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LOWER AND MIDDLE DEVONIAN CONODONTS FROM THE BROKEN RIVER EMBAYMENT NORTH QUEENSLAND, AUSTRALIA

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With 16 plates, 6 tables, and 9 text-figures

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ABSTRACT. Limestones of the Siluro-Devonian Graveyard Creek and Broken River Formations in the Broken River Embayment, north Queensland, contain diverse, though unevenly distributed, conodont faunas. Seven major units, the Jack Limestone Member of the Graveyard Creek Formation and the Martin’s Well, Dip Creek, Chinaman Creek, Lockup Well Limestone Members and lenses Dmb_E and Dmb_F of the Broken River Formation were examined. Seventy-seven conodont form species and subspecies, referable to twenty form genera, are described; seven species (Coelocerodontus reduncus, Neopanderodus aequabilis, Ozarkodina playfordi, Scolopodus erectus, Spathognathodus paleithorpei, Spathognathodus n. sp. A, Synprioniodina scalena) and one subspecies (Polygnathus foveolatus serotinus) are new. Although a continuous conodont succession could not be established, eight stratigraphically significant conodont faunas are recognizable. These comprise (in ascending order, with deduced ages): the eosteinhorennis (Ludlovian), pesavis (middle–late Siegenian), exiguas (middle–late Siegenian), Spathognathodus n. sp. (early Emsian), foveolatus-paleithorpei (late Emsian), linguiformis cooperi (early Couvinian), pseudofoliatus (late Couvinian–early Givetian), and brevis (Givetian) faunas. The faunas allow an accurate appraisal of stratigraphical relationships within the Broken River Embayment and, though hampered by the apparent endemism of certain form species, their correlation within eastern Australia is effected. Intercontinental correlation shows that eastern Australian early Devonian conodont faunas are better related to western North American faunas than to those of the European type sequences; this may indicate some degree of conodont provincialism. Middle Devonian conodonts of eastern Australia appear to have close affinities with both North American and European forms.
INTRODUCTION

ONLY during the last decade have conodonts been employed in biostratigraphic analyses of lower and middle Devonian limestone sequences of eastern Australia. Philip (1965, 1966), Philip and Jackson (1967), Flood (1969), Pedder et al. (1970b), Duce (1970b), and Savage (1973) have described lower Devonian conodont faunas from New South Wales and Victoria, while middle Devonian conodonts from northern New South Wales have been documented by Philip (1967) and Pedder et al. (1970a). Duce (1970a) and Telford (1972) gave preliminary accounts of lower Devonian faunas from central and southern Queensland, but conodonts from other lower and middle Devonian limestones of that state have hitherto been largely neglected, except for brief mention in review articles (Duce and Wilson 1967; Philip and Pedder 1967c).

The most extensive development of Devonian limestones in Queensland occurs in the Broken River area, about 240 km north-west of Charters Towers. Here limestones were formed within a probably geomorphic Palaeozoic structure, the Broken River Embayment. Geology of the region has been described by various authors

TEXT-FIG. 1. Devonian sedimentation in Australia, and the location of the Broken River Embayment.
(White 1965; Wyatt and Jell 1967; Jell 1968) and Jell (unpublished Ph.D. Queensland University, 1967) studied the morphology and stratigraphic distribution of rich coral faunas from many of the limestones. However, no detailed consideration has yet been given to conodont faunas already noted to occur in the embayment's Devonian sequence (Wyatt and Jell 1967, table 1). Of particular importance is the essentially uninterrupted nature of the succession, ranging from the upper Silurian through to the middle Devonian (Wyatt and Jell 1967).

Carbonate deposition was widespread in the Tasman Geosynclinal Zone of eastern Australia during late Silurian and Devonian time, but it was mostly confined to small, widely separated regions so that geographically extensive and stratigraphically continuous limestone sequences are rare (text-fig. 7). Indeed, deposition of few Devonian limestone sequences continued for longer than one stage (Philip and Pedder 1967c, figs. 2, 3). Therefore conodont studies of the thick limestone units in the Broken River Embayment were originally intended to provide definition of an uninterrupted succession of Siluro-Devonian faunas, and so establish a biochronological standard for eastern Australia. Unfortunately gaps, caused by disconformities or unfossiliferous strata, were found to occur in the sequence, preventing definition of a continuous zonal scheme. Thus, rather than formal zones, a number of stratigraphically useful conodont faunas are proposed (Table 4) and described herein. These faunas are also effective in interbasinal and intercontinental correlation.

