First East Gondwanan record of *Strepsodus* (Sarcopterygii, Rhizodontida) from the Lower Carboniferous Ducabrook Formation, central Queensland, Australia

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KEY WORDS
Strepsodus,
Rhizodontidae,
Carboniferous,
Queensland,
East Gondwana,
Laurentia.

ABSTRACT

Postcranial rhizodontid remains from Middle Paddock (central Queensland, mid-Viséan) show closest affinity to those of *Strepsodus*, known from the Carboniferous of Britain and eastern Canada, latest Devonian of Turkey and Upper Devonian of Colombia and Iran. The Queensland *Strepsodus* marks the appearance of the Rhizodontidae (a derived taxon within the Rhizodontida including *Strepsodus*, *Rhizodus* and *Screbodinus*) in East Gondwana; tetrapod, xenacanth and lungfish taxa from Middle Paddock also include groups not previously described from East Gondwana. This is a contribution to IGCP 421.

RÉSUMÉ

Premières observations pour le Gondwana oriental sur Strepsodus *(Sarcopterygii, Rhizodontida) du Carbonifère inférieur de la Formation Ducabrook, Queensland central, Australie.*

Des restes postcrâniens de rhizodontides de Middle Paddock (Queensland central, Viséen moyen) présentent les plus étroites affinités avec ceux de *Strepsodus*, du Carbonifère de Grande-Bretagne, du Canada oriental, du Dévonien terminal de Turquie et du Dévonien supérieur de Colombie et d'Iran. Le *Strepsodus* du Queensland marque l'apparition des Rhizodontidae (un taxon dérivé au sein des Rhizodontida, et qui inclut *Strepsodus*, *Rhizodus* et *Screbodinus*) dans le Gondwana oriental ; des taxons de tétrapodes, xénacanthes et dipneustes de Middle Paddock incluent aussi des groupes jusqu'alors inconnus dans le Gondwana oriental. Ceci est une contribution au PICG 421.

MOTS CLÉS
Strepsodus,
Rhizodontidae,
Carbonifère,
Queensland,
Gondwana oriental,
Laurentia.

INTRODUCTION

Collecting at the mid-Viséan Middle Paddock site (Drummond Basin, central Queensland, Fig. 1) since 1995 has revealed a diverse freshwater fauna (at least one tetrapod taxon, xenacanth and other sharks, palaeoniscids, lungfish and acanthodians), including relatively abundant rhizodontid specimens. These are dominated by shoulder girdle material, opercular and gular bones, teeth and scales, preserved due to their robustness or flatter shape (less readily transported in moving water). Of these, the shoulder girdle specimens are most readily recognizable as rhizodonts. They can be referred to the Rhizodontida on the basis of the characteristic "reverse double overlap" of the anteroventral margin of the cleithrum onto the clavicle, followed ventrolaterally and dorsally by an overlap of the clavicle onto the cleithrum. A third overlap occurs as a dorsal extension of the clavicle overlaps the anterior margin of the cleithrum (Andrews & Westoll 1970: fig. 10).

The Rhizodontida is a somewhat enigmatic group of tetrapodomorph (*sensu* Ahlberg 1991) sarcopterygian fishes known since the middle of the nineteenth century, but originally described largely from teeth and scales (Owen 1840). This created considerable taxonomic confusion (Andrews 1985), occurring even when other cranial and postcranial material was available.

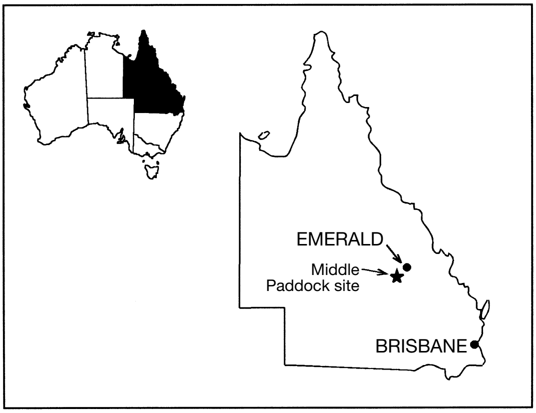

FIG. 1. — Map showing location of Middle Paddock fauna, Drummond Basin, central Queensland.

