Biogeographic and Biostratigraphic Implications of the *Serratognathus bilobatus* Fauna (Conodonta) from the Emanuel Formation (Early Ordovician) of the Canning Basin, Western Australia

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**ABSTRACT.** Discovery of *Serratognathus bilobatus* in the Early Ordovician Emanuel Formation of the Canning Basin, Western Australia, has regional biogeographic and biostratigraphic implications. Distribution of *Serratognathus* indicates a close biogeographic link between Australia and adjacent eastern Gondwanan plates and terranes during the latest Tremadocian to early Floian (Early Ordovician), and the formation of the so-called “Australasian Province”, a distinctive biogeographic entity that existed throughout most of the Ordovician. The *S. bilobatus* fauna from the Canning Basin is much more diverse in comparison with those assemblages bearing *Serratognathus* from coeval Chinese Lower Ordovician successions and probably represents an assemblage inhabiting relatively deeper water (mid-outer shelf) environments. The Canning Basin fauna contains many pandemic forms, and bridges the gap in the regional correlation of this widely distributed fauna across eastern Gondwana.

This well-preserved, diverse fauna includes *Serratognathus bilobatus* and 23 associated species: *Acodus deltatus*?, *Acodus? transitans*, *Bergstroemognathus extensus*, *Cornuodus* sp., *Drepanodus arcuatus*, *Drepanoistodus* sp. cf. *D. nowlani*, *Fahraeusodus adentatus*, *Lissoepikodus nudus*, *Nasusgnathus dolonus*, *Paltodus* sp., *Paracordyodus gracilis*, *Paroistodus parallelus*, *Paroistodus proteus*, *Prioniodus adami*, *Protopanderodus gradatus*, *Protosiricodius simplicissimus*, *Scolopodus houlianzhaiensis*, *Semiacontiodus* sp. cf. *S. cornuformis*, *Stiptognathus borealis*, *Triangulodus bifidus*, *Tropodus australis*, gen. et sp. indet. A and gen. et sp. B. A *P. adami-S. bilobatus* Biozone is defined within the middle and upper Emanuel Formation. Correlation of this biozone suggests an early Floian (late *P. proteus* Biozone to possibly earliest *P. elegans* Biozone) age for the middle and upper members of the Emanuel Formation.


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Conodonts are abundant, diverse, and well-preserved in the Early Ordovician Emanuel Formation of the Canning Basin in Western Australia. In the nearly sixty years since the discovery of the fauna (Guppy & Opik, 1950), this rich fauna has formed the subject of several important studies, particularly on the prioniodontids by McTavish (1973) and by Nicoll & Ethington (2004), rhipidognathids by Zhen et al. (2001), Jumudontus brevis by Nicoll (1992), and Stiptognathus borealis (Repetski, 1982) by Ethington et al. (2000). As documentation of the entire fauna represented by a huge collection recovered from several measured sections and subsurface core material is still in progress, the current contribution focuses only on *Serratognathus bilobatus* Lee, 1970 and the associated fauna recovered from three samples of the Emanuel Formation.

The discovery of *S. bilobatus* in the Emanuel Formation, which was deposited in relatively deep water, mid-outer shelf settings, provides crucial new biostratigraphic data to more precisely date and correlate the *Serratognathus* faunas widely distributed in eastern Gondwana and adjacent Peri-
Regional geological setting and lithostratigraphy

The Canning Basin is an intracratonic sag basin, bounded by Precambrian rocks of the Kimberley Block to the north and the Pilbara Block to the south, occupying about one-sixth of Western Australia’s onshore area (Fig. 1). Sparsely inhabited and covered largely by flat-topped hills and sand dunes, it is dominated by a Palaeozoic-Mesozoic sedimentary succession more than 15 km in thickness. Extensive geological investigations have been carried out in the region for more than a century (Purcell, 1984), spurred on by its high potential for fossil fuel reserves.

The Early Ordovician Prices Creek Group, representing the oldest stratigraphic unit in the basin, is only exposed along its northern margin (Lennard Shelf) where it rests unconformably on Precambrian basement. This basal contact is observable only in drillcore. The Prices Creek Group is overlain paraconformably by the Middle Devonian (Givetian) Cadjebut Formation (Hocking et al., 1996). The group was initially subdivided into a lower Emanuel Limestone (subsequently renamed Emanuel Formation) and an upper Gap Creek Dolomite (later amended to Gap Creek Formation) with a measured thickness of 595 m for the Emanuel Formation in the type section along Emanuel Creek (Guppy & Öpik, 1950; Guppy et al., 1958). Exploration drill holes in the area revealed an additional unexposed section between the Emanuel Formation and metamorphic rocks of the Precambrian basement, comprising a dolomitic interval 88 m thick underlain by 82 m of arkose (Veevers & Wells, 1961; Henderson, 1963; McTavish & Leg, 1976; Towner & Gibson, 1983). Nicoll et al. (1993) formally named the dolomitic unit the Kudata Dolomite and the arkose unit the Kunian Sandstone, and revised the Emanuel Formation as consisting of limestone intercalated with shale and siltstone with a total thickness of 435 m exposed in the type section (Fig. 1).

Regionally the Emanuel Formation conformably overlies the Kudata Dolomite and is conformably overlain by the Gap Creek Formation of mid-late Floian age (Fig. 2). The basal arkose of the Kunian Sandstone was deposited in a major transgressive phase flooding the Canning Basin during the Tremadocian (Nicoll et al., 1993). This age determination was based on the regional tectonic framework and event stratigraphy, as well as fossil evidence from the overlying Kudata Dolomite, as no fossils were found in the arkose unit. The Emanuel Formation was subdivided into three informal members (Nicoll et al., 1993). However, in the type area, both lower and upper members with intercalated shale, siltstone and limestone (or nodular limestone in the upper member) are poorly exposed, whereas the limestone-dominated middle member with a thickness of 143 m is better exposed forming a more or less continuous section. The Emanuel Formation has not only yielded a rich conodont fauna, but also trilobites (Legg, 1976; Laurie & Shergold, 1996a, 1996b), graptolites (Thomas, 1960; Legg, 1976), nautiloids (Teichert & Glenister, 1954), gastropods (Gilbert-Tomlinson, 1973; Jell et al., 1984; Yu, 1993), brachiopods (Brock & Holmer, 2004) and various other invertebrate and microfossil groups (Guppy & Öpik, 1950; Brown, 1964; Schallreuter, 1993a, 1993b).
Age and correlation of the conodont fauna

McTavish (1973) described 20 multi-element conodont species and subspecies from the Emanuel Formation and lower part of the Gap Creek Formation; 19 of these were referred to prioniodontid genera, namely Acodus, Baltoniodus, Prioniodus and Protopriioniodus, and one to Periodontidae. On the basis of correlation with Balto-Scandian and North America Mid-continent successions McTavish (1973) determined a Latorpian age (latest Tremadocian to Floian in current terminology) for the Emanuel Formation and lower part of the Gap Creek Formation; 19 of these were species and subspecies from the Emanuel Formation and McTavish (1973) described 20 multi-element conodont species WCB705/133 WCB705/243 161–166 m Total

<table>
<thead>
<tr>
<th>species</th>
<th>WCB705/133</th>
<th>WCB705/243</th>
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<th>Total</th>
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<td>527</td>
<td>970</td>
<td>119</td>
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</table>

Also from the Emanuel Formation, Oepikodus communis (Ethington & Clark, 1982) was found in the upper part of the Emanuel Formation (Table 1), Paroistodus paralellus, Acodus deltatus?, Tropodus australis, Protopanderodus gradatus, Stiptognathus borealis, Bergstroemognathus extensus, and Drepanodus arcuatus dominate the fauna, whereas Serratognathus bilobatus is relatively rare. As shown in Table 2, among the 24 species recorded in this study, 11 species were also recorded in the Honghuayuan Formation in the Yangtze Platform of South China (An, 1987, Ding et al. in Wang, 1993; Zhen et al., in press a), seven in the Liangjiashan Formation of the North China Platform (An et al., 1983), only three in the Qianzhongliangzi Formation of the Ordos Basin of North China Plate (An & Zheng, 1990), and four in the upper subgroup of the Qiliag Group of the Tarim Basin (Zhao et al., 2000). Recently a fauna closely comparable with that documented herein (with 12 species in common including S. bilobatus) was found in the Mooroonga Formation in the offshore Arafura Basin, north Australia (Nicoll unpublished material), indicating wide distribution of this species in western and northern Australia.