All specimens are housed in the micropalaeontological collection of the Department of Geology and Mineralogy, University of Queensland, St. Lucia, Brisbane. Figured specimens, including holotypes and paratypes of new taxa, have catalogue numbers prefixed by Y. Each conodont-bearing sample was assigned a Ct number. All samples from a single measured section are designated with the same geographical locality, which is given a locality number prefixed by L. Section or individual sample localities are shown on text-fig. 2; distribution of conodont species is indicated on Tables 1–3. The Ct-numbered samples of each rock unit and section locality are listed in Appendix 1.

**STRATIGRAPHY**

Originally defined by Hill (1960), the Broken River Embayment constitutes a south-westerly directed offshoot of the generally northward trending Tasman Geosyncline. Strata of the embayment consist of a sequence of Palaeozoic sedimentary rocks, overlapping Precambrian igneous and metamorphic rocks of the Georgetown Inlier (White 1961) in the headwater regions of Gray Creek and of Broken and Clarke Rivers. The first major geological study of the embayment took place between 1956 and 1959 when combined field parties of the Bureau of Mineral Resources and Geological Survey of Queensland mapped the Georgetown, Einasleigh, Gilberton, and Clarke River 1:250,000 Sheet areas (the embayment lies almost entirely within the Clarke River Sheet area). Results of this work were embodied in a report by White (1965) on the geology of the Georgetown–Clarke River area, which also contains a summary of previously published geological information on the region.

The geology of the Georgetown–Clarke River area consists of a western region of Archaean high-grade metamorphic rocks and Proterozoic sediments and metasediments overlapped in the east by Palaeozoic sediments and volcanics of the Tasman Geosyncline. Late Ordovician to early Carboniferous marine and terrestrial strata constitute the sequence of the Broken River Embayment; and, except for minor
occurrences of Tertiary laterites and Quaternary alluvium, no younger sediments are represented. During the late Ordovician, late Silurian, and early and middle Devonian, limestones were extensively developed (text-fig. 2) and prolific invertebrate faunas have been obtained from them (White 1965; Wyatt and Jell 1967). Limestone units relevant to the present study are as follows:

**EARLY–MIDDLE DEVONIAN**

- Broken River Formation (White 1959b)
  - Martin’s Well Limestone Member
  - Dip Creek Limestone Member
  - Chinaman Creek Limestone Member
  - Lockup Well Limestone Member

**LATE SILURIAN–EARLY DEVONIAN**

- Graveyard Creek Formation (White 1959a)
  - Jack Limestone Member (White 1959a)

In addition, several small unnamed limestone lenses occur in the lower and upper parts of the Graveyard Creek Formation, and near the base of the Broken River Formation, near Pandanus Creek homestead, Martin’s Well, and Lockup Well (text-fig. 2). The younger ones in the Graveyard Creek Formation are in a comparable stratigraphical position to the Jack Limestone. The limestones are situated in three principal regions, ‘Pandanhas Creek’ area, ‘Jessey’s Springs’ area (between ‘Pandanhas Creek’ homestead and the Broken River), and the Broken River area itself (text-fig. 2).

‘Pandanhas Creek’ area. Within this area faulting has been intense, especially in a zone parallel to Gray Creek, between ‘Pandanhas Creek’ and Martin’s Well. The strata have also been strongly folded into a series of southward plunging anticlines and synclines, which are highlighted by prominent, almost continuous limestone outcrops. Following the regional mapping of the Clarke River Sheet area (White 1962, 1965), Jell (1968) examined the limestones and their coral faunas in the ‘Pandanhas Creek’—Martin’s Well—Lockup Well region. Jell established four major units, the Martin’s Well, Dip Creek, Chinaman Creek, and Lockup Well Limestone Members of the Broken River Formation, together with several small, but biostratigraphically significant, unnamed lenticular bodies in the lower and upper parts of the Graveyard Creek Formation, and near the base of the Broken River Formation.

