Early Ordovician Conodonts
from Far Western New South Wales, Australia

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ABSTRACT. Thirty species (representing 19 genera) of Early Ordovician conodonts are described and illustrated from Mount Arrowsmith and Koonenberry Gap in the northwestern part of New South Wales. One new genus, Cooperignathus, and the new species Oepikodus pincallyensis, are established. Acodus sp. cf. emanuelensis predominates in 35 samples from the Tabita Formation and upper beds of the underlying Yandaminta Quartzite at Mount Arrowsmith, associated with ramiform and pectiniform taxa including species of Cooperignathus, Prioniodus, Oepikodus, Erraticodon, and Baltoniodus. The Koonenberry Gap fauna is dominated by coniform species, particularly Protopanderodus nogamii, P. gradatus, and Scolopodus multicostatus. Both faunas span an age range from latest Bendigonian to Chewtonian (evae Zone); their compositional differences are probably related to slight variations in water depths and depositional environments. Species endemic to the shallow water Australian cratonic region, represented by Bergstroemognathus kirki, Triangulodus larapintinensis, Acodus sp. cf. emanuelensis and Prioniodus sp. cf. amadeus, support a correlation with Early Ordovician faunas of central and western Australia, particularly those from the lower Horn Valley Siltstone of the Amadeus Basin. Biogeographically significant species in the western New South Wales faunas include Cooperignathus nyinti, C. aranda and Scolopodus multicostatus, which provide linkages with counterparts in North America and South China. Cosmopolitan elements in the documented collections are represented by Cornuodus longibasis, Drepanoistodus bariovalis, and Scolopodus quadratus. Only one species, Scalpellodus latus, from Mount Arrowsmith appears to be otherwise confined to Baltoscandia (northern Europe).

Fig. 1. Localities and geological maps of the studied areas. Maps of Australia and New South Wales, showing location of Mount Arrowsmith (B) and Koonenberry Range (C) areas to the north of Broken Hill. A. geological map of the Mount Arrowsmith area (modified after unpublished mapping by B. Stevens and K.J. Mills, Geological Survey of NSW Broken Hill office), showing locations of conodont samples collected from the Yandaminta Quartzite and Tabita Formation, Australian Map Grid coordinates from Mount Arrowsmith 7237 orthophotomap (first edition, 1978). B. map of the Koonenberry Gap area showing locations of samples collected for conodonts, Australian Map Grid coordinates from Wonnaminta 7336 orthophotomap (first edition, 1978).
Introduction
Geological setting and previous investigations

Conodont elements, the tooth-like remains of a long-extinct group of marine animals apparently with chordate affinities, are abundant microfossils in many Palaeozoic rocks (Sweet, 1988). Their global distribution and often-restricted time ranges make them ideal for biostratigraphic and biogeographic studies. During the Early Ordovician Epoch conodonts ranged widely in shallow seas across the Australian craton. Conodont faunas of this time from the edge of the craton, exposed in far western New South Wales, are here systematically described, enabling precise correlation with regional and international successions.

The cratonic rocks form part of the Upper Proterozoic–Middle Palaeozoic Koonenberry Belt (previously called the Wonominta Block, sensu Mills 1992), which trends southeast from near Tiboburra to between Broken Hill and White Cliffs, in the northwestern part of New South Wales (Fig. 1). In this region of mostly poor outcrop and low relief, Koonenberry Belt sediments are generally inconspicuous or largely buried beneath younger regolith. Mount Arrowsmith, situated at the northwestern extremity of this belt, is a prominent exception, being mainly composed of Proterozoic alkaline volcanic rocks—the Mount Arrowsmith Volcanics, including basaltic pillow lavas and tuffs—interposed between an eastern and western belt of metasediments (Kara Beds of Mills, 1992), also of probable late Neoproterozoic age.

Wopfner (1967) first described the Middle Cambrian and Lower Ordovician sediments on the western side of Mount Arrowsmith. Wopfner’s mapping has remained the most detailed published documentation of the outcrop of these Palaeozoic units, although his informal stratigraphic nomenclature has been updated. The Middle Cambrian strata, preserved only on the southwest flank of Mount Arrowsmith, are now included within the Gnalta Group, while the Lower Ordovician sediments (which are well exposed in a syncline west of the Mount Arrowsmith summit) are correlated with the Mootwingee Group. Shergold (1971) and Webby et al. (1981) substituted stratigraphic names introduced in unpublished Ph.D. research by Warris (1967) to formalize the stratigraphic subdivisions introduced by Wopfner (1967). The Cambrian section is faulted against the Lower Ordovician Yandaminta Quartzite (member E of Wopfner), which is overlain by the Tabita Formation (member F) (Fig. 2) and in turn conformably succeeded by the Pingbilly Formation (Wopfner’s member G). The exact nature of the boundary between the Yandaminta Quartzite and the Tabita Formation is open to interpretation; in most places the contact appears to be conformable and intergradational, but in some outcrops there is definite evidence of a subtle angular (perhaps structurally induced) relationship (K.J. Mills and R. Glen, pers. comm.). These Mootwingee Group strata unconformably overlie the western belt of the Kara Beds.

Pioneering palaeontological and biostratigraphical studies of the northwestern part of New South Wales were undertaken by Warris (1967) but much of this work remains unpublished. A brief outline of the fossil distribution at Mount Arrowsmith was given by Warris (1969), who provided an insight into the abundance and diversity of the Early Ordovician faunas, comprising mainly nautiloids, bivalves, gastropods, brachiopods, trilobites, ostracodes, and conodonts. Only a nautiloid, Anthoceras warburtoni, from the Tabita Formation (Crick & Teichert, 1983) and a new species of the problematical genus Janospira, J. acuosiphon, from the Yandaminta Quartzite (Paterson, 2001a) of this rich fauna have previously been formally described.
Conodonts from a single sample (16 specimens) collected from the basal beds of the Tabita Formation were first identified by E.C. Druce (in Wopfner, 1967: 168, 170), who established a possible upper “Arenig” age and noted similarities with the conodonts of the Horn Valley Formation in the Amadeus Basin. Independent identifications of the same form genera determined by Druce, together with many additional form taxa, were made by Warris (1967) in a major study of the Mount Arrowsmith conodonts, based on collections of nearly 4500 identifiable specimens obtained from three measured sections in the area. In his published listing of the Mount Arrowsmith fauna, Warris (1969) emphasized forms not found in the solitary sample analysed by Druce and noted the presence of five new species of “fibrous” genera from throughout the Tabita Formation. Warris also recognized three biostatigraphically distinct conodont zones in the formation, the lower two of early “Arenig” age, and the upper one of late “Arenig” age. Jones et al. (1971), in a brief reference to the Mount Arrowsmith conodonts, interpreted their age as broadly mid to late “Arenig”. Further studies of the Warris conodont collection were undertaken by Kennedy in the 1970s, but the revised systematics employing a combination of apparatus and form species taxonomy remains unpublished (Kennedy, 1976). Repeated requests for the return of the Warris collection to Australia have been ignored, so the original material remains unavailable for study. Accordingly, we have not relied on Kennedy’s (1975) listing of 16 taxa from the area, nor have we referred to his now mainly outdated thesis research.

Our study of conodonts from Mount Arrowsmith commenced in 1999 as part of a broader program of research on the Early Ordovician biotas of western New South Wales. Conodont resampling focussed on a number of measured sections and spot localities in the Yandaminta Quartzite and the Tabita Formation (Fig. 2). Recovery of 3076 identifiable elements substantially increases knowledge of the fauna, enabling for the first time an accurate age determination and correlation of the succession with others in Australia and elsewhere in the world.

The Koonenberry Gap area, some 80km to the east of Mount Arrowsmith (Fig. 1), has received much less palaeontological attention. Packham (1969: 68) mentioned limestones at Koonenberry Mountain from which the late Brian Daily (University of Adelaide) had identified a small conodont fauna of late Early Ordovician or early Middle Ordovician age; it is not certain whether this sample was collected from the section exposed at the Gap. The prominence of Koonenberry Mountain above the surrounding flat plains is due to the northwest-southeast trending Koonenberry Fault with uplift delineating the west margin of the mountain, while a subparallel splay of this fault forms its east boundary. Webby et al. (1988) described a trilobite fauna of latest Cambrian-basal Ordovician (Tremadocian) age from silstones of the Wattles Bore Formation, adjacent to the faults. Well-bedded dolomitic limestones stratigraphic unit not yet formalized at Koonenberry Gap have previously yielded the conodont Bergstroemognathus kirki (Zhen et al., 2001). The conodont fauna from Koonenberry Gap (determined from 446 identifiable specimens), like the Mount Arrowsmith assemblages, is of evae Zone age (late Bendigonian–Chewtonian), broadly equivalent to the middle “Arenig” or uppermost Ibexian (Webby, 1995, fig. 1).

Early Palaeozoic regional geography
Following the Delamerian Orogeny in Middle–Late Cambrian time (Q.Z. Wang et al., 1989, fig. 3), the Lower Ordovician Mootwingee Group was deposited on the Gnalta Shelf, as part of the east-facing margin of the Australian craton, which represented also the eastern edge of the Gondwanan supercontinent. Webby (1976, 1978, 1983) interpreted quartzose clastic sedimentation, which dominates much of the Mootwingee Group to the south of Koonenberry Mountain, as derived from the Delamerian uplands to the (present) southwest, and deposited in an extensive delta. Broadly contemporaneous impure carbonates in the Tabita Formation at Mount Arrowsmith, and dolomitic limestones at Koonenberry Gap, are the only known remnants preserved of what might have been an extensive shallow shelf depositional setting extending to the northwest (Webby, 1976, fig. 6B; 1983, fig. 1). Environments probably ranged in water depth from strandline to sub wave base, in relatively sheltered situations such as protected bays or very shallow gradient shorelines, inferred from complete preservation of diverse macrofossils in the Tabita Formation. There is no convincing evidence of areas with restricted circulation or enhanced salinity, except that numerical dominance in the Tabita samples of a single species (Acodus sp. cf. emanuelensis, Fig. 4) may indicate some sort of specialized environment. Any differences in faunal content between localities of essentially the same age are therefore most plausibly related to variation in water depth.

Elsewhere on the Australian craton at this time, the Larapintine Sea provided a shallow marine connection linking the Gnalta Shelf through the Amadeus and Georgina Basins westwards to the Canning Basin (for discussion on the development of this concept refer to Webby, 1978: 55). Contemporaneous conodont faunas in the central Australian basins have been described from the Horn Valley Siltstone of the Amadeus Basin (Cooper, 1981; Nicoll & Ethington, in press; Stewart & Nicoll, in press), and the Coolibah Formation of the Georgina Basin (Sait & Druce, 1993). The known Canning Basin faunas are both slightly older (late Lancefieldian–Bendigonian: McTavish, 1973; Nicoll et al., 1993) and younger (Darriwilian: Watson, 1988) than those from western New South Wales. Compositional differences in conodont faunas from these regions can be interpreted as due in part to water temperature variations, as cooler, more temperate waters entered the Larapintine Sea from the Canning Basin side to mix with warm equatorial currents flowing across the Gnalta Shelf. Local variations in faunal distribution are more likely due to water depth fluctuations, as discussed below.

Conodont ecology and biogeography
Among the 30 species recorded from the Mount Arrowsmith area, 20 (including nearly all those with relatively restricted age ranges) were also found in the Koonenberry Gap samples (Fig. 5), and hence these two assemblages are considered more or less contemporaneous in age. There are, however, some significant differences between their overall faunal composition, diversity, and relative abundance. For example, the fauna from the Tabita Formation at Mount Arrowsmith is the more diverse, including coniform, ramiform and pectiniform elements, while the Koonenberry
Fig. 3. Distribution of conodont taxa and specimens in samples from the upper Yandaminta Quartzite and the overlying Tabita Formation at Mount Arrowsmith, and from the unnamed dolomitic limestone unit at Koonenberry Gap, western New South Wales. Samples from limestone nodules in the upper Yandaminta Quartzite are labelled Y1 and W5; all other samples are from the Tabita Formation, except for C1611–C1613 which are from Koonenberry Gap.

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Zhen et al.: Ordovician conodonts—western NSW
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The Koonenberry Gap fauna is dominated by robust coniform elements. Particularly noticeable is the absence of *Oepikodus pinicallensis*, *Prioniodus* cf. *amadeus*, *Prioniodus* sp. A and *Baltoniodus* sp. A from the Koonenberry Gap fauna. Furthermore, approximately half the total number of elements recovered from Mount Arrowsmith samples can be assigned to just one species, *Acodus* sp. cf. *emanuelensis* (Figs. 3, 4), whereas this species is much less common in the Koonenberry Gap samples. In the latter, *Protopanderodus nogani* is the dominant species (nearly 30% of the fauna), while in the Mount Arrowsmith fauna, this species is very rare (Fig. 3). *Triangulodus* sp. A, *Scolopodus multitcostatus*, and *Protopanderodus gradatus* are also relatively abundant at Koonenberry Gap compared to Mount Arrowsmith (Fig. 4).

Such compositional differences between the conodont faunas of the two localities probably reflect biofacies variations. Johnston & Barnes (1999), in a study of contemporaneous conodont faunas of western Newfoundland, recognized a *Diaphorodus* biofacies that represents a shallow-subtidal environment. *Diaphorodus* is here regarded as a junior synonym of *Acodus*—see Zhen *et al.* (in press). The domination of *A. sp. cf. emanuelensis* at Mount Arrowsmith suggests that the western New South Wales faunas generally inhabited a similar shallow-subtidal environment. However, the presence of *O. pinicallensis* and several species of *Prioniodus*, in association with abundant sponge spicules in some samples of the Tabita Formation, suggests interfingering of a somewhat deeper subtidal biofacies. In contrast, the absence of deeper water forms such as species of *Oepikodus* and *Prioniodus* from the Koonenberry Gap fauna, together with the abundance of robust coniform elements, probably indicates the presence of shallower, near-shore conditions in that area.

*Bergstroemognathus kirki*, *Triangulodus larapintensis*, *Acodus* sp. cf. *emanuelensis* and *Prioniodus* sp. cf. *amadeus* were probably endemic to Australia. Numerically, these four species constitute slightly more than half of the western New South Wales faunas. They are widely distributed in the intracratonic basins of Australia, typically (except for *P. sp. cf. amadeus*) inhabiting shallow water environments (Cooper, 1981; Stait & Druce, 1993). Accompanying cosmopolitan species, including *Cornuodus longibasis*, *Drepanoistodus basiovalis*, *Scolopodus quadratus* and *Ansella jemtlandica*, together comprise only a minor component (about one-tenth) of the Mount Arrowsmith and Koonenberry Gap faunas.

Domination of endemic taxa in the cratonic shelf of western New South Wales is in striking contrast to the composition of deeper water faunas inhabiting offshore parts of the Gondwanan margin; for example, the conodonts of the Hensleigh Siltstone (*elegans* Zone) in central New South Wales where cosmopolitan and widespread species are overwhelmingly dominant (Zhen *et al.*, 2001, in press). In correlating faunas from the cratonic platform and margins, those non-endemic species which are not long-ranging cosmopolitan forms, assume critical importance. These comprise the remaining third of the western New South Wales shelf margin fauna, with many exhibiting particularly important biogeographic relationships (discussed below). *Cooperignathus nyinti* and *C. aranda* are widely distributed in Australian cratonic successions, as well as being represented in South China (An, 1987), North American Midcontinent successions (Ethington & Clark, 2003 in press).