Recent work has resulted in the description of well-preserved rhizodont skull material for the East Gondwanan taxa *Barameda decipiens* Long 1989 and *Gooloogongia loomesi* Johanson & Ahlberg 1998. Skull material of Laurentian forms is less well known, although this will be remedied in part by the preparation and description of the skull of *Screbodinus ornatus* (Traquair, 1878) by J. Jeffrey (in prep.). Nevertheless, many taxa are best known from the robust shoulder girdle specimens (e.g., Andrews & Westoll 1970) and comparable material from Middle Paddock will be the focus of this preliminary report. All material collected from Middle Paddock is housed at the Queensland Museum.

ABBREVIATIONS

QMF	Queensland Museum, Brisbane;
NMV P	National Museum of Victoria, Melbourne;
AMF	Australian Museum, Sydney.

SYSTEMATIC PALEONTOLOGY

Classe SARCOPTERYGII Romer, 1955
Order RHIPIDISTIA Cope, 1887

Family RHIZODONTIDAE Traquair, 1881

Shoulder girdle material has been described or figured for a large number of Late Devonian and Carboniferous Rhizodontida including *Strepsodus sauroides* (Binney, 1841), *Screbodinus ornatus* (Andrews & Westoll 1970; Andrews 1985), *Rhizodus hibberti* Owen, 1840 (Andrews & Westoll 1970), ?*Strepsodus anculonamensis* Andrews, 1985, *Strepsodus* sp. (Janvier *et al.* 1984) (these taxa are assigned to the Rhizodontidae, a derived family within the Rhizodontida), *Sauripteris taylori* Hall, 1843 (Andrews & Westoll 1970), *Barameda decipiens* (Long 1989), *Gooloogongia loomesi* (Johanson & Ahlberg 1998) and "*Notorhizodon*" *macelveyi* Young *et al.*, 1992 (this taxon may be restricted to assigned shoulder girdle material [Johanson & Ahlberg, in press]). Undescribed rhizodontid shoulder girdle material (cleithra) from Horton Bluff (Tournaisian, Nova Scotia, Canada) has also been examined (by Johanson & Warren) and will be included in comparisons below.

One variable feature among these taxa is the degree of development of the unornamented and depressed flange along the posterior margin of the cleithrum. Of these taxa, *Screbodinus* and *Barameda* are said to have relatively smaller flanges (Fig. 2E, H). This is also the morphology seen in the ?*Strepsodus anculonamensis* and "larger Foulden form", associated with (and closely related to) ?*S. anculonamensis* (Fig. 2A, B) (Andrews 1985: 85, figs 11b-e; 13a-c). The widest portion of these smaller flanges (visible in lateral view) appears to mirror the dimensions of the posterior scapulocoracoid attachment on the internal surface of the cleithrum (see below); dorsal to this, the flange narrows sharply. This widest point occurs at the narrowest part of the main body of the cleithrum (the pectoral incision [Andrews 1985]). It should be noted that the posterior flange figured for *Barameda* (Long 1989: fig. 9B) may be nearer to the scapulocoracoid and the pectoral incision than indicated (based on NMV P181699). This flange in *Barameda* (Long 1989: fig. 7E) is probably smaller than that of ?*Strepsodus anculonamensis* and the "larger Foulden form" (Andrews 1985: fig. 11). The posterior flange on the Horton Bluff cleithra is most similar to ?*Strepsodus anculonamensis* and the "larger Foulden form". That of *Strepsodus* sp. from the latest Devonian of Turkey (Janvier *et al.* 1984 : pl. 2.12) also appears to be smaller, especially when compared with *Strepsodus sauroides* (see below). These species can be separated from *Screbodinus ornatus*, which has a small posterior flange but lacks a pectoral incision (Andrews 1985) (Fig. 2E). The smaller flange in *Barameda* may be associated with the absence of a raised or distinct posterior scapulocoracoid attachment (Long 1989: fig. 7C; see below).

Gooloogongia loomesi lacks a posterior flange entirely (Fig. 2G) (Johanson & Ahlberg 1998), while "*Notorhizodon*" *macelveyi* appears to have a thin posterior unornamented area that is not depressed relative to the dorsal lamina of the cleithrum (Fig. 2F) (Young *et al.* 1992: fig. 40A). This may represent an incipient posterior flange. The posterior flange of *Sauripteris taylori* is not readily evaluated, as the specimen described is visible only in internal view (e.g., Andrews & Westoll 1970: pl. 8C). A new specimen of *Sauripteris* figured by Daeschler & Shubin (1997) may have more information in this regard following preparation.