Coral faunas from the unnamed limestones of the Graveyard Creek Formation were thought by White (1965) and Jell (unpublished Ph.D. 1967) to indicate a range of middle Silurian to early Devonian for the unit. The largest and most diverse of these faunas was obtained from a small lens about 6 km north of ‘Pandalhas Creek’ (L. 3684 on text-fig. 2). Conodonts proved to be far more abundant in this lens than in others of the Graveyard Creek Formation, although in none of them were specimen yields very great (Table 1). All of these lenses consisted mainly of massive, crinoidal, or coralline limestone, which is commonly so recrystallized that fossil preservation is poor. Both White (1965) and Jell (1968) noted evidence of a considerable time interval between deposition of the Graveyard Creek Formation and Martin’s Well Limestone Member, the oldest major fossiliferous unit of the Broken River Formation; but there is no suggestion of angular discordance between the two formations.
TEXT-FIG. 2. Limestone units of the Broken River Embayment. A, Martin’s Well Member; B, Dip Creek Member; C, Lockup Well Member; D, Chinaman Creek Member; E–I, unnamed units; J, Jack Member. Conodont-bearing samples from the various localities are listed in the Appendix. Section thicknesses and conodont abundances are given in Tables 1–3.
TABLE 1. Distribution of conodonts in limestone lenses of the Graveyard Creek Formation. All limestone units indicated on this and the following tables were sampled at 2-5 m intervals (in most cases by 0-5 m channel samples) but space does not permit individual documentation of the more than 500 samples, whose details are in the author’s unpublished Ph.D. thesis at the University of Queensland 1972.

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<th>3684</th>
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<td>14</td>
<td>15</td>
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<td>6</td>
<td>21</td>
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<td>1</td>
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<tr>
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<td>6</td>
<td>3</td>
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<tr>
<td>Plectospathodus alternatus</td>
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<td></td>
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<td>2</td>
<td></td>
</tr>
<tr>
<td>Spathognathodus eastleinhornensis</td>
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<td>3</td>
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<tr>
<td>Spathognathodus eugnius</td>
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<tr>
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<td></td>
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<tr>
<td>Trichonodella inconstans</td>
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</tbody>
</table>

Jell (1968) provided details of lithological character and distribution of the limestone members of the Broken River Formation. Their thicknesses, which vary from 80 m for the Martin’s Well Limestone Member to as much as 700 m for the Chinaman Creek Limestone Member, are indicated on Tables 1-3. No realistic estimate of thickness could be made for the Lockup Well Limestone Member as its basal part is obscured by Cainozoic basalt (text-fig. 2). The Martin’s Well Limestone Member differs markedly from the other three. It consists mainly of thinly bedded detrital limestones and shales, while the others are more massive, containing reef-like and biothermal structures, and have little interbedded terrigenous material. In addition, the invertebrate megafossil faunas, including tabulate and rugose corals, stromatoporoids, sponges, crinoids (both stems and calices are usually present), brachiopods, bivalves, trilobites, and nautiloids, are more diverse in the Martin’s Well Limestone than in the other limestones whose faunas are dominantly corals, stromatoporoids, and crinoids with minor brachiopods and bivalves. Similarly, conodonts were found to be consistently more abundant in the Martin’s Well Limestone Member. One sampled section (L. 3658 on text-fig. 2) coincides with the type section defined by Jell (1968).