Jumudontus brevis Nicoll, 1992 ranges from the middle member to lower part of the upper member of the Emanuel Formation. It is a pandemic species, also found in Early Ordovician rocks in Utah and Texas (Ethington & Clark, 1982), Newfoundland (Stouge & Bagnoli, 1988), western Canada (Norford et al., 2002), Baltoscandia (Bergström, 1988) and Greenland (Smith, 1991). In the Fillmore Formation of Utah, J. brevis first appears three m above the FAD of O. communis and extends to 237.7 m above the base of the formation at section H, suggesting a correlation with the lower O. communis Biozone (Ethington & Clark, 1982). In Newfoundland, it occurs in the upper part of Bed 9 (upper P. elegans Biozone) and lower part of Bed 11 (O. evae Biozone) of the Cow Head Group (Stouge & Bagnoli, 1988), an interval slightly higher than its occurrence (= upper P. proteus Biozone to lower P. elegans Biozone) in the Emanuel Formation.

Stiptognathus borealis (Repetski, 1982) is present from the upper part of the middle member to the basal part of the upper member of the Emanuel Formation, a range slightly shorter than that of J. brevis (Ethington et al., 2000; Nicoll & Ethington, 2004). It was also recorded from the Great Basin (Ethington & Clark, 1982; Ethington et al., 2000), western
Table 2. Comparison of occurrence of conodont species of the *Serratognathus* fauna from the Emanuel Formation with their distribution in other *Serratognathus* faunas recognized in China and other coeval successions referred to in the text.

<table>
<thead>
<tr>
<th>species</th>
<th>mid-upper part of Emanuel Formation</th>
<th>mid-upper part of Marathon Limestone of Texas</th>
<th>mid Qian-Zhongliangzi Formation Ordos Basin</th>
<th>uppermost Meitan Formation in South China (Zhen et al., 1987)</th>
<th>South China</th>
<th>North China</th>
<th>uppermost Qiulitag Group Formation Ordos Basin</th>
<th>uppermost Arafura Basin</th>
<th>northern Australia (Nicoll, unpublished material)</th>
<th>Setul Limestone</th>
<th>Malaysia</th>
<th>uppermost Topui Formation</th>
<th>Newfoundland</th>
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<td><em>Bergstroemognathus extensus</em></td>
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Texas (Repetski, 1982), and the Argentine Precordillera (Lehnert, 1995; Albanesi in Albanesi et al., 1998). According to Ethington et al. (2000), it occurs in the Fillmore Formation of Utah, in the upper quarter of the El Paso Group and in the upper member of the Marathon Limestone of Texas, and in the Mountain Springs Formation of Nevada, constrained within an interval of upper *Acodus deltatus*/*Oneotodus costatus* Biozone to lower *O. communis* Biozone (early Floian age). However, in the Argentine Precordillera, earliest occurrence of *S. borealis* occurs in the upper *P. proteus* Biozone within the Tremadocian/Floian boundary interval.

*Scolopodus houlanzhaiensis* An & Xu in An et al., 1983 occurs abundantly in the Liangjiashan Formation of North China with a similar stratigraphic range to that of *Serratognathus bilobatus* (An et al., 1983), and was also reported from the Honghuayuan Formation in Guizhou (South China) in association with *Serratognathus diversus* (Zhen et al., in press a). As both the Liangjiashan Formation and Honghuayuan Formation were deposited in shallow subtidal settings, faunas recovered from these two units are dominated by endemic forms, and it is difficult to directly correlate them with either the Balto-Scandian or North American Mid-continent successions. Thus the presence of *S. houlanzhaiensis* in association with *Serratognathus bilobatus* in the Emanuel Formation is critical to bridging this correlation gap.

*Triangulodus bifidus* Zhen in Zhen et al., 2006 is a morphologically distinctive species occurring throughout the Honghuayuan Formation and also into the lower part of the overlying Meitan Formation in South China (Zhen et al., 2006, 2007a). It is apparently a rare species in the Emanuel Formation, represented by only a few specimens (Fig. 15I–K), and will be reported from the *S. bilobatus* fauna in the Arafura Basin of northern Australia (Nicoll unpublished material).

Co-occurrence of *Paroistodus proteus* and *P. parallelus* in the Emanuel Formation also suggests a correlation with the upper part of the *P. proteus* Biozone of the Balto-Scandian succession. Löfgren (1997) indicated that in Sweden, *Paroistodus parallelus* makes its first appearance in the uppermost *P. proteus* Biozone, often associated with *P. proteus*, and extends to the upper middle *O. evae* Biozone. More specifically, occurrence of *Prioniodus adami* in the upper part of the Emanuel Formation allows a direct correlation with the *P. adami* Biozone (= upper *P. proteus* Biozone) recognized in the Cow Head Group of Newfoundland (Stouge & Bagnoli, 1988). There, *P. adami* was reported ranging through the lower to upper part (but not top) of Bed 9 in the Ledge-Point of Head Section (Stouge & Bagnoli, 1988, fig. 3), and the *P. adami* Biozone (succeeded by the *P.
Biozone in the lower part of the Setul Limestone in Malaysia (Metcalfe, 1980, 2004), in the Mooroongga Formation (subsurface) of the Arafura Basin off the north coast of Australia (Nicoll unpublished material), and in the Emanuel Formation of the Canning Basin, Western Australia (this study). Zhylkaidarov (1998, p. 65) indicated the occurrence of *S. bilobatus* from the Shabakty Formation in Maly Karatau of southern Kazakhstan. However, as neither illustrations nor other information of the species from this locality are available, this Kazakhstan occurrence is considered doubtful at present. *Serratognathus diversus* is recorded in the Honghuayan Formation and coeval units in South China (An et al., 1985; An, 1987; Zhen et al., in press a), Liangjiashan Formation of North China (An et al., 1983), and the upper subgroup of the Qultiat Group of the Tarim Basin (Zhao et al., 2000). *Serratognathus extensus*, possibly representing the most advanced of the three species, has been reported only from the Liangjiashan Formation of North China Platform (An et al., 1983).

The type material of *S. bilobatus* was described from the Dumugol Formation in the Taebaeksan Basin in the central-eastern part of the Korean Peninsula (Lee, 1970; Choi et al., 2005). The Dumugol Formation (also called the Dumugol Shale) consists of shale and intercalated limestone whose thickness varies from 150 to 270 m across the region and contains cyclic successions shifting from the near-shore to the deeper subtidal facies on a low-relief carbonate shelf, which was believed to be part of an extension of the North China Platform during the Early Ordovician (Choi et al., 2001, 2005). It yielded abundant conodont and trilobite faunas closely comparable to the late Tremadocian to early Floian faunas of North China (Lee, 1970, 1975; An et al., 1983; Zhou & Fortey, 1986; Seo et al., 1994; Choi et al., 2005). Occurrence of the *Archaeoscyphia-Calathium* association (occasionally forming isolated bioherms) in the Dumugol Formation also supports a close biogeographic link with North China (Choi et al., 2005). Based on rich and diverse conodont assemblages, Seo et al. (1994) divided the Dumugol Formation into four conodont biozones (in ascending order): *Chosonodina herfurthi-Rossodus manitouensis* Biozone, *Colaptoconus quadraplicatus* Biozone, *Pararycopelodus gracilis* Biozone, and *Triangulodus dumugolensis* Biozone, with an age ranging from late Tremadocian to early Floian. They correlated the *Triangulodus dumugolensis* Biozone at the top of the Formation to the *S. bilobatus* Biozone of North China, but unfortunately *S. bilobatus* was not recovered from any of their studied samples, and the type horizon of this species described by Lee (1970) in the region was not pinned down in their new biostratigraphic scheme of the Dumugol Formation. However, Seo et al. (1994, p. 606) indicated that *S. bilobatus* also occurs in the overlying Maggel Formation as reported in two unpublished postgraduate theses.

In North China, *S. bilobatus* was widely reported as occurring in the Liangjiashan Formation within an interval correlated to the upper *P. proteus* Biozone to lower *P. elegans* Biozone of the Balto-Scandian conodont succession (Zhen et al., in press a). The Liangjiashan Formation is best exposed in the Zhaoqezhuang Section near Tangshan, Hebei Province, where it consists of a 160 m sequence of a thick-bedded lower limestone member and an upper dolomite member (Chen Xu et al., 1995) that conformably overlies the Yeli (Yehil) Formation of Tremadocian age and is overlain by the Beianzhuang Formation of the
late Floian to Dapingian age. An et al. (1983) subdivided the formation into four conodont biozones (in ascending order): (1) Scalpellodus tarsus Biozone; (2) Serratognathus bilobatus Biozone; (3) Serratognathus extensus Biozone; and (4) Paraserratognathus paltodiformis Biozone. The S. bilobatus Biozone is confined to the lower part of the Liangjiashan Formation with a total thickness of 30 m in the Zhaogezhuang Section; the overlying S. extensus Biozone ranges through the middle part of the formation with a total thickness of 50 m (An et al., 1983, p. 26).

