absent	large weak
sulcus	absent, or	absent, or	absent or	absent	absent	absent	absent	absent
interarea	orthocline to anacline, usually curved	orthocline (approx.)	orthocline	orthocline	orthocline	anacline, curved	anacline	anacline
spines/side	oblique up to 7	oblique, up to 5	oblique, ≥4	upright, 4	?	?	oblique, c. 5–6	oblique, c. 5–6
ribs/5 mm	8–9	10–11	7–12	15 (type)	11–13	c. 8	5–7	7–10
med. septum	(max. 14) short, thin, fairly low	(max. 13) to Ls/3; thin, high	short, thin?	Ls/4; thin, high	to Ls/4; thin, high	?	c. Ls/5; low	<ls 3;<br="">low, detached</ls>
age	Pragian	Lochkovian to Pragian	Emsian	Pragian	Pragian	Emsian	Emsian	Emsian

<sup>1</sup>The one ventral internal mould of *P*.? suavis is not nearly as convex as that of *P*.? bowieae, but ornament, median septum and teeth are comparable.



**Figure 13**. **a–c**, **e–k**: *Parachonetes baragwanathi*; **a**, holotype NMV P52367, longitudinally compressed ventral internal mould; **b**, NMV P47592, ventral internal mould; **c**, NMV P60870, latex from ventral internal mould; **e**, NMV P47585, latex from ventral internal mould; **f–h**, NMV P47590, dorsal external mould (also showing ventral interarea) in posterior and ventral aspects, and latex replica in posterodorsal aspect showing interareas and myophore; **i**, NMV P60869, damaged and laterally compressed ventral internal mould; **j,k**, NMV P60938, incomplete dorsal internal mould and latex replica. Kilgower Member, Tabberabbera Formation; Pragian. **d**: ? *P. baragwanathi*, NMV P60908, latex from incomplete distorted ventral internal mould. Dead Bull Member, Tabberabbera Formation; Pragian. Scale bars 2 mm (c,d) and 5 mm.

line; commonly with rounded alae and broad, shallow ventral sulcus; hinge spines robust, oblique; ventral median septum short, thin, teeth small but strong; dorsal median septum low, relatively short; cardinal process high, arched over prominent cardinal process pit, continuous with straight, robust inner socket ridges; straight anderidia fused to inner socket ridges, diverge at about 25°, with small spines at highest points.

**Description**. Shell large (Ls over 20 mm, Ws over 30 mm), strongly concavo-convex (Ls/Ds 2.4–2.6), moderately elongate (Ls/Ws about 0.6–0.8). More or less prominent rounded alae and broad shallow ventral sulcus commonly present; hinge width equal to or slightly less than maximum width, which is usually in front of hinge line. Ventral beak

incurved, prominent; interarea usually curved, orthocline to anacline. Delthyrium open, apical angle about 90°, with bounding ridges in some specimens. Dorsal interarea  $\frac{1}{3}-\frac{1}{2}$ height of ventral interarea, hypercline. Myophore quadrilobate. Chilidial plates very narrow in small shells, in larger shells prominent, almost meeting medially, and covering proximal third of cardinal process. Hinge spines orthomorph or gently geniculate, oblique (*contra* Gill, 1949),  $\alpha$  apparently varying from 75° to as low as 40°; spines symmetrically placed. Shell thin.

Radial ornament costellate; ribs strong, coarse, rounded and often sinuous or irregular (generally 8 or 9 in 5 mm at 5 mm radius; 10–16 per cm anteromedially), separated by narrower furrows; 50 or more ribs marginally in large shells. Details of increase on ventral valves obscure, but bifurcation occurs, most commonly anterolaterally. On dorsal valve, increase tends to be by intercalation medially, bifurcation laterally (most distinctly on alae).

Ventral interior with variably developed median septum, mostly thin, short, and not particularly high. Only reasonably well preserved interior, NMV P47585, shows what appears to be an ovate adductor field with weak bounding ridge, extending beyond median septum; generally, however, internal reflection of ribs strong enough to obscure traces of musculature. Papillae numerous, small, most abundant laterally and marginally, without obvious regular arrangement. Teeth small but strong, triangular in section, slightly elongate parallel to hinge, rounded distally.

Dorsal median septum low, short in one of two available dorsal interiors, longer and expanded anteriorly in other. Prominent anderidia diverge at about 25°, in one specimen showing what appear to be very short spines at their highest points (in front of their midlength). Outer socket ridges narrow but distinct. Robust inner socket ridges, fused to anderidia posteriorly, merge with short, high, inwardly bifid cardinal process arched over distinct cardinal process pit. Small papillae, as in ventral valve.

**Discussion**. The specimens are all strongly distorted and often incomplete, but do include internal and external moulds of both valves. As recognised by Johnson (1966), the overall appearance and details of the cardinalia are typical of *Parachonetes*. Johnson suggested that *Chonetes*? *suavis* Talent, 1963, may be a synonym of *P. baragwanathi*, with the only difference being the latter's "split dorsal septum". Both are large, coarsely costellate, and come from the Kilgower Member, but Talent's species differs in having a much longer and more robust dorsal median septum (which can develop a median groove posteriorly), anteriorly geniculate anderidia which posteriorly diverge at about twice the angle found in *P. baragwanathi*, a more prominent cardinal process, and more robust inner socket ridges whose distal ends are turned laterally, almost parallel to the hinge line.

The small incomplete ventral internal mould described as *Chonetes*? sp. B by Talent (1963), while flattened and incomplete, is close to *P. baragwanathi* in its short, fine, posteriorly slightly enlarged median septum, robust triangular teeth, and robust spine bases—compare NMV P60870, figured by Talent (1963, pl. 37, fig. 7). I tentatively place the two forms in synonymy.

## Parachonetes robustus (Chapman, 1903)

#### Figs. 14, 15a-o

*Chonetes robusta* Chapman, 1903: 76–77, pl. 12, fig. 8; Gill, 1945: 134; Gill, 1949: 109, pl. 3, figs. 15, 17; Boucot & Harper, 1968: 151.

Chonetes (Chonetes) killarensis Gill, 1945: 140–141, pl. 8, fig. 14; Boucot & Harper, 1968: 151.

*Chonetes (Chonetes) productoida* Gill, 1945: 141–142, pl. 8, figs. 3, 7, 12.

**Type material**. HOLOTYPE NMV P1417 (Fig. 15a–c), a damaged steinkern (part ventral internal mould, part dorsal external mould) from NMV PL1803, "Hughes Quarry (north of Lilydale)". This is at the summit of a low hill near

the middle of the block of land bounded by Edward, Coldstream West and Victoria Roads, Chirnside Park, north of Melbourne; Christmas Hills 1:25,000 sheet 7922–1–3, grid reference 528.239.

**Type material of "***C." productoida* **Gill**. HOLOTYPE NMV P14520 (Fig. 15d–f), a rather worn and distorted ventral internal mould, and PARATYPE P14521 (Fig. 15g,h), a ventral internal mould. Both are from NMV PL1803, the type locality of *C. robustus*.

**Type material of "C."** *killarensis* **Gill**. HOLOTYPE,: NMV P123067 (Fig. 15k–m; formerly MUGD 1915), a ventral internal mould from NMV PL1834, "Syme's Tunnel", Healesville district; Healesville 1:100,000 sheet 8022, grid reference 684199.

**Other material**. Topotypes NMV P1418A & B (adjacent valves); also P25569 (NMV PL1824, Victoria Road Cutting), 33103 (NMV PL1813, Hull Road, Mooroolbark), 33107 (NMV PL1834), 80125 (W of Hull Road), 142029 and 142031–32 (Kilsyth).

**Stratigraphic distribution**. Humevale Formation, Melbourne Trough, central Victoria.

Age. Lochkovian to Pragian, Early Devonian.

**Diagnosis**. *Parachonetes* close to *P. baragwanathi*, differing in its smaller size, and in having its greatest width towards midlength even in alate shells.

Description. Shell medium-sized; greatest observed Ls 17.7 mm (corresponding Ws 21.2 mm) in holotype of Chonetes killarensis. Outline rather elongate, with Ls/Ws varying between 0.66 and c. 0.85 (8 specimens); some large shells have rounded alae. Shallow ventral sulcus. Greatest width usually in front of hinge, even in alate shells, in some lying as far forward as about 0.4Ls, but Wh little less than Ws. Longitudinal profile strongly concavo-convex (Ls/Ds 1.9-4.3, for five good specimens 2.1-3.0). Ventral beak prominent, incurved; interarea orthocline or nearly so (may be anacline or apsacline), and flat. Delthyrium rather narrow, apical angle 70-90°; apparently open. Dorsal interarea very narrow, attitude uncertain; chilidium and myophore obscure. Up to five symmetrically placed spines seen to each side of umbo, of oblique orthomorph type and apparently weakly geniculate (see Racheboeuf, 1981),  $\alpha$  c. 70°, but spines mostly not preserved. Shell thin.