The Dip Creek Limestone Member lies 600 m stratigraphically above the Martin’s Well Limestone Member. It is an intensely folded unit extending from south-west of Martin’s Well to Lockup Well in the east (text-fig. 2), and it is well-exposed, occurring as prominent bluffs; one sampled section (L. 3667) was parallel to, but about 100 m south of, the type section (Jell 1968) along Dip Creek. The Dip Creek Limestone Member is dominantly massive limestone, with individual beds up to 6 m thick, and occasional biothermal mounds, which are common in section L. 3666 near Martin’s Well. Thinly bedded detrital limestone or shale intercalations were infrequent in all sections.
The Chinaman Creek Limestone Member, the thickest member of the Broken River Formation, occurs only in the western part of the ‘Pandanus Creek’ area extending north from near ‘Pandanus Creek’ homestead as a series of low ridges (text-fig. 2). The member consists mostly of thickly bedded limestone including numerous biohermal structures; thinly bedded detrital limestone is uncommon, occurring mainly in the lower part. The limestones are separated into three distinct units by two series of sandstone beds. These were present in similar positions in both measured sections (text-fig. 2), indicating some lateral continuity of the beds. Boundaries between limestone and sandstone are gradational over several metres.

Extending south-west from Lockup Well (text-fig. 2) is a limestone body called the Lockup Well Limestone Member by Jell (1968), but whose stratigraphic relationships with the other limestones are uncertain. The base of the unit is obscured by Cainozoic basalt and associated lateritic soils. The southern end is similarly obscured, while poor outcrop near Lockup Well prevents accurate delineation of the northern margin. In this northern region there are outcrops of other separate limestone bodies which may represent either the Lockup Well or Martin’s Well Limestone Members. Conodont and coral faunas are prolific at these localities (L. 3675, Table 2). The Lockup Well Limestone Member is similar to the Dip Creek Limestone Member, being thickly bedded with numerous biohermal structures, and with only few detrital limestones. The top 3–5 m consists of thinly bedded, conodont-rich, crinoidal limestone which can be traced laterally for several kilometres and was encountered in sections at L. 3673 and L. 3674. The section at L. 3672 approximately coincides with the type section of the unit, and allowing for the difficulties in selection of the lowermost beds, the measured thickness of 390 m accords with 430 m estimated by Jell (1968).

Distribution of conodonts in the Dip Creek, Chinaman Creek, and Lockup Well Limestone Members is irregular (Table 2), and large faunas were obtained only sporadically. This distribution can be correlated with the occurrence of thinly bedded detrital limestone or biostromal mounds rich in crinoidal debris. The great algal and coralline growth, which was mainly responsible for formation of the limestones, was apparently not conducive to flourishing conodont communities. Only in strata richer in terrigenous material, perhaps representing forereef or interreef facies, are the microfossils abundant.

‘Jessey’s Springs’ area. The basalt covering part of the Lockup Well Limestone Member extends south for about 4 km and is, in turn, overlain by lateritic soils which extend a further 6 km. At the southern margin of this lateritic material, near ‘Jessey’s Springs’, more limestones of the upper Graveyard Creek Formation and of the Broken River Formation crop out (text-fig. 2). Those in the former are small lenticular bodies, equivalent in stratigraphical position to the Jack Limestone Member which occurs further south. The large, partly lateritic soil covered, limestone body in the Broken River Formation is unnamed, but was referred to by White (1965) as lens Dmb£. He described it as consisting of light-grey limestone, with poorly developed bedding, cropping out over about 6.5 sq. km, this fairly large area being the result of complex folding. Because of its isolation from them, the relationships of lens Dmb£ with lenses in the ‘Pandanus Creek’ area have not previously been clarified, although Jell (unpublished thesis, 1967) noted a coral fauna at ‘Jessey’s Springs’ that he correlated
<table>
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<th>Location</th>
<th>Stratiographic Interval (M)</th>
<th>Limestone Member</th>
<th>Location</th>
<th>Stratiographic Interval (M)</th>
<th>Limestone Member</th>
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<tr>
<td>Martin's Well</td>
<td></td>
<td></td>
<td>Dip Creek</td>
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<td></td>
</tr>
<tr>
<td>Dip Creek</td>
<td></td>
<td></td>
<td>Chinaman Creek</td>
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</tr>
<tr>
<td>Lockup Well</td>
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</tr>
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</table>