<table>
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<th>Unichnodus simplex sp. cf. (total)</th>
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**Fig. 3.** Continued.
Gondwana and Laurentia. To their short stratigraphic range, but are also valuable 2000). They are not only biostratigraphically significant due to their short stratigraphic range, but are also valuable for their widespread distributions in deeper water successions (Pohler, 1994; Johnston & Barnes, 1982; Repetski, 1982) and in peri-Laurentian offshore successions (Dzik, 1994), and from a lower stratigraphical level (middle Ordovician age in the Langkawi Islands, Malaya (Igo & Koike, 1967). Also, in the Argentine Precordillera, Serpagli (1974) recorded Protopanderodus nogamii in a post-evae zone occurrence.

Elements of typical Baltoscandian faunas are represented only by Scalpellodus latus, which is a minor component of the Mount Arrowsmith fauna. This species was also recorded from the Horn Valley Siltstone of the Amadeus Basin (Cooper, 1981).

**Biostratigraphy and regional correlation**

Given that the most abundant species in the faunas under discussion are confined to Australia (Figs. 4, 5), it is not surprising that their precise age determination and international correlation are difficult. Zonal index species of neither the North Atlantic nor North American Midcontinent biostratigraphic successions are recognizable in the western New South Wales conodont faunas. However, co-occurrence of Oepikodus communis, Cooperignathus nyinti, C. aranda, and Jumudontus gananda in the Tabita Formation suggests a latest Bendigonian to Chewtonian age, corresponding to the evae Zone of the North Atlantic faunal scheme, or the andinus to aranda zones (top Ibexian) of the North American Midcontinent succession. No evidence exists in these Tabita Formation faunas to support the earlier contention of Warris (1969) that the formation spanned three conodont zones.

Within the Australian craton, the Mount Arrowsmith and Koonenberry Gap conodont faunas correlate well with the Horn Valley Siltstone fauna of the Amadeus Basin, central Australia, for which Cooper (1981) suggested an age ranging from the Oepikodus evae Zone to Baltoniodus navis/triangulis Zone. While this age assignment remains acceptable, presence of the index species O. evae and B. navis cannot be confirmed in the Horn Valley Siltstone, based on Cooper’s illustrated specimens. Re-examination of a large toptotype collection of the Horn Valley specimens, provided courtesy of Dr Barry Cooper, has also failed to reveal these

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**Fig. 4. Bar charts illustrating relative species abundances in the Lower Ordovician conodont faunas of western New South Wales.**
The stratigraphic range of *O. pincallyensis* (a transitional form morphologically between *O. evae* and *O. communis*), occurring in the Horn Valley Siltstone. In the western New South Wales conodont faunas, suggesting that *O. evae* extends upwards into the upper biostratigraphic association in the Coolibah Formation, where the first appearances of *C. nyinti*, *C. aranda*, *D. costatus*, and *S. quadratus* also occur. These species also range into the upper biostratigraphic association in the Gap faunas with those of the Coolibah Formation of the Georgina Basin (Stait & Drue, 1993) is based on co-occurrence in both regions of *B. vonwikeri*, *C. aranda*, *D. multispinosus*, and *D. arima*. Of the three biostratigraphic associations recognized in the Gap faunas, where the first appearances of *C. nyinti*, *C. aranda*, *D. costatus*, and *S. quadratus* also occur. These species also range into the upper biostratigraphic association in the Gap faunas with those of the Coolibah Formation of the Georgina Basin (Stait & Drue, 1993) is based on co-occurrence in both regions of *B. vonwikeri*, *C. aranda*, *D. multispinosus*, and *D. arima*. Of the three biostratigraphic associations recognized in the western New South Wales conodont faunas, the western New South Wales faunas are most closely aligned with those of the middle Coolibah Formation. Although Stait & Drue (1993) recognized a new species of *Oepikodus* apparently closely related to *O. pincallyensis*, occurring in the Horn Valley Siltstone. In the western New South Wales conodont faunas, suggesting that *O. evae* extends upwards into the upper biostratigraphic association in the Coolibah Formation, where the first appearances of *C. nyinti*, *C. aranda*, *D. costatus*, and *S. quadratus* also occur. These species also range into the upper biostratigraphic association in the Gap faunas with those of the Coolibah Formation of the Georgina Basin (Stait & Drue, 1993) is based on co-occurrence in both regions of *B. vonwikeri*, *C. aranda*, *D. multispinosus*, and *D. arima*. Of the three biostratigraphic associations recognized in the western New South Wales conodont faunas, the western New South Wales faunas are most closely aligned with those of the middle Coolibah Formation. Although Stait & Drue (1993) recognized a new species of *Oepikodus* apparently closely related to *O. pincallyensis*, occurring in the Horn Valley Siltstone.
correlated the uppermost Coolibah Formation with the lower Horn Valley Siltstone, our study (Fig. 6) concludes that the Mount Arrowsmith and Koonenberry Gap conodont faunas were contemporaneous with the assemblages of the middle to upper Coolibah Formation and the lower Horn Valley Siltstone.

Many of the Lower and Middle Ordovician conodonts from the Canning Basin remain undescribed, so hindering precise correlation with western New South Wales faunas. The conodont fauna from the Emanuel Formation (McTavish, 1973; Nicoll, 1992; Zhen et al., 2001) spans from late Lancefieldian (La3) to middle Bendigonian (Be2) according to Nicoll (in Shergold et al., 1995), with at least the middle part of the formation corresponding to the interval from the A. deltatus–O. costatus to lower O. communis conodont zones of the North American Midcontinental faunal succession (Ethington et al., 2000). A late Bendigonian (O. communis Zone) age was assigned to the overlying Gap Creek Formation by Nicoll (in Shergold et al., 1995). The conodont faunas described by Watson (1988) are mainly from stratigraphically younger, Darriwilian, units including the Nita and Goldwyer formations.

As previously discussed, the western New South Wales faunas of the shallow cratonic shelf margin exhibit significant differences from the slightly older (elegans Zone) fauna of the Hensleigh Siltstone in central New South Wales, which inhabited deeper water, lower slope environments of an offshore island arc setting (Zhen et al., in press). At species level, the only forms common to these two regions are Cornuodus longibasis, Protopanderodus gradatus, P. leonardii and Scolopodus quadratus, which are all long-ranging or cosmopolitan in extent (Fig. 5).

Globally, the Lower Ordovician conodont faunas of far western New South Wales are most closely correlated with those from the San Juan Formation (upper part of assemblage B to lower part of assemblage C) of the Argentine Precordilleran (Serpagli, 1974), the Cow Head Group (Bed 11) of Newfoundland (Johnston & Barnes, 1999), and the Ibex area of Utah through the Jumadontus gananda–Reutterodus andinus interval (Ethington & Clark, 1982) (Fig. 5). These assemblages occupy either the interval from the andinus Zone to basal flabellum/laevis Zone of a shallow, warm water “North American mid continent” type setting, or the correlative evae Zone of the cooler and/or deeper water “North Atlantic” type setting.

**Material and methods**

Nineteen samples (average weight 5kg) collected at Mount Arrowsmith yielded well preserved, moderately abundant conodonts. Locations of all samples from this area (Fig. 1) refer to grid references (GR) on the Mount Arrowsmith 7237 1:100 000 orthophotomap (first edition, 1978). Samples Y1 (GR 556150mE 6670200mN) and W5 (GR 556720mE 6669500mN) were collected from limestone nodules within shales and mudstones exposed below the topmost beds of the Y andaminta Quartzite, which forms distinctive linear topographic ridges in the area. Due to deep weathering of the shales, their direct contact with the overlying quartzite beds cannot be established. According to the stratigraphic definition given by Warris (1967), these two samples should lie within the upper Yandaminta Quartzite. Seven samples (M/A11-1 to M/A11-7) were collected from a hill slope section (centred on GR 557000mE 6663000mN) on the southwestern flank of Mount Arrowsmith. In both

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**Fig. 6.** Correlation of Lower to Middle Ordovician (pre Darriwilian) successions in the Amadeus, Georgina and Canning basins of Australia with the Tabita Formation (including at its base the Yandaminta Quartzite) at Mount Arrowsmith, based on global graptolite and conodont zonations.
the Y4 and M/A11 sections (Fig. 2), the contact between the predominantly calcareous Tabita Formation and the underlying Yandaminta Quartzite is shown, but the boundary with shales of the overlying Pingbilly Formation is not exposed due to deep weathering and alluvium cover. Spot sample M/A7 (GR 557700mE 6664250mN) is from a laminated thinly bedded limestone near the middle part of the Tabita Formation, on the northeast side of the synclinal axis (Fig. 1). Two other spot samples (M/A3 and M/A4), which are five metres apart stratigraphically, were collected from thinly bedded limestones within green shale exposed in a creek near the axis of the syncline (GR 557800mE 6663700mN) about 600 m south of sample M/A7. All these samples were completely dissolved in 10% acetic acid, with residues separated and concentrated using sodium polytungstate. Fifteen additional samples were collected at Mount Arrowsmith from a measured section TAB1 which crosses the site of Department of Mineral Resources borehole DMR Koonenberry RDH/DDH7 at GPS GR 558300mE 6662200mN (Figs. 1, 2). One sample (T2, GR 557850mE 6663750mN) was taken from the top of the Tabita Formation close to the boundary with the overlying Pingbilly Formation. These 16 samples, collected and processed by J. Paterson (Paterson, 2001b), were only partially dissolved in 10% acetic acid. At Koonenberry Gap (GR 624950mE 6624500mN, Wonnaminna 7336 1:100 000 orthophotomap, first edition 1978) approximately 800 m northwest of Koonenberry Mountain trig station, three samples (C1611, C1612, C1613) were collected from a continuous section (Fig. 1) of as yet unnamed thickly bedded dolomitic limestones. These samples were dissolved in a solution of 10% acetic acid buffered with 5% formic acid to break down the dolomitic matrix.

A total of 3522 identifiable conodont specimens were obtained from the 35 samples collected in the Mount Arrowsmith and Koonenberry Gap areas (Fig. 3). All photographic illustrations shown in Figs. 7–29 are SEM photomicrographs captured digitally. Figured specimens bear the prefix AMF and are deposited in the collections of the Palaeontology Section at the Australian Museum in Sydney.

A septimembrate species of Acodus, consisting of acodiform Pa and Pb, makellate M, and costate S elements bearing two (Sc), three (Sa and Sb), and four (Sd) strong, blade-like costae. Description. Pa element with robust, laterally compressed, erect or slightly proclined cusp, anteroposteriorly extended base and moderately open basal cavity; cusp slightly curved inwards with straight, sharp anterior margin and nearly straight and sharp posterior margin; base triangular in outline in lateral view, formed by adenticulate posterior process and triangular anticusp; posterior process with straight or gently arched upper margin meeting straight posterior margin of the cusp at an angle of 90–115°; basal margin straight, forming an angle of about 50° with anterior margin; inner lateral face typically with a prominent, rounded-faced mid costa; outer lateral face smooth or with weak mid carina (Fig. 7A–F). Pb element similar to the Pa, but with its cusp slightly reclined, and also more curved inwards (Fig. 7G); in lateral view, curvature of anterior margin variable; posterior margin also curved, forming an angle of 50–90° with upper margin of the posterior process; anticusp less pointed, with an angle of 60–65° between basal and anterior margins (Fig. 7I–L). M element makellate,
anteroposteriorly compressed, with broad, smooth anterior face (Fig. 7N, O), and a weak basal buttress on the posterior face (Fig. 7H, M); anticusps triangular in outline; outer lateral process low, adenticulate with straight or slightly arched upper margin. *S* element symmetrical, triconodelliform, with broad anterior face, a blade-like costa on each lateral face and a third costa along the posterior margin; the three costae extended basally as short adenticulate processes (Fig. 7P–R). *Sb* element like the *Sa*, but asymmetrical (Fig. 7S, T). *Sc* element laterally compressed with a sharp costa along anterior and posterior margins, which extend basally merging into the upper margin of a low posterior process and an anticusp-like shorter anterior process; cusp slightly inner laterally curved, with smooth lateral faces (Fig. 7U, V). *Scd* element asymmetrical with four blade-like costae, which extend basally into shallow adenticulate processes (Fig. 7W–Y); costa along the posterior margin stronger than others; one costa on each lateral face, and the fourth costa along the anterior margin, but inner laterally curved (Fig. 7W).

**Remarks.** Specimens from western New South Wales are identical with those described as *A. emanuelensis* from the Horn Valley Siltstone of central Australia (Cooper, 1981). Although generally comparable with the type material from the Emanuel Formation of the Canning Basin, the New South Wales specimens do not develop the prominent thin blade-like arched upper margin of the posterior process displayed by the figured specimens from the Canning Basin. The Horn Valley material will be described as a new species by R.S. Nicoll (in prep.), to which the western New South Wales specimens would be assigned. Pending completion of that study, the present material is left in open nomenclature. *Acodus* sp. cf. *emanuelensis*, the most common species in the Mount Arrowsmith fauna, exhibits a wide range of variation. Specimens from samples with associated sponge spicules, such as M/A7 (inferred to represent relatively deeper water environments) are smaller, with costae extended basally into adenticulate processes in the *S* elements (Fig. 7Y). Specimens from other, presumably shallower water, samples are larger with more weakly developed processes (Fig. 7W).

***Acodus*** sp.  
**Fig. 8M–Q**

**Material.** 16 specimens (S elements) from the Tabita Formation at Mount Arrowsmith; two from an unnamed dolomitic limestone unit at Koonenberry Gap.

**Remarks.** Multicostate coniform elements referred to herein as *Acodus* sp. are symmetrical or nearly so. At least two types can be distinguished: a quadricostate element (Fig. 8Q) with an anterior costa, posterior costa, and one median costa on each lateral side; and a septicostae element (Fig. 8M–P) with rounded anterior face, a costa along the posterior margin, and three costae on each lateral side. An additional pentacostate element was also recovered. It has a broad anterior face, two costae on each side and a posterior costa along the posterior margin, and cusp star-shaped in cross section. These specimens show some resemblance to the *S* elements of *Acodus compta* (Branson & Mehl), but with less strongly developed costae in comparison to that species. They might represent a separate species, but the material available now precludes a complete description.

***Ansellia Fähræus & Hunter, 1985***

**Type species.** *Belodella jemtlandica* Löfgren, 1978.

**Ansellia jemtlandica** (Löfgren, 1978)  
**Fig. 8K,L**

“*Belodella*” sp. A Serpagli, 1974: 38, 39, pl. 8, fig. 7, pl. 20, fig. 10. *Belodella jemtlandica* Löfgren, 1978: 46–49, pl. 15, figs. 1–8, fig. 24A–D (cum syn.).

*Belodella jemtlandica* –Cooper, 1981, pl. 26, fig. 14.  
*Ansellia jemtlandica* Fähræus & Hunter, 1985: 1173–1175, pl. 1, figs. 1–5, 9, pl. 2, fig. 12a,b, text-fig. 1 (cum syn.).

*Ansellia jemtlandica* –Albanesi, in Albanesi et al., 1998: 160, pl. 1, figs. 18–23, text-fig. 27 (cum syn.).

**Material.** Four specimens (Sa elements) from the Tabita Formation at Mount Arrowsmith, and an additional specimen (Sa) from the unnamed dolomitic limestone unit at Koonenberry Gap.

**Remarks.** This species is rare in our collections, only the symmetrical *Sa* element being recovered. It has a proclined cusp, an anterolateral costa on each lateral side, and a thin posterior margin basally bearing a row of small, closely spaced denticles. The specimen illustrated from the Horn Valley Siltstone (Cooper, 1981) is a weakly asymmetrical, acostate *Sc* element of the same species.

***Baltoniodus*** Lindström, 1971

**Type species.** *Prioniodus navis* Lindström, 1955.

**Baltoniodus** sp. A  
**Fig. 11P–X**

?*Baltoniodus navis* –Cooper, 1981: 168, pl. 30, fig. 2.