Radial ornament coarsely costellate, ribs strong, rounded and often slightly sinuous (5–7 in 5 mm anteromedially, may be wider but lower on alae); intervening furrows as wide, also rounded. Twenty-six to thirty-two costae, lateral costae originating along cardinal margin (and radial to a point posterior to the ventral beak). Ribs increase by bifurcation, mostly towards margin of larger shells, but with no clear pattern and increase not extensive; up to 42 ribs marginally. Growth lines generally obscure.

Ventral interior with relatively short median septum (up to a third of valve length but generally shorter), thin and high posteriorly, falling fairly steeply towards valve floor, but not significantly prolonged as myophragm. Teeth small but relatively strong, triangular in section, slightly elongate parallel to hinge, rounded distally. Muscle field obscured by strong reflection of external ornament, but visceral cavity generally impressed. Papillae low, most abundant marginally, otherwise show no clear organisation.

Dorsal interior not known.

**Discussion**. Preservation, as moulds in mudstone, is generally mediocre; consequently quoted dimensions in many cases are only best estimates, and the total number of hinge spines is rarely visible. The ventral valves and dorsal exterior of *P. robustus* are almost indistinguishable from

those of *P. baragwanathi*, despite the distortion the latter have suffered, and I am confident in referring the former to *Parachonetes. Parachonetes baragwanathi* differs in its moderately greater size, and in features probably related to that, such as greater convexity and number of spines, and in the predominantly curved anacline interarea. As already noted, it is therefore very likely that the two forms are synonymous.

Only four specimens are known from the type locality, of which two comprise the total material for "*Chonetes*" *productoida* (Fig. 15d–h), and the others are the holotype



Figure 14. Scatter diagrams of length against width and depth against length for measurable species of the *Parachonetes robustus* group.



**Figure 15**. **a–o**: *Parachonetes robustus*; **a–c**, holotype NMV P1417, damaged internal mould in ventral and lateral aspects (a, c) and latex replica in dorsal aspect (b); **d–f**, holotype of *Chonetes productoida*, NMV P14520, ventral internal mould in lateral and ventral aspects (d, f) and latex replica in posterodorsal aspect; **g,h**, paratype of *Chonetes productoida*, NMV P14521, ventral internal mould in ventral and posterior aspects; **i,j**, topotypes NMV P1418A (above) NMV P1418B (below), latex replica and ventral internal moulds; **k–m**, holotype of *Chonetes killarensis*, NMV P123067, ventral internal mould in posterior and ventral aspects (k,l) and latex replica (m); **n,o**, NMV P80125, latex from ventral internal mould in posterodorsal and dorsal aspects. Humevale Formation; Lochkovian to Pragian. Scale bars 5 mm. **p**: *Parachonetes*? sp. cf. *robustus*; NMV P33109, ventral internal mould. Humevale Formation; Lochkovian. Scale bar 5 mm.

(Fig. 15a–c) and a topotype (Fig. 15i,j) of "*C*." robustus. The former differ from all specimens previously assigned to "*Chonetes*" robustus in being somewhat larger, prominently alate and a little more convex, and in having slightly anacline interareas. Gill (1945: 141–2) considered productoida differed significantly in having a recurved beak and high umbonal area, but comparison of the holotypes shows no difference in umbonal convexity, and only slight difference in the attitude of the interarea (either side of orthocline). The two specimens appear to me to lie within

the range of variability of shells assigned to *P. robustus*, and so I consider the species to be synonymous.

The one specimen of "*Chonetes*" *killarensis* (Fig. 15k– m) lacks alae, as do some *robustus*, but is otherwise identical with the latter; it is relatively well preserved, and shows 5 oblique spines ( $\alpha$  c. 70°) to either side of the umbo. The currently available material does not support Gill's (1945) contention that the main difference lies in the hinge spines: short, fine and sinuous in *killarensis*, long, strong and straight in *robustus*. 272 Records of the Australian Museum (2000) Vol. 52

Parachonetes? sp. cf. robustus (Chapman, 1903)

Fig. 15p

**Material**. NMV P33109, a ventral internal mould from PL1802, "Wilson's", an excavation in Albert Hill Road about 400 m east of the intersection with Victoria Road, Lilydale.

**Stratigraphic distribution**. Humevale Formation (in pale khaki mudstone), Melbourne Trough, central Victoria.

## Age. Lochkovian, Early Devonian.

**Description**. The valve is of moderate size (Ls 11.5 mm, Ws 18.6 mm), strongly convex (Ds/Ls 0.47), ovate in outline and slightly alate. Greatest width separated from equally wide hinge margin by shallow re-entrants, such that cardinal angles are acute (c.  $70^{\circ}$ ), alae small. Shallow V-shaped sulcus. Interarea low, orthocline; delthyrium wide; small apical pseudodeltidium. Probably four spines each side; bases oblique, but spines for most of their course upright, straight or possibly gently curved.

Radial ornament of costellate ribs strong, rounded, spaced medially eight in 5 mm at 5 mm radius; ribs radiate from inner part of hinge, rare bifurcation bringing number to 33 marginally. Ribs straight medially, slightly sinuous laterally, weak towards alae.

Ventral median septum short (c. ¼ Ls), strong and high, not prolonged as myophore. Valve floor very finely papillose, muscle field obscure. Teeth robust, supported by very short dental plates.

Dorsal valve unknown.

**Comparison**. The deep convexity, strong ribs, shallow but distinct sulcus, basally oblique but distally more nearly upright spines, orthocline interarea and short strong median septum make this single specimen closely comparable with *Parachonetes robustus* and, to a lesser extent, *P. baragwanathi*. It differs in having small sharp alae and possibly gently cyrtomorph hinge spines, and in having short dental plates. *Parachonetes flemingi* and *P. konincki* have short dental plates, but their hinge spines are more oblique, and they lack ventral sulci.

#### Parachonetes buchanensis (Gill, 1951)

## Figs. 14, 16

Chonetes buchanensis Gill, 1951: 68–70, pl. 3, figs. 17, 20; Talent, 1956: 45.

**Type material**. HOLOTYPE NMV P47628 (Fig. 16a–c; formerly GSV 48690), a partly decorticated and somewhat damaged ventral valve in limestone "from the big eastward bend in the Gelantipy Road, ½ mile south of Murrindal State School", Buchan district, East Gippsland; figured Gill (1951, pl. 3, fig. 17); Murrindal Limestone. PARATYPE NMV P47627 (GSV 48824) from the same locality, a damaged ventral valve figured Gill (1951, pl. 3, fig. 20).

**Other material**. Figured specimen NMV P34621 (GSV 48825B) a damaged ventral valve from the ridge east of Rocky Camp, 65.5 m above the Buchan Caves Limestone;



**Figure 16. a**–**e**: *Parachonetes buchanensis*; **a**–**c**, holotype NMV P47628, partially decorticated ventral valve in posterior, lateral and ventral aspects; **d**, NMV P34621, damaged ventral valve; **e**, NMV P80100, partially decorticated ventral valve with greatly extended alae. Buchan Group; Emsian. Scale bars 5 mm.

figured Gill (1951, text-fig. 8). Topotypes NMV P79735–41 (fragmentary specimens from the same limestone block, GSV 48690, as the holotype), and 80100 (GSV 48691; a partly decorticated ventral valve).

**Stratigraphic distribution**. Apparently Murrindal Limestone and Taravale Mudstone (see VandenBerg, p. 139, in Douglas & Ferguson, 1988), Buchan Rift, eastern Victoria.

Age. Emsian, Early Devonian.

**Diagnosis**. *Parachonetes* differing from *P. baragwanathi* in having more prominent alae, more rounded ribs, and less commonly occurring ventral sulcus.

**Description**. Shell large (Ws over 30 mm), strongly concavo-convex (Ds/Ls 0.29–0.39), with length about  $\frac{2}{3}$  width; weak ventral sulcus in one specimen. Alae broadly rounded, prominent. Ventral interarea flat, orthocline and relatively low, with open delthyrium having apical angle of about 70–80°; no other details known. Three to four hinge spines on each side; to judge by preserved bases, they were fairly robust and steeply oblique ( $\alpha$  about 75°?). Radial

ornament coarsely costellate, ribs rather low, rounded, often rather sinuous distally, radiating from umbo and inner hinge line; 7 to 12 ribs in 5 mm at 5 mm radius, 40 to 50 ribs marginally. Ribs increase infrequently by bifurcation. Growth lines subdued, irregular.

Ventral muscle field apparently impressed at least posterolaterally; probable short, fine median septum. Valve floor, at least laterally, finely papillose. Teeth apparently well developed.

One partly decorticated fragment of the dorsal interior (NMV P79735) shows signs of what could be both median septum and cardinal process pit.