In the Honghuayuan Formation (the coeval strata on the Yangtze Platform of South China), S. bilobatus is rare and has been reported only from the Lower Yangtze Valley (An & Ding, 1982, 1985). A closely related species, S. diversus, is dominant in the fauna. Recent studies (Zhen et al., in press a) of the conodonts from the Honghuayuan Formation at its type locality and several other sections in Guizhou resulted in the recognition of three conodont biozones in the Formation (in ascending order): Triangulodus bifidus Biozone, Serratognathus diversus Biozone and Prioniodus honghuayuanensis Biozone. In the type section of the Honghuayuan Formation, S. diversus is confined to an interval of 13.5 m in the middle part of the Formation which is correlated to the upper P. proteus Biozone of the Balto-Scandian succession (Zhen, 2007; Zhen et al. in press a).

When correlating the conodont fauna from the Emanuel Formation and the lower Gap Creek Formation with well-studied Balto-Scandian and North America Mid-continent conodont successions, McTavish (1973, p. 31) was puzzled by the fact that Balto-Scandian Lower Ordovician successions were condensed, while North America Mid-continent successions, although with "comparable thickness to the Emanuel Formation" had faunas "of limited value for precise age determination". At the time, he did not attribute these faunal differences and difficulties in correlation to either ecological or biogeographical reasons. It is now understood that distribution of conodont animals was largely controlled by the water temperature and the water depth of their habitats (see Zhen & Percival, 2003). Higher resolution of the faunal correlation can only be achieved by comparing faunas from the same biogeographical province and Domain or at least from the same realm, otherwise ecological and biogeographical overprints should be removed or discounted when comparing faunas from different biogeographical settings.

A restricted distribution of Serratognathus in eastern Gondwana (Fig. 3) strongly supports the concept that the so-called "Australasian Province" became evident in the latest Tremadocian and early Floian, and persisted through
most of the Ordovician (Nowlan et al., 1997; Zhen et al. in Webby et al., 2000). Restriction of S. diversus primarily to the South China and the Tarim plates also indicates a closer biogeographic relationship between these two Chinese plates in the early Floian, and agrees with the recent biogeographic analysis based on the trilobite geographical and stratigraphical distribution data from the Chinese Cambrian (Zhou et al., 2008) and Ordovician (Zhou & Zhen, 2008). Trilobite data (Zhou & Zhen, 2008; Zhou et al., 2008) suggested that a broad undifferentiated biogeographic entity persisted in the Chinese plates and terranes positioned in eastern Gondwana from Cambrian to Tremadocian time, and became more diversified in the early Floian when two subprovinces (North China and South China) could be recognized (Zhou et al., 2008, fig. 2). Trilobite distributional patterns and sharing of several endemic forms also support a closer biogeographic tie between Australia and North China (Choi et al., 2001; Zhou & Zhen, 2008; Zhou et al., 2008).

Material and methods

All photographic illustrations shown in Figs 4 to 16 are SEM photomicrographs captured digitally (numbers with the prefix 'IY' are the file names of the digital images). Conodont specimens for this study are from three samples from the Emanuel Formation that bear S. bilobatus. Both WCB705/113 and WCB705/243 are from Section WCB 705 measured by following the line of the type section (Guppy & Öpik, 1950; Grid Ref. for base: 18°39’50”S 125°54’00”E; and top: 18°39’12”S 125°55’05”E), and sample 161–166 m is from a drillhole (BHP/PDH, grid 125°54’00”E; and top: 18°39’12”S 125°55’05”E), and in the northern margin of the Canning Basin. Figured specimens bearing the prefix CPC are housed in the Palaeontology Collection of Geoscience Australia in Canberra. Those bearing the prefix “AM “F” (Figs 12–14) are deposited in the collections of the Palaeontology Section at the Australian Museum, Sydney, and were collected from the Honghuayuan Formation in Guizhou (see Zhen et al. in press a for sampling locations and stratigraphic details). Several species documented herein only by illustration are rare in the collection. Among these species are introduced by Nicoll (1990, 1992).

**Phylum Chordata Balfour, 1880**

**Class Conodonta Pander, 1856**

**Acodus Pander, 1856**

_Diaphorodus Kennedy, 1980: 51._

**Type species.** _Acodus erectus_ Pander, 1856.

**Remarks.** The name _Acodus_, although widely cited in Ordovician conodont literature, has been a subject of debate and has remained one of the most controversial conodont genera for many years. As its type species _A. erectus_ was poorly known, Kennedy (1980) regarded _Acodus as a nomen dubium_, and this view was accepted by several subsequent workers (e.g., Sweet, 1988), while others (e.g., Lindström in Ziegler, 1977; Ji & Barnes, 1994; Zhen et al., 2004) retained _Acodus_ as a valid genus, but with varying definitions.

During the late Tremadocian to early Floian, conodonts evolved rapidly and experienced the greatest diversification event in their evolutionary history of some 300 million years. Several important clades, particularly the Prioniodontida, evolved from forms previously grouped with _Acodus_. Understanding of the apparatus composition and structure of _Acodus_ and related taxa is crucial in depicting the phylogenetic relationships and evolutionary history of these related clades (Stouge & Bagnoli, 1999). Therefore, a narrower rather than broader generic concept is needed for _Acodus_, which is restricted herein to forms with the same apparatus composition and structure as _Prioniodus_ but typically consisting of adenticulate elements.

Recent study by Nicoll & Ethington (2004) shows that Oepikodontidae diverged from the main clade of Prioniodontoida in the late Tremadocian through an adenticulate stage represented by _Lissoepikodus_ (recognized in the Emanuel Formation), and supports the hypothesis that both Prioniodontoida and Balognathoidea might have evolved from a common ancestor (Stouge & Bagnoli, 1999), most likely _Acodus_ (= _Diaphorodus + "Acodus" deltatus_ of Stouge & Bagnoli, 1999).

As Pander’s type specimens of the genotype, _A. erectus_, are lost, our current understanding of _Acodus_ is largely based on several subsequent works on _A. deltatus_ Lindström, 1955 and other related species documented by McTavish (1973),

[Fig. 4, caption continued]. (G), P element (short based), CPC39796, inner lateral view (IY129-024); (H), Sa element; (I), CPC39797, lateral view (IY129-009); (J), CPC39798, lateral view (IY129-11); (K), CPC39799, basal view (IY129-014). (L), P element (short based), CPC39800, inner lateral view (IY129-020). (M), Lb element, CPC39801, inner lateral view (IY129-018). (N), Pb element; MNCPC39802; (O), basal-out lateral view (IY126-018); (P), outer lateral view (IY126-020). (Q), CPC39803, inner lateral view (IY126-029); (R), CPC39804, basal-out lateral view (IY126-022); (S), CPC39805, outer lateral view (IY126-023). (T), M element, CPC39806, 161–166 m, posterior view (IY130-034); (U), Sb element, CPC39807, WCB705/243, outer lateral view (IY130-045); (V), P element; V, W, CPC39809, 161–166 m; (V), anterior view (IY130-037); (W), inner lateral view (IY130-038); (X), CPC39810, 161–166 m, outer lateral view (IY130-028). Scale bars 100 µm.
Fig. 4. A–F, Bergstroemognathus extensus (Graves & Ellison, 1941). All from sample WCB705/243. (A), M element, CPC39790, posterior view (IY116-046). (B), Sa element, CPC39791, posterior view (IY116-047). (C), Sb element, CPC39792, inner lateral view (IY116-048). (D), Sc element, CPC39793, inner lateral view (IY116-049). (E), Pb element, CPC39794, inner lateral view (IY116-042). (F), Pa element, CPC39795, inner lateral view (IY116-043). G–L, Cornuodus sp. All from WCB705/243; ...[continued on facing page]
van Wamel (1974), Lindström (in Ziegler, 1977), Stouge & Bagnoli (1999), Zhen et al. (2003), Nicoll & Ethington (2004) and Zhen et al. (2005). McTavish (1973) described *A. deltatus* and several other species of *Acodus* from the Emanuel Formation of the Canning Basin, and suggested a seximembrate apparatus for *A. deltatus* including prioniodiform (= P of our interpretation), ramiform (trichonodiform = Sa, gothodiform = Sb, cordyloform = Sc, and tetrapri-}

niodiform = Sd of our interpretation), and oistiform (= M of our interpretation) elements. Based on the stratigraphical distribution and morphological changes of various *Acodus* species recognized in the Emanuel Formation, McTavish (1973, fig. 7) indicated that both *Prioniodus* and *Baltoniodus* might have evolved from *Acodus*. Some authors went even further by attributing *A. deltatus* to either *Prioniodus* (van Wamel, 1974) or *Baltoniodus* (Bagnoli et al., 1988). In their revision of *A. deltatus*, Bagnoli et al. (1988) considered it to have a seximembrate apparatus without an Sa element, and included in this species some specimens from the Emanuel Formation illustrated by McTavish (1973). Subsequently Stouge & Bagnoli (1999) indicated that forms referred to *A. deltatus* by McTavish (1973), Ethington & Clark (1982) and
Acodus? transitans McTavish, 1973

Fig. 4M–R

Acodus transitans McTavish, 1973: 41, 42, pl. 1, figs 10, 11, 15, 17, 19, 21, 24, text-fig. 3 m–o.