**Material.** Thirteen specimens (11 P, 2 M) from the Tabita Formation at Mount Arrowsmith.

**Description.** Only P and M elements recovered; the P element is pastinate with denticulate anterior and posterior processes, and adenticulate outer lateral process; cusp more or less triangular in cross section (Fig. 11T, U), with sharp anterior and posterior margins, and smooth inner lateral side; the outer lateral face with a broad costa which extends basally into a short denticulate process; anterior process extending downward with three or four stout denticles; posterior process longer, bearing five to seven stout denticles; basal cavity open, rather deep. *M* element strongly geniculate, bearing a long anticusp with fine saw tooth-like denticles on its upper margin (Fig. 11Q, R); base of denticles with distinctive surface sculpture (Fig. 11P).

**Remarks.** The species is assigned to *Baltoniodus* based on its wide basal cavity and orientation of the anterior and posterior processes essentially in a single plane. The P element of this species differs from those of *Oepikodus pincallyensis* in having a much smaller cusp, an adenticulate outer lateral process, and a more open basal cavity. The anterior and posterior processes are more or less straight within a single plane, whereas in the P elements of *Oepikodus pincallyensis* the anterior process is strongly curved inward. The P element described herein is close to the specimen referred to *Baltoniodus navis* illustrated by
Remarks. A septimembrate apparatus of limestone unit at Koonenberry Gap. The originally described P elements of Baltoniodus navis Lindström, 1955 possess long denticulate outer lateral processes which meet the anterior process at an angle of about 30°, whereas the Tabita Formation species has an adenticulate, short outer lateral process, which is almost normal to the anterior and posterior processes; the anterior process is in the same plane with the posterior process (Fig. 1T,V), or only very slightly curved inner laterally (Fig. 11X).

_Bergstroemognathus Serpagli, 1974_  
_Type species._ Oistodus extensus Graves & Ellison, 1941.

_Bergstroemognathus kirki_ Stait & Druce, 1993  
_Fig. 8A–J_

_Bergstroemognathus extensus_ (Graves & Ellison).–Cooper, 1981: 161, pl. 31, fig. 12, pl. 32, figs. 9–11, non fig. 7. _Bergstroemognathus kirki_ Stait & Druce, 1993: 302–303, figs. 12H, 16D,F–H,J.

_Bergstroemognathus kirki._–Zhen et al., 2001: 201–204, figs. 4.14–4.20, 8.1?, 8.2–8.22.

_Material._ Five specimens (1 M, 4 Sc) from limestone nodules within shales of the upper Yandaminta Quartzite, and 26 specimens (4 Pa, 6 Pb, 4 Sa, 8 Sb, 3 Sc, 1 Sd) from the overlying Tabita Formation at Mount Arrowsmith; seven and 26 specimens (4 Pa, 6 Pb, 4 Sa, 8 Sb, 3 Sc, 1 Sd) from nodules within shales of the upper Y andaminta Quartzite, distinguished by their P elements, those of similarity of their S and M elements. The two genera are Protoprioniodus as indicated by the general symmetrical Sa, slightly asymmetrical Sb, and asymmetrical crest(s); basal cavity shallow, represented by a small basal open basal cavity.

_By an increase in the area of the basal surface, and secondly by the displacement of this area from the basal lateral side to the underside of the P elements (Fig. 9). The Cooperignathus apparatus appears to be the earliest form with planate elements, and phylogenetically might represent an early stage of evolutionary development of the Polyplacognathidae clade._

_Two species, C. aranda and C. nyinti, are included in Cooperignathus. They are widely distributed in the Early Ordovician (O. evae Zone) of Australia, South China and North America. Because the diagnostic P elements are relatively rare, both species were previously ascribed to Protoprioniodus based on the M and S elements._

_Occurrence._ Horn Valley Siltstone, Amadeus Basin (Cooper, 1981), Coolibah Formation, Georgina Basin (Stait & Druce, 1993) in central Australia; Tabita Formation at Mount Arrowsmith, and unnamed dolomitic limestone unit at Koonenberry Gap, western New South Wales (herein); Dawan Formation, Hubei Province, South China (An, 1987); Wah Wah Limestone, Ibex area of western Utah (Ethington & Clark, 1982), Juab Limestone, Utah (Sweet et al., 1971; Ethington & Clark, 1982); E1 Paso Group, western Texas and southern New Mexico (Repetski, 1982); Broken Skull and Sunblood formations, southern District of Franklin, Canada (Tipnis et al., 1978); upper part of the Eleanor River and Ship Point formations, Arctic Canada (Barnes, 1974); Cow Head Group (Pohler, 1994; Johnston & Barnes, 2000), and St. George Group (Stouge, 1982; Ji & Barnes, 1994), western Newfoundland, Canada.

_Cooperignathus nyinti_ (Cooper, 1981)  
_Figs. 10A–N, 11A–O_

_New genus A Sweet et al., 1971: partim only pl. 1, fig. 19._

_New genus A Sweet et al., 1971.–Repetski, 1982: 56, partim only pl. 27, figs. 3, 4._

_Protoprioniodus nyinti_ Cooper, 1981: 176, pl. 29, figs. 1–8, 11, 12.

_Protoprioniodus nyinti._–Stait & Druce, 1993: partim only fig. 19N,O.

_Protoprioniodus aranda._–Ethington & Clark, 1982: 87, partim only pl. 9, figs. 24–26, 30.

_Protoprioniodus aranda._–Johnston & Barnes, 2000: partim only pl. 6, figs. 23, 24.

_Material._ Six specimens (3 M, 1 Sa, 1 Sb, 1 Sc) from limestone nodules within shales of the upper Yandaminta Quartzite, and 62 specimens (6 Pa, 7 Pb, 19 M, 7 Sa, 11 Sb, 12 Sc) from the overlying Tabita Formation at Mount Arrowsmith; one additional specimen (M) from unnamed dolomitic limestone unit at Koonenberry Gap.

**Diagnosis.** A ramiform-pectiniform species consisting of a seximembrate apparatus including modified anguliplanate P elements, makellate M element, alate Sa, and modified tertioedate Sb and Sc elements; all elements albid, with adenticulate processes, and a ledge-like costa lying parallel to and slightly above the basal margin to define the basal surface, which is represented by a shallow groove between this costa and the basal margin.

**Description.** P elements are modified anguliplanate units, arched and crescentic in outline in lateral view, with convex outer lateral face and concave inner lateral face; upper surface with a thin anteroposteriorly extended blade-like crest which lacks recognizable cusp and denticiles and curves inwards, and also with its upper margin gently bowed inward; ledge-like costa on each side extending throughout the whole unit, more or less parallel to the basal margin, to define a groove-like basal surface on each side between costa and the basal margin in lateral view, and a narrow platform in the upper view; on the concave side, the groove-like basal surface is more strongly developed and extends
Fig. 10. *Cooperignathus nyinti* (Cooper, 1981): A–C, Pa element, AMF120319, M/A7, A, basal, outer lateral view; B, basal view; C, antero-outer lateral view; D, Pa element, AMF120320, M/A7, inner lateral view; E–G, Pa element, AMF120321, M/A7, E, close up showing the basal cavity and outer lateral process, F, outer lateral view; G, upper, outer lateral view; H, Pb element, AMF120322, M/A7, outer lateral view; I–K, Pb element, AMF120323, Y4–2, I, outer lateral view, J, basal view, K, upper, outer lateral view; L–N, Pb element, AMF120324, M/A7, L, inner lateral view, M, inner lateral-basal view, N, showing reticulate surface structure. Scale bars 100 µm, unless otherwise indicated.

continuously from anterior to posterior extremities; underneath the element, the basal margins on both sides narrow to define a small, shallow basal pit at mid curvature and a narrow groove extending towards the distal ends of the anterior and posterior processes; on the convex side, the Pa element displays a short ridge-like outer lateral process (Fig. 10G) developed between the horizontal, ledge-like costa and the basal margin to divide this groove-like area into a slightly shorter anterior part and a longer posterior part, and basally this short process forms a prominent basal buttress (Fig. 10A–C,E); in the Pb element this outer lateral process is much weaker or even absent (Fig. 10I); surface of the P elements ornamented by reticulation which is best developed near the ledge-like costa (Fig. 10L,N). *M element* anteroposteriorly compressed, with a robust outer laterally strongly recurved cusp, an adenticulate outer lateral process and an adenticulate, anticusp-like inner lateral process; cusp also slightly curved posteriorly, and inner- and outer-lateral processes curved slightly anteriorly; anterior and posterior faces bearing a round-faced costa; basally, the costa on the posterior face is truncated by a strong, ledge-like horizontal costa.
extending from the outer lateral process to the inner lateral process, with an acute angle (about 30°) between them; posteriorly, the broad basal buttress defining a more or less triangular opening of the basal cavity (Fig. 11B). *S* elements bearing a tricostate cusp, a sharp costa along the posterior margin, and a costa along the anterolateral corner on each lateral face, and with a broad anterior face; three costae extending basally into three adenticulate processes, which are tripod-like in lateral view; posterior process long, straight or inner laterally curved; lateral processes extending...
basally and laterally, ornamented with fine striae which are vertically arranged more or less parallel to the axis of the cusp in anterior view (Fig. 11J); in upper view, the three processes meet the cusp in a T- or Y-shaped junction; three processes with a prominent costa on each side more or less parallel the basal margin to define the basal surface. Three morphotypes are recognized, based mainly on curvature of the posterior process; Sa element symmetrical with straight posterior process; Sb element slightly asymmetrical, with posterior process slightly curved inward and a more strongly downwardly extended inner lateral process; Sc like the Sb, but asymmetrical with a more strongly inwardly curved posterior process.

Remarks. In the Horn Valley Siltstone, *C. nyinti* is very common while *C. aranda* is less so, but always occurs with *C. nyinti* except in the lowest stratigraphic horizons (Cooper, 1981). Morphologically, *C. nyinti* and *C. aranda* are very similar. The latter was originally defined only on S and M elements. No P elements were formally recognized previously for this species, although Cooper (1981: 175) stated that the P element of *C. aranda* might be very similar to its counterpart in *C. nyinti* with differences “solely in size, degree of thickening, and robustness”. The S elements of *C. nyinti* and *C. aranda* are similar, except that those of *C. aranda* have an indentation at the junction between the posterior margin of the cusp and the upper margin of the posterior process. The M elements of these two species are also very similar. Both have a strong posterior costa, a basal buttress, and a strong costa paralleling the basal margin to define a basal groove on the posterior face. However, the M element of *C. nyinti* has a more strongly outer-laterally reclined cusp, and a straight or slightly arched basal margin, whereas that of *C. aranda* has a longer inner lateral process with the lowest point of the basal margin underneath the basal buttress, and with a more strongly arched upper margin to the outer lateral process.

The P elements illustrated from the Horn Valley Siltstone (Cooper, 1981) show a distinctive short outer lateral process on the convex outer lateral side that links the horizontal ledge-like costa and the basal margin to divide the groove into two parts. These specimens are referred herein to the Pa position. Re-examination of a large topotype collection of this species confirms that Pa and Pb elements of *C. nyinti* are also represented at the type locality. Like the Horn Valley Siltstone samples, P elements are relatively rare in the Mount Arrowsmith samples, with a similar situation noted in the Wah Wah and Juab formations of the Ibex area, Utah (Ethington & Clark, 1982). These latter authors recorded a ratio of about 8(S):11(M):1(P) for the species (*C. nyinti* + *C. aranda*), and argued that the P elements must have been very minor constituents of the apparatus. Hence they regarded *P. nyinti* as a probable junior synonym of *P. aranda*, and suggested that the differences on which Cooper (1981) distinguished these two species might merely represent a broad spectrum of morphologic variation within the one species apparatus. Repetski (1982), and Johnston & Barnes (2000) expressed similar views. However, recovery of two additional types of pectiniform elements from the Mount Arrowsmith samples, which are now referred to as the Pa and Pb elements of *C. aranda*, strongly suggests the coexistence of the two species of *Cooperignathus*.

**Cooperignathus aranda** (Cooper, 1981)

Fig. 12A–P


**Material.** Two specimens (1 M, 1 Sa) from limestone nodules within shales of the upper Yandaminta Quartzite, and 25 specimens (5 Pa, 2 Pb, 10 M, 3 Sa, 4 Sb, 1 Sc) from the overlying Tabita Formation at Mount Arrowsmith; four specimens (1 Pa, 2 M, 1 Sc) from unnamed dolomitic limestone unit at Kooneberry Gap.

**Diagnosis.** A ramiform-pectiniform species with a seximbrate apparatus, including albid, pastiniplanate P elements, makellate M element, alate Sa, and modified tertiopepate Sb and Sc elements; S elements with a distinctive indentation at the conjunction of the posterior margin of the cusp with the upper margin of the posterior process.

**Description.** *P elements* bearing a longer anterior process, a posterior process and a shorter posterolaterally extended outer lateral process; each process with a wide platform and an adenticulate blade-like crest, which join at the centre, but without a recognizable cusp; basal cavity small, represented by a weak keel with a narrow groove underneath each process to join a shallow basal pit (Fig. 12E); zone of recessive basal margin not recognized on the basal surface; the Pa element has a wider platform, with anterior and posterior processes strongly curved inwards meeting at an angle of 90–120°; distal end of the posterior process bent sharply downwards; the inner lateral margin of the platform forming a discernible niche at the curvature (Fig. 12B,D). *Pb element* has a narrower platform, and with anterior and posterior processes much less inner laterally curved, meeting at an angle of about 150–160° (Fig. 12F). *M element* anteroposteriorly compressed, with a robust cusp and adenticulate inner and outer lateral processes; in posterior view, the outer lateral process bears a blade-like crest with strongly arched upper margin (Fig. 12J); sharply pointed, inner lateral process (Fig. 12L,K); basal costa extends more or less parallel to the basal margin from distal end of the outer lateral process to the tip of inner lateral process on both anterior and posterior faces (Fig. 12I–K); cusp reclined outer laterally and also slightly curved posteriorly, with a ridge-like costa along the anterior and posterior faces; the costa on the anterior face extends basally to join the basal costa and then merges into a weakly
Fig. 12. *Cooperignathus aranda* (Cooper, 1981): A–D, Pa element, AMF120333, Y4–4, A, close up showing reticulate surface structure, B, inner lateral view, C, outer lateral view, D, inner lateral, upper view; E, Pa element, AMF120334, C1611, basal view; F–H, Pb element, AMF120335, TAB1/39.5, F, upper view, G, inner lateral view, H, outer lateral, upper view; I, M element, AMF120336, W5, anterior view; J, M element, AMF120337, M/A7, posterior view; K, M element, AMF120338, C1612, basal posterior view; L, Sa element, AMF120339, TAB1/65.2, lateral view; M,N, Sb element, AMF120340, M/A7, M, lateral view, N, close up, lateral view; O,P, Sc element, AMF120341, Y4–4, O, lateral view, P, basal lateral view. Scale bars 100 µm, unless otherwise indicated.
developed basal buttress; the costa on the posterior face generally much stronger, truncated by the basal costa and merging with a more strongly developed basal buttress, with an angle of 50–65° between the posterior costa and the basal costa on the outer lateral process; in posterior view, the basal margin curves upwards distally, with the buttress at the lowest point. S elements ramiform, but adenticulate, with a prominent suberect or proclined cusp, a long posterior process, and a lateral process on each side along the anterolateral corner; a basal costa developed on each side of both processes, more or less parallel to the basal margin, so defining a shallow groove on each side just above the basal margin; posterior process gently curved downwards distally, bearing a blade-like crest, with gently arched upper margin forming a distinct cleft at its junction with the posterior margin of the cusp (Fig. 12M,N); lateral processes shorter, extending from tip of the cusp as a blade-like costa on each side and produced basally into a short adenticulate process (Fig. 12O,P); in upper view, the three processes join the cusp to form a T- or Y-shaped junction; Sa element symmetrical (or nearly so) with straight posterior process and equally developed lateral processes; Sh element slightly asymmetrical with posterior process gently curved inner laterally; Sc element asymmetrical with more strongly inner laterally curved posterior and inner lateral processes.