**Discussion**. The specimens are all either fragmentary or partly decorticated and slightly damaged ventral valves in limestone. Little is known of the dorsal valve, or of the ventral interior. When describing this species, Gill recognised that it was closely related to the "C." robustus group, and especially "C." baragwanathi. I concur, and so despite its being poorly known I am confident that "C." buchanensis is a species of Parachonetes.

Gill (1951) distinguished "C." buchanensis from "C." baragwanathi on the lack of a ventral sulcus, more rounded ribs, and different proportions. However, one of his specimens shows what could be a sulcus, a feature not always present in baragwanathi. Moreover, comparison of proportions is made difficult by differences in preservation: baragwanathi is known from rather distorted moulds in mudstone, buchanensis from undistorted but somewhat damaged valves in limestone. If allowance is made for this, and an estimate of width over alae in the latter is made, the two are not readily distinguished on Ls/Ws (about 0.67) or Ds/Ls (about 0.3–0.4). The appearance of the ribs has also probably been affected by greater distortion of the shells preserved in mudstone. As noted above, the two are probably synonymous.

## Parachonetes? sp. cf. buchanensis (Gill, 1951)

"Chonetes" sp. Flood, 1974: 118-119, pl. 2, figs. 5-6.

**Material**. AM F77156 (formerly UNE 11071, figured pl. 2, fig. 6) and F77148 (formerly UNE 11072, figured pl. 2, fig. 5), incomplete ventral valves from the north side of Point Hibbs. The cited specimen UNE 11073 was apparently not transferred to the Australian Museum (R. Jones, pers. comm., 21 May 1998).

**Stratigraphic distribution**. Point Hibbs Limestone, Western Tasmania Terrane, southwestern Tasmania.

Age. Eognathus sulcatus Zone, early Pragian, Early Devonian.

**Discussion**. Flood's (1974) specimens are fairly small (the figured specimens are about 7 and 8 mm long), strongly convex, with coarse ribs (about 12 in 5 mm at 5 mm radius in F77156) radiating from the hinge; there could be small alae. In the absence of preserved hinge spines, dorsal valve or internal details, assignment to *Parachonetes* must be uncertain, but the known structures are typical of the Australian species here assigned to *Parachonetes*. Flood compared his material with *P. robustus* and *P. baragwanathi*, but the pattern of bifurcation of the ribs is most like that in

some specimens of *P. buchanensis*, with which it is here formally compared.

#### Parachonetes konincki Chatterton, 1973

Fig. 17

Parachonetes konincki Chatterton, 1973: 67-69, pl. 15, figs. 1-8, 15.

**Type material**. HOLOTYPE ANU 18942, a silicified shell from Chatterton's locality Cyrillic-V or Cyrillic-G, "Bloomfield" property, parish of Warroo, east side of Burrinjuck Reservoir west of Yass (34°59'37"–35°S 148°49'52–55"E); figured Chatterton (1973, pl. 15, figs. 4, 8). PARATYPES ANU 18941a–e, CPC 10556–57, same locality; figured Chatterton (pl. 15, figs. 1–3, 5–7, 15).

**Stratigraphic distribution**. Basal *Receptaculites* Limestone Member, Taemas Formation, Canberra-Yass Shelf, south-eastern New South Wales.

Age. *Polygnathus perbonus* Zone, middle Emsian, Early Devonian.

**Diagnosis**. Very large coarsely ribbed *Parachonetes* with strongly oblique hinge spines; pseudodeltidium small, apical; short dental plates, short low ventral median septum, distinct ridges between ventral adductor and diductor scars; dorsal median septum prominent, anderidia with well-developed low-angle spines.

**Summary description**. Shell very large, ovate, strongly concavo-convex; Ls/Ws about 0.8; greatest width in front of hinge line, Wh/Ws c. 0.87. Ventral umbo broad, beak very subdued; cardinal extremities weakly convex; interarea low, flat, anacline; delthyrium wide, pseudodeltidium small, apical. Dorsal umbo flat, small elongate protegular node common; interarea very low, hypercline; notothyrium wide, filled by quadrilobate myophore flanked by chilidial plates; myophore projects into delthyrium. Hinge spines numerous (up to 6 each side?), oblique, obliquity increasing outwards to as low as 30°; outer spines curved to extend almost parallel to cardinal margin.

Ornament costellate; ribs low, rounded, 5–7 in 5 mm at 5 mm radius, radiating from umbo and adjacent hinge line. Increase mainly by bifurcation on ventral valve, intercalation on dorsal, but usually not frequently enough laterally to produce sinuous ribs. Ribs only moderately expressed internally.

Ventral interior with triangular teeth of moderate size, somewhat elongate parallel to hinge, supported by short, widely divergent dental plates. Muscle field moderately impressed posteriorly, obscure anteriorly, bounded posterolaterally by short, low, widely divergent ridges; low ridges also separate adductor and diductor scars. Median septum low, especially posteriorly, reaches c. <sup>1</sup>/<sub>5</sub> valve length. Valve floor anterolaterally papillose.

Dorsal interior with high, bilobed cardinal process roughly rectangular, expanded myophore angled so as to be visible from directly above valve interior; cardinal process arches over moderately deep cardinal process pit at rear of low notothyrial platform. Cardinal process lobes long, prolonged forward as distinct ridges which converge to fuse with strong median septum. Anderidia arise from prolongations of cardinal process lobes, diverge at c. 40°, and are much shorter than median septum, which is highest anteriorly and reaches to c. <sup>1</sup>/<sub>3</sub> valve length. Anderidia highest at about their midlength, whence project distinct forward-pointing spines. Strong inner socket ridges diverge from posterior sides of cardinal process lobes, and rapidly die out distally; outer socket ridges low and short, overhanging deep sockets. Valve floor anterolaterally papillose.

**Comparison**. Chatterton's figures are excellent, so are not reproduced here. *Parachonetes konincki* resembles *P. baragwanathi* in its short dental plates, but the former is more coarsely ribbed, and has anderidia and dorsal septum which are of similar width and height. It is closer to *P. flemingi*—the differences are discussed below.

## Parachonetes flemingi Chatterton, 1973

## Fig. 17

Parachonetes cf. P. macrostriatus.-Johnson, 1966: 369, pl. 63, figs. 9-14.

Parachonetes flemingi Chatterton, 1973: 64–67, pl. 15, figs. 9–14, 16–23.

**Type material**. HOLOTYPE ANU 18944, a silicified shell from Chatterton's locality Cyrillic-G, "Bloomfield" property, parish of Warroo, east side of Burrinjuck Reservoir west of Yass, NSW (34°59'37"S 148°49'55"E); figured Chatterton (1973, pl. 15, figs. 10, 14, 21). PARATYPES ANU 18943a–e, CPC 10553–55, figured Chatterton (1973, pl. 15, figs. 9, 11–13, 15–20, 22–23).

**Stratigraphic distribution**. Lower *Receptaculites* Limestone Member, Taemas Formation, Canberra-Yass Shelf, southeastern New South Wales.

Age. *Polygnathus perbonus* Zone, middle Emsian, Early Devonian.

**Diagnosis**. Large coarsely ribbed alate *Parachonetes* with strongly oblique hinge spines, small apical pseudodeltidium, prominent myophore; dental plates short; ventral median septum low; dorsal median septum long, narrow; anderidia with short low-angle spines at mid-length; valve floors strongly corrugated.

Summary description. Shell large, elongate semi-ovate, strongly concavo-convex; usually alate, maximum width at hinge line. Alae generally small, angular, somewhat flatter than remainder of shell. Ls to 30 mm, Ws to 35 mm, Ls/Ws c. 0.7-0.85, Ds/Ls to 0.5. Ventral beak low, umbo broad; interarea low, anacline; delthyrium wide, pseudodeltidium small, apical. Dorsal umbo flat; interarea very low, hypercline; notothyrium wide, almost filled by strongly protruding quadrilobed myophore, edged by narrow triangular chilidial plates. Hinge spines numerous (up to six each side?), steeply oblique orthomorph near umbo, obliquity increasing outwards ( $\alpha$  as low as 30°); outer spines geniculate, turned outwards almost parallel with hinge line.

Ornament rather coarsely costellate; ribs rounded, somewhat irregular, medially 7–10 in 5 mm at 5 mm radius, radiating from umbo and nearby hinge line, weaker on ears.

Ribs increase by both bifurcation and intercalation, most frequently laterally so that lateral ribs are distinctly sinuous. Ribs strongly corrugate valve interiors.

Ventral interior with broadly triangular, distally rounded teeth slightly divergent from hinge, supported by very short dental plates not fused to valve floor. Muscle field moderately impressed posteriorly. Median septum low, extends forward no more than <sup>1/3</sup> valve length, may be flattened proximally. Valve floor posterolaterally papillose.