Material. Four specimens from three samples WCB705/133 (Table 1).

Remarks. Acodus transitans is characterized by having a number of small and rudimentary denticles on the posterior process of its P and S elements, and represents a transitional form between Acodus and Prioniodus. Only a small number of specimens were available in this study (Fig. 4M–R). A comprehensive revision of Acodus species from the Emanuel Formation will be undertaken in a separate contribution.

Drepanodus Pander, 1856

Type species. Drepanodus arcaucusus Pander, 1856.

Drepanodus arcaucusus Pander, 1856

Fig. 5A–F

Drepanodus arcaucusus Pander, 1856: 20, pl. 1, figs 2, 4–5, 17, 30; ?31; Löfgren & Tolmacheva, 2003: 211–215, figs 2, 3A–C, E–H, 5K–V, 6M–U, 7H–N, 8A–G (cum syn.); Zhen et al., 2004: 52–53, pl. 3, figs 1–12; Zhen et al., in press a: fig. 5A–N (cum syn.).

Material. 95 specimens from three samples (Table 1).

Remarks. Recently revised as having a septimembrate apparatus (Löfgren & Tolmacheva, 2003), D. arcaucusus is a pandemic species widely distributed in various environments from inner shelf to slope (or basinal) settings with a long stratigraphic range from the late Tremadocian to Late Ordovician. It is a fairly common species in the Emanuel Formation, generally larger in comparison with those of other taxa. The cusp of the Sa element varies from proclined (Fig. 5B) to reclinend (Fig. 5A), the Sd element has a twisted cusp and inwardly flexed anterobasal corner (Fig. 5C, D), the Pb element is characterized by having a strongly reclined cusp and a more or less square base in lateral view with basal margin curved into a right angle, and the Pa element bears a flared base with a shallower basal cavity (Fig. 5F).

Acodus deltatus? Lönström, 1955

Fig. 4S–X

Acodus deltatus deltatus Lönström.—McTavish, 1973: 39, pl. 1, figs 1–9, 12–14, text-fig. 3p–t.

Material. 209 specimens from three samples (Table 1).

Remarks. By assigning the Emanuel material to Acodus deltatus Lindström, 1955, McTavish (1973) defined A. deltatus as having a seximembrate apparatus. However, in a later revision of this Baltic species, Bagnoli et al. (1988) suggested that only some illustrated specimens referred to A. deltatus deltatus by McTavish (1973) might be doubtfully assignable to A. deltatus. Stouge & Bagnoli (1999) further indicated that the Emanuel material referred to A. deltatus was not conspecific with the type specimens from Sweden. As revision of the Acodus species described by McTavish (1973) and other related coniform taxa occurring in the Emanuel Formation is still in progress and will be presented elsewhere, the currently material is only tentatively referred to A. deltatus.
Fig. 6. A–F, Paracordylodus gracilis Lindström, 1955. All from sample WCB705/243. (A), M element, CPC39827, anterior view (IY116-050). B–E, S elements; B–C, CPC39828, (B), inner lateral view (IY116-051); (C), close up showing chevron-shaped pattern of striae adjacent to anterior margin (IY126-052); (D), CPC39829, inner lateral view (IY126-053); (E), CPC39830, outer lateral view (IY126-054); (F), P element, CPC39928, outer lateral view (IY1160S55). G.H.L, Prioniodus adami Stout & Bagnoli, 1988. G.H, Pa element, CPC39831, WCB705/243, (G), antero-outer lateral view (IY118-020); (H), outer lateral view (IY118-021). I–K, Sa element, CPC39832, WCB705/243, posterior view (IY128-021). M–R, Protoprioniodus simplicissimus McTavish, 1973. All from sample WCB705/243. M, N, Sc element; (M), CPC39833, outer lateral view (IY118-020); (N), CPC39834, inner lateral view (IY118-030). O–P, Pa element, CPC39835, (O), inner lateral view (IY118-025); (P), upper-outer lateral view (IY118-023). Q.R, M element; (Q), CPC39836, anterior view (IY129-022); (R), CPC39837, posterior view (IY118-029). I–K, Sa element, CPC39838, WCB705/133, (I), lateral view (IY127-012); (J), anterior view, close up showing striae on the broad anterior face (IY127-011); (K), anterior view (IY127-010). S, Sc element, CPC39839, 161–166 m, inner lateral view (IY130-001). (T), Sb element, CPC39840, 161–166 m, outer lateral view (IY130-002). U, V, Sd element, CPC39841, 161–166 m, (U), inner lateral view (IY130-005); (V), outer lateral view (IY130-006). Scale bars 100 µm unless otherwise indicated.
**Drepanoistodus Lindström, 1971**

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

**Drepanoistodus sp. cf. Drepanoistodus nowlani**

*Ji & Barnes, 1994*

Fig. 5G–P

*Drepanoistodus sp. cf. Drepanoistodus nowlani* Ji & Barnes.—Zhen et al., 2007b: 132–134, pl. 2, figs 1–21, pl. 3, figs 1–9 (*cum syn.*).

**Material.** 52 specimens from three samples (Table 1).

**Remarks.** The Emanuel specimens are comparable with those described from the Honghuayuan Formation of Guizhou as *D*. sp. cf. *D. nowlani* except for the less extended basal-anterior corner in the P elements (Fig. 5N–P).

**Fahraeusodus Stouge & Bagnoli, 1988**

**Type species.** ?*Microzarkodina adentata* McTavish, 1973.

**Fahraeusodus adentatus** (McTavish, 1973)

Fig. 6I–K, S–V


**Fahraeusodus adentatus** (McTavish).—Stouge & Bagnoli, 1988: 119, pl. 4, figs 12–14 (*cum syn.*); Lehnert, 1995:89, pl. 7, fig. 20A, 20B.

**Material.** Seven specimens from two samples (Table 1).

**Remarks.** Specimens representing the asymmetrical Sb element with a lateral costa on the outer lateral face (Fig. 6T), the strongly asymmetrical Sc element without a lateral costa on each side (Fig. 6S), and the asymmetrical Sd element with a costa on each side (Fig. 6U, V) were recovered in the two samples from the Emanuel Formation. A specimen representing the triform Sa element with a broad, nearly flat anterior face and with a sharp anterolateral costa on each side (Fig. 6I–K) is also assigned to this species. McTavish (1973) recognized a quinquimembrate apparatus including oistodiform (= M element), ozarkodiniform (= P element), trichonodelliform (= Sa element), cordylodiform (= Sc element), and tetraproniodiform (= Sd element), and doubtfully assigned it to *Microzarkodina*. Stouge & Bagnoli (1988) proposed *Fahraeusodus* and selected ?*M. adentata* as the type species. However, only a few specimens were recovered in the upper part of Bed 9 (*O. evae* Biozone) of the Cow Head Group in Newfoundland, an interval stratigraphically slightly younger than the occurrence in the Emanuel Formation. The flat anterior face and edge-like anterolateral costa on each side of the Sa element are comparable with some specimens referred to *Fahraeusodus marathenensis* by Stouge & Bagnoli (1988, e.g., pl. 4, fig. 15) from the Cow Head Group.

**Paracordylodus Lindström, 1955**

**Type species.** *Paracordylodus gracilis* Lindström, 1955.

**Paracordylodus gracilis** Lindström, 1955

*Fig. 6A–F*


**Paracordylodus gracilis** Lindström, 1955: p. 584, pl. 6, figs 11–12; Tolmacheva & Löfgren, 2000: 1117–1119, figs 5, 7; Tolmacheva & Purnell, 2002: 209–228, text-figs 1–10; Zhen et al., 2004: p. 56, pl. 4, figs 19–22 (*cum syn.*).