Remarks. Cooper (1981), who described and illustrated only the M and S elements of this species, suggested the possible P element might be similar to its counterpart in the typical North American Midcontinent faunas. Löfgren (1999) suggested that Cornuodus was most closely related to Protopanderodus and Drepanodus, assigning it to the Family Protopanderodontidae, Lindström, 1970.

**Cornuodus longibasis** (Lindström, 1955)

Fig. 13A–D

“**Cornuodus**” longibasis Serpagli, 1974: 43, pl. 7, fig. 2a,b, pl. 20, fig. 21. Cornuodus longibasis.—Cooper, 1981: 161, pl. 26, figs. 10–11. Cornuodus longibasis.—Löfgren, 1999: 175–184, pls. 1–3 (cum syn.). Cornuodus longibasis.—Johnston & Barnes, 2000: 15, pl. 7, figs. 3, 4, 8, 9 (cum syn.).

**Cornuodus longibasis**.—Zhen et al., in press: pl. 2, fig. 19 (cum syn.).

**Material.** Five specimens from limestone nodules within shales of the upper Yandaminta Quartzite, and 109 specimens from the overlying Tabita Formation at Mount Arrowsmith; three specimens from unnamed dolomitic limestone unit at Koonenberry Gap.

**Remarks.** Löfgren (1999) recently defined a septimembrate apparatus for the species. However, we experienced great difficulties in differentiating our specimens, which all seem to be S elements. No P elements have been confirmed in the western New South Wales collections.

**Drepanodus Pander, 1856**

**Type species.** Drepanodus arcuatus Pander, 1856.

**Drepanodus sp.**

Fig. 13E–I

**Material.** Eight specimens (2 arcuiform, 2 graciliform, 4 sculponeaform) from limestone nodules within shales of the upper Yandaminta Quartzite, and 52 specimens (23 arcuiform, 17 graciliform, 12 sculponeaform) from the overlying Tabita Formation at Mount Arrowsmith; ten specimens (5 arcuiform, 3 graciliform, 2 sculponeaform) from unnamed dolomitic limestone unit at Koonenberry Gap.

**Remarks.** This species of Drepanodus comprises small, albid, laterally compressed, conical units with sharp anterior and posterior margins and smooth lateral sides. The basal cavity is relatively deep, extending to near the maximum curvature of the cusp. Three morphotypes have been recovered. The arcuiform element is nearly symmetrical with a proclined cusp. The graciliform element is asymmetrical with a slightly reclined cusp, and the sculponeaform element is nearly symmetrical and has a recurved cusp. Elements resemble those of the type species of the genus, but lack a prominent mid-carina on the lateral faces (van Wamel, 1974). Arcuiform elements referred to D. arcuatus, illustrated from the Ningoo Formation of southeast China (Z.H. Wang & Bergström, 1999, pl. 2, figs. 4, 5), also have smooth lateral faces, but the Chinese specimens exhibit a posteriorly reclined cusp.

**Drepanoistodus Lindström, 1971**

**Type species.** Oistodus forceps Lindström, 1955.

**Remarks.** Nicoll (1994) suggested that most euciconodonts in the Order Protopanderodontida comprised seximembrate coniform-coniform apparatuses including S (Sa, Sb, Sc, Sd) and P (Pa, Pb) elements. However, this configuration for
coniform species has not subsequently been widely accepted. Hence the commonly used notation schemes are followed for the two species of *Drepanoistodus* documented herein.

*Drepanoistodus basiovalis* (Sergeeva, 1963)  
Fig. 14A–K  
*Oistodus basiovalis* Sergeeva, 1963: 96, pl. 7, figs. 6, 7, text-fig. 3.  
*Drepanoistodus basiovalis* Löfgren, 1978: 55, pl. 1, figs. 11–17, fig. 26B,C (*cum syn.*).  
*Drepanoistodus suberectus* Cooper, 1981: 164, pl. 26, figs. 1, 2, 6.  
*Drepanoistodus basiovalis*.–Johnston & Barnes, 2000: 18, pl. 11, figs. 10, 11, 15, 16 (*cum syn.*).

**Material.** Thirteen specimens (4 P, 1 M, 1 Sa, 3 Sb, 4 Sc) from limestone nodules within shales of the upper Yandaminta Quartzite, and 123 specimens (11 P, 31 M, 21 Sa, 41 Sb, 19 Sc) from the overlying Tabita Formation at Mount Arrowsmith; 21 specimens (3 P, 4 Sa, 8 Sb, 6 Sc) from unnamed dolomitic limestone unit at Koonenberry Gap.

**Description.** Apparatus quinquimembrate, all elements are hyaline, laterally compressed with sharp anterior and posterior margins, non-costate lateral faces, and have an open basal cavity. The *P element* (Fig. 14A,B,D–F,H) is asymmetrical with a reclined cusp and an extended anterobasal corner, triangular in outline. The M element is geniculate with a short outer lateral process, and a rounded inner lateral corner; a mid-carina may develop on the anterior and posterior faces (Fig. 14J,K). The *S elements* consist of a symmetrical (or nearly so) Sa element with an erect cusp (Fig. 14G), an asymmetrical Sb element with a reclined cusp and an oval-shaped opening of the basal cavity (Fig. 14C), and an asymmetrical Sc element with a strongly recurved, more laterally compressed cusp, having a narrower opening of the basal cavity (Fig. 14I).

**Remarks.** The definition of this widely distributed species given by Löfgren (1978) is followed here. However, the element with an outer lateral costa (Löfgren, 1978, pl. 1, fig. 12) is not recognized in our collections. The *P element* corresponds to the scandodiform element of many previous authors (e.g., Stouge & Bagnoli, 1990, pl. 5, fig. 19). Compared with their material from Sweden, M elements from western New South Wales are characterized by a shorter outer lateral process.

*Drepanoistodus costatus* (Abaimova, 1971)  
Fig. 15A–R  
*Drepanodus costatus* Abaimova, 1971: 490, pl. 10, fig. 6, text-fig. 3.  
*Scolopodus cornutiformis* Lee, 1976: 172, pl. 2, fig. 18.  
*Drepanodus pitjanti* Cooper, 1981: 162, pl. 26, figs. 3–5, 7, 8.  
*Scolopodus flexilis* An, 1981: 216, pl. 3, figs. 1, 2.  
*Scolopodus flexilis*.–An *et al.*, 1983: 142, pl. 14, figs. 13–18, pl. 33, fig. 4.  
*Scolopodus ordosensis* Z.H. Wang & Luo, 1984: 284, pl. 4, figs. 22, 23.  
*Drepanodus pitjanti*.–Watson, 1988: 111, pl. 3, figs. 14, 16, 17, pl. 5, fig. 15.  
*Scolopodus flexilis*.–An & Zheng, 1990: 173, pl. 5, figs. 1–6 (*cum syn.*).  
*Drepanodus? costatus*.–Smith, 1991: 30, fig. 17k.  
*Drepanoistodus costatus* Stait & Druce, 1993: 303, figs. 12LM, 17J,K,M,N,T,L (*cum syn.*).  
Material. One specimen (Sa) from limestone nodules within shales of the upper Yandaminta Quartzite, and 71 specimens (8 M, 9 Sa, 21 Sb, 20 Sc, 13 Sd) from the overlying Tabita Formation at Mount Arrowsmith; 20 specimens (6 M, 4 Sa, 6 Sb, 3 Sc, 1 Sd) from unnamed dolomitic limestone unit at Koonenberry Gap.

Remarks. Specimens from western New South Wales appear identical to the type material of D. pitjanti, from the Horn Valley Siltstone, for which Cooper (1981) recognized a quinquimembrate apparatus consisting of an M and four S elements. Albanesi (in Albanesi et al., 1998) reinterpreted the Sb element originally defined by Cooper (1981), as occupying the P position of the apparatus.

Cooper (1981) suggested that D. pitjanti and Drepanodus costatus are closely related, but that the latter lacks a costatus the Sb element originally defined by Cooper (1981), as to Sd) apparatus for Druce (1993) also recognized a quinquimembrate (M, Sa to Sd) apparatus for Drepanodus costatus, and referred this species to Drepanoistodus. They suggested that D. costatus could be differentiated from D. pitjanti mainly by its more strongly costate cusp. Stait & Druce (1993) correctly regarded Sclopopodus flexilis An—widely distributed in the Liangiaishan Formation and the Beianzhuang Formation (Lower Majiagou Formation) of North China—as a junior synonym of D. costatus. With its less strongly developed costa, S. flexilis is very similar morphologically to the type material of D. pitjanti. The M element of the Chinese species (An & Zheng, 1990, pl. 5, fig. 2; referred to as a graciliform element) is almost identical with the M element of D. costatus illustrated from the Coolibah Formation (Stait & Druce, 1993), except that only one strong costa and an additional much weaker costa are developed on the posterior face, whereas the illustrated Coolibah specimen (Stait & Druce, 1993, fig. 17J) shows three much less strongly developed costae. The M element (Fig. 15E–H) of the Mount Arrowsmith and Koonenberry Gap material is identical to that of D. pitjanti from the Horn Valley Siltstone, both forms being characterized by a single strong costa on the posterior face. They also have a cusp more strongly outer laterally curved than do corresponding elements illustrated from the Georgina Basin and North China. The complex variations in the number of costae and other morphological details of M elements in the taxa discussed above suggest that such characters are of little or no use in differentiating these species.

Drepanoistodus sp.

Fig. 14L

Material. Four specimens from limestone nodules within shales of the upper Yandaminta Quartzite, and four specimens from the Tabita Formation, at Mount Arrowsmith; an additional specimen from unnamed dolomitic limestone unit at Koonenberry Gap.

Remarks. Specimens of a large suberect element, here identified as Drepanoistodus sp. (Fig. 14L), are asymmetriclic with the basal cavity inflated inner-laterally and with an undulose basal margin at the inner side. Löfgren (1978) noticed some variations among Swedish specimens assigned to the P element of D. basiovalis. Some forms showing a flaring anterobasal corner (Löfgren, 1978, pl. 1, fig. 13), are comparable with the elements here referred to D. sp. This element might occupy the Pa position to complete a siximembrate apparatus for D. basiovalis.

Erraticodon Dzik, 1978


Diagnosis. Septimembrate apparatus with a ramiform-ramiform structure including digyrate (or modified) P, makellate M, alate Sa, bipennate Sb and Sc, and tertioapedate Sd, hyaline elements with a prominent cusp, discrete peg-like denticles on the processes, and a shallow basal cavity.

Remarks. The type material of E. balticus was recovered from an erratic boulder found near Kartuzy, Pomerania, Poland, but believed to be transported from the Baltic region. Dzik (1978) originally recognized a seximembrate apparatus for the species, consisting of a makellate M, which has a denticulate outer lateral process but apparently lacks an anticusp (Dzik, 1978, pl. 15, fig. 5, text-fig. 6d), bipennate Sb and Sc with a denticulate posterior process and an anterolateral process, tertioapedate Sa and Sd with a denticulate posterior process and a lateral process on each side, and digyrate Pb elements (Dzik, 1978, text-fig. 2, spathognathiform element). Subsequently, Dzik (1991) indicated that the species had a septimembrate composition, but unfortunately provided neither description nor further details of the revised apparatus. Based on his schematic illustration (Dzik, 1991, p. 299, text-fig. 12A), both Pa and Pb elements are digyrate; the Pb (Dzik, 1991, text-fig. 12 A-sp) has a straight basal margin, and an anterior costa which extends to the anticusp, while the Pa (Dzik, 1991, text-fig. 12A-oz) has a rather strongly arched basal margin and lacks an anticusp. The other elements he illustrated are reinterpreted here as n=M, tr=Sa, pl=Sd, ke-hi=Sb, and lo=Sc.

Watson (1988, pl. 8, fig. 13) recovered a very rare bipennate element with a long, curved posterior process from the Goldwyer Formation of the Canning Basin which he attributed to E. balticus. This may represent a variant of the Sb element.

Erraticodon balticus is characterized by having an accentuated denticle on the posterior process of the Sa, Sb and Sc elements. The species is widely distributed in the Baltic region and the Siberian Platform (Dzik, 1978), the Canning Basin of Western Australia (Watson, 1988), South China (Ding et al., in Wang, 1993), Argentine Precordillera (Lehnert, 1995; Albanesi, in Albanesi et al., 1998), Utah (Ethington & Clark, 1982), and western Newfoundland (Stouge, 1984; Pohler, 1994; Johnston & Barnes, 2000).

Three additional named species are ascribed to Erraticodon. Locally these include E. patu Cooper, of O. evae Zone age, from the Horn Valley Siltstone (Cooper, 1981), the Tabita Formation at Mount Arrowsmith and an unnamed unit at Koonenberry Gap. Records of this species outside Australia are in need of reassessment. The stratigraphically younger E. balticus supposedly co-occurs with E. patu at the top of the San Juan Formation in the Argentine Precordillera, but of the four illustrated specimens, only an Sa element (Lehnert, 1995, pl. 10, fig. 11) can be assigned doubtfully to E. patu. Illustrated P elements from the Suri Formation (navis Zone) in the
A potential fifth species of the genus, referred to herein as *E.* sp. A, is a rare component in the Tabita Formation fauna, but due to limited material is not formally named. Features distinguishing it from *E. patu* are discussed below.

**Erraticodon patu Cooper, 1981**

Figs. 16A–K, 17A–O

*Erraticodon patu* Cooper, 1981: 166, pl. 32, figs. 1–6, 8. *Erraticodon patu.—*Nicoll, 1990, fig. 2.1.

?*Erraticodon patu.—*Albanesi & Vaccari, 1994: 137, pl. 1, figs. 11–16.

?*Erraticodon patu.—*Lehnert, 1995: 88, pl. 10, partim only fig. 11.

**Material.** 314 specimens (48 Pa, 29 Pb, 44 M, 29 Sa, 50 Sb, 59 Sc, 55 Sd) from the Tabita Formation at Mount Arrowsmith, and eight specimens (1 Pb, 1 M, 1 Sa, 1 Sb, 2 Sc, 2 Sd) from unnamed dolomitic limestone unit at Koonenberry Gap.

**Diagnosis.** A species of *Erraticodon* with a septimembrate ramiiform-ramiform apparatus, consisting of digyrate *Pa* and *Pb* elements, makellate *M*, alate *Sa*, bipennate *Sb* and *Sc*, and tertiopedate *Sd* elements; all hyaline with a prominent cusp, and two or three denticulate processes bearing discrete peg-like denticles; cusp bearing two or three thin, flange-like costae which extend basally to form the upper margin of the processes; basal cavity shallow, extending as shallow grooves towards the tips of the processes.

**Description.** *Pa element* digyrate with a less prominent cusp than the *Pb* element; the inner lateral process extending horizontally, with a straight basal margin which is normal to the axis of the cusp; the outer lateral process extending downwards at an angle of about 130° to the cusp, with a gently arched basal margin. The cusp varies from straight and erect (Fig. 16A,B) to prominently curved posteriorly (Fig. 16C); in the latter variation, denticles on the lateral processes also curve posteriorly; cusp and denticles have broad anterior and posterior faces and a flange-like costa on each lateral face; in cross section, cusp and denticles vary from rounded near the base to anteroposteriorly compressed towards the tips; shallow basal cavity represented by a small pit beneath the cusp, extending as a faint basal groove underneath each of the lateral processes. 