Dorsal interior with high, arcuate, bilobed cardinal process arching over wide, shallow cardinal process pit. Anterolateral ends of cardinal process lobes form limits to low notothyrial platform, and merge with long straight anderidia which diverge forward at 30–40°. Sides of cardinal process lobes fused to low, straight inner socket ridges which broaden distally to merge with valve floor and define posterolateral limits of muscle field. Anderidia increase in height to about their midlength, where they form short blunt spines; anderidia much lower beyond spines, extend forward to no more than <sup>1</sup>/<sub>4</sub> valve length. Notothyrial platform sometimes medially grooved; long, narrow median septum extends from it to about <sup>1</sup>/<sub>3</sub> valve length. Valve floor finely papillose outside anteriorly ill-defined muscle field.

**Comparison**. Chatterton's illustrations are good, so are not reproduced here; the summary description (using modern terminology) is provided to facilitate comparison with other species. Chatterton (1973: 65-66) and Johnson (1966) distinguished P. flemingi from the type species P. macrostriatus by its thinner shell and consequent stronger corrugation of the interior surfaces; moreover it has a shallower cardinal process pit, and less prominent papillae. Chatterton distinguished P. flemingi from P. baragwanathi by its less obviously papillose valve floors, and equally prominent dorsal median septum and anderidia, and from P. suavis by its greater size, shorter dorsal median septum but longer ventral median septum, straight inner socket ridges, and more strongly corrugated valve floors. As already discussed, it differs from both (and from all representatives of the "robustus" species-group) in its consistently anacline ventral interarea, greatly reduced alae, non-sulcate ventral valve, and lower ventral median septum

Chatterton's two species *P. konincki* and *P. flemingi* are close, and are found at similar stratigraphic levels; the former is distinguished by larger size (Chatterton reported fragmentary specimens significantly larger than those plotted here in Fig. 17), valve floors less strongly corrugated by the external ribs, alae rudimentary or more usually absent, longer spines on the anderidia, and distinct ridges separating ventral adductor and diductor scars.

## Parachonetes? bowieae (Gill, 1945)

## Fig. 18

*Chonetes (Chonetes) bowieae* Gill, 1945: 136, pl. 8, figs. 1–2. *Chonetes bowieae.*–Gill, 1951: 61–62, pl. 3, fig. 16.

**Type material**. HOLOTYPE NMV P123141A+B (counterparts, formerly MUGD 1908, 1909), somewhat distorted ventral internal and external moulds in mudstone from locality PL1835, Syme's Quarry, Seville East, east of Lilydale.



Figure 17. Scatter diagrams for length against width and depth against length for species of *Parachonetes* not assigned to the *P. robustus* group.



**Figure 18**. *Parachonetes? bowieae*; holotype, counterparts NMV P123141B (ventral external mould) and NMV P123141A (ventral internal mould); the valve has been laterally compressed. Humevale Formation; Pragian. Scale bar 5 mm.

The specimen figured by Gill (1951) and the material from localities other than the type locality referred to by him in 1945, have not been found.

**Stratigraphic distribution**. Humevale Formation, Melbourne Trough, central Victoria.

Age. Boucotia loyolensis–Nadiastrophia Assemblage Zone (Garratt & Wright, 1988); Pragian, Early Devonian.

**Diagnosis**. Medium-sized relatively finely costellate *Parachonetes?* in which the lateral costae radiate from very close to the umbo; hinge spines robust, upright orthomorph; alae and ventral sulcus absent.

**Description**. Only available specimen a laterally compressed and damaged ventral valve 17 mm long, and at least 19 mm wide; valve strongly convex, especially medially. Cardinal extremities flattened, apparently not extended as alae, so cardinal margin less than maximum width. Umbo low, beak small and barely projecting beyond cardinal margin. No sulcus. Shell costellate; ribs rounded, laterally rather sinuous, extend from umbo and possibly immediately adjacent cardinal margin. At 5 mm radius, 15 ribs in 5 mm; increase by both bifurcation and intercalation; about 60 ribs marginally. Interarea not well preserved, apparently flat and orthocline. Delthyrium open. Four hinge spines each side of umbo; spines robust, long, upright but with oblique bases, orthomorph and fairly evenly spaced.

Thin ventral median septum, fairly high posteriorly, extends forward to about <sup>1</sup>/<sub>4</sub> valve length. Teeth apparently well developed, supported by short downwards-divergent dental plates. Muscle field obscure. Distal parts of valve floor finely and densely papillose.

**Discussion**. In the absence of a dorsal valve, and with costae which appear to radiate from at or very close to the beak, the generic position of this species remains uncertain. It is tentatively assigned to *Parachonetes*, and to the "*robustus*" group, described above, because of the strong similarity of the single ventral valve to those of members of that group. The ribs are a little finer, but not strikingly so (counts of ribs in 5 mm are as high as 13 in *P. robustus*, 14 in *P. baragwanathi*), and the damaged state of the valve means

the existence of extended cardinal extremities cannot be ruled out. The long, distally upright hinge spines are distinctive but, other than for one specimen of *P. baragwanathi* with clearly oblique spines, only the spine bases in representatives of the "*robustus*" group are known, so this is an unreliable factor.

## Parachonetes? suavis (Talent, 1963)

## Figs. 14, 19

Chonetes? suavis Talent, 1963: 69, pl. 38, figs. 4–9. Parachonetes suavis.–Johnson, 1966: 366; Chatterton, 1973: 67.

**Type material**. HOLOTYPE: NMV P147841 (Fig. 19a,b; formerly GSV 57123), an incomplete dorsal internal mould and counterpart ventral external mould from NMV PL576 (Talent's locality 56), near the source of Pat Creek (a tributary of the Mitchell River), Parish of Cobbannah, Tabberabbera district, East Gippsland; figured Talent (1963, pl. 38, fig. 5). PARATYPES NMV P47599 (GSV 57121; Talent, pl. 38, fig. 7), NMV P60876 (GSV 57135; Talent, pl. 38, fig. 4) and counterpart NMV P74171 (GSV 57137; Talent, pl. 38, fig. 6), NMV P147842 (GSV 57117; Talent, pl. 38, fig. 9), and GSV 57131 (Talent, pl. 38, fig. 8; this specimen was not registered on transfer, and was still missing in November 1997), all from the type locality.

**Stratigraphic distribution**. Lower Kilgower Member, Tabberabbera Formation, Tabberabbera Zone, eastern Victoria.

Age. Pragian, Early Devonian.

**Diagnosis**. Small to medium-sized, strongly concavo-convex, costellate shells with strong ribs radiating from at or near beak, crowded medially, sinuous and less crowded laterally; teeth prominent, ventral median septum short, narrow, posteriorly high; prominent arched cardinal process supported by strong, curved inner socket ridges and long, sharply geniculate anderidia, divergence proximally 50°, distally >90°; small cardinal process pit; long dorsal median septum.

**Description**. Shell small to medium-sized (Ls to 11 mm, Ws to 20 mm), strongly concavo-convex (Ds/Ls about 0.4). Small shells subcircular (Ls/Ws c. 0.9), with greatest width in front of hinge (Wh c. 0.9Ws), larger shells alate and so relatively wider (Ls/Ws 0.5), but alae rounded, so that width at hinge equals greatest width. Ventral interarea low, orthocline; delthyrium apparently open but apically bisected by median septum; apical angle about 100°. Dorsal interarea very narrow, hypercline; cardinal process prominent, myophore quadrilobate, flanked by large, upright, triangular chilidial plates which are conjunct apically. Hinge spines, known only by their bases, symmetrical placed. Shell thin.

Radial ornament costellate; ribs sharply rounded, high, separated by rounded furrows; ribs more crowded and prominent medially than laterally, where somewhat sinuous, least prominent on alae, and originate at or very near beak. Ribs 9–11 in 5 mm anteromedially, increase in number from about 34–38 costae to more than 50 ribs marginally by bifurcation on ventral valve, intercalation on dorsal valve.

Ventral interior with small, prominent teeth, triangular in section, slightly elongate parallel to hinge. Median septum



**Figure 19**. **a**–**g**: *Parachonetes? suavis*; **a,b**, holotype NMV P14781, dorsal internal mould and latex replica (shows remnants of ventral valve laterally); **c**, paratype NMV P60876, latex from incomplete dorsal external mould; **d**,**e**, paratype NMV P47599, distorted ventral internal mould and latex replica; **f**,**g**, paratype NMV P74171, counterpart to P60876, incomplete dorsal internal mould and latex replica. Lower Kilgower Member, Tabberabbera Formation; Pragian. Scale bars 2 mm.

narrow, high (especially posteriorly, where it reaches level of interarea), but short (no longer than ¼ valve length). Muscle field gently impressed posteriorly, very faint anteriorly, probably flabellate, extends forward to about ¼ valve length. The one reasonable interior lacks large endospines, but there is a suggestion of numerous fine papillae; valve floor strongly corrugated by external ornament.