**Material.** 35 specimens from sample WCB705/243 (see Table 1).

**Remarks.** *Paracordylodus gracilis* is one of the best known species in the Early Ordovician. The reconstructed apparatus initially was based on interpretation of collections of discrete specimens documented successively by Sweet & Bergström (1972), McTavish (1973), and van Wamel (1974). Their collective interpretations were confirmed nearly 30 years later by the *in situ* bedding plane assemblages (Tolmacheva & Löfgren, 2000; Tolmacheva & Purnell, 2002). Its species composition and structure based on numerous clusters from deep water radiolarian cherts in central Kazakhstan revealed important data about its evolutionary affinities (Tolmacheva & Purnell, 2002). *Paracordylodus gracilis* is widely distributed (see Tolmacheva & Löfgren, 2000; Tolmacheva & Purnell, 2002), ranging from the late Tremadocian (late *P. proteus* Biozone) to late Floian (mid *O. evae* Biozone). It was most common in the Open Sea Realm (from shelf edge to basin setting), with typical examples reported in central Kazakhstan (Tolmacheva & Purnell, 2002) occurring as the dominant species making up 90–99% of the specimen numbers. It is present in similar deep water oceanic settings in cherts of turbiditic successions (Percival et al., 2003), and also in allochthonous limestone or calcareous siltstone of slope settings (Zhen et al., 2004) in eastern Australia on the margins of eastern Gondwana. *Paracordylodus gracilis* was also common in the shallow marine environments within the Cold Domain of the Shallow-Sea Realm, such as in the Baltos-Scandian Province (Löfgren, 1978; Tolmacheva & Löfgren, 2000). Its occasional presence in outer shelf environments or more rarely in inner shelf habitats within Temperate or even Tropical domains can be attributed to up-welling of cold ocean currents.

**Paracordylodus Lindström, 1971**

**Type species.** *Oistodus parallelus* Pander, 1856.

**Paracordylodus parallelus** (Pander, 1856)

*emend. Löfgren, 1997*

*Fig. 7A–S*

*Oistodus parallelus* Pander, 1856: 27, pl. 2, fig. 40.

**Paracordylodus parallelus** (Pander).—Lindström, 1971: 47, fig. 8; Löfgren, 1997: 923–926, pl. 1, figs 1–12, 17, 21, text-fig. 5A–G (*cum syn.*); Albanesi in Albanesi et al., 1998: 144, pl. 8, figs 27–30; Johnston & Barnes, 2000: 31–32, pl. 10, figs 10.11,15–17, 20; Tolmacheva et al., 2001: fig. 4.12–4.13; Viira et al., 2006: pl. 1, fig. 5.
Fig. 7. *Paroistodus parallelus* (Pander, 1856). All from sample WCB705/133. A–D, M element; (A), CPC39842, anterior view (IY117-002); B,C, CPC39843, (B), anterior view (IY117-005); (C), basal view (IY117-006); (D), CPC39844, posterior view (IY117-008). E–G, Sa element; E,F, CPC39845, (E), lateral view (IY117-010), (F), basal view (IY117-011); (G), CPC39846, lateral view (IY117-009). H–J, Sb element; (H), CPC39847, outer lateral view (IY117-017); I,J, CPC39848, (I), inner lateral view (IY117-016), (J), basal view (IY117-018). K–M, Sc element; K,L, CPC39849, (K), basal view (IY117-014), (L), inner lateral view (IY117-013); (M), CPC39850, outer lateral view (IY117-012). N,O, Sd element; (N), CPC39851, inner-basal view (IY117-025); (O), CPC39852, outer lateral view (IY117-029). P, Pb element; CPC39873, outer lateral view (IY132-020). Q–S, ?Pa element; (Q), CPC39854, basal view (IY117-036), (R), CPC39855, outer lateral view (IY117-030); (S), CPC39856, inner lateral view (IY117-034). Scale bars 100 µm.
**Material.** 457 specimens from three samples (Table 1).

**Remarks.** The species as revised by Löfgren (1997) possesses a septimembrate apparatus (including makellate M and drepanodiform or paroistodiform S and P elements), which can be distinguished from the other species of *Paroistodus* by having prominent lateral costae on the sides of its constituent elements. Zhen et al. (in press b) preferred to describe the S and P elements as paroistodiform in the *Paroistodus* species which show a sharp anterior costa extending basally into the basal cavity and forming a ridge-like structure (Zhen et al., 2007b, p. 137) at the anterior end of the basal cavity. However this character is not shown in the material of the two *Paroistodus* species (similar to *Paroistodus* sp. recently documented from the Honghuayuan Formation in South China) reported herein from the Emanuel Formation, although the anterior part of base often exhibits a zone of recessive basal margin (Figs 7A–C, 8H). *Paroistodus parallelus* occurs abundantly in the Emanuel Formation, where it is found in association with *P. proteus* although the latter is rare (Table 1).

*Paroistodus proteus* (Lindström, 1955)  
emend. Löfgren, 1997

**Remarks.** *Paroistodus parallelus* is relatively rare in the Emanuel samples, and can be easily differentiated from associated *P. parallelus* mainly by lacking a prominent costa on the lateral faces. *Paroistodus proteus* was revised by Löfgren (1997) as having a septimembrate apparatus. After a review of previously reported occurrences of this species in the Honghuayuan Formation and other coeval stratigraphic units in South China and comparison with Baltic material of *P. proteus*, Zhen et al. (2007b) concluded that *Paroistodus* is represented in the Honghuayuan Formation by a rare form that they identified as *Paroistodus* sp. It differs from *P. proteus* in having a smooth lateral face without a carina and having a more open basal cavity which lacks the distinctive so-called paroistodiform character. The material from the Emanuel Formation is transitional between typical *P. proteus* from the late Tremadocian to Floian of Balto-Scandia and *Paroistodus* sp. from the Honghuayuan Formation of South China. It is comparable with *P. proteus* in having a prominent carina (Fig. 8A–E) or even a weak costa (Fig. 8J) on the lateral faces, but similar to *Paroistodus* sp. from the Honghuayuan Formation in lack of the paroistodiform feature. As mentioned above, absence of the paroistodiform character in species of *Paroistodus* co-occurring in the Emanuel Formation may indicate that this feature is caused by ecological adaption rather than as a phylogenetically significant trait for *Paroistodus*. Interestingly, *P. proteus* from the Emanuel Formation of Western Australia and from the Latorp Limestone and Tøyen Shale of Sweden and *Paroistodus* sp. from the Honghuayuan Formation of South China come from three contrasting ecological/sedimentological settings; they may represent three populations or subspecies of *P. proteus*. The typical latest Tremadocian and early Floian *P. proteus*-bearing successions in Sweden (e.g., Diabsbrottet area) were deposited in the outer shelf settings of the Cold Domain (Bergström et al., 2004), and the mid-upper part of the Emanuel Formation might be largely deposited in deep subtidal settings, while the Honghuayuan Formation with *Paroistodus* sp. apparently represents typical shallow subtidal environments. Therefore, in consideration of the relationship between their morphological variation and their ecological/geographical distributions, the material from the Emanuel Formation is considered as conspecific with type material of *P. proteus*, and *Paroistodus* sp. from the Honghuayuan Formation (Zhen et al., 2007b) might be better treated as a separate subspecies of *P. proteus*.

**Prionioidus Pander, 1856**

**Type species.** *Prionioidus elegans* Pander, 1856.

*Prionioidus adami* Stouge & Bagnoli, 1988

**Remarks.** Based on a large collection from Bed 9 of the Cow Head Group of western Newfoundland, Stouge & Bagnoli (1988) established *P. adami* as having a septimembrate apparatus (pastinate Pa, and Pb, ramiform S and geniculate M elements), and also included in it the material from the Emanuel Formation that McTavish (1973), ascribed to *Prionioidus* sp. C except for the oisto-diform element (his pl. 3, fig. 11, text-fig. 6j) which bears a short, adenticulate inner lateral process. *Prionioidus adami* is characterized by bearing small, closely-spaced denticles on the long posterior process of the S and P elements, as well as on the anterior and outer lateral processes of the P elements and the inner lateral process of the M element. The Pa element (Fig. 6G, H) from the Emanuel Formation is identical with those illustrated by McTavish (1973, pl. 3, figs 5, ?16), but exhibits less closely spaced denticles on the processes in comparison with the holotype (Stouge & Bagnoli, 1988, pl. 11, fig. 8). The M element from the Cow Head Group shows a long adenticulate outer lateral process and a long, denticulate inner lateral process with small, closely-spaced denticles, similar to those on the processes of the P and S elements, but no M element has been recovered from the samples of this study.
**Protopanderodus Lindström, 1971**

*Type species.* *Acontiodus rectus* Lindström, 1955.