*Pb element* is a modified digyrate element with a lateral process on each side, bearing up to five denticles, and a shorter anterior process generally bearing three denticles; cusp erect (Fig. 16E), rounded or water drop-like in cross section near the base (Fig. 16G), with a sharp anterior margin, broadly rounded posterior face (Fig. 16D,G,H), and a thin flange-like lateral costa on each side which extend downwards to form the upper margin of the lateral process; anterior process inner laterally curved, in the same plane as the outer lateral process, and forming an angle of 60–70° with the inner lateral process in upper view (Fig. 16G,H); denticles on the lateral processes more or less rounded in cross section near the base, but towards tips they become anteroposteriorly compressed with sharp lateral margins marked by a flange-like costa, and broad anterior and posterior faces; denticles on the anterior process compressed laterally with sharp anterior and posterior margins, marked by a flange-like costa extending from the tip of the cusp, along its anterior margin and the upper...
margin of the anterior process, to the distal end of the process (Fig. 16J,K). *M* element makellate with a shorter inner lateral process bearing one or two denticles, and an outer lateral process bearing three to five denticles (Fig. 17A,B); cusp robust, anteroposteriorly compressed, and slightly curved posteriorly, with broad anterior and posterior faces, and sharp lateral margins; basal margin straight; basal buttress weakly developed. *Sa* element alate, symmetrical (or nearly so) bearing a posterior process and a lateral process on each side (Fig. 17F,G); cusp more or less rounded in cross section with broad anterior margin, a sharp posterior costa and a median costa on each lateral face; costae extending downwards to form the upper margins of the processes; lateral processes bearing two or three antero-posteriorly compressed denticles; posterior process bearing three or more, smaller, laterally compressed denticles; the posterior process of all *Sa* elements studied from western New South Wales is broken. *Sb* element bipennate, with a posterior process bearing three to five denticles and a downward extending and strongly inner laterally curved anterior process (Fig. 17K–O); cusp robust, posteriorly inclined, with posterior and anterior costa; anterior costa and anterior process strongly curved inner-laterally so that in lateral view, they appear to be more inner lateral than anterior in position (Fig. 17K). *Sc* element bipennate with a strongly downwardly extended anterior process bearing three or more denticles and a posterior process bearing three or more denticles (Fig. 17C–E); cusp suberect, laterally compressed with sharp anterior and posterior margins; thin anterior margin sharply curved inner-laterally; basal margin
Fig. 17. *Erraticodon patau* Cooper, 1981: A, M element, AMF120378, Y4–6, anterior view; B, M element, AMF120379, Y4–6, posterior view; C, Sc element, AMF120380, Y4–6, inner lateral view; D, Sc element, AMF120381, M/A11-6, outer lateral view; E, Sc element, AMF120382, Y4–6, outer lateral view; F, Sa element, AMF120383, M/A11-5, anterior view; G, Sa element, AMF120384, Y4–4, posterior view; H, Sd element, AMF120385, Y4–8, anterior view; I, Sd element, AMF120386, M/A11-3, posterior view; J, Sd element, AMF120387, Y4–7, posterior view; K, Sb element, AMF120388, Y4–7, inner lateral view; L, Sb element, AMF120389, Y4–7, outer lateral view; M, Sb element, AMF120377, Y4–6, posterobasal view; N, O, Sb element, AMF120390, M/A11-5, N, postero-inner lateral view, O, antero-inner lateral view. Scale bars 100 µm.
strongly arched with the two processes nearly normal to each other. \textit{Sd element} tertiopedate, asymmetrical, with a short inner lateral process bearing two or three denticles, and a longer outer lateral process bearing three to six denticles (Fig. 17H–J); two lateral processes extending downwards forming an angle of about 60 to 70°; posterior process bearing two or more denticles; cusp erect, oval in cross section with broad anterior margin, a posterior costa, and a mid-lateral costa on each side; costae extending downwards to mark the upper margins of the processes.

\textbf{Remarks.} Specimens from the Tabita Formation are identical with the type material from the Horn Valley Siltstone. The majority of the Mount Arrowsmith elements bear a basal attachment, and similarly, many of the Horn Valley specimens also have well preserved attachment cones (Nicoll, 2002, pers. comm.). Cooper (1981) originally described the \textit{Pb element} as having three processes—antero, posterior, and a lateral. However, Sweet (1988) correctly indicated that the \textit{Pb element} is actually a modified digyrate element, with a lateral process on each side and a strongly curved anterior process. This morphology is also clearly illustrated in the holotype of the species (Cooper, 1981, pl. 32, fig. 6). Close examination of specimens of the \textit{Pb element} from Mount Arrowsmith has confirmed that these lack a posterior process.

Cooper (1981) described the \textit{M element} as neoprioniodiform. Subsequently, Nicoll (1990) introduced the term makellate for the element occupying the \textit{M} position, and suggested that the \textit{M element} of \textit{E. patu} was a typical makellate element. In the Mount Arrowsmith specimens, however, the anticus is actually an antero-inner lateral process bearing one or two denticles. The basal buttress on the posterior face is generally weak (Fig. 17B).

The stratigraphically older \textit{E. patu} is readily distinguished from the type species, \textit{E. balticus}, from the Middle Ordovician by having a distinct \textit{Pb element} with a denticulate anterior process, \textit{M element} with a denticulate inner lateral process, and by absence of an accentuated denticle on the posterior process in the \textit{Sa}, \textit{Sb} and \textit{Sc} elements.

The \textit{Pb element} of \textit{E. tangshanensis} Yang & Xu, in An \textit{et al.}, 1983 is a modified digyrate form (originally termed plecostopathognathiform, but including both \textit{Pb} and \textit{Sd} elements) which resembles the same element in \textit{E. patu}, but the elements of \textit{E. tangshanensis} have much more robust denticles and some \textit{Sd} elements bear an accentuated denticle on the posterior process. The alate \textit{Sa} element of this Chinese species has a short lateral process, represented by a single stout denticle, on each side, while the \textit{M} element is more comparable with that of \textit{E. balticus} in lacking an inner lateral process.

\textbf{Erraticodon sp. A}

Fig. 18A–G

\textbf{Material.} Five specimens (1 \textit{Pa}, 1 \textit{Pb}, 2 \textit{Sa}, 1 \textit{Sc}? ) from the Tabita Formation at Mount Arrowsmith.

\textbf{Description.} \textit{Pa element} digyrate, with a long posterior process bearing three or more peg-like widely spaced and posteriorly inclined denticles (Fig. 18C,D); cusp oval in cross section, slightly twisted inward, with a sharp anterior margin, which extends basally into a short anticusp; inner lateral side bearing a long process with three or more peg-like, widely spaced denticles which are anteroposteriorly compressed and distally rather sharply curved inward. \textit{Pb} element modified digyrate, with a longer inner lateral process bearing three or more widely spaced, peg-like denticles, and a short outer lateral process with a single denticle; anterior process also short and represented by a single denticle (Fig. 18A,B); cusp and denticles curved posteriorly. \textit{Sa} element alate, symmetrical, with a robust cusp, a denticulate posterior process, and lateral processes on each side bearing a small denticle (Fig. 18F,G). \textit{Sc} element possibly represented by a poorly preserved specimen with a short anterior process bearing a single denticle, and a posterior process with three or more, long, posteriorly reclined denticles (Fig. 18E).

\textbf{Remarks.} This species is rare in the Tabita fauna, with only \textit{Pa}, \textit{Pb}, \textit{Sa} and a doubtful \textit{Sc} element recovered. It can be easily differentiated from the co-occurring \textit{E. patu} by having widely spaced denticles, a short anterior process in the \textit{Pb} element, and a laterally compressed cusp with a prominent anticus in the \textit{Pa} element. Although possibly a new species, formal designation is deferred pending recovery of all element types.

\textbf{Jumudontus Cooper, 1981}

\textbf{Type species.} \textit{Jumudontus gananda} Cooper, 1981.

\textit{Jumudontus gananda} Cooper, 1981

Fig. 18H–J

\textit{Jumudontus gananda} Cooper, 1981: 170, pl. 31, fig. 13.

\textit{Jumudontus gananda}—Nicoll, 1992: 216–223, figs. 4–8 (cum syn.).

\textit{Jumudontus gananda}—Pohler, 1994, pl. 3, figs. 15, 16.

New genus A n. sp. 1 s.f. Pohler, 1994: 42, pl. 7, fig. 29, text-fig. 15T,U (= S elements).

New genus An. sp. 2 s.f. Pohler, 1994: 42, pl. 7, figs. 27, 28, text-fig. 15R,S (= Pb element).

New genus C n. sp. 1 s.f. Pohler, 1994: 43, pl. 7, fig. 26, text-fig. 15X (= Pb element).

\textit{Jumudontus gananda}—Johnston & Barnes, 2000, pl. 4, fig. 22.

\textit{Jumudontus gananda}?—Zhen \textit{et al.}, in press: pl. 3, fig. 19 (cum syn.).

\textbf{Material.} Six specimens (all \textit{Pa}) from the Tabita Formation at Mount Arrowsmith, and eleven specimens (10 \textit{Pa}, 1 \textit{Pb}) from an unnamed dolomitic limestone unit at Koonenberry Gap.

\textbf{Remarks.} \textit{Jumudontus gananda} was originally described (Cooper, 1981) as a form species with only the \textit{Pa} element recognized from the Horn Valley Siltstone of the Amadeus Basin. Nicoll (1992) revised the species as consisting of a septimembrate coniform-pectiniform apparatus, also based on a collection from the Horn Valley Siltstone, with a recovered element ratio of 60(Pa):21(Pb):2(M):1(Sa):5(Sb):3(Sc):8(Sd). In samples from western New South Wales, the species is comparatively rare, and only the more common \textit{Pa} and \textit{Pb} elements were recovered. Pohler (1994) briefly documented some \textit{Pb} and \textit{Sd} elements of this species, assigning them to three informal form species without knowledge of Nicoll’s (1992) revision.
Oepikodus Lindström, 1955

**Type species.** *Oepikodus smithensis* Lindström, 1955.

**Remarks.** Revision of the original form species concept (Lindström, 1955) led to recognition of a trimembrate apparatus consisting of prioniodiform, oepikodiform, and oistodiform elements (Lindström, 1971; Lindström, in Ziegler, 1975; Lindström, in Ziegler, 1977; Bergström & Cooper, 1973; van Wamel, 1974). Subsequently, Sweet (1988) and Johnston & Barnes (2000) interpreted the genus as consisting of a quinquimembrate apparatus incorporating three morphotypes of ramiform S elements. Further recognition of two pastinate (Pa and Pb) elements (Stouge & Bagnoli, 1988; Albanesi, in Albanesi et al., 1998) and four morphotypes of ramiform S (Sb1, Sb2, Sc, and Sd) elements (Repetski, 1982) imply a seximembrate or septimembrate apparatus for the genus, including pastinate Pa and Pb, makellate M, and ramiform S elements. In a more recent revision (Stewart & Nicoll, in press; Nicoll & Ethington, in press), *Oepikodus* was defined as consisting of a septimembrate apparatus, including pastinate Pa and Pb, makellate M, and quadriramate or modified quadriramate S elements. Nicoll & Ethington (in press) suggested that *Oepikodus* can be distinguished from *Prioniodus* (and *Baltoniodus*) mainly on the basis of the morphology of their Sa elements, those of *Oepikodus* being quadriiform alate, while Sa elements in the other two genera are triform alate.

**Oepikodus communis** (Ethington & Clark, 1964)

Fig. 19 O

*Gothodus communis* Ethington & Clark, 1964: 690–692, pl. 114, figs. 6, 14, text-fig. 2F.

*Oepikodus equidentatus* Ethington & Clark, 1964: 692–693, pl. 113, figs. 6, 8, 10, 11, 14.


*Oepikodus communis.*—Ethington & Clark, 1982: 61–62, pl. 6, figs. 18, 22, 25 (cum syn.).

*Oepikodus communis.*—Smith, 1991: 42, figs. 24a–f,i,j, 25, 26 (cum syn.).
Fig. 19. A–N, *Oepikodus pincallyensis* Zhen sp. nov.: A, M element, paratype, AMF120399, M/A7, anterior view; B, C, Pa element, paratype, AMF120401, Y4–2, B, outer lateral view, C, anterior view; D, E, Pa element, paratype, AMF120402, Y4–2, D, outer lateral view, E, upper view; F, Pa element, paratype, AMF124210, M/A7, basal view; G, H, paratype, Pb element, AMF124211, Y4–2, G, outer lateral view, H, anterior view; I–L, Pb element, Holotype, AMF120398, Y4–2, I, antero-lateral view, J, inner lateral view, K, upper view, L, outer lateral view; M, N, M element, paratype, AMF120400, M/A7, M, posterior view, N, postero-inner lateral view, showing basal buttress. O, *Oepikodus communis* (Elhington & Clark, 1964): Pb element, AMF120403, M/A11-2, outer lateral view. Scale bars 100 µm.
Material. One Pb element, from the Tabita Formation, at Mount Arrowsmith.

Remarks. Oepikodus communis is extremely rare at Mount Arrowsmith; the single Pb element recovered (sample M/A11-2) has a denticulate posterior process, and adenticulate outer lateral and anterior processes (Fig. 19O). Morphological differentiation and apparatus composition of O. evae, O. communis and O. intermedius have been widely discussed in Ordovician conodont literature. Serpagli (1974) considered O. intermedius to be transitional between O. evae and O. communis, showing O. intermedius first appearing in the San Juan Formation directly above the last appearance of O. evae. He further correlated the range of O. intermedius in the San Juan Formation with the O. communis Zone of the North American Midcontinent faunal succession, and suggested an evolutionary trend from O. evae–O. intermedius–O. communis. More recently, however, the O. communis Zone has been correlated in part with the P. elegans Zone, below the O. evae Zone (Webby, 1995), implying that O. intermedius might be the youngest species of the three. Although Serpagli (1974) distinguished O. intermedius from O. communis on curvature of processes on the P elements and curvature of the basal margin of the M elements, we agree with most subsequent authors (Ethington & Clark, 1982; Repetski, 1982; Smith, 1991) that these details are within the variation of O. communis. However, merging of these two species has the effect of extending the range of O. communis upwards into the flabellum/laevis Zone.

Oepikodus pinclallyensis Zhen n.sp.

Figs. 19A–N, 20A–R

Etymology. After Pincally Homestead (Fig. 1), which is located southwest of the type locality (Y4).

Material. Three specimens (1 M, 1 Sa, 1 Sc) from limestone nodules within shales of the upper Yandaminta Quartzite, and 92 specimens (13 Pa, 11 Pb, 16 M, 16 Sa, 10 Sc, 17 Sb, 9 Sd) from the overlying Tabita Formation at Mount Arrowsmith, western New South Wales, including the holotype AMF120398 (Pb element), from sample Y4–2 (C1822), and 15 paratypes AMF120399–120402, AMF120404–120411, AMF124210–124212.

Diagnosis. A species of Oepikodus consisting of a septimembrate apparatus with a ramiform-pectiniform structure; all elements albid; both Pa and Pb elements pustinate with a longer denticulate posterior process, a shorter denticulate outer lateral process, and an inner-laterally curved anterior process which is adenticulate (Pa) or denticulate (Pb); S elements typical (Sa and Sd) or modified (Sb and Sc) quadrimariate.