In contrast, both *Strepsodus sauroides* and *Rhizodus* have more strongly developed posterior flanges of the cleithrum (Fig. 2C, D). That of *Rhizodus* does not narrow, but extends around the dorsal margin of the cleithrum (Andrews & Westoll 1970: pl. 6). This is the best developed posterior flange in the Rhizodontida. In *Strepsodus sauroides* (Andrews & Westoll 1970:

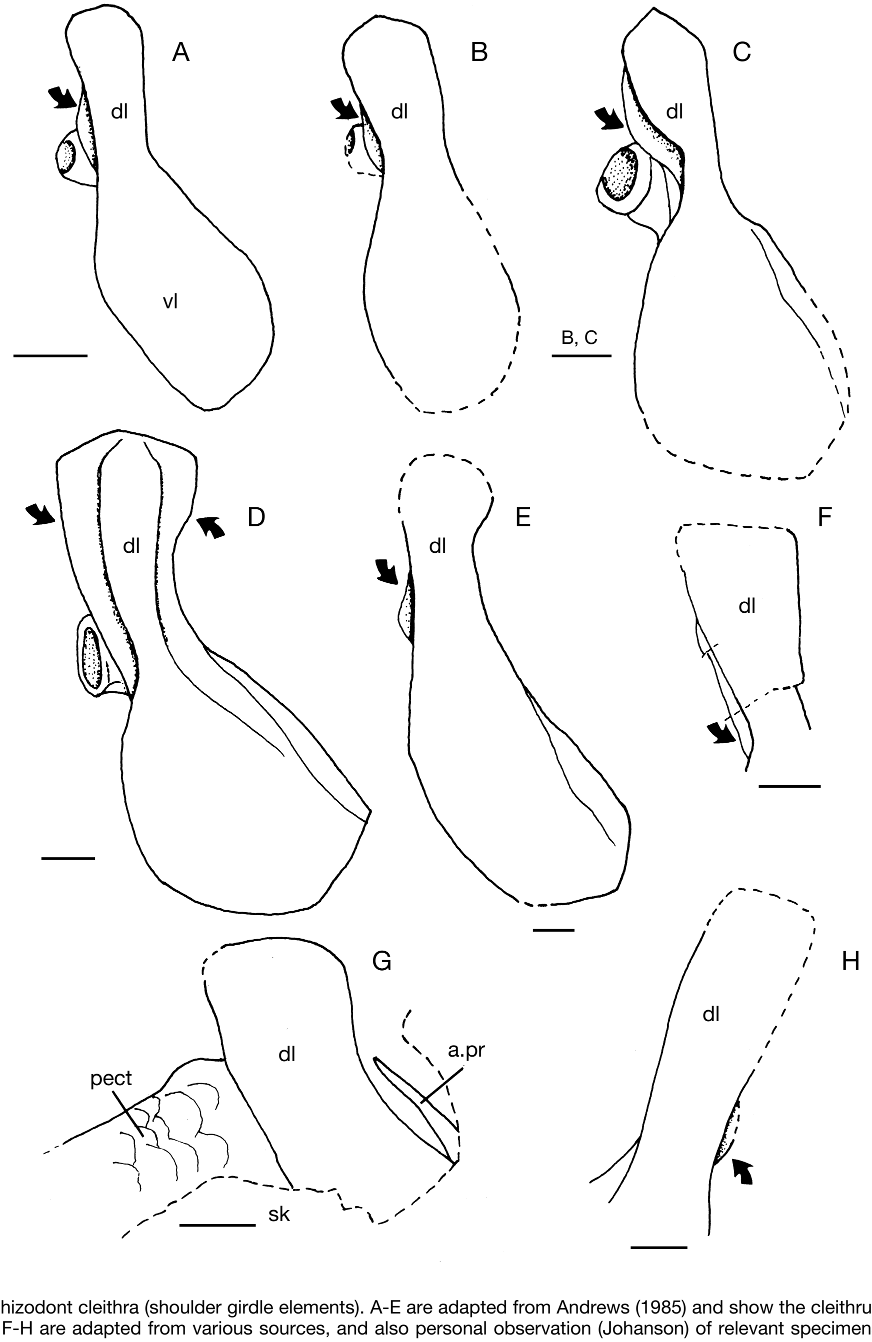

FIG. 2. — Rhizodont cleithra (shoulder girdle elements). A-E are adapted from Andrews (1985) and show the cleithrum flattened into one plane. F-H are adapted from various sources, and also personal observation (Johanson) of relevant specimens. Dermal ornament is omitted. **A**, ?*Strepsodus anculonamensis*, right cleithrum (Andrews 1985: fig. 11b); **B**, "larger Foulden form", right cleithrum (Andrews 1985: fig. 11a); **C**, *Strepsodus sauroides*, right cleithrum (Andrews 1985: fig. 13h); **D**, *Rhizodus hibberti,* right cleithrum (Andrews 1985: fig. 13d); **E**, *Screbodinus ornatus,* right cleithrum (Andrews 1985: fig. 13g); **F**, "*Notorhizodon*" *mackelveyi* (AMF54333, Young *et al*. 1992), dorsal lamina of right cleithrum; **G**, *Gooloogongia loomesi*, right cleithrum (Johanson & Ahlberg 1998: fig. 1a); **H**, *Barameda decipiens,* left cleithrum (Long 1989: fig. 7E). Arrows indicate unornamented flange of cleithrum (except in G where it is believed to be absent). Abbreviations: **a.pr**, ascending process of the clavicle; **dl**, dorsal lamina of cleithrum; **pect**, pectoral fin; **sk**, skull; **vl**, ventral lamina of cleithrum. Scale bars: A, 0.5 cm; B-C, 2 cm; D, 3 cm; E-H, 1 cm.

pl. 11; Andrews 1972: pl. 1C), the flange also extends dorsally but does not reach the dorsal margin of the cleithrum. This is the widest flange among species of *Strepsodus* (compare the "larger Foulden form" with *S. sauroides* [Andrews 1985: fig. 13a-c, h]).