**Protopanderodus gradatus** Serpagli, 1974

*Fig. 9A–P*

*Protopanderodus gradatus* Serpagli, 1974: 75, pl. 15, figs 5a–8b, pl. 26, figs 11–15, pl. 30, figs 1a–b; text-fig. 17; Zhen et al., 2004: 56–57, pl. 5, figs 1–10 (cum syn.); Zhen & Percival, 2006: fig. 9A–C; Zhen et al., in press a: fig. 8A–Q.

*Material.* 126 specimens from two samples (Table 1).

*Remarks.* *Protopanderodus gradatus* is common in one (WCB705/243) of the samples studied from the Emanuel Formation. This material is identical with the types described from the San Juan Formation (Early Ordovician) of Argentine Precondillera (Serpagli, 1974), and those recently documented from the Honghuayuan Formation of Guizhou, South China (Zhen et al., in press a, fig. 8A–Q). An additional element (Fig. 9J–P) bearing a more compressed cusp and a less extended base with a rounded basal margin has also been recognized in the Emanuel material. It also shows rather prominent striation in the area immediately anterior to the lateral costa, and a weakly developed chevron-shaped pattern of striae adjacent to the anterior margin (Fig. 9K, O). As these distinctive characters are not observed in the other elements of *P. gradatus*, it is tentatively assigned herein to the M position of *P. gradatus*. Some specimens bear rounded holes of about 3–4.5 µm in diameter, presumably representing the boring structure made by an unknown organism (Fig. 9O, P).
Scolopodus Pander, 1856

Type species. Scolopodus sublaevis Pander, 1856.

Scolopodus houlianzhaiensis
An & Xu in An et al., 1983

Fig. 10A–K

Scolopodus rex houlianzhaiensis An & Xu in An et al., 1983: 148, pl. 12, figs 23–27, text-fig. 11.7. 11.8; ?Ding, 1987: pl. 6, fig. 23; non Ding et al. in Wang, 1993: 205, pl. 14, figs 13–15.

Scolopodus houlianzhaiensis An & Xu.—Zhen et al., in press a: fig. 9G–L.

Material. 19 specimens from three samples (Table 1).

Remarks. The multicoastate Sa (symmetrical) and Sb (asymmetrical) elements of Scolopodus houlianzhaiensis show some resemblance to S. quadratus, but the distinctive Sc element has a strongly compressed cusp and lateral costae restricted to near the anterior margin (Fig. 10J, K). An & Xu (in An et al., 1983) considered this species as a subspecies of Scolopodus rex Lindström, 1955, which is now regarded as a junior synonym of Scolopodus striatus Pander, 1856 (see Fåhraeus, 1982, Zhen et al., 2004; Tolmacheva, 2006).

An & Xu (in An et al., 1983) suggested a bimembrate apparatus including symmetrical and asymmetrical elements. Three morphotypes, representing symmetrical multicoastate Sa, asymmetrical multicoastate Sb, and strongly asymmetrical Sc elements, can be recognized among our Emanuel material. The Sa element (Fig. 10A–D) has a broad anterior face, five or six sharp costae on each side and a costa along the posterior margin, and is identical with the symmetrical element defined by An et al. (1983, pl. 12, figs 23–25) from the Liangjiashan Formation of North China. The Sb element
Fig. 11. *Serratognathus bilobatus* Lee, 1970. (A), Sa element, CPC39898, 161–166 m, anterior view (IY116-041). B–F, Sb element; B–E, CPC39899, WCB705/133, (B), posterior view (IY116-002), (C), outer lateral view (IY116-006), (D), upper view showing the tip of the cusp (IY116-012), (E), upper view (IY116-011), (F), CPC39900, WCB705/133, anterior view (IY116-028). G–L, Sc element, CPC39901, WCB705/133, (G), posterior view (IY116-013), L, upper view (IY116-023), (H), basal-posterior view (IY116-018), (I), posterior view of the cusp (IY116-014), (J), posterior view, close up showing fine striae (IY116-015), (K), basal view showing ring-like basal node (IY116-022). Scale bars 100 µm unless otherwise indicated.
Fig. 12. *Serratognathus diversus* An, 1981. All from the Honghuayuan Formation in Guizhou. A–C, Sa element; (A), AM F.135048, THH7, anterobasal view (IY119-004); (B), AM F.135044, THH7, lateral view (IY119-002); (C), AM F.135047, THH10, posterior view (IY119-040). (D), Sb element, AM F.135049, THH7, outer lateral view (IY119014); E–H, broken specimens showing overlapping laminar layers on the surface of breakage. E,F, Sb element, AM F.135815, THH7, (E), postro-lateral view (IY133-035), (F), upper view (IY133-037); G,H, Sc element, AM F.135816, THH9, (G), inner lateral view (IY133-040), (H), close up showing the surface of breakage (IY133-041); (I), Sc element, AM F.135817, YTH10, showing the partition between laminar layers and the fine laminar structure within each laminar layer (IY133-033). Scale bars 100 µm unless otherwise indicated.

[Fig. 13 caption continued]... G,H, Sb element, AM F.135823, WHC36, (G), antero-outer lateral view, bearing 10 laminar layers (IY133-013), (H), close up showing denticles along anterior margin of each laminar layer (IY133-014). I,J, Sc element, AM F.135824, WHC36, (I), antero-outer lateral view, bearing 17 laminar layers (IY133-006), (J), posterior view (IY134-001). K, L, Sc element, AM F.135825, THH12, (K), anterior view, bearing 20 laminar layers (IY133-044), (L), posterior view (IY134-029). (N), Sc element, AM F.135826, WHC35, close up showing the small ring-like node representing the initial stage of the element (IY134-014). (O), Sc element, AM F.135817 (same specimen as Fig. 12I), YTH10, close up showing the rounded pit-like initial stage of the element (IY133-028). Scale bars 100 µm, unless indicated otherwise.
Fig. 13. *Serratognathus diversus* An, 1981. All from the Honghuayuan Formation in Guizhou. Showing size variation; A–E, G, I, K and M are magnified equally. (A), Sb element, AM F.135818, AFI983A, anterior view, bearing six laminar layers (IY133-046). (B), Sb element, AM F.135819, THH10, anterior view, bearing six laminar layers (IY133-038). C, M, Sc element, AM F.135820, YTH5, (C), anterior view, bearing eight laminar layers (IY133-024), (M), posterior view (IY134-019). (D), Sa element, AM F.135821, AFI986, upper-anterior view, bearing eight laminar layers (IY133-050). E, F, Sc element, AM F.135822, YTH4, (E), anterior view, bearing 10 laminar layers (IY133-021), (F), close up showing denticles along anterior margin of each laminar layer (IY133-022). …[continued on facing page]
Semiacontiodus Miller, 1969

Type species. Semiacontiodus nogamii Miller, 1969.

Semiacontiodus sp. cf. Semiacontiodus cornuformis (Sergeeva, 1963)

Figure 15L–T

Scolopodus cornuformis Sergeeva.—An, 1987: 183, pl. 7, figs 10–11, 13–16; Ding et al. in Wang, 1993: 202, pl. 5, fig. 33; Zhen et al., in press a: fig. 9D–F.

Material. 26 specimens from three samples (Table 1).

Remarks. Three morphotypes of this species are recognized in the Emanuel samples representing a symmetry transition series including symmetrical Sa (Fig. 15L,M), asymmetrical Sb (Fig. 15N,O), and strongly asymmetrical and laterally more compressed Sc (Fig. 15P–T) elements. Although these specimens have relatively shorter bases, they otherwise resemble those of S. cornuformis (Sergeeva, 1963), which was revised as consisting of a septimembrate apparatus (Löfgren, 1999).

Serratognathus Lee, 1970

Type species. Serratognathus bilobatus Lee, 1970.

Serratognathus bilobatus Lee, 1970

Figure 11A–L

Serratognathus bilobatus Lee, 1970: 336, pl. 8, figs 6, 7; Metcalfe, 1980: pl. 1, figs 16–19; An, 1981: pl. 2, fig. 26; An & Ding, 1982: pl. 5, fig. 25; An et al., 1983: 149, pl. 16, figs 20–22, pl. 17, figs 1, 2; An, 1987: 189, 190, pl. 18, fig. 11; Ding, 1987: pl. 6, fig. 16; An & Zheng, 1990: pl. 7, fig. 13; Ding et al. in Wang, 1993: 207, pl. 20, fig. 5; Chen & Wang, 1993: fig. 2Q, 2U; Wang et al., 1996: pl. 2, figs 1–7, 9; Nicoll & Metcalfe, 2001: fig. 6.19–6.22; Metcalfe, 2004: pl. 2, figs 9–10.