Table 2: Distribution of conodonts in limestone members of the Broken River Formation, Pandanus Creek region.
with faunas in the middle part of the Chinaman Creek Limestone Member and upper parts of the Dip Creek and Lockup Well Limestone Members. Conodonts are prolific in the middle part of lens Dmb_E, where there is a thinly bedded sequence with abundant terrigenous material and crinoidal debris (Table 3). The conodonts and associated coral faunas suggest correlation of the upper parts of the Dip Creek and Lockup Well Limestone Members with lens Dmb_E, yet the latter is situated relatively lower in the Broken River Formation than these other limestones. Conodont faunas from limestones of the Graveyard Creek Formation near 'Jessey's Springs' are similar to those from the unnamed lenses in the 'Pandanus Creek' area, so that a larger disconformity between the Silurian-Devonian formations is indicated in the southern region.

**Broken River area.** The first description of limestones now known to constitute portions of the Graveyard Creek and Broken River Formations was by Daintree (1872) who recorded 23 000 ft (7500 m) of Devonian strata exposed in the Broken River, and along the stage route from 'Wandovale' to 'Pandanus Creek'. Jack (1887) in his description of the Devonian strata of the region especially considered the sequence in the Broken River north of the 'Wandovale'-'Pandanus Creek' road crossing. Here the river runs perpendicular to the strike of the beds, affording good exposure of the Silurian and Devonian formations (text-fig. 2). White (1959b) designated part of this succession as the type section of the Broken River Formation. For the present study only the Jack Limestone Member, which crops out to form the walls of the Broken River gorge, and the lowermost limestone lens of the Broken River Formation—Lens Dmb_F (White 1965)—were sampled. Conodonts were present but rare in the Jack Limestone Member, which is mainly very thickly bedded and poorly fossiliferous. One small zone of thinly bedded coralline limestone in the central part of the unit had the best conodont faunas, but they were still rarer than from the more terrigenous limestones of the Broken River Formation. Lens Dmb_F was described by White (1965) as being at least 1150 ft (350 m) thick and containing siltstone, sandstone, and pebble quartz conglomerate interbedded with the limestone. In the section sampled along the Broken River the unit is thinly bedded with silty material. Conodonts are common and the faunas are similar to those from lens Dmb_E, again indicating the presence of a larger disconformity between the Graveyard Creek and Broken River Formations than is evident in the northern 'Pandanus Creek' region.

**Classification of Conodonts**

In order to achieve a natural classification of conodonts a system of multi-element grouping of form species has been instituted. Initial efforts centred about Ordovician conodonts (Bergström and Sweet 1966; Schopf 1966; Webers 1966) but increased interest has prompted revision of Silurian and Devonian faunas (Walliser 1964, 1972; Jeppsson 1969, 1971, 1972; Klapper and Philip 1971, 1972; Mashkova 1972; Bultynck 1972). Also, Lindström (1970) produced a detailed, if somewhat preliminary, suprageneric classification based on multi-element taxonomy. Agreement was reached among many conodont workers on conceptual and nomenclatural complexities imposed by the new taxonomic system (Lindström and Ziegler (eds.) 1972). Nevertheless, in examination of new, diverse conodont faunas some difficulties still
TABLE 3. Distribution of conodonts in lenses $Dmb_E$ and $Dmb_F$ of the Broken River Formation; Jessey's Springs and Broken River regions respectively.

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<th>LIMESTONE MEMBER</th>
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persist and these are reflected in the present study. The faunas from the Broken River Embayment are diverse though relatively sparse (Tables 1–3). However, a virtual prerequisite of multi-element grouping, especially in the institution of new groups, is large specimen collections. Where conodont yields are low there must be doubts on the application or foundation of any groups. Hence in these cases the individual
elements can only be recorded in anticipation that later studies, with larger numbers of specimens, may produce multi-element groupings which can be extrapolated back to the smaller collections.