Of the taxa just described, the better preserved Middle Paddock rhizodontid cleithra (QMF34611, QMF36762 and QMF34602) show closest similarity to *Strepsodus*, with a well-developed pectoral incision and posterior flange. Of these, QMF36762 (Fig. 3A-C) is the best preserved. The width of this flange decreases more rapidly above the scapulocoracoid attachment than does that of *S. sauroides,* and may be more similar to ?*Strepsodus anculonamensis*, the "larger Foulden form" and the Horton Bluff rhizodontid, where the main width of the flange occurs at the pectoral incision in external view (Fig. 3A). On the other hand, QMF34611 (Fig. 3D) and QMF34602, although more damaged, appear to show a better developed flange, and differences in the morphology of the dorsal cleithrum and scapulocoracoid attachment (see below) that may indicate the presence of more than one species at Middle Paddock. Comparisons between these two cleithra and *S. sauroides* are difficult due to damage in the former; still, the flanges of these appear better developed than QMF36762 and other species of *Strepsodus*.

Other differences exist among known rhizodont cleithra. For example, the dorsal cleithrum is more triangular in the best preserved specimen of *Strepsodus sauroides* (Andrews & Westoll 1970: pl. 11A), rounder in ?*S. anculonamensis* and the "larger Foulden form" (Andrews 1985: fig. 11d) but squarer in the Middle Paddock (Fig. 3) and Horton Bluff specimens.

The morphology of the scapulocoracoid attachment also differs among these, although it is always located on the dorsal lamina of the cleithrum at the pectoral incision (Andrews 1985). This position is consistent among the Rhizodontida. The morphology of the scapulocoracoid attachment on the Middle Paddock cleithra is somewhat variable. In certain specimens (QMF34611, Fig. 3E, arrow), ridges form a V- or U-shaped structure posteriorly (attachment for the glenoid buttress). A low anterior ridge forms the attachment for the supraglenoid and infraglenoid buttresses of the scapulocoracoid. In another specimen (QMF36762, Fig. 3C), the posterior attachment area is flatter and less clearly composed of ridges. The area between the anterior and posterior attachment areas is slightly concave in QMF36762 but less well-developed in other Middle Paddock cleithra.