Dorsal interior with prominent, curved inner socket ridges, distally parallel with hinge line, proximally fused to prominent, arched, bilobed cardinal process. Outer socket ridges low, short. Cardinal process pit small but distinct. Prominent anderidia arise at base of cardinal process and diverge at about 50°; proximally low and wide, they rise steadily to about ½ valve length, where each bears a very short spine (c. 0.5 mm). Beyond that point, anderidia low, narrow, diverging at >90° to reach about 60% Ld. Median septum prominent, long (reaches two thirds valve length); posterior half broad, rising forward, and in one of two specimens bears shallow median furrow; anterior half narrow, can develop one or two short lateral spurs. Papillae variable, radially arrayed below inter-rib furrows, may be large anteromedially. Musculature obscure.

**Discussion**. Johnson (1966) unequivocally placed *Chonetes? suavis* in *Parachonetes*, but the type of hinge spine is unknown, and the ornament (more or less radial from the umbo) is atypical for the genus. Johnson also suggested that it could be synonymous with *P. baragwanathi*, but there are significant differences, not least in details of the cardinalia

(*suavis* has longer, more divergent anderidia, whose proximal and distal ends meet at a distinct angle; longer and posteriorly expanded dorsal median septum; curved inner socket ridges) and ornament (the ribbing in *suavis* is finer, and increases exclusively by intercalation on the dorsal valve). The two species are known from different localities in the same formation.

## Parachonetes? spooneri (Talent, 1956)

## Figs. 17, 20

Chonetes spooneri Talent, 1956: 44–45, pl. 3, fig. 9. Parachonetes spooneri.–Chatterton, 1973: 66.

**Type material**. HOLOTYPE NMV P122903 (Fig. 20a,b; formerly MUGD 2186), a dorsal valve from Spooner Creek about 400 m below the western contact between limestone and the Snowy River Volcanics due south of McRae's homestead, The Basin, Buchan, East Gippsland; figured Talent (1956, pl. 3, fig. 9). PARATYPE NMV P122904 (MUGD 2219), a worn and auloporoid-overgrown ventral valve; same locality.

**Stratigraphic distribution**. Buchan Caves Limestone (in muddy limestone about the middle of the formation), Buchan Rift, eastern Victoria.

**Age**. *Polygnathus dehiscens* Zone (Mawson *et al.*, 1992), Early Emsian, Early Devonian.



**Figure 20. a**–**d**: *Parachonetes? spooneri*; **a**,**b**, holotype NMV P122903, dorsal interior in dorsal and posterior aspects; **c**,**d**, paratype NMV P122904, auloporoid-encrusted ventral valve in ventral and posterior aspects, the latter showing prominent teeth and narrow arcuate pseudodeltidium (both partly obscured by corallites). Buchan Caves Limestone; Emsian. Scale bars 5 mm.

**Diagnosis**. Large, strongly concavo-convex coarsely costellate shell, ribs radiating from hinge line close to umbo; teeth robust; cardinal process elevated, posteriorly directed, deeply bifid; cardinal process pit shallow, elongate; sockets short, deep, divergent, inner socket ridges straight, extended as low broad ridges laterally; anderidia short, geniculate, proximally diverge at 30°; dorsal median septum long, widened posteriorly around cardinal process pit.

**Description**. Shell large (Ls to 27 mm, Ws to 30 mm), strongly concavo-convex (Ds/Ls c. 0.5), slightly wider than long (Ls/Ws c. 0.9), with cardinal angles obtuse and greatest

width at about midlength. Ventral beak low, interarea anacline, concave; delthyrium wide, parabolic, with narrow, arcuate, apical pseudodeltidium. Dorsal interarea very low, attitude uncertain. Cardinal process relatively small; posteriorly directed myophore of two triangular lobes separated by a deep furrow; posterior face of each lobe weakly bifid, with adaxial ridge higher than abaxial ridge; narrow chilidial plates flank myophore. Hinge spines and spine bases unknown.

Radial ornament coarsely costellate; ribs rounded and fairly regular, separated by narrow furrows, radiate from beak and immediately adjacent cardinal margin. Increase by bifurcation on ventral valve, apparently by intercalation on dorsal valve. Rib spacing medially about eight in 5 mm at 5 mm radius, coarsening outwards; number of ribs at shell margin not known.

Teeth small but prominent, triangular in section, slightly elongate parallel to hinge; remainder of ventral internal structures unknown.

Dorsal interior irregularly radially corrugated by impression of ribs. Cardinal process prominent, posteriorly directed, deeply bilobed. Outer socket ridges triangular, short but relatively prominent, overhang small, deep, divergent dental sockets: inner socket ridges short, straight, proximally narrow and fused with cardinal process, distally expanded into very subdued ridges. Median septum low but wide proximally, supporting cardinal process and medially depressed by small, elongate cardinal process pit; septum rises gently to about its midlength, extends to about <sup>2</sup>/<sub>3</sub> valve length. Anderidia short, narrow, arise at junction of median septum with inner socket ridges and cardinal process lobes, diverge at about  $30^\circ$ , and reach about 1/5valve length: distal ends turn inwards almost parallel with median septum. Adductor muscle field smoother than remainder of valve floor, anterolaterally bounded by low, wide ridge. Outside muscle field, valve floor densely covered by small radially elongate papillae.

**Discussion**. This species is represented by only two specimens, one of which is encrusted by an auloporoid coral, and the ventral interior remains essentially unknown. Chatterton thought *P.? spooneri* close to his new species *P. flemingi*, but the cardinal process pit is much smaller, and the cardinal process does not strongly over-arch it in the manner so typical of *Parachonetes*. The anderidia are relatively shorter than in *P. flemingi*, and the dorsal septum is not nearly as wide posteriorly. It also differs from typical *Parachonetes* in that the ribs radiate from a relatively short median section of the hinge line; in that, it resembles *P.? bowieae* and *P.? suavis*, species only tentatively assigned to the genus but in many other ways similar to the *P. robustus* species-group.

There is some similarity to the notiochonetine *Allanetes neozelanica* Boucot & Johnson, 1967 (Emsian, New Zealand), a strongly concavo-convex coarsely ribbed form with a similarly elevated cardinal process, small but distinct cardinal process pit, long median septum and weakly divergent anderidia. However, unlike in *P.? spooneri* its cardinal process is flanked by strong cardinal crests (interpreted as widely disjunct chilidial plates by Boucot & Johnson, and by Racheboeuf, 1998: 76; Boucot & Johnson's pl. 22, figs. 6–7, shows that they are not attached to the edge of the notothyrium), and the dorsal valve floor is not strongly corrugated by the exterior ornament as in *P.? spooneri*. Moreover, *A. neozelanica* has (unusually) a ventral fold and dorsal sulcus.

## Parachonetes? sp.

?Devonochonetes sp. 1 Lenz & Johnson, 1985: 58–59, pl. 16, figs. 1–4, 6–8.

**Material**. AM F64783–87, from between 520 and 825 m above the base of the Garra Formation in the composite section of Lenz & Johnson (1985: 38–39) Wellington Caves, near Wellington.

**Stratigraphic distribution**. Garra Formation, Molong High, central New South Wales.

Age. Probably *Eognathus sulcatus* Zone (see Lenz & Johnson, text-fig. 4), early Pragian, Early Devonian.

**Summary description** (modified after Lenz & Johnson, 1985). Shell small (Ls to 8 mm, Ws to 10 mm), strongly concavo-convex, subovate to transverse, with small alae. Ornament finely costellate (15–17 in 5 mm at 5 mm radius); ribs rounded, increasing in width forward, occasionally bifurcating, radiating from hinge line near umbo. Ventral umbo rounded; interarea low, concave, apsacline; delthyrium small, open. Dorsal interarea very low, hypercline; myophore trilobed. Hinge spines bases steeply oblique, few, robust, asymmetrically placed. Shell thin, valve interiors strongly corrugated.

Ventral interior with small triangular teeth, short low median septum. Ventral muscle field obscure, not impressed.

Dorsal interior with strong, straight, widely divergent inner socket ridges; cardinal process wide, directed posteriorly, distally bilobed, the lobes not deeply separated, and posteriorly weakly furrowed. No obvious cardinal process pit. Anderidia low, narrow, arise just in front of cardinal process, diverge forward at c. 40°, extend to about 1/5 valve length. Low breviseptum arises at c. <sup>1</sup>/<sub>3</sub> valve length.

**Discussion**. In several important aspects the above description differs from the original (despite the original illustrations being quite good), especially regarding the dorsal interior. The authors were clearly very uncertain about the position of this form, and were probably persuaded to refer it tentatively to *Devonochonetes* because they perceived the cardinal process to have a trilobed myophore. However, AM F64785 and F64786 (pl. 16, figs. 3, 4) clearly show what has usually been called a quadrilobed myophore (see Racheboeuf, 1998: 14). Moreover, Devonochonetes characteristically has distinctly oblique hinge spines, a strongly impressed ventral muscle field, a large pseudodeltidium, and a long dorsal median septum. Racheboeuf (1998: 41) assigned this form to *Johnsonetes*, but that genus lacks the first spine on the left side, which does not appear to be the case with the present species, and it also has a well-developed dorsal median septum. The shell shape and ornament, and the asymmetrically placed probably steeply oblique orthomorph spines all recall Parachonetes, but that genus also has a distinctive cardinal process arched above a deep cardinal process pit. The generic position of this species therefore remains very uncertain, but on balance is closest to *Parachonetes*, to which I tentatively refer it.