Material. Seven specimens from three samples (Table 1).

Diagnosis. Species of Serratognathus with a trimembrate apparatus, including symmetrical Sa, asymmetrical Sb, and strongly asymmetrical Sc elements; all elements semi-conical in outline with fan-shaped array of small, closely spaced denticles along anterior and lateral edges of overlapping lamellar layers; cusp small, posteriorly positioned and anterolaterally enclosed by up to 16 vertically overlapping laminar layers, which are anterobasally divided by a broad median groove into two lobe-like lateral processes; basal cavity absent.

Description. Trimembrate apparatus, including symmetrical Sa, asymmetrical Sb, and strongly asymmetrical Sc elements which form a symmetry transition series; each element semi-conical in outline, formed by upwardly overlapping layers, resembling a half-cut onion; composed of the cusp and a gently posterolaterally extended lobe-like lateral process on each side. Cusp small or indistinctive, weakly compressed laterally with a broad posterior face, and the anterior margin embedded in up to 16 surrounding overlapping layers, which are bordered by small, closely spaced denticles along the anterior and lateral margins. Discrete denticles surround the cusp in a semicircle, representing the anterolateral edge of each overlapping layer. Node-like denticles weakly developed on posterior face, may be absent towards the base (Fig. 11B, E, G, I); fine striae microstructure best developed on the posterior face in the area above the basal margin (Fig. 11 I, J). Denticulate anterior margin of each layer turned upwards. Basal face smooth, wide, and distally arched; crescentic in outline in basal view; bisected by anteroposteriortly directed median groove extending anterobasally to separate into two lobes underneath each lateral process. Basal cavity absent; basal end of the cusp represented by a small ring-like node (Fig. 11K), but in one specimen basal cavity represented by a small, shallow pit underneath the cusp (Fig. 11B).

Sa element symmetrical, outline crescentic in upper view with convex anterior face and concave posterior face, and tower-like in anterior view (Fig. 11A). Cusp small, located postero-medially with a short lobe-like process on each side, which extends posterolaterally; in anterior view, two processes separated anterobasally by a prominent rather deep median groove (Fig. 11A). Basal face smooth, bisected by the median groove into two symmetrical lobes.

Sb element (Fig. 11B–F) like Sa, but asymmetrical; inner lateral process shorter in posterior view (Fig. 11B), extending laterally with basal margin nearly horizontal; outer lateral process longer extending posterolaterally (Fig. 11C). Basal margin of the two processes forming an angle of 125° or more in the upper view (Fig. 11E). Basal face asymmetrical, with a longer lobe under outer lateral process and a shorter lobe under inner lateral process. One specimen (Fig. 11B) exhibits a small and shallow basal cavity.

Sc element (Fig. 11G–L) similar to Sb, but strongly asymmetrical with longer and more strongly posteriorly extended lateral processes. In upper view, the basal margins of the two lateral processes form a rather narrower angle of about 70–80° (Fig. 11G, L); outer lateral process longer (Fig. 11G, L).

Remarks. Lee (1970) illustrated two specimens of Serratognathus bilobatus from the Dumugol Formation of South Korea, with the figured holotype (Lee, 1970, pl. 8, fig. 7a–d) assignable to the asymmetrical Sb element defined herein and the other figured paratype (Lee, 1970, pl. 8, fig. 6) is a symmetrical Sa element. Both specimens are identical with those from the Emanuel Formation. Serratognathus bilobatus differs from S. diversus An, 1981 (Figs 12–14) from the Honghuayan Formation of South China mainly in having a smaller, often indistinct, cusp (Fig. 11G, H).
Fig. 14. *Serratognathus diversus* An, 1981. All from the Honghuayuan Formation in Guizhou. (A), Sb element, AM F.135050, THH7, basal-posterior view, showing fine growth laminar preserved on the lateral and posterior surfaces of the cusp (IY119-022). (B), Sc element, AM F.135825 (same specimen as Fig. 13K,L), THH12, close up showing growth laminar along the posterobasal margin (IY134-037). (C), Sc element, AM F.135816 (same specimen as Fig. 12G, H), THH9, closing up showing fine growth laminar on the posterior face (IY134-049). (D,E), Sa element, AM F.135048, THH7, (D), close up showing fine growth laminar on the posterior face (IY119-006), (E), close up showing the small ring-like node representing the initial stage of the element (IY119-012). Scale bars 10 µm.
Fig. 15. A–H, Stiptognathus borealis (Repetski, 1982). (A), M element, CPC39902, WCB705/243, posterior view (IY129-033). B–D, Sa element; B,C, CPC39903, WCB705/243, (B), upper-posterior view (IY118-006), (C), upper-anterior view (IY118-007); (D), CPC39904, WCB705/243, upper view showing the cross section of the cusp (IY118-004). E–G, Sb element, E,G, CPC39905, WCB705/133, (E), basal-posterior view (IY117-041), (G), posterior view (IY117-039). (F), CPC39906, WCB705/243, basal view (IY118-015). (H), Pb element, CPC39907, WCB705/243, antero-inner lateral view (IY118-008). I–K, Triangulodus bifidus Zhen in Zhen et al., 2006. Sd element, CPC39908, WCB705/133, (I), basal view (IY116-056), (J,K), posterolateral views (IY116-058, IY116-057). L–T, Semiacontiodus sp. cf. S. cornuformis (Sergeeva, 1963). L,M, Sa element, CPC39909, WCB705/133, (L), posterior view (IY126-027); (M), posterolateral view (IY126-028). N,O, Sb element; (N), CPC39910, 161–166 m, inner lateral view (IY132-012); (O), CPC39911, 161–166 m, outer lateral view (IY132-014). P–R, Sc element; P–R, CPC39912, 161–166 m, (P), inner lateral view (IY132-016); (Q), basal view (IY132-018); (R), outer lateral view (IY132-017). S,T, CPC39913, WCB705/133, (S), inner lateral view (IY127-018); (T), close up showing fine striae (IY127-019). Scale bars 100 µm unless otherwise indicated.
Serratognathus diversus An, 1981

Figs 12–14

*Serratognathus* sp. A An et al., 1981: pl. 1, fig. 10.
*Serratognathus diversus* An, 1981: 216, pl. 2, figs 23, 27.
30; Zhen et al., in press a: figs 10A–K, 11A–K, 12D–M (cum syn.).
*Serratognathus obliquidens* Chen, Chen & Zhang, 1983: 136, pl. 1, fig. 18.
*Serratognathus tangshanensis* Chen, Chen & Zhang, 1983: 136–137, pl. 1, figs 14–17; Chen & Zhang, 1989: 223, pl.5, fig. 12.

Remarks. Both *Serratognathus obliquidens* and *S. tangshanensis* were erected as form species from the Honghuayuan Formation exposed in the Nanjing Hills (Chen et al., 1983).

We consider them to be junior synonyms of *S. diversus*, representing the asymmetrical elements (Sb + Sc) of our current notation.

Based on a large collection of *S. diversus* from the Honghuayuan Formation, Zhen et al. (in press a) recognized a trimembrate apparatus including symmetrical Sa, asymmetrical Sb and strongly asymmetrical Sc elements (Fig. 12). Material of *S. bilobatus* from the Emanuel Formation shows the same apparatus. Morphologically, *S. diversus* and *S. bilobatus* are closely comparable except that the former has a much more prominent, laterally compressed cusp. Their elements are resembling a half-cut onion with a posteriorly located cusp enveloped anterolaterally by numerous overlapping laminar layers (varying from 6 to 20, see Fig. 13). The upper margins of these laminae are progressively lower anterolaterally. Laminae are ornamented with
tooth-like denticles (Fig. 13) along their anterior and lateral margins, and by blunt node-like denticles along the posterior margins (Fig. 14D). Underneath each specimen is a wide, smooth, distally arched basal face (Fig. 12A, G), which is crescentic in outline and divided anteroposteriorly into two lobes (lateral processes; Fig. 13 A–E, K) by a broad, median groove. Typically a small ring-like node underneath the cusp represents the initial stage of the element (Figs 13N, 14E), without basal cavity.

Natural breakage surfaces on some of the specimens show these lamellar layers to be tightly compacted (Fig. 12G, H) with partitions generally observed only near the edge of each layer (Fig. 12E–H). In most cases, no microstructure is observable on the surface of the breakage. However, some specimens show fine laminations (growth lamellae) formed by flattened crystallites (Fig. 12I).