On a smaller specimen of *Strepsodus* sp. from Turkey (Janvier *et al.* 1984: pl. 2.10), the posterior scapulocoracoid attachment appears to be composed of two short, obliquely oriented and parallel ridges. The anterior ridge runs to about the level of these two ridges, forming a shallow V-shaped area between them. The comparable area on described specimens of *Strepsodus sauroides* and ?*S. anculonamensis* is either covered by the scapulocoracoid (Andrews & Westoll 1970: pl. 11A) or not visible (Andrews & Westoll 1970: pl. 11H; Andrews 1985). The attachment on the "larger Foulden form" appears flat and not clearly composed of distinct ridges (Andrews 1985: fig. 11e), as in QMF36762 (Fig. 3C, arrow). The nature of the anterior ridge is not clear. The posterior scapulocoracoid attachment in the Horton Bluff specimens is similar to the "larger Foulden form" and QMF36762. These areas are distinctly separate from the main body of the cleithrum. As noted above, this is not the case for *Barameda* (NVM P181699, Long 1989: fig. 7C). On the Horton Bluff specimens, the anterior ridge for the supraglenoid and infraglenoid buttresses is sharply developed and separated from the posterior by a deep and rounded groove. The scapulocoracoid is preserved on certain of these specimens and appears firmly fused to the cleithrum. That is, no fossae are present between the scapulocoracoid and the cleithrum. The presence or absence of these fossae in *Strepsodus sauroides* (Andrews & Westoll 1970: 442) is not well established. The scapulocoracoid is entirely absent from the Middle Paddock cleithra.

Young *et al.* (1992: fig. 47) restricted the British Carboniferous rhizodonts, including *Screbodinus*, *Strepsodus* and *Rhizodus* to the Rhizodontidae,