Description. Pa element has a prominent, slightly proclined, laterally compressed cusp which is triangular in cross section, with sharp posterior and anterior margins; an inwardly curved blade-like costa extends along the anterior margin, merging downward into the upper margin of an adenticulate, inwardly curved, anterior process (Fig. 19E); outer lateral face has a rounded distinctive costa that extends downwards to merge into the upper margin of the outer lateral process (Fig. 19B); the outer lateral process extends anterolaterally forming an obtuse angle with the posterior process (Fig. 19E); small, closely spaced denticles developed on the posterior and outer lateral processes (Fig. 19B–E); in upper view, these processes meet at a Y-shaped junction; basal cavity triangular in outline (Fig. 19F); none of the specimens recovered have processes preserved for their full length. Pb element similar to the Pa, with denticulate outer lateral and posterior processes, but with the cusp more or less erect or slightly reclined, also with a blade-like anterior costa that extends basally to merge into a shorter, denticulate, anterior process (Fig. 19G–L); outer lateral process extending more or less normal to the posterior process (Fig. 19K). M element geniculate, makellate, with a long adenticulate outer lateral process and a shorter, triangular adenticulate inner lateral process (anticusp) (Fig. 19A,M,N); cusp robust, inclined outer laterally, and also slightly curved posteriorly, anteroposteriortly compressed with sharp lateral margins, and a strong rounded costa on the anterior and posterior faces; surface ornament of fine striae; anterior costa extending to the basal margin, becoming stronger and wider on the base; posterior costa extending into a moderately developed basal buttress; outer lateral process with a sharp, gently arched upper margin and costa extending from cusp to distal end of the process on each of its sides, and more or less parallel to the basal margin; inner lateral process with a sharp upper margin which is a continuously straight extension of the inner lateral margin of the cusp; basal cavity shallow, extending as narrow grooves underneath the lateral processes, with only slightly arched basal margin. Sa element symmetrical or nearly so, and quadrimariate; cusp slightly proclined, more or less diamond-shaped in cross section with sharp anterior and posterior margins and a sharp costa on each lateral side; anterior margin extended basally into a long downwardly directed anticusp; sharp lateral process extending basally into a weakly developed rudimentary adenticulate lateral process on each side; posterior process long, denticulate, bearing closely spaced and erect denticles of different sizes, larger denticles about two or three times as wide as the smaller denticles in the lateral view, typically with three to five smaller denticles between two larger denticles; basal margin of the posterior process nearly straight, forming an angle of about 40 to 50° with the basal margin of the anticusp (Fig. 20A–D). Sb element asymmetrical, with a weak carina on the inner lateral face, an inner laterally curved posterior process, and a proclined cusp; on the outer lateral face a prominent costa is developed which extends basally into a short adenticulate outer lateral process (Fig. 20I–M). Sc element similar to Sb, modified quadrimariate, asymmetrical with cusp and anticusp slightly curved inwards; cusp erect or slightly proclined with sharp anterior and posterior margins, smooth outer lateral face and a weak carina on the inner lateral face; posterior process long, extending posteriorly as well as downwards, with a slightly arched upper margin, bearing numerous small, laterally compressed, and closely spaced denticles; none of the specimens examined have the full length of the posterior process preserved; anticusp long, triangular in shape, extending anteriorly and downwards, forming an angle of about 70–80° with the posterior process (Fig. 20E–H). Sd element quadrimariate, like the Sa but asymmetrical, with cusp and the anterior process (anticusp) prominently curved inward, and with a long denticulated posterior process, a sharp anterior margin extended basally into a strongly downwardly directed anticusp; cusp
proclined, more or less diamond-shaped in cross section, with sharp posterior and anterior margins, and a strong costa on each lateral face, which extends basally into a rudimentary adenticulate lateral process on each side (Fig. 20N–R).

Remarks. S and M elements of O. evae, O. communis and the new species O. pincallyensis closely resemble each other. Oepikodus evae was revised recently in detail (Stewart & Nicoll, in press) based on material from Australia and Sweden including well preserved bedding-plane assemblages. Compared with the revised concept of O. euae, the new species has a short anticusp in the M and S elements, and the Sb and Sc elements exhibit only rudimentary development of the lateral processes, which are reduced to a weakly developed carina on the inner lateral face of the Sb and Sc elements. Denticles on the posterior process in the S elements of O. communis are regular in size, whereas Sa elements of O. pincallyensis display variably sized denticles. Instead of a rather arched basal margin in the M elements of both O. evae and O. communis, O. pincallyensis shows a more or less straight basal margin. However, differentiation of these three species is mainly reliant on the P elements, specifically the absence of denticles on both the anterior and outer lateral processes on the P element of O. communis. The new species differs from O. evae in having smaller, rudimentary denticles on the anterior and outer lateral processes of the P elements. Furthermore, the anterior and outer lateral processes in the P element of O. evae, as shown by the type material from the Lower Ordovician of south-central Sweden (Lindström, 1955) and newly documented specimens from Australia (Stewart & Nicoll, in press), extend strongly downwards. In possessing smaller denticles and much less downwardly extended anterior and outer lateral processes on the P elements, the new species more closely resembles Oepikodus communis (Ethington & Clark, 1964), and Oepikodus intermedius Serpagli, 1974, but both of these latter species (which are probably conspecific) have adenticulate anterior and outer lateral processes.

In a recent study of the conodonts from the Horn Valley Siltstone of central Australia, Nicoll & Ethington (in press) recognized another new species of Oepikodus, previously recorded by Cooper (1981) as O. euae. It differs from O. pincallyensis and other Oepikodus species in having a pronounced v-shaped cleft separating the posterior margin of the cusp and the first denticle of the posterior process in the S and P elements. Rudimentary denticles are also developed on the anterior process of some Sc, Sb and M elements of this species from Horn Valley Siltstone.

**Oneotodus Lindström, 1955**


**Oneotodus sp.**

Fig. 24E,F

Oneotodus sp. Cooper, 1981: 172, pl. 27, figs. 1, 2.

Material. Six specimens from the Tabita Formation at Mount Arrowsmith, and one specimen from unnamed dolomitic limestone unit at Koonenberry Gap.

Remarks. The generic concept of *Oneotodus* adopted here follows that given by Ethington & Brand (1981) and Sweet (1988: 52). The western New South Wales species is comparable with specimens illustrated from the Horn Valley Siltstone (Cooper, 1981). It is a simple cone unit, with shallow but flaring basal cavity, which is rounded in basal view (Fig. 24E); in cross section, the cusp is rounded near the base and laterally compressed distally. Some elements display weak costae on the lateral faces (Fig. 24F).

**Prioniodus Pander, 1856**

Type species. *Prioniodus elegans* Pander, 1856.

Remarks. Generic concepts and the apparatus compositions of *Prioniodus* and *Baltoniodus* Lindström, 1971 have long been debated. Fähraeus & Nowlan (1978), and Cooper (1981) regarded the two as separate genera, based mainly on differentiation of the P elements, and also on the nature of the basal cavity. This definition has been more or less accepted by Löfgren (1978), Clark *et al.* (1981), Sweet (1988), and Stouge & Bagnoli (1988). However, Serpagli (1974) considered *Baltoniodus* to be a subgenus of *Prioniodus*, while van Wamel (1974) regarded *Baltoniodus* as a junior synonym of *Prioniodus*. Many authors (Cooper, 1981; Sweet, 1988; Dzik, 1994; Nicoll & Ethington, in press) considered that both genera might have been derived independently from species of *Acodus*, while *Oepikodus* may have evolved from *Prioniodus* (Dzik, 1983; Sweet, 1988) or also from *Acodus* (Stouge & Bagnoli, 1999). In a recent revision of *Oepikodus*, Nicoll & Ethington (in press) suggested the triform alate Sa elements, and relatively larger basal cavity distinguish both *Prioniodus* and *Baltoniodus* from *Oepikodus*. Sa elements of *Prioniodus* and *Baltoniodus* have a lateral process on each side and a long posterior process, but lack an anterior process.
Prioniodus sp. cf. P. amadeus Cooper, 1981

Fig. 21A–L

Material. One specimen (P) from limestone nodules within shales of the upper Yandaminta Quartzite and 47 specimens (27 P, 1 M, 19 S) from the overlying Tabita Formation at Mount Arrowsmith.

Description. The pastinate P elements are not differentiated into Pa and Pb due to limited material. They have a prominent, strongly laterally compressed, blade-like cusp with sharp anterior and posterior margins, and a sharp costa on the outer lateral face. The anterior and posterior margins, and the outer lateral extend basally into three processes (Fig. 21A–D). The posterior and outer lateral processes are longer and have several (up to seven) small denticles; anterior process shorter with a few small rudimentary denticles; cusp triangular in cross section with sharp anterior and posterior margins, and a sharp-edged costa on the outer lateral face; anterior process slightly curved inward, and outer lateral process extending anterolaterally, forming a more or less Y-shaped outline in upper view. M element makellate, with a long adenticulate outer lateral process, which has a straight basal margin and an arched upper margin, and a short inner lateral process, which is triangular in outline in anterior view (Fig. 21IL); cusp anteroposteriorly compressed, with a broad costa on the anterior and posterior faces, and a straight inner lateral margin forming an acute angle (about 40–45°) with the basal margin of the outer lateral process. Sa element triform alate, symmetrical, with a long denticulate posterior process, a broad anterior face, and a sharp ridge-like costa on each lateral face, which extends basally into a short adenticulate process (Fig. 21J,K). Sb element modified bipennate, strongly asymmetrical with a slightly proclined cusp, inner laterally curved anterior margin, a straight denticulate posterior process and a short adenticulate anticusp-like anterior process (Fig. 21E,F). Sc element modified bipennate, similar to Sb but slightly asymmetrical with a long denticulate posterior process and a short, anticusp-like adenticulate anterior process; cusp erect, laterally compressed, with sharp anterior and posterior margins; anterior process slightly curved inward, and posterior process slightly arched with denticles of uniform size pointed posteriorly (Fig. 21G). Sd element tertiopedate, asymmetrical with a denticulate posterior process; cusp proclined, and inner laterally curved, with broad anterior margin and a blade-like costa on each lateral side, which extends basally into a lateral process; inner lateral process more prominent, with a few rudimentary denticles distally (Fig. 21H,I).

Remarks. This species, consisting possibly of a septimembrate apparatus, is relatively uncommon in the Mount Arrowsmith collections. Although the modified bipennate Sb and Sc elements resemble those of P. amadeus Cooper, 1981 from the Horn Valley Siltstone of the Amadeus Basin (see especially Cooper, 1981, pl. 31, fig. 6), that species differs in inclusion of quadriramate elements in the apparatus, and its P elements have a less laterally compressed cusp and an adenticulate anterior process.

Some broad similarities are apparent between P. sp. cf. amadeus and Oepikodus pincallyensis. However, S elements of the former (differentiated into a triform alate Sa, modified bipennate Sb and Sc, and tertiopedate Sd) are generally larger, with more robust posterior processes bearing posteriorly pointed denticles of uniform size. S elements of O. pincallyensis are quadriramate, or modified quadrirame. The P elements of P. sp. cf. amadeus have a more laterally compressed blade-like cusp compared to O. pincallyensis, and exhibit a shorter and less inner laterally curved anterior process, and a relatively larger and deeper triangular basal cavity.

Prioniodus sp. A

Fig. 21M–Q

Material. Four specimens (3 Pa, 1 Pb) from the Tabita Formation at Mount Arrowsmith.

Description. Both Pa and Pb elements have a robust, erect cusp with sharp anterior and posterior margins; Pb element with a more laterally compressed blade-like cusp, and short posterior and outer lateral processes, with four denticles on the former and a single denticle on the latter; the anterior process long, inner laterally curved, bearing more than ten denticles (Fig. 21M,N). Cusp of Pa element more or less triangular in cross section, with a sharp mid-costa along the outer lateral face, which extends basally into a long denticulate outer lateral process (Fig. 21P,Q); long denticulate posterior process bearing closely spaced denticles which are erect and laterally compressed; outer lateral process normal to the posterior process (Fig. 21O), bearing over ten closely spaced denticles which are anteroposteriorly compressed, with tips slightly curved posteriorly; neither anticusp nor denticles developed at the anterobasal corner.

Remarks. The Pa element is well defined and is distinguished from those of other species of the genus by its long denticulate posterior and outer lateral processes. The Pb element of this species is characterized by a prominent cusp, and long denticulate anterior process. It shows some resemblance to the P element of Prioniodus sp. A. McTavish, 1973 from the Emanuel Formation of the Canning Basin (McTavish, 1973, pl. 2, fig. 4), but has an even longer anterior process with prominent denticles, and a much shorter outer lateral process.

Protopanderodus Lindström, 1971

Type species. Acontiodus rectus Lindström, 1955.

Protopanderodus gradatus Serpagli, 1974

Fig. 22A–K

Protopanderodus gradatus Serpagli, 1974: 75, pl. 15, figs. 5a–8b; pl. 26, figs. 11–15, pl. 30, fig. 1a,b; text-fig. 17.

Material. Ten specimens (4 Sb, 4 Sc, 2 Sd) from limestone nodules within shales of the upper Yandaminta Quartzite, and 69 specimens (11 Sa, 16 Sb, 17 Sc, 25 Sd) from the overlying Tabita Formation at Mount Arrowsmith; 31 specimens (1 Sa, 7 Sb, 12 Sc, 11 Sd) from unnamed dolomitic limestone unit at Koonenberry Gap.

Remarks. This species was recently reported from the slightly older (upper *P. elegans* Zone) Hensleigh Siltstone of central New South Wales, where five morphotypes were recognized (Zhen *et al.*, in press). Four elements have been recovered from the western New South Wales samples, and are regarded as occupying S positions in the species apparatus. The Sa element (termed element “d” by Zhen *et al.*, in press) is symmetrical or nearly so with a posterolateral
Fig. 22. A–K, *Protopanderodus gradatus* Serpagli, 1974: A, Sa element, AMF120436, M/A11-1, posterolateral view; B, Sd element, AMF120437, C1612, outer lateral view; C,D, Sb element, AMF120438, C1612, C, inner lateral view, D, outer lateral view; E,F, Sc element, AMF120439, C1612, E, inner lateral view, F, outer lateral view; G, Sd element, AMF120440, C1612, outer lateral view; H–J, Sa element, AMF120441, Y4–2, H,J, lateral views, J, close up showing the fine striae; K, Sd element, AMF120442, C1612, inner lateral view. L–R, *Protopanderodus leonardii* Serpagli, 1974: L, Sa element, AMF120443, M/A11-3, lateral view; M, Sb element, AMF120444,
costa and an anterolateral costa on each side (Fig. 22A–H–J). The Sb element (element “c” of Zhen et al., in press) is weakly asymmetrical, with a lateral costa on each side and slightly inner laterally curved cusp (Fig. 22C,D). Specimens referred to as element “b” by Zhen et al. (in press) may represent a variant of the Sb element; they are not recognized here. The Sc element is strongly asymmetrical with a smooth outer face and a costate inner face (Fig. 22E,F). It is similar to element “a” from the Hensleigh Siltstone, but the latter is more strongly twisted with a smooth inner face and a costate outer face. The Sd element (element “e” of Zhen et al., in press) is similar to the Sa with a posterolateral costa and an additional anterolateral costa on each side, but apparently asymmetrical (Fig. 22B,G,K).

Our specimens are identical with the type material from the San Juan Formation of Argentina (Serpagli, 1974). In lateral view, elements of *P. gradatus* from the Hensleigh Siltstone are less laterally compressed with the basal margins more or less straight, rather than gently curved as shown by the types from the Argentine Precordillera.

**Protopanderodus leonardii** Serpagli, 1974

Fig. 22L–R

*Protopanderodus leonardii* Serpagli, 1974: 77, pl. 16, figs. 1a–4c, pl. 27, figs. 12–16, text-fig. 6.

*Protopanderodus leonardii*.—Zhen et al., in press: pl. 4, figs. 23, 24 (cum syn.).

**Material.** Six specimens (1 Sa, 3 Sb, 2 Sc) from the Tabita Formation at Mount Arrowsmith.

**Remarks.** This species differs from *P. gradatus* mainly in having sharp anterior margins. Serpagli (1974) initially recognized a trimembrate apparatus consisting of a symmetrical bicostate Sa, asymmetrical bicostate Sb, and asymmetrical acostate Sc elements. However, his illustrations depict two distinct forms of elements. The holotype (Serpagli, 1974, pl. 27, fig. 15) and a paratype (Serpagli, 1974, pl. 27, fig. 14) have an extremely short base, and are interpreted as PElements. The other three figured paratypes have a relatively longer base supporting a more or less erect cusp, and represent a symmetry transition series of S elements.