This species differs from all other Australian species assigned to *Parachonetes* in smaller size, finer ribs, and lack of a distinct cardinal process pit. Lenz & Johnson (1985) drew comparisons with *Devonochonetes zeravshanicus* Gratsianova (in Gratsianova & Rzhonsnitskaya, 1977), but that species is much larger, with numerous sharply oblique hinge spines and a better developed ventral median septum.

## Anopliidae Muir-Wood, 1962

Holynetinae Racheboeuf, 1981

## Septachonetes Chatterton, 1973

**Type species**. *Septachonetes melanus* Chatterton, 1973, pp. 77–78; pl. 14, figs. 18–25; pl. 17, figs. 1–2. Emsian, New South Wales.

**Diagnosis** (modified from Racheboeuf, 1998: 62). Very small elongate semi-oval shell with fine costellate ornament, two upright spines on right side only; dorsal interior with deep cardinal process pit, no median septum, weak widely divergent anderidia and three to five pairs of irregular sinuous accessory septa developed anteromedially.

**Remarks**. *Holynetes* Havlíček & Racheboeuf, 1979, from the Eifelian of Bohemia, is externally very similar, but rather larger and more strongly concavo-convex; moreover the capillae increase in number rather than size distally. Internally it differs in having shorter and less well-developed anderidia, and a single pair of long accessory septa which do not extend beyond midlength, instead of the several anteriorly placed pairs in *Septachonetes*.

## Septachonetes melanus Chatterton, 1973

Septachonetes melanus Chatterton, 1973: 77–78; pl. 14, figs. 18–25; pl. 17, figs. 1–2.

**Type material**. HOLOTYPE ANU 18940, a silicified ventral valve from Chatterton's locality A, on the east side of a creek flowing south into Burrinjuck Reservoir about 3 km south of Good Hope, west of Yass, NSW (34°57'14"S 148°48'55"E); figured Chatterton (1973, pl. 14, fig. 20). PARATYPES ANU 18939a–d, CPC 10566–68.

**Stratigraphic distribution**. Warroo Limestone Member, upper Taemas Formation, Canberra-Yass Shelf, southeastern New South Wales.

Age. Emsian, Early Devonian.

**Diagnosis**. Moderately concavo-convex *Septachonetes* with anderidia diverging at 70°, and 3–4 pairs well-developed anteriorly placed accessory septa.

**Remarks**. The species has been well described and illustrated by Chatterton. In summary, the shell is up to 4 mm long, 5.5 mm wide, Ls/Ws about 0.75, Ds/Ls c. 0.3. The two hinge spines are apparently slightly intraverse and may be weakly cyrtomorph. Ornament is very fine—Chatterton records about 45 ribs at the margin of a shell 5

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mm wide—with the ribs increasing in size with shell growth, but only rarely in number. The ventral interior is simple, with a short, low median septum and small teeth. The short, narrow anderidia diverge at about  $70-80^{\circ}$ . In front of them is a median zone with coarse papillae, flanked by several pairs of pustulose accessory septa.

Because of the pattern of hinge spines, Chatterton thought this species may have arisen by neoteny from *Protochonetes latus*, but the internal features of both valves are very different. The two species co-exist in the Warroo Member.

Septachonetes micrus (Gill, 1951)

#### Fig. 21

Chonetes micrus Gill, 1951: 62-63, pl. III, figs. 6-11.

**Type material**. HOLOTYPE NMV P14698 and counterpart P14699 (Fig. 21a,b), ventral internal and external moulds, from locality PL1813, Hull Road, Mooroolbark, north of Melbourne (a cutting on the east side of Hull Road just north of its intersection with Taylor Road); Kilsyth 1:25,000 sheet, grid reference 521166; figured Gill (1951, pl. III, figs. 9–11). PARATYPE NMV P14700 and counterpart P14701, dorsal internal and external moulds, same locality; figured Gill (1951, pl. III, figs. 6–8).

**Other material**. Topotypes NMV P14705–6, cited Gill (1951: 63); NMV P14702, cited Gill (1951: 62), probably from PL1802 (Gill's locality 2: "Wilson's" on Albert Hill Road near Lilydale, north of Melbourne).

**Stratigraphic distribution**. Humevale Formation, Melbourne Trough, central Victoria.

Age. Pragian, Early Devonian.

**Diagnosis**. Strongly concavo-convex species of *Septachonetes* with nearly smooth cardinal extremities, short dental plates, prominent anderidia diverging at about 55°, low irregularly developed accessory septa.

**Description**. Shell small (Ls to 5 mm, Ws to 6.5 mm), suboval (Ls/Ws c. 0.8), strongly concavo-convex (Ds/Ls about 0.4). Cardinal angles either moderately obtuse, when Wh/Ws greater than 0.9 and greatest width towards midlength, or bluntly alate. Ventral umbo low, beak small but sharp, interarea and delthyrial structures unknown. Dorsal umbo flat, with small elongate protegular node; interarea almost linear, anacline; notothyrium filled by protruding quadrilobed myophore and narrow triangular chilidial plates. Two thin, more or less upright, weakly intraverse cyrtomorph spines on right side of beak.

Ornament finely costellate; capillae rounded, radiating from beaks, separated by deep narrow furrows, and increasing in number by bifurcation on ventral valve, intercalation on dorsal valve. Over 40 capillae at margin of large shells (16–17 in 5 mm).

Ventral interior with small triangular teeth apparently supported by short divergent dental plates. Muscle field obscure; median septum posteriorly high and thin, prolonged forward as a fine ridge to about a quarter of valve length. Traces of external furrows posterolaterally subdued



**Figure 21**. **a**–**d**: *Septachonetes micrus*; **a**,**b**, holotype NMV P14699, latex from ventral external mould, and counterpart P14698, ventral internal mould; **c**,**d**, paratype NMV P14701, latex from dorsal external mould, and counterpart NMV P14700, latex from dorsal internal mould. Humevale Formation; Pragian. Scale bar 2 mm.

and bear coarse, slightly radially elongate and rather sparse papillae. Rest of valve floor fairly strongly reflects external ornament, and traces of furrows bear numerous much finer papillae.

Dorsal interior with small, raised, proximally bilobed cardinal process arched over shallow but well-developed cardinal process pit. Inner socket ridges prominent, straight, diverging at about 150° from sides of cardinal process lobes; initially thin and high, becoming low and broad distally. Prominent anderidia diverge at about 55°, and extend from forward ends of cardinal process lobes to about a fifth of valve length. Structure between anderidia on paratype, thought by Gill (and Chatterton, 1973: 77) to be low, flattopped median septum, is not aligned with valve mid-line,

**Comparison**. As considered likely by Chatterton (1973: 77), S. micrus is very close to S. melanus. Of similar outline and ornament, externally they differ only in the former being slightly larger and more strongly convex, so that smaller shells would be difficult to distinguish. The faint ventral sulcus reported by Gill for S. micrus is not continuous to the anterior margin, but confined to the centre of the valve, so is probably not a true sulcus but either teratogenic or a preservational artefact. The internal structures of the two species are also very similar, although the reflection of the external ornament is stronger in S. micrus. Moreover its teeth appear to be less transverse and are supported by narrow dental plates, and the coarse papillae on the lateral floor of the ventral valve are less numerous. In the dorsal interior the anderidia are less divergent, the accessory septa not as strongly developed.

## Chonetoidea incertae sedis

## "Chonetes" taggertyensis Gill, 1945

#### Figs. 22, 23

Chonetes (Chonetes) taggertyensis Gill, 1945: 137–138, pl. VIII, figs. 6, 8, 13.

? Chonetes? sp. A Talent, 1963: 69, pl. 41, figs. 5-6.

**Type material**. HOLOTYPE NMV P27979A+B (Fig. 22ae; formerly MUGD 1910, 1911), an incomplete ventral internal mould and counterpart external mould, from Blue Hills, Taggerty, about 85 km northeast of Melbourne (37°19'S 145°43'E); figured Gill (1945, pl. VIII, figs. 8, 13). PARATYPE NMV P27980 (formerly MUGD 1912), an incomplete ventral internal mould figured Gill (1945, pl. VIII, fig. 6); same locality.

**Other material**. Possibly NMV P60907 (Fig. 23; formerly GSV 57316), a ventral internal mould from locality NMV PL576 (Talent's locality 56), near the source of Pat Creek (a tributary of the Mitchell river), Parish of Cobbannah, Tabberabbera district, East Gippsland, figured Talent (1963, pl. 41, figs. 5, 6).