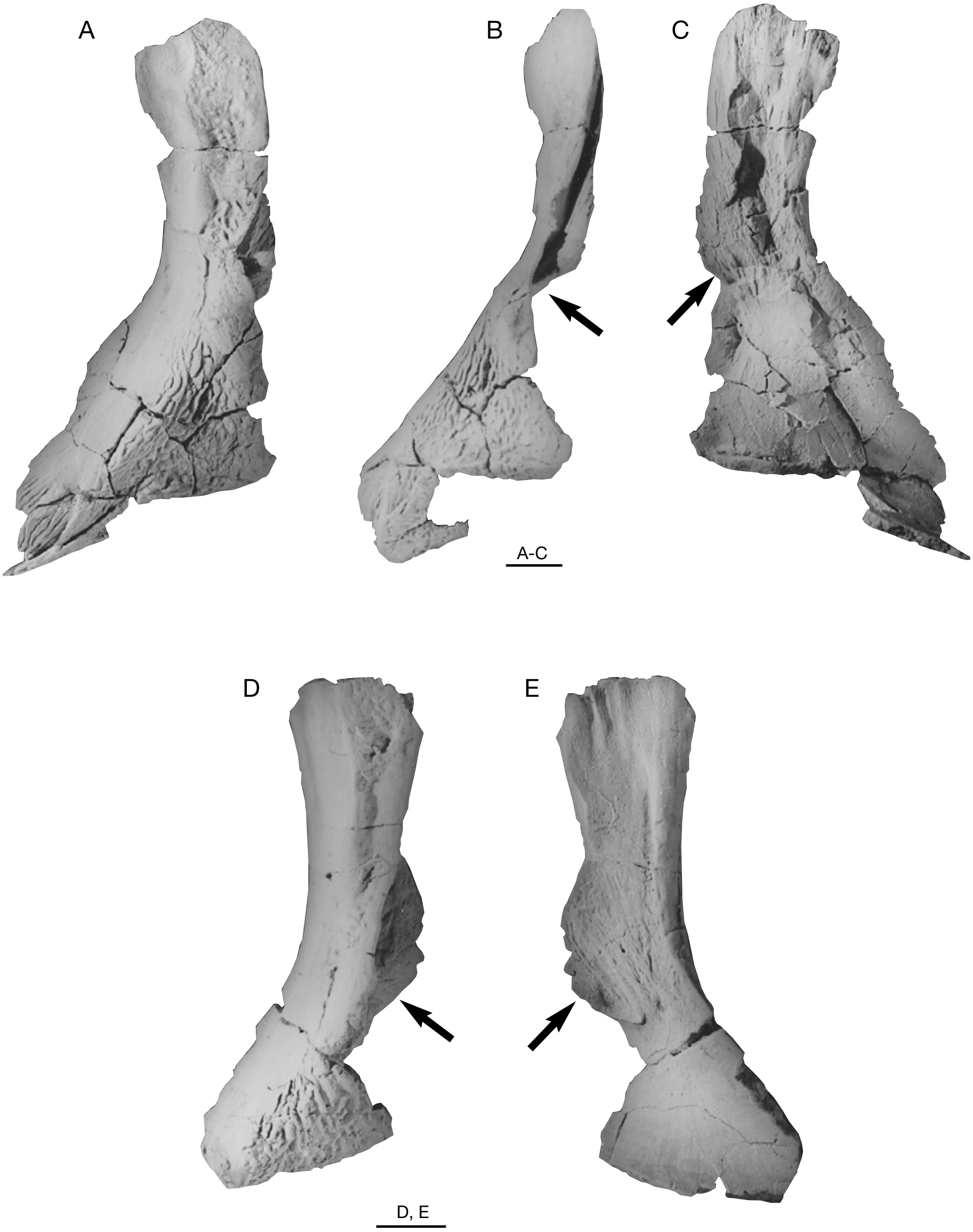

FIG. 3. — Cleithra of Middle Paddock rhizodonts (Ducabrook Formation, mid-Viséan, Drummond Basin, Queensland). A-C, QMF36762, left cleithrum similar to ?*Strepsodus anculonamensis* in size of unornamented flange; **A**, external view; **B**, posterolateral view; **C**, internal view; D-E, QMF34611, left cleithrum more similar to *Strepsodus sauroides* in size of posterior unornamented flange; **D**, external view; **E**, internal view. Arrow in B and D marks position of posterior flange; arrow in C and E marks position of posterior part of the scapulocoracoid attachment. Scale bars: 1 cm.

with other rhizodonts (including *Barameda*) forming more inclusive, basal branches within the Rhizodontida. Johanson & Ahlberg (1998) established that *Gooloogongia* was phylogenetically the most basal rhizodont, with *Barameda* forming a polytomy with the Rhizodontidae. Problematic in these phylogenetic analyses is *Gooloogongia*, which has little information on the nature of the pectoral fin supports, and *Sauripteris*, for which information is limited entirely to the latter. This results in uncertainty in character state codings and unresolved phylogenetic relationships.

One thing that can be established is that *Rhizodus* and *Strepsodus* represent the most derived rhizodonts, for example, in the development of the posterior flange of the cleithrum, and in the course of the postotic canal crossing onto the postparietal bone of the skull roof. This canal runs along the bones flanking the postparietal in *Barameda* and *Gooloogongia* (Young *et al.* 1992; Johanson & Ahlberg 1998). *Screbodinus ornatus*, although also possessing a reduced posterior flange (Andrews & Westoll 1970), shows a similar course of the postotic canal to *Rhizodus* and *Strepsodus* (Andrews 1985: fig. 7c).

BIOGEOGRAPHICAL REMARKS

Skull material from Middle Paddock is still under investigation; nevertheless, the similarity in shoulder girdle material suggests that the Middle Paddock rhizodontid is more closely related to the Rhizodontidae (although the number of species at Middle Paddock and their affinities within *Strepsodus* are difficult to determine at this time) than to other eastern Gondwanan taxa, which appear to be primitive in a variety of characters including those mentioned above.

The age of eastern Gondwanan rhizodonts ranges from Givetian-early Frasnian ("*Notorhizodon*" *macelveyi*) to late Frasnian (*Gooloogongia*) and into the Carboniferous (*Barameda*, ?Tournaisian; Middle Paddock specimens, mid-Viséan). The referral of the Middle Paddock specimens to *Strepsodus* extends the range of this taxon, previously described from numerous northern hemisphere localities (Andrews 1985), including shoulder girdle material from the late Tournaisian Calciferous Sandstones at Foulden, Scotland (?*S. anculonamensis* and the closely related "larger Foulden form" [Andrews 1985]) and various Late Carboniferous localities in the British Coal Measures (Bashkirian-Westphalian; Andrews & Westoll [1970]; Andrews [1985]). Among the Rhizodontida, shoulder girdle material (cleithra) from Horton Bluff (Nova Scotia, early Tournaisian) also shows strongest similarity to *Strepsodus.* This distribution indicates interchange between Laurentian localities and East Gondwana in the Carboniferous. This is supported by the presence of *Strepsodus* sp. in Upper Devonian (latest Famennian) deposits of Turkey (Janvier *et al.* 1984) and Iran (Dashtban 1996; Janvier pers. comm.), along the northern margin of Gondwana.