_Serratognathus extensus_ Yang in An et al., 1983 differs from _S. diversus_ in having a more robust cusp and a long, laterally extended process on each side. This species is similar to _S. diversus_ and _S. bilobatus_ in that the anterior face bears 2–3 rows of denticles that extend continuously from the end of one lateral process to the other, and in lack of a basal cavity. Yang’s type material included 14 specimens from the Liangjiashan Formation in Hebei Province (An et al., 1983, tables 6–7). An et al. (1983, p. 26) suggested that _S. extensus_ might be directly evolved from _S. bilobatus_, and recognized the _S. extensus_ Zone succeeding the _S. bilobatus_ Zone in the Liangjiashan Formation.

**Tropodus Kennedy, 1980**


**Type species.** _Tropodus comptus_ (Branson & Mehl, 1933).

**Remarks.** _Tropodus_ Kennedy, 1980 is treated herein as a valid genus, having a rather different species apparatus as that of _Acodus_, particularly its S elements that exhibit a much wider variation characterized by the occurrence of multi-costate elements, and the P elements typically with weaker development of a lateral costa that may be represented by a broad carina. _Tropodus_ was proposed to consist of a bimembrate apparatus (comprising comptiform and pseudoquadratiform elements) with _Paltodus comptus_ Branson & Mehl, 1933 as the type species (Kennedy, 1980). Although the genus was originally defined as consisting of a symmetry transition series of elements bearing “three or more, prominent keel-like costae” (Kennedy, 1980, p. 65), both elements of his revised _T. comptus_ have five costae, likely representing only part of a species apparatus. The comptiform element (= Sc herein) was represented by the form species _P. comptus_, an asymmetrical element with costate anterior and posterior margins, and with two costae on the outer face and one on the inner face (Kennedy, 1980, pl. 2, figs 21–24), and the pseudoquadratiform element (= Sd herein) by the form species _Scelopodus pseudoquadra-tus_ Branson & Mehl, 1933, a symmetrical quiniquistostate element with a broad anterior face and a costate posterior margin (Kennedy, 1980, pl. 2, figs 25–27).

The other species originally included in _Tropodus_ was _Walliserodus australis_ which was defined as consisting of a transitional series from tristate to multistate elements (Serpagli, 1974, p. 89). Kennedy (1980) admitted that “the two types of elements in _T. comptus_ are very similar to two of the many morphologies of elements in _T. australis_ (Serpagli, 1974)” although the latter presented “a multitude of variably costate forms.” Serpagli (1974) originally defined a quinquimembrate apparatus for _T. australis_ including asymmetrical tristate (= Sb1 herein), asymmetrical quadri-costate (= Sb2 herein), strongly asymmetrical, laterally compressed multistate (= Sc herein) and a nearly symmetrical quiniquistostate (= Sd) elements; Sa, P and M elements were originally not recognized in either species.

Based on material from the Cow Head Group of Newfoundland, Bagnoli et al. (1988) and Stouge & Bagnoli (1988) included P and M elements in the species apparatus of _Tropodus_. Stouge & Bagnoli (1988) also revised both _T. comptus_ and _T. sweeti_ (Serpagli, 1974), and suggested that _W. australis_ proposed by Serpagli (1974) comprised elements belonging to both _T. comptus_ and _T. sweeti_. As Smith (1991) correctly pointed out, distinguishing between S elements belonging to these species is rather uncertain, as Stouge & Bagnoli (1988) had included the holotype (tristate element) of _W. australis_ in the synonymy lists of both _T. comptus_ and _T. sweeti_. However, the P elements they defined for _T. comptus_ and _T. sweeti_ show remarkable differences. The P elements of _T. comptus_ illustrated from the Cow Head Group (Stouge & Bagnoli, 1988, pl. 16, fig. 2) and also from Utah (Ethington & Clark, 1982, text-fig. 22, pl. 11, figs 6, 7) are more or less scandodiform bearing a smooth, convex outer face and a concave inner face with a broad, prominent mid carina, while the P element of _T. sweeti_ is a typical acodiform element with a prominent costa on one side (Serpagli, 1974, pl. 14, figs 13, 14, pl. 24, figs 8–10). Smith (1991) restricted _Tropodus_ to Kennedy’s original definition by including only costate elements in the species apparatus and proposed _Chionoconus_ to accommodate those elements which Stouge & Bagnoli (1988) defined as the P elements of _T. comptus_.

Zhen et al. (2004) reported the occurrence of _T. australis_ (assigned to _T. comptus_) and _T. sweeti_ from two samples within the Early Ordovician Hensleigh Siltstone in central New South Wales. The P and M elements of both these species are comparable with those described by Serpagli (1974) from the San Juan Formation of Precordilleran Argentina and by Stouge & Bagnoli (1988) from Newfoundland. However, Zhen et al. (2004), following Ji & Barnes (1994), applied a rather different concept for the S elements by including a symmetrical Sa element in the apparatuses. These studies also raised uncertainties about the definition of the constituent species of _Tropodus_. Firstly, if P elements of _Tropodus_ are confined to “scandodiform” elements as Stouge & Bagnoli (1988) originally proposed, _T. sweeti_ should be excluded from it. Secondly, although Kennedy (1980) suggested that _Triangulodus_ consisted of hyaline elements, if _Tropodus_ is considered as bearing “scandodiform” P elements, it would be very similar to _Triangulodus_, if it is not considered as a junior synonym of the latter. Among the specimens from the Hensleigh Siltstone, two types of P elements were recognized for _T. australis_ (Zhen et al., 2004). Both Pa and Pb elements
have a broad convex outer face and a concave inner face with a thin anterior margin curved inward. The lateral costa is weak, and may even be represented only as a broad carina on the inner side of the Pa element (Zhen et al., 2004, pl. 1, figs 1, 3) which is comparable with those illustrated by Stouge & Bagnoli (1988, pl. 16, fig. 2) and those from the Emanuel Formation (Fig. 16L–P). However, the lateral costa is plainly evident in the Pb element (Zhen et al., 2004, pl. 1, fig. 4). Similar variations among the P elements of *T. comptus* were also observed in the material from the St. George Group (Ji & Barnes, 1994). Therefore, *Tropodus* is defined herein as consisting of a genulate M element, a series of highly variable S elements (in respect to the number of the costae), and acodiform P elements with a lateral costa on the inner side varying from weak to well developed.

**Tropodus australis** (Serpagli, 1974)

Fig. 16A–P

Walliserodus serpaglii Serpagli, 1974: 89–91, pl. 19, figs 5a–10c, pl. 29, figs 8–15, text-figs 23, 24.

*Tropodus australis* (Serpagli).—Albanesi et al., 1998: 151, pl. 13, figs 12–18.

*Tropodus comptus australis* (Serpagli).—Stouge & Bagnoli, 1988: 141, 142, pl. 16, figs 3–5; Löfgren, 1993: fig. 9; o, t; Lehner, 1993: pl. 4, fig. 5; Lehret, 1995: 129, 130.

*Acodus comptus* (Branson & Mehl, 1933).—Zhen et al., 2004: 50, 51, pl. 1, figs 1–19.

Scolopodus ?rex Lindström.—Percival et al., 1999: 13, fig. 8.9.

*Tropodus ?sweeti* (Serpagli).—Percival et al., 1999: 13, fig. 8.10.

**Material.** 190 specimens from three samples (Table 1).

**Remarks.** Specimens from the Emanuel Formation are identical with those recovered from the Hensleigh Siltstone of central New South Wales (Zhen et al., 2004, pl. 1, figs 1–19). Stouge & Bagnoli (1988) regarded *W. australis* as a subspecies of *T. comptus*. In the Emanuel Formation samples, only one species of *Tropodus, T. australis* is represented, exhibiting similar variation of the S elements (Fig. 16C–K) as was documented by Serpagli (1974), and the P elements (Fig. 16L–P) that are comparable with those described by Stouge & Bagnoli (1988) from the Cow Head Group of Newfoundland.

*Tropodus australis* differs from typical *T. comptus* of the North American Mid-continent (Kennedy, 1980; Ethington & Clark, 1982; Landig & Wesrop, 2006) mainly in having a strongly laterally compressed, muti-costate (Sc) element. Landig & Wesrop (2006) documented *T. comptus* from the Fort Cassin (Early Ordovician, Floian) of northeastern New York, and defined it as consisting of a septimembrate apparatus including S, M and P elements, and also illustrated a scandomiform element as representing the Sc position (see Landig & Wesrop, 2006, fig. 6.15). In the study of conodont faunas from the Jefferson City and other equivalent units in Oklahoma (Kindblade), Ethington (2009, per. com.) recognized the possible P elements of *T. comptus* and noticed their considerable difference from those of *T. australis* illustrated herein from the Emanuel Formation. He suggested that elements of *T. australis* tended to be heavier whereas those of *T. comptus* were more subdued.

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**References**