**Stratigraphic distribution**. The type locality is in an uncertain Lower Devonian horizon in the eastern Melbourne Trough, central Victoria; Talent's specimen is from the lower Kilgower Member, Tabberabbera Formation, Tabberabbera Zone, eastern Victoria.

Age. Pragian, Early Devonian.

**Diagnosis**. Medium-sized relatively convex capillate chonetoid with flat orthocline ventral interarea, prominent arcuate pseudodeltidium; hinge spines few, probably oblique; teeth prominent, triangular; ventral muscle field large, posteriorly deeply impressed, smooth; prominent



**Figure 22. a**–**g**: "*Chonetes*" *taggertyensis*; **a**–**e**, holotype NMV P27979A–B (counterpart ventral internal and external moulds): internal mould in ventral, lateral and posterior aspects (b, d,e) and latex replica (a), latex from external mould (c); **f**,**g**, paratype NMV P27980, incomplete ventral internal mould and latex replica (in slightly anteroventral aspect, showing raised arcuate pseudodeltidium). Pragian? Scale bars 5 mm.

ventral median septum high, thickened against valve floor, prolonged anteriorly as long, low myophragm; ventral valve floor peripherally heavily papillate outside zone of weak radial ridges; large papillae posterolateral to muscle field. Dorsal valve unknown.

**Description**. Shell medium-sized (Ls to 15 mm, calculated Ws 18.4 and 20.9 mm), ovate, Ls/Ws about <sup>2</sup>/<sub>3</sub>. Greatest width apparently at about midlength (Wh/Ws about 0.8), cardinal angles obtuse. Rather strongly convex, Ds/Ls about 0.4; convexity greatest at midlength, much reduced towards margin and cardinal extremities. Ventral beak small, low, rounded; interarea orthocline, flat, triangular; delthyrium triangular, partly closed by prominent arcuate pseudo-deltidium. Hinge spines not preserved, but bases (four each side) oblique.

Ornament finely costellate, of low rounded capillae radiating from umbo and increasing in size distally; about 16 in 5 mm at 5 mm radius, and 15/cm at anterior margin. Increase in number by intercalation, rare before midlength. Ribs fainter towards cardinal extremities.



**Figure 23**. ?"*Chonetes*" *taggertyensis*; NMV P60907, ventral internal mould in posterior and ventral aspects. Tabberabbera Formation; Pragian. Scale bar 5 mm.

Ventral interior with prominent, wide, subtriangular teeth buttressed against valve floor on either side of muscle field. Inner margins of teeth (and delthyrium) diverge at about 80°. Muscle field large, widely flabellate, posteriorly deeply impressed, anteriorly poorly differentiated; floor smooth; length about 0.4Ls. Narrow, raised, ovate adductor scars faintly visible to either side of well-developed median septum. Median septum high, basally thickened, tapering upwards, extends to about 1/4 valve length, prolonged as well-developed myophragm bordered by narrow furrows (vascula media?) to valve midlength or beyond. Valve floor beyond muscle field faintly radially furrowed. Visceral cavity bounded distally by zone of radially arranged papillae concentrated below inter-rib furrows. On paratype, marginal zone strongly marked off from visceral cavity and valve floor near cardinal angles by concentric furrows. Papillae significantly coarser posterolateral to muscle field.

Dorsal valve unknown.

**Discussion**. Only two incomplete ventral valves are known. In the absence of dorsal valves and details of the hinge spines, the generic and even familial position of "*Chonetes*" *taggertyensis* remains highly uncertain. Boucot & Harper (1968: 151) thought it could be either *Chonetes* or *Protochonetes*, but the latter is unlikely in view of the long ventral median septum and prominent pseudodeltidium. With fine ribs radiating from the beak, it is clearly not a parachonetine. It cannot be excluded from the Strophochonetinae, but would be unusual for that subfamily in its lack of an accentuated median rib, its relatively strong convexity, and its prominent teeth and ventral median septum.

The distinct papillose marginal zone, otherwise nearly smooth valve floor (including the cardinal extremities), and concentration of particularly large papillae posterolateral to the muscle field in "*C*." *taggertyensis* can be seen in a number of described Devonian species belonging to several chonetid subfamilies, such as *Plebejochonetes* sp. 2 of

Racheboeuf (1976, especially pl. 2, fig. 2-but the median septum is shorter); the type species *Plebejochonetes* semiradiatus (Sowerby, 1842), especially the syntype valves figured by Racheboeuf & Fuchs (1988: pl. 1, fig. 3b; pl. 2, fig. 2b); topotypes of the type species Chonetes sarcinulatus (Schlotheim, 1820) figured by Racheboeuf (1978, figs, 3[6] and 4[1-3]); Devonochonetes? kerfornei (Renaud, 1942) of Racheboeuf (1981, especially pl. 23, figs. 11, 20-22 and pl. 24, fig. 1); and ventral valves of Notiochonetes falklandica (Morris & Sharpe, 1846) figured by Isaacson (1977, pl. 5, figs. 4–6). This diversity (both taxonomic and palaeogeographic) simply makes it clear that the position of Gill's species (which does not appear to be close to any other Australian Silurian-Devonian species) cannot be clarified in the absence of data on hinge spines and the dorsal valve.

The single ventral internal mould NMV P60907 (Fig. 23) from the Kilgower Member, described as Chonetes? sp. A by Talent, 1963, is strongly convex, subovate (Ls = 9.8 mm, Ws = 12.8 mm, Ls/Ws 0.77), with robust oblique spine bases, and triangular teeth supported by dental plates which continue forward as weak ridges posterolaterally bounding the gently impressed flabellate muscle field. The valve floor is flattened near lateral margins. A short, high, thick median septum starts in front of the beak and is bordered by narrow grooves. These grooves also define the margins of the distinct raised ovate diductor scars which are immediately in front of the median septum. The valve floor is densely papillose, the papillae aligned below the inter-rib furrows and very coarse posterolaterally. The overall shape, the shape of the median septum, the distribution of papillae on the valve floor, and the distinct diductor scars all recall "C." taggertyensis. The obvious differences are the strong internal reflection of the external ribs, implying that the ribs themselves are much stronger, and the distinct dental plates. Talent's form is closer to "C." taggertyensis than to any other Australian species, and they are here tentatively placed in synonymy, but without more material this is far from established.

#### "Chonetes" ruddockensis Gill, 1945

#### Fig. 24a,b

Chonetes (Chonetes) ruddockensis Gill, 1945: 139–140, pl. 8, fig. 10.

non Chonetes aff. ruddockensis.-Gill, 1950: 249, pl. I, fig. 36.

**Type material**. HOLOTYPE NMV P122947 (Fig. 24a; formerly MUGD 1914), a ventral internal mould in siltstone from locality PL1820, "Ruddock's Quarry", on hillside c. 200 m west of Edward Road and 400 m north of intersection with Switchback Road, Chirnside Park; Kilsyth 1:25,000 sheet 7922-2-IV, grid reference 516215; figured Gill (1945, pl. VIII, fig. 10); Humevale Formation.

**Other material**. NMV P122948 (formerly MUGD 1916), a poorly preserved ventral external mould in silty sandstone from near Strath Creek, Kinglake.

**Stratigraphic distribution**. Humevale and Killingworth Formations, Melbourne Trough, central Victoria.



**Figure 24. a,b**: "*Chonetes*" *ruddockensis*; **a**, holotype NMV P122947, ventral internal mould; **b**, NMV P122948, latex from ventral external mould. Humevale and Killingworth Formations; Lochkovian. **c**: *Chonetes* aff. *ruddockensis* of Gill (1950); NMV P14804, ventral internal mould. Bell Shale, Tasmania; Lochkovian. Scale bars 5 mm.

Age. Lochkovian, Early Devonian.

**Description** (holotype). Shell small (Ls 5.5 mm, Ws 7.2 mm), subquadrate (Ls/Ws 0.76), greatest width at about midlength (Wh/Ws 0.97), cardinal angles extended as small ears. Profile fairly strongly convex (Ds/Ls 0.33). Interarea unknown. At least four pairs of long, thin, slightly sinuous, more or less upright hinge spines. External ornament of low, rounded, even capillae (about 23 in 5 mm at 5 mm radius), increasing by bifurcation, separated by narrow furrows; about 54 capillae at margin.

Ventral internal details not well preserved, obscured by limonite. Teeth small. Median septum very subdued, fine, extending to about midlength, apparently widened posteriorly. Valve floor probably papillose marginally, but density and pattern unknown.

Dorsal valve unknown.

**Discussion**. NMV P122948 is a poorly preserved and doubtfully complete ventral external mould 8.8 mm wide that adds little to the above description. The maximum width is at the hinge line, and the ears appear to be slightly more prominent and more rounded than in the holotype. Gill referred to specimens from a number of other localities, but these have not been recognised in the university and museum collections.