Thulborn *et al.* (1996) noted that the Middle Paddock fauna was similar to faunas included in Milner's (1993) Mississippian Tetrapod Province, previously restricted to Laurentia (North America and western Europe). If correct, a significant extension of the Mississippian Tetrapod Province into East Gondwana is indicated during, or prior to, the Viséan. The Ducabrook rhizodontids show similarities to both Mississippian (Foulden, Horton Bluff) and Pennsylvanian/Late Carboniferous (*Strepsodus sauroides*, Coal Measures of Britain) species of *Strepsodus*. This may indicate links or interchange beyond the Mississippian. Further study of the remainder of the Middle Paddock fauna, and description of other taxa from faunas of the Mississipian Tetrapod Province (e.g., from Iowa, West Virginia and Nova Scotia [Schultze & Bolt 1996; Clack & Carroll in press]) will help to clarify these suggestions.

Nevertheless, the presence of *Strepsodus* in the Middle Paddock fauna marks the appearance of the Rhizodontidae in East Gondwana. This might represent a distinct faunal change within East Gondwana from the Devonian to the Carboniferous, and perhaps more specifically, within the Carboniferous. The Middle Paddock fauna includes the most derived East Gondwana rhizodont known in association with at least one tetrapod.

By comparison, the rhizodont *Barameda* occurs in the Lower Carboniferous Mansfield Group of Victoria; tetrapods are absent. Although there is some uncertainty as to the phylogenetic position of *Barameda* (see above), a referral to the Rhizodontidae (with *Strepsodus* and *Rhizodus*) is unlikely. This upper level of the Mansfield Group may be older than previously accepted (possibly Devonian), with the Carboniferous age based largely on the absence of placoderm material present in lower levels (Long & Campbell 1985). Undoubted Lower Carboniferous localities (Tournaisian-early Viséan, and so older than the Middle Paddock fauna) in the Upper Telemon and Raymond Formations of the Narrien Range, northern Drummond Basin, Queensland, contain an osteolepid, actinopterygians, acanthodians, xenacanths and other sharks and possibly rhizodonts (Turner 1993; Fox *et al.* 1995), but again, no tetrapod material.

With regards to other taxa, a ctenodont lungfish is present at Middle Paddock (Turner *et al.* 1999), while in the Mansfield Group, the lungfish *Delatitia* Long & Campbell 1985 appears less derived in characters such as the course of the supraoccipital commissure through the A rather than the B bone at the back of the skull (Schultze & Bolt 1996: character 3). The ctenodont lungfish *Tranodis* Thomson 1965 from the Goreville (Illinois) and Delta (Iowa) localities (Viséan-Namurian) is associated with taxa that are also found at Middle Paddock, including tetrapods, rhizodonts, palaeoniscids, xenacanths, hybodonts, other sharks and gyracanthid acanthodians (Schultze & Bolt 1996; S.T. pers. obs.). The former localities were included in Milner's (1993) Mississipian Tetrapod Province and a comparison between the rhizodonts here and those from Middle Paddock will be important.

The differences just described suggest some type of major change in East Gondwana within the Early Carboniferous. This may not be entirely due to variation in the position of Laurentia and Gondwana, as strong evidence exists for an association between these landmasses in the late Frasnian and into the Famennian. This is based upon the presence of the lungfish *Soederberghia* Lehman, 1955 as well as tristichopterid sister taxa (Tetrapodomorpha) in New South Wales and various Laurentian sites (Ahlberg & Johanson 1997; Johanson & Ahlberg 1997; Ahlberg *et al.* in press).

The presence of *Strepsodus* in the Carboniferous of Middle Paddock, eastern Canada and Britain, and in the Upper Devonian of Turkey and Iran corroborates suggested interchange between Laurentian and Gondwanan landmasses in the Late Devonian and Carboniferous. Additionally, Frasnian-aged *Strepsodus*-like material has been recovered from South America (in Colombia, Janvier & Villarroel 1998). The absence of *Strepsodus* or other more derived rhizodontid taxa from the Upper Devonian East Gondwana (Australia + Antarctica, Young [1981]) may require further explanation, as *Strepsodus* was probably already established in western and northern Gondwana during this time.

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