This species is uncommon at Mount Arrowsmith. Three types of S elements were recovered, but no P elements have been recognized. The Sa element is symmetrical or nearly so with a posterolateral costa on each side (Fig. 22L). The Sb element is similar to the Sa, but asymmetrical, with cusp curved inwards and slightly twisted (Fig. 22M,N). The Sc element is asymmetrical with sharp anterior and posterior margins, and a more expanded base; it has a posterolateral costa on each side, and a thin inner-laterally curved anterior edge (Fig. 22 O–R).

**Protopanderodus nogamii** (Lee, 1975)

Fig. 23A–P, ?Q

*Scopelodus cf. bassleri* Igo & Koike, 1967: 23, pl. 3, figs. 7, 8, text-fig. 6B.


*Panderodus* sp. Serpagli, 1974: 59, pl. 24, figs. 12, 13, pl. 30, figs. 12, 13.

*Scopelodus nogamii* Lee, 1975: 179, pl. 2, fig. 13.

*Protoperanerodus primitus* Druce (MS), in Cooper, 1981 (nomen nudum): 174, pl. 27, figs. 3, 4 (cum syn.).

*Scopelodus euspinus* Jiang & Zhang, in An et al., 1983: 140, pl. 13, fig. 27, pl. 14, figs. 1–8 (cum syn.).

*Protopanderodus nogamii*.—Watson, 1988: 124, pl. 3, figs. 1, 6.

*Scopelodus euspinus*.—An & Zheng, 1990: 170, pl. 2, figs. 7–11, 13, 14, 16.

*Protoperanerodus primitus*.—Stait & Druce, 1993: 307, figs. 13A–C, 18D,E,G–K (cum syn.).

*Paraperanerodus paracornuformis*.—Albanesi, in Albanesi et al., 1998: 116, partim pl. 12, fig. 13, 8?–10?, non 11, 12.

**Material.** Three specimens (2 Sb, 1 Sc) from the Tabita Formation at Mount Arrowsmith, and 128 specimens (12 Pa, 18 Pb, 35 Sa, 55 Sb, 5 Sc, 3 Sd) from unnamed dolomitic limestone unit at Koonenberry Gap.

**Description.** A species of *Protopanderodus* consisting of a sixmembrane apparatus; all elements with a distinctive deep and narrow furrow on one lateral side (Sc) or both sides (other elements); surface coarsely striated, with striae more prominent on the base. *P elements* slightly asymmetrical, more laterally compressed, with a median furrow on each side and a shorter base; cusp with a broad anterior face, and a sharp blade-like posterior margin; basal cavity peanut-like in outline (Fig. 23I,N); some specimens (Fig. 23J) with a prominent rounded costa situated posterior to the furrow on the inner lateral face. The Pa element (Fig. 23I–N) has a subrect cusp and shorter base, the curvature between the posterior margin of the cusp and the base is about 90° or slightly less; the Pb element (Fig. 23 O,P) has a more or less proclined cusp with a longer base, and a more gradational curvature between the posterior margin of the cusp and the base. *S elements* are less laterally compressed, with a longer base, and a more or less rounded posterior margin. Sa element (Fig. 23A,B) symmetrical with a furrow on each side; Sb element similar to Sa, but with a more laterally compressed base (Fig. 23C,D); Sc element (Fig. 23E,F) asymmetrical, with a furrow only on inner lateral face; Sd element similar to Sb but asymmetrical, with cusp slightly twisted and curved inward (Fig. 23G,H).

**Remarks.** This species is characterized by having a distinctive deep furrow on one or two lateral faces, and by its coarsely striate surface. The furrow is not a true panderodontid furrow, and disappears just before reaching the basal margin, as do also the coarse striae.
Fig. 23. A–P, *Protopanderodus nogamii* (Lee, 1975): A, Sa element, AMF120430, C1611, basal view showing the basal cavity; B, Sa element, AMF120428, C1612, lateral view; C, D, Sb element, AMF120427, C1612, C, lateral view of the basal part showing furrow and striation, D, lateral view; E, F, Sc element, AMF120431, Y4–2, E, inner lateral view, F, outer lateral view; G, H, Sd element, AMF120429,
Although Cooper (1981) figured two S elements of *Protopanderodus primitus* Druce (MS), he provided neither adequate description nor designation of the types in the expectation that the species would be fully described by Druce in a subsequent publication. However, the species was not formally introduced until Stait & Druce (1993) designated the specimen figured by Cooper (1981, pl. 27, fig. 4) as the lectotype and the other figured specimen (Cooper, 1981, pl. 27, fig. 3) as the paratype for *P. primitus*. They also cited Cooper as the original author of the species, rather than Druce. Jiang & Zhang (in An et al., 1983) in the meantime had erected *Sclopopodus euspinus*, based on material from the Beijianzhuang Formation (approximately Chewtonian to Castlemainian age) of Hebei Province, North China, without knowledge of Cooper's work. Jiang & Zhang (in An et al., 1983) described *S. euspinus* as a form species characterized by a furrow on each side and a low costa immediately anterior to it. Among their figured specimens, two morphotypes can be recognized—one, represented by the holotype (An et al., 1983, pl. 14, fig. 3) and two other illustrated specimens (pl. 14, figs. 1, 2), is more laterally compressed with a wider base (referred to herein as the P elements), while the other morphotype (assigned here to the S elements) is less laterally compressed with a longer base (see An et al., 1983, pl. 14, figs. 4, 5).

Stait & Druce (1993) correctly considered *S. euspinus* conspecific with *P. primitus*, but the Chinese species has priority over *P. primitus* which in 1983 was a nomen nudum. They revised this species in terms of multielement terminology, referring the laterally compressed symmetrical form to the Pa element, and also recognized an asymmetrical Pb element. The less laterally compressed symmetrical form was assigned to the Sa element. Two additional asymmetrical elements, one uni-furrowed (here referred to as Sc) and a tri-furrowed form were also recovered from the Coolibah Formation to form the first symmetry transition series (Stait & Druce, 1993). The Sc element is comparatively rare in the western New South Wales faunas. The Sb element defined by Stait & Druce (1993) is similar to the Sa, but slightly asymmetrical with the furrow on the outer lateral face situated more towards the posterior margin and with the cusp slightly curved inward—it is recognized here as the Sd element. Their figured tri-furrowed Sd element (Stait & Druce, 1993, fig. 18K) is regarded as representing the Pb position, being laterally compressed with a proclined cusp and a shorter base. The rounded second costa posterior to the furrow on the inner side is not considered a distinctive feature. It may occur in either Pa (Fig. 23J herein) or Pb (Stait & Druce, 1993, fig. 18K) elements, and in our material is relatively weak in comparison with the specimen illustrated by Stait & Druce (1993).

Watson (1988) interpreted *Protopanderodus euspinus* as a junior synonym of *Protopanderodus nogamii* (Lee, 1975). Jiang & Zhang (in An et al., 1983) differentiated *P. nogamii* from *P. euspinus* mainly on its shorter base and reclined cusp. They stated that whereas both species generally co-occur over an extended stratigraphic range in North China, from the Liangjiaoshan Formation (Bendigonian) to the Fengfeng Formation (Gisbornian) of North China, only *P. nogamii* was recorded from South China (An, 1987), and therefore, the species were treated as separate.

*Protopanderodus nogamii* was originally described from the Nandal Formation, of suggested Middle Ordovician age, in North Korea. Based on the illustration of the holotype and only figured specimen (Lee, 1975, pl. 2, fig. 13), the following differences in comparison with the type material of *P. euspinus* are noticed. The holotype of *P. nogamii* is a larger specimen (width of the base 570 µm), with a reclined cusp, and coarser striae (8/100 µm) which are developed only on a shorter, posteriorly more extended base. In contrast, the holotype of *P. euspinus* is smaller (width of the base 150 µm) with a proclined or suberect cusp, and bears finer striae (20–25/100 µm). Otherwise, the two species are closely comparable, with *P. nogamii* representing one extreme morphotype in the species apparatus (Albanesi pers. comm., 2002). Therefore, despite being defined on a solitary element, *P. nogamii*—according to strict application of nomenclatural priority—takes precedence over *P. euspinus* and all other synonyms mentioned in this discussion.

An & Zheng (1990: 173) included two specimens designated as *Protopanderodus* sp. by Ethington & Clark (1982) from the Lehman Formation of the Ibex area, Utah, with *Protopanderodus euspinus*. Since both specimens appear to have a true panderodontid furrow situated on the posterior face, it seems that this reassignment is unjustified.

One specimen (Fig. 23Q) from Koonenberry Gap (C1612) is a symmetrical element resembling *P. nogamii*, but is doubtfully assigned due to its much shorter proclined cusp, and a curved lateral costa and furrow on each side. These variations might reflect some kind of pathological deformation.

*Protoprioniodus* McTavish, 1973

**Type species.** *Protoprioniodus simplicissimus* McTavish, 1973.

**Remarks.** As pointed out by Smith (1991), interpretations of the apparatus composition of the genus and its phylogenetic relationships vary considerably. It is clear that at least three distinct species groups have been previously assigned to *Protoprioniodus*. The first group, represented by the type species, *P. simplicissimus* McTavish, 1973, and *P. yapu* Cooper, 1981, have a pastinate P element with a robust cusp, similar to the P elements of *Prioniodus* but with adenticulate processes in this and all other elements. Based on this interpretation, which was followed by Cooper (1981), Ethington & Clark (1982), and Smith (1991), the apparatus has a ramiform-pectiniform configuration. Material from the western New South Wales collections supports the interpretation of Sweet (1988: 61) who
envisaged the apparatus as consisting of pectiniform P elements, makellate M element and adentriculate ramiform S elements.

The second group, including P. nyinti and P. aranda from the Amadeus Basin previously referred to the genus by Cooper (1981), have the P positions occupied by pectiniform elements, but in lacking a recognizable cusp they do not conform to the concept of Protoprioniodus. These species are now distinguished as the new genus Cooperignathus, in which the anterior, posterior and outer lateral processes are characterized by having blade-like crests on upper surfaces, rather than rows of nodes in more derived forms like Eoplacognathus.

The third species group is represented by P. papiliosus (van Wamel, 1974) and P. cowheadensis Stouge & Bagnoli, 1988. These latter authors, as well as Johnston & Barnes (2000), regarded the genus as including oistodiform elements in both the P and M positions, implying a ramiform-ramiform configuration.

Some authors (McTavish, 1973; Cooper, 1981) have suggested that Protoprioniodus might have evolved from Acodus based on general similarity of their P elements, although in Protoprioniodus these have a more strongly developed adentriculate outer-lateral process. An alternate proposal (Sweet, 1988: 61) related Protoprioniodus more closely to Oistodus, citing the geniculate nature of their skeletal elements.

**Protoprioniodus yapu** Cooper, 1981

Fig. 24A–D

*Protoprioniodus yapu* Cooper, 1981: 178, pl. 30, figs. 3–5, 8, 9, 11, 13.

*Protoprioniodus costatus* An, 1987: 174, *partim* only, pl. 14, figs. 1, 4, pl. 16, fig. 25.

†*Protoprioniodus yapu*.—An, 1987, pl. 16, fig. 27.

*Protoprioniodus costatus*—Ding et al., *in* Wang, 1993: 197, pl. 14, fig. 27.

*Protoprioniodus yapu*.—Ding et al., *in* Wang, 1993, pl. 15, figs. 10, 12.

*Protoprioniodus aranda*.—Johnston & Barnes, 2000: 42, *partim* only, pl. 6, fig. 22.

**Material.** Seventeen specimens (5 Pb, 10 M, 2 doubtful S) from the Tabita Formation at Mount Arrowsmith.

**Remarks.** Nicoll (2002, pers. comm.) indicated that *Protoprioniodus yapu* may belong to part of the species apparatus of either *P. nyinti* or *P. aranda* (both transferred to the new genus Cooperignathus herein). As *P. yapu* is relatively rare in the Tabita Formation, Cooper’s (1981) definition is retained herein pending further study of the type material from the Horn Valley Siltstone.

In erecting *P. yapu*, Cooper (1981) illustrated two morphotypes of the P elements, both of which are highly modified pastinate units with a prominent cusp. The paratype (Cooper, 1981, pl. 30, fig. 11) with rudimentary denticulate outer lateral processes is here designated as the Pa element. The holotype (Cooper, 1981, pl. 30, fig. 9) lacks an outer lateral process, and is assigned to the Pb position (Fig. 24B–D). The M element is characterized by having a strongly inner laterally recurved cusp and an adenticulate, long outer lateral process, and apparently lacks an anticusp or inner lateral process (Fig. 24A). The strongly laterally compressed S elements (not identified with certainty at Mount Arrowsmith) have a strong mid-costa on the inner-lateral face.

*Protoprioniodus* was distinguished by An (1987) from *Oelândodus* van Wamel, 1974 by having a prominent ridge-like costa above the basal margin. Comparison of the two species originally ascribed to *Oelândodus* shows that the type species, *O. elongatus* (Lindström, 1955), apparently lacks this feature, while its presence in *O. costatus* van Wamel, 1974 justifies An’s (1987) reassignment of this species to *Protoprioniodus*. The P elements of *P. costatus* and *P. yapu* are similar in morphology, but their S and M elements are easily distinguished. The S element of *P. costatus* shows some resemblance to the S elements of *C. nyinti*; both have a tricostate cusp, costae extending basally to a lateral process on each side, and a long posterior process. The M element has a long pointed anticusp, straight basal margin and a strongly outer laterally recurved cusp. On this basis, the P, S and M elements referred to *P. costatus* by An (1987) from China are identical with those of *P. yapu*, rather than conspecific with the Swedish type material of *P. costatus*. 

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**Fig. 24.** A–D. *Protoprioniodus yapu* Cooper, 1981: A, M element, AMF120448, M/A7, posterior view; B, C, Pb element, AMF120449, Y4–2, B, outer lateral view, C, inner lateral view; D, Pb element, AMF120450, M/A7, outer lateral view. E, F, *Oneotodus* sp.: E, AMF120451, M/A11-3, posterolateral view; F, AMF124226, C1612, inner lateral view. Scale bars 100 µm.
Scalpellodus Dzik, 1976

**Type species.** Protopanderodus latus van Wamel, 1974.

*Scalpellodus latus* (van Wamel, 1974)

Fig. 25A–J

*Protopanderodus latus* van Wamel, 1974: 91, pl. 4, figs. 1–3.

*Scalpellodus latus*.–Łośgren, 1978: 99, pl. 5, figs. 10, 14, pl. 6, figs. 1–4, 7, 21 (*cum syn.*).

*Scalpellodus latus*.–Cooper, 1981: 179, pl. 27, figs. 7–10, 13–15.

**Material.** One specimen (Sa) from limestone nodules within shales of the upper Yandaminta Quartzite and 28 specimens (1 P?, 2 Sa, 12 Sb, 5 Sc, 6 Sd) from the overlying Tabita Formation at Mount Arrowsmith.

**Remarks.** This coniform species is similar to *Cornuodus longibasis*, but is more laterally compressed, and ornamented with fine striae (Fig. 25A,H), which is a critical character in recognition of this species. Of the three morphotypes distinguished by Cooper (1981), we also recognize a symmetrical Sa element with a broad anterior face, a sharp costa on each lateral face, and a costa along the posterior margin (Fig. 25A,B). All three costae on the Mount Arrowsmith specimens are relatively weakly developed in comparison with the Sa element illustrated from the Horn Valley Siltstone (Cooper, 1981, pl. 27, figs. 7, 9). Asymmetrical forms (defined as the Sb element by Cooper), with a sharp posterior margin and an anterolateral costa only on the inner lateral side, can be segregated into an Sb element (Fig. 25C,D) with a proclined cusp, and another type with an erect cusp and a more laterally compressed base—here referred to the Sd element (Fig. 25E,F,H,I). The nearly symmetrical element with sharp anterior and posterior margins, which Cooper (1981) identified as the Sc element, is also recognized (Fig. 25J). A small, nearly symmetrical specimen with a recurved cusp (Fig. 25G) possibly occupied the P position of this species.