With such inadequate material, and no dorsal valves, the generic and even family position of this species is also highly uncertain. Boucot & Harper (1968: 151) thought it could be either *Chonetes* or *Protochonetes*. *Protochonetes* has a short ventral median septum while that in *C. (Chonetes)* is long, but both have oblique hinge spines (more variable in *Protochonetes*). *Protochonetes* has a posteriorly enlarged ventral median septum, as does *Strophochonetes*, which tends to be larger and usually has an enlarged median rib.

Gill (1950) thought that NMV P14804 (Fig. 24c) from the Bell Shale in Zeehan, Tasmania, was comparable with "C." *ruddockensis*. It is a poorly preserved ventral internal mould 7.9 mm wide, non-alate (Wh/Ws 0.96), strongly convex (Ds/Ls 0.58) with strong radial capillae (17 in 5 mm at a radius of 5 mm) increasing by both intercalation and bifurcation; there are fairly strong papillae towards the cardinal angles and possibly submarginally. Information on hinge spines and internal details is wanting, so generic assignment is impossible, but on shape and ornament alone I do not consider it at all close to *C*. (*C*.)? ruddockensis.

## "Chonetes" foedus Talent, 1963

## Fig. 25

Chonetes? foedus Talent, 1963: 68–69, pl. 37, figs. 8–16, pl. 38, figs. 1–3; Johnson, 1966: 366.

Allanetes? foedus.-Boucot & Johnson, 1967: 142.

**Type material**. HOLOTYPE NMV P60871 (Fig. 25b; formerly GSV 57100), a ventral internal mould from Talent's locality 48, Tabberabbera area; this is on a tributary gully of the left branch of Dead Bull Creek 2.65 km south-southeast of its junction with the Wentworth River, Parish of Nungatta; figured Talent (1963, pl. 37B, figs. 9, 15). PARATYPES NMV P47601 (GSV 57112), a distorted dorsal external mould figured Talent (pl. 37B, fig. 8); NMV P74170 (GSV 57102), an incomplete ventral internal mould figured Talent (pl. 38, fig. 2).

**Other material**. Figured topotypes NMV P47600 (GSV 57111), 60872–74 (GSV 57095, 57104, 57106), 74168–69 (GSV 57109, cited as 57103, and 57007).

**Stratigraphic distribution**. Basal Dead Bull Member, Tabberabbera Formation, Tabberabbera Zone, eastern Victoria.

Age. Pragian, Early Devonian.

**Description**. Shell medium-sized (Ls to 12 mm, Ws to 21 mm), semiovate (Ls/Ws c. 0.6), greatest width towards midlength (Wh/Ws c. 0.9). Ventral valve strongly convex, with flattened (but not laterally extended) cardinal extremities, sometimes with weak sulcus. Dorsal valve slightly concave; body cavity relatively deep. Ventral interarea obscure, possibly low orthocline; delthyrial structures unknown. Dorsal interarea narrow, catacline to hypercline; small quadrilobate myophore flanked by triangular disjunct chilidial plates. Hinge spines apparently upright or slightly inwards-oblique, probably straight.

Radial ornament costellate, most pronounced medially on both valves, becoming very faint towards cardinal angles. About 22–24 high costae (anteromedian spacing 15–17/cm) irregularly radial medially, sharply rounded with narrow interspaces. Ribs increase by bifurcation on ventral valve, intercalation on dorsal valve, such that there are about twice as many ribs marginally as on umbo. Laterally, rapid increase in ribs beyond about 4 mm radius causes distinct change in rib direction. Change in rib direction gradual on ventral valve, such that ribs are markedly curved, but quite abrupt on dorsal valve, such that ribs are straight or only weakly curved distally. Distinct dorsal protegular node.

Teeth small. Median septum narrow, high and somewhat swollen posteriorly in some specimens, does not extend beyond ¼ valve length. Muscle field obscure. A few large papillae on inner surfaces of ears.



**Figure 25. a–c:** "*Chonetes*" *foedus*; **a**, topotype NMV P47600, latex from ventral external mould; **b**, holotype NMV P60871, ventral internal mould; **c**, paratype NMV P47601, latex from dorsal external mould. Dead Bull Member, Tabberabbera Formation; Pragian. Scale bars 5 mm.

Dorsal interior poorly known. Very fine median septum may reach valve midlength; anderidia fine, low, diverge at 35° or more, reaching ¼ valve length. Muscle field obscure. Large elongate papillae aligned along impressions of coarser external ribs, absent from beneath externally smooth posterolateral areas; arrangement of papillae thus opposite of that in ventral valve.

**Discussion**. Talent could find no species with which to compare his material, and this remains the case. Johnson (1966: 366) commented "There remains some uncertainty regarding generic affinities ...", whereas Boucot & Johnson (1968) questionably assigned it to *Allanetes* on the basis of the similarity of the ribbing, quoting Talent's "... pronounced differentiation between the main body of the

shell and the weakly ornamented posterolateral slopes". I agree with those authors that the ornament is not that of *Parachonetes*—in fact it is very distinctive, and also unlike that of *Allanetes*. In the latter, moreover, there are (unusually) a ventral fold and dorsal sulcus. Talent's species has a ventral sulcus, and a nearly flat dorsal valve. Unusual also is the depth of its body cavity, more like that of many productoids. It is likely that this species represents a new genus but, in view of the many gaps in present knowledge of its structure (e.g., spine type, presence or absence of a cardinal process pit), it would be premature to erect one.

## Species rejected from the Chonetoidea

#### Chonetes bipartita Chapman, 1913

Chonetes bipartita Chapman, 1913: 104–105, pl. X, figs. 8–10. Stropheodonta bipartita.–Gill, 1942: 41, pl. V, figs. 7, 9, pl. VI, figs. 8–10. Plectodonta bipartita.–Gill, 1950: 249, pl. I, figs. 21–23.

**Remarks**. Gill (1942) recognised that Chapman's specimens were not a chonetoidean, but they were not finally referred to *Plectodonta* until after Brown (1949) redescribed the Yass species; the brief synonymy given above shows only the changes in generic position. Specimens assigned to *P. bipartita* have subsequently been described from a number of successions in southeastern Australia, but the original material has not been re-described or re-figured.

## Chonetes concinna Chapman, 1904

#### Fig. 26a

Chonetes concinna Chapman, 1904: 223, pl. XXI, fig. 3. Eoörthis concinna.–Chapman, 1917: 95.

**Type material**. HOLOTYPE NMV P26016 (formerly MDV 296), an internal mould of a dorsal valve from allotment 3i, section W, Parish of Knowsley, near Heathcote.

**Stratigraphic distribution**. Knowsley East Formation, Heathcote Greenstone Belt, central Victoria.

Age. Ptychagnostus gibbus Zone, Undillan, Middle Cambrian.

**Discussion**. Chapman thought in 1917 (but not 1904?) that the single small and poorly preserved specimen was a sulcate ventral valve. It is a dorsal valve, with a deep sulcus flanked by several plications. The hinge is close to the greatest width, and the interarea is narrow, anacline, divided by a wide notothyrium, and may be denticulate. The brachiophores are small plates diverging ventrally and also forwards, while the sockets are quite small. Nothing can be seen of the cardinal process or muscle field. In the absence of a ventral valve and details of the exterior, the specimen cannot reliably be placed even at the family level. As Chapman recognised, it is not a chonetoid.



**Figure 26. a**: *Chonetes concinna*; holotype NMV P26016, latex from incomplete dorsal internal mould. Knowsley East Formation; Undillan (Middle Cambrian). **b,c**: *Chonetes (Chonetes) gaskini*; holotype NMV P123068; **b**, profile of shell, showing close resemblance to *Spinella buchanensis*—scale bar 5 mm; **c**, external mould of tentaculitid thought originally to be a corrugated hinge spine—scale bar 2 mm. Buchan Group; Emsian. Scale bar 2 mm.

#### Chonetes (Chonetes) gaskini Gill, 1945

#### Fig. 26b,c

Chonetes (Chonetes) gaskini Gill, 1945: 142, pl. VIII, figs. 9, 11.

**Type material**. HOLOTYPE NMV P123068 (formerly MUGD 1913) from the scarp along old Hut Creek, Bindi near Buchan, East Gippsland.

**Stratigraphic distribution**. Buchan Group, Buchan Rift, eastern Victoria.

Age. Emsian, Early Devonian.

**Discussion**. Described by Gill as a large incomplete ventral valve with a single annular hinge spine, the specimen is an incomplete spiriferid dorsal valve. As can be clearly seen by the profile figured here (Fig. 26b), there is a narrow flat fold, and numerous rounded lateral plications; it is probably *Spinella buchanensis* Talent, 1956. The "annular spine" is an adjacent tentaculitid (Fig. 26c).

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