A number of lower and middle Devonian multi-element groups recorded by Klapper and Philip (1971, 1972) can be recognized in faunas from limestone units of the Broken River Embayment; also the dimorphic nature of conodont elements, described by Jeppsson (1972), is apparent. But in addition there are numerous form species which do not belong to any known multi-element apparatus and specimen yields were not great enough to allow reliable grouping of them. This could be alleviated by more extensive sampling of the rock units. Therefore in the following systematic descriptions all genera and species are treated as form-elements, and listed alphabetically, with consideration given to phylogenetic lineages and prominent multi-element affinities. With this system, as in the past, the disjunct conodonts may be used in detailed biostratigraphic analyses.

SYSTEMATIC DESCRIPTIONS

Genus Belodella Ethington, 1959


Type species. Belodus devonicus Stauffer, 1940 (p. 420, pl. 59, figs. 47-48) from a clay bed overlying the middle Devonian Cedar Valley Limestone of Minnesota; by original designation.


Multi-element relationships. Belodella has an irregular distribution, often being abundant at some localities to the complete exclusion of other forms (e.g. Telford 1972). Seddon and Sweet (1971) interpreted this as due to dependence on a particular environmental situation; this would suggest that the host organism of Belodella contained representatives of this form genus alone. Occurrences of Belodella devonica (Stauffer, 1940), B. resina (Philip, 1965), and B. triangularis (Stauffer, 1940) in limestones of the Broken River Embayment did not show any mutual association, so perhaps these form species represent separate natural taxa or multi-element groups.

Belodella devonica (Stauffer, 1940)

Plate 1, figs. 5-9

1940 Belodus devonicus Stauffer, p. 420, pl. 59, figs. 47-48.
1957 Belodus erectus Rhodes and Dineley, p. 359, pl. 38, fig. 8.
1964 Belodella sp. of Serpagli and Greco, p. 199, pl. 37, figs. 3-4.
1966 Belodus asiaticus Moskalenko, p. 83, pl. 11, fig. 4, text-fig. 1a.
1966 Belodella devonica (Stauffer); Barnett et al., p. 436, pl. 58, fig. 1.
1966 Belodella devonica (Stauffer); Clark and Ethington, p. 677, pl. 82, figs. 8-9.
1966 Belodella sp. cf. B. devonica (Stauffer); Philip, p. 444, pl. 1, figs. 22-24.

Emended diagnosis. A species of Belodella consisting of a symmetrical recurved cone, with a narrowly biconvex cross-section and a deep, thin anterior keel; denticles of the posterior edge vary greatly in size and may be partly fused or discrete.
Remarks. Dentition of Belodella devonica is variable but it is gradational between specimens and further subdivision of the species does not seem warranted. Hence B. erecta (Rhodes and Dineley 1957) is synonymous with B. devonica, as its supposedly distinctive, discrete denticles merely represent one variety of a morphological series. Serpagli (1967) also proposed a morphological transition series, based on cross-sectional outline, which suggested synonymy of B. devonica, B. resima, and B. triangularis. Specimens of Belodella from the Broken River Embayment exhibit only three distinct cross-sectional outlines, biconvex, narrowly triangular, and broad symmetrically triangular (text-fig. 3). Savage (1973) encountered the same situation. Thus it seems preferable to consider these outlines as characterizing three distinct form species, B. devonica, B. resima, and B. triangularis respectively.

![Cross-sections of Belodella species](image)

**Text-fig. 3.** Cross-sections, at about midheight, of form species of Belodella from the Broken River Embayment.

**Belodella resima** (Philip, 1965)

Plate 1, figs. 10–16; Plate 2, figs. 3–4

1961 *Belodus triangularis* Stauffer; Budurov, p. 261, pl. 3, fig. 7.
1965 *Belodus resimus* Philip, p. 98, pl. 8, figs. 15–17, 19; text-fig. 2e–f.
1966 *Belodella triangularis* (Stauffer); Barnett et al., p. 436, pl. 58, fig. 4.
1966 *Belodus multitentatus* Moskalenko, p. 85, pl. 11, figs. 6–7; text-fig. 1c.
1966 *Belodella resima* (Philip); Philip, p. 444, pl. 1, figs. 14–17.
1968 *Belodus triangularis* Stauffer; Schulze, p. 185, pl. 16, fig. 14.