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Fig. 25. *Scalpellodus latus* (van Wamel, 1974): A,B, Sa element, AMF120452, Y4–2, A, inner lateral view of the basal part showing the fine striae, B, lateral view; C, Sb element, AMF120453, Y4–2, inner lateral view; D, Sb element, AMF120454, M/A11-1, inner lateral view; E,H, Sd element, AMF120455, M/A7, E, inner lateral view, H, close up showing fine striae; F, Sd element, AMF120456, M/A7, posterior view; G, P element, AMF120457, TAB1/39.5, inner lateral view; I, Sd element, AMF120458, M/A7, inner lateral view; J, Sc element, AMF120459, Y4–2, lateral view. Scale bars 100 µm, unless otherwise indicated.
Scolopodus Pander, 1856

Type species. Scolopodus sublaevis Pander, 1856.

Scolopodus multicostatus Barnes & Tuke, 1970

Fig. 26A–R

Scolopodus multicostatus Barnes & Tuke, 1970: 92, pl. 18, figs. 5, 9, 15, 16, text-fig. 6D.

Material. 85 specimens (8 Pa, 14 Pb, 17 Sa, 17 Sb, 17 Sc, 12 Sd) from the Tabita Formation at Mount Arrowsmith, and 48 specimens (3 Pa, 7 Pb, 6 Sa, 15 Sb, 12 Sc, 5 Sd) from the unnamed dolomitic limestone unit at Koonenberry Gap.

Diagnosis. A species of Scolopodus consisting of a sixmembrane apparatus including two laterally compressed sciodiform P elements with a short base, and multicostate S elements with a longer base and a broad anterior margin; symmetrical Sa and Sd elements more or less rounded in cross section, asymmetrical Sb and Sc elements laterally more compressed.

Description. P elements sciodiform with erect cusp; Pa element with a smooth outer lateral face; inner face multicostate with a median costa, an anterolateral costa, a posterior costa and a number of interposed weaker costae (Fig. 26A,B). Pb element has a stronger, more or less blade-like antero-inner lateral costa, and a costa along the posterior margin (Fig. 26C–E); outer lateral face smooth or with a few short costae near the base. Sa element symmetrical, with a reclined cusp which is more or less rounded in cross section, a broad smooth anterior face, and bearing three or more costae on each posterolateral face (Fig. 26F–I). Sb element slightly asymmetrical, laterally compressed; cusp proclined with a broad anterior face and sharp posterior margin; inner lateral face with two to four stronger costa and several finer ones in between; outer lateral face with a stronger anterolateral costa and several finer ones posterior to it (Fig. 26J,K,M,N). Sc element asymmetrical, laterally compressed; cusp suberect with a sharp posterior costa along the posterior margin and a sharp anterolateral costa on the inner side (Fig. 26L), as well as a number of weaker costae (typically three or four) on each lateral face; costae on the outer lateral face weaker than those on the inner lateral face (Fig. 26O). Sd element nearly symmetrical, less laterally compressed in comparison with the Sb and Sc elements; basal cavity opening rounded (often flared); broad anterior face, a costa along the posterior margin, with several costae on each of the lateral faces; the anterolateral costa on each side stronger than others (Fig. 26Q,R).

Remarks. Two species of Scolopodus are present in western New South Wales; S. multicostatus is distinguished in generally having fewer costae, which are also much weaker and not as sharp-edged as in the co-occurring S. quadratus. The Newfoundland type specimens of S. multicostatus figured by Barnes & Tuke (1970), which are all slightly asymmetrical with a short base and erect cusp, are identical to the New South Wales Sb elements. Stait & Druce (1993) recognized a sixmembrane apparatus for S. multicostatus from the Coolibah Formation of the Georgina Basin, including sciodiform (Pa), posteriorly keeled sciodi- form (Pb), acontiodiform (Sa), planoconvex (Sb), laterally compressed paltoadiform (Sc) and equidimensional paltoadiform (Sd) elements. The Coolibah Formation material generally exhibits more numerous, strongly developed costae than do the specimens in western New South Wales; however, Pa elements from both areas are identical. Specimens referred to the symmetrical Sa element in our collections have weakly developed costae, a broader anterior face, and a more strongly reclined cusp in comparison with the Sa element illustrated from the Coolibah Formation (Stait & Druce, 1993, fig. 19L).

Scolopodus quadratus Pander, 1856

Fig. 27A–O

Scolopodus quadratus Pander, 1856: 26, pl. 2, fig. 6a–d, pl. A, fig. 5d. Scolopodus costatus Pander, 1856: 26, pl. 2, fig. 7a–d, pl. A, fig. 5e. Scolopodus striatus Pander, 1856: 26, pl. 2, fig. 8a–d, pl. A, fig. 5f. Scolopodus rex Lindström, 1955: 595, 596, pl. 3, fig. 32. Scolopodus rex var. paltoadiformis Lindström, 1955: 596, pl. 3, figs. 33, 34. Scolopodus quadratus.—Fåhraeus, 1982: 21, pl. 2, figs. 1–14, pl. 3, figs. 1–8, 15. Scolopodus rex.—Seo et al., 1994, fig. 10.10–10.12. Scolopodus rex.—Albanesi, in Albanesi et al., 1998: 133, pl. 12, figs. 14–17 (cum syn.). Scolopodus quadratus.—Zhen et al., in press: pl. 5, figs. 15–21 (cum syn.).

Material. One specimen (Sd) from limestone nodules within shales of the upper Yandaminta Quartzite and 37 specimens (4 Pb, 12 Sa, 12 Sb, 1 Sc, 8 Sd) from the overlying Tabita Formation at Mount Arrowsmith; two specimens (1 Sa, 1 Sd) from the unnamed dolomitic limestone unit at Koonenberry Gap.

Remarks. Five element types have been recovered from the Tabita Formation, including a sciodiform Pb element with a proclined cusp, four costae on the inner lateral face and a smooth outer lateral face (Fig. 27A–C), and four sciodiform elements: the symmetrical Sa (Fig. 27D–F), nearly symmetrical Sb (Fig. 27G–J), laterally compressed nearly symmetrical Sc element (Fig. 27M–O), and asymmetrical Sd element with slightly twisted cusp (Fig. 27J–L). However, the species is highly variable, and there are intermediate morphotypes varying in the number of costae, symmetry, curvature of the cusp, and degree of lateral compression. Scolopodus quadratus also occurs in the slightly older Hensleigh Siltstone of the Lachlan Fold Belt (Zhen et al., in press).

Triangulodus van Wamel, 1974

Type species. Paltodus volchovensis Sergeeva, 1963.

Triangulodus larapintinensis (Crespin, 1943)

Fig. 28A–V

Material. 259 specimens (41 Pa, 31 Pb, 42 M, 31 Sa, 57 Sb, 41 Sc, 16 Sd) from the Tabita Formation at Mount Arrowsmith, and 43 specimens (6 Pb, 10 M, 2 Sa, 10 Sb, 15 Sc) from unnamed dolomitic limestone unit at Koonenberry Gap.

Description. Apparatus septimembrate; the Pa element scantodiform with erect cusp, and sharp anterior and posterior margins (Fig. 28A,B). Pb element similar to the Pa, but with cusp curved inward and inner laterally twisted and the posterior margin showing a rounded gradational curvature towards the base (proclined near the base, Fig. 28C,D). M element geniculate with a short adenticulate outer lateral process (Fig. 28E,F). Sa element symmetrical, with a broad anterior face, a posterior costa, and a lateral costa on each side (Fig. 28G–K). Sb element asymmetrical with a broad anterior face, a weak costa along the posterior margin and a sharp costa on the inner lateral face near the anterior margin, and with a smooth outer lateral face (Fig. 28L–O). Sc element asymmetrical with a suberect cusp, having a sharp costa along the posterior and anterior margins; base more inflated on the outer side with anterior margin laterally curved (Fig. 28P–S). Sd element similar to Sc, but strongly asymmetrical and less laterally compressed with a twisted cusp (Fig. 28T–V).

Remarks. The type material from the Waterhouse Range, central Australia, which was poorly illustrated by Crespin.
(1943), was re-examined by Cooper (1981) who assigned the species to *Trigonodus Nieper, in Hill et al., 1969*. However, as C.Y. Wang (1992) pointed out, that name is pre-occupied by the Triassic bivalve *Trigonodus Sandberger, in Alberti, 1864*, leaving *Triangulodus* as the valid genus. A brief discussion of the complex nomenclatural history of Crespin’s species, provided by Strusz (1994: 132, 252), suggests further study (probably involving recollec-


Inflation at the type locality is needed to fully resolve the species concept. As this is beyond the scope of the present work, we are reliant on Cooper’s concept of the species, together with comments kindly provided by R.S. Nicoll who is in the process of reviewing Crespin’s and Cooper’s types.

The material from western New South Wales is identical with that of the species illustrated from the Horn Valley Siltstone, except that the Pb element from central Australia has a much more strongly twisted cusp (Cooper, 1981, pl. 27, fig. 11). Cooper (1981) recognized a quadricostate asymmetrical Sc element, which he did not illustrate. The asymmetrical Sc element (Cooper, 1981, pl. 27, fig. 5), described as tricostate (anterior, posterior, and one lateral), is here regarded as the Sb element. Cooper’s Sd element (1981, pl. 27, fig. 12) is the most laterally compressed specimen, with a sharp costa along the posterior margin, and an inner laterally curved costa along the anterior margin. It is now reassigned to the Sc position. An asymmetrical element like Sc but with a twisted cusp from the western New South Wales fauna is interpreted as the Sd element (Fig. 28T–V); it is also distinguished by its less laterally compressed base.

**Triangulodus sp. A**

**Material.** 15 specimens (4 Sa, 5 Sb, 5 Sc, 1 Sd) from the Tabita Formation at Mount Arrowsmith. 64 specimens (11 Sa, 30 Sb, 21 Sc, 2 Sd) from unnamed dolomitic limestone unit at Koonenberry Gap.

**Description.** Only S elements are recognized for this species, characterized by having an open, slightly inflated basal cavity. Sa element symmetrical, tricostate, with a costa along the posterior margin, a broad anterior face, and a costa on each lateral side (Fig. 29A–E); cusp suberec, triangular in cross section. Sb element asymmetrical, bicostate, with an anterolateral costa on the inner lateral side, a posterolateral costa on the outer lateral side, and with broad anterior and posterior surfaces (Fig. 29F–I). Sc element asymmetrical, with a sharp costa along the anterior and posterior margins, and with the most laterally compressed base of all elements recognized; anterior costa inner laterally curved; a broad carina also developed on the inner lateral face (Fig. 29J–M). Sd element nearly symmetrical, with broad anterior and posterior margins, and with a sharp costa on each lateral face (Fig. 29N–P).

**Remarks.** This species, especially the Sa and Sc elements, somewhat resembles *T. larapintinensis*, but generally all elements are less laterally compressed with an open, slightly inflated basal cavity.

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**Ulrichodina Furnish, 1938**

**Type species.** Acontiodus abnormalis Branson & Mehl, 1933.

**Ulrichodina sp. cf. simplex Ethington & Clark, 1982**

*Fig. 14M–O*

“Drepanodus” sp. 3 Serpagli, 1974: 45, pl. 10, fig. 7a–b, pl. 21, fig. 15.


*Ulrichodina ?simplex*.–Smith, 1991: 71, fig. 40d.

*Ulrichodina n.sp. 3 Repetski, 1982: 56, pl. 26, fig. 7a–c, fig. 8H.

**Material.** A single specimen from limestone nodules within shales of the upper Yandaminta Quartzite at Mount Arrowsmith.

**Remarks.** Due to limited material, neither generic nor specific identification is certain. This specimen may well correspond to the Sa element of a *Drepanoistodus* species. However, based on its distinctive basal cavity shape and the notch on each side, it is tentatively ascribed to *Ulrichodina*. The specimen is a symmetrical, hyaline coniform unit with a laterally compressed, stout, erect cusp, having a distinctive, short, strongly posteriorly curved anticusp-like projection, which has a narrow but rounded anterior corner, and a distinct notch on the basal margin of both sides. It is nearly identical to a specimen referred to as *Drepanodus* sp. 3 from the San Juan Formation of the Argentine Precordillera (Serpagli, 1974). However, it is about twice the size of the San Juan specimen, and has the anticusp-like projection at the anterobasal corner more strongly curved posteriorly.

Ethington & Clark (1982) doubtfully assigned Serpagli’s San Juan specimen to their new species, *?Ulrichodina simplex*, which was based on four elements from the Fillmore Formation of the Ibex area, Utah. The three figured type specimens are rather poorly preserved. The holotype is a very large element (about three times as large as the San Juan specimen), has a much weaker development of the notch on each side of the basal margin, and a more laterally compressed cusp with sharp anterior and posterior margins. *Ulrichodina simplex* was also reported from the El Paso Group (Repetski, 1982), and from the Wandel Valley Formation of Greenland (Smith, 1991). In all these occurrences, it is represented by just a few specimens. The figured Greenland specimen, even more doubtfully assigned to *U. simplex*, is an albid element, with a laterally flared buttress on each side, rather than exhibiting a notch deeply carved into the base, as in the Mount Arrowsmith specimen.
Fig. 29. *Triangulodus* sp. A, A, Sa element, AMF124220, TAB1/8.1, A, basal view, B, posterolateral view; C–E, Sa element, AMF124221, Y4–8, C, D, posterolateral view, E, basal view; F, Sb element, AMF120483, Y4–2, inner lateral view; G, H, Sb element, AMF120485, C1613, G, upper, inner lateral view, H, upper, outer lateral view; J, Sb element, AMF120486, C1613, postero-inner lateral view; J, K, Sc element, AMF124222, C1613, J, basal view, K, inner lateral view; L, M, Sc element, AMF124223, C1613, L, inner lateral view, M, postero-inner lateral view; N–P, Sd element, AMF120487, M/A7, N, anterolateral view, O, posterolateral view, P, close up showing the fine striae. Scale bars 100 µm, unless otherwise indicated.
ACKNOWLEDGMENTS. Fieldwork by YYZ & BDW at Mount Arrowsmith was undertaken with the support of the Australian Research Council (grant A39600788 to BDW). The study was also supported by a Research Fellowship to YYZ kindly provided by the Sydney Grammar School. John Paterson (Macquarie University) is thanked for providing some additional conodont material from a measured section in the Mount Arrowsmith area. IGP sampled the Koonenberry Gap section under the guidance of Kingsley Mills (Geological Survey of New South Wales). Barry Cooper (Primary Industry & Resources Department of South Australia) kindly made available additional Horn Valley Siltstone collections for comparative study. Gary Dargan (Geological Survey of New South Wales) assisted with acid leaching, residue separation and other laboratory work. Scanning electron microscope photographs were prepared in the Electron Microscope Unit of the Australian Museum; Sue Lindsay is thanked for providing helpful assistance with the SEM work. Helen Beare is thanked for kindly carrying loan material to and from Adelaide. We are grateful for detailed reviews provided by Bob Nickoll (Australian National University) and Guillermo Albanesi (CONICET, Cordoba, Argentina) which markedly contributed to our understanding of several species. IGP publishes with permission of the Director General, NSW Department of Mineral Resources. This is a contribution to IGP Project no. 410: the Great Ordovician Biodiversification Event.

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