**Diagnosis.** See Philip (1966, p. 444).

Less compressed specimens of Belodella resima, whose dentition has been partly removed by abrasion, resemble examples of Coelocerodontus reduncus sp. nov. that have been similarly abraded to produce a pseudodenticulated posterior margin. The flat-topped nature of the broken denticles of B. resima usually serves to distinguish the species.

**Belodella triangularis** (Stauffer, 1940)

Plate 1, figs. 1–4; Plate 2, figs. 1, 2

1940 *Belodus triangularis* Stauffer, p. 420, pl. 59, fig. 49.
1965 *Belodus cf. triangularis* Stauffer; Philip, p. 99, pl. 8, figs. 22, 26–28; text-fig. 2c–d.
1966  *Belodus subtriangularis* Moskalenko, p. 84, pl. 11, fig. 5; text-fig. 16.
1967  *Belodella erecta* (Rhodes and Dineley); Serpagli, p. 54, pl. 11, figs. 5–6.
1970  *Coelocerodontus triangularis* (Stauffer); Bultynck, p. 85, pl. 27, figs. 6, 9, 16.
1971  *Belodella devonica* (Stauffer); Fähraeus, p. 674, pl. 78, figs. 30–31 only (figs. 28–29 = *B. devonica*).

**Emended diagnosis.** A species of *Belodella* with a broadly triangular cross-section; antero-lateral margins are keeled and denticles along the posterior edge are small, fused, and laterally compressed.

**Remarks.** Nomenclatural problems and morphological separation of *Belodella triangularis*, *B. devonica*, and *B. resima* have been previously outlined. The most diagnostic feature of *B. triangularis* is its broadly triangular cross-section, so that some specimens with obviously triangular cross-sections, illustrated by Serpagli (1967) as *B. erecta* and by Fähraeus (1971) as *B. devonica*, may be considered conspecific with *B. triangularis*.

**Genus BRYANTODUS** Bassler, 1925

1925  *Bryantodus* Bassler, p. 219.
1926  *Bryantodus* Ulrich and Bassler, p. 21.
1968  *Bryantodus* Bassler; Huddle, p. 9.

**Type species.** *Bryantodus typicus* Bassler, 1925, p. 219, from the upper Devonian Rhinestreet Shale Member of the West Falls Formation, New York State; by original designation. Lectotype of type species illustrated by Huddle (1968, pl. 3, fig. 1).

**Diagnosis.** See Huddle (1968, p. 9).

**Bryantodus cf. pravus** (Bryant, 1921)

Plate 6, figs. 12–14

cf. 1921  *Prioniodus pravus* Bryant, p. 18, pl. 8, fig. 5 (not seen).
cf. 1957  *Bryantodus pravus* (Bryant); Bischoff and Ziegler, pp. 51–52, pl. 13, fig. 5; pl. 14, figs. 1–2; pl. 21, fig. 19.
cf. 1967  *Bryantodus* sp. cf. *pravus* (Bryant); Philip, p. 153, pl. 2, figs. 15, 18, 19, 21.

The unit is a denticulated, shallowly arched, bowed bar. It is thick and robust with a broad oral face and sharp aboral margin forming a roughly triangular cross-section. Development of some features shows variation, but this can usually be related to specimen size. Lateral flanges are present on all specimens. On large specimens they

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**Explanation of Plate 1**

All figures are lateral views unless indicated otherwise.

Figs. 1–4. *Belodella triangularis* (Stauffer). 1, Y. 1637 (Ct 230), ×55. 2–3, Y. 1638 (Ct 417), ×80 and ×45.

4, Y. 1639 (Ct 329), cross-sectional view, ×80.

Figs. 5–9. *Belodella devonica* (Stauffer). 5, Y. 1640 (Ct 208), ×90. 6, Y. 1641 (Ct 252), ×75. 7, Y. 1642 (Ct 299), ×90. 8, Y. 1643 (Ct 354), ×90. 9, Y. 1644 (Ct 285), ×90.

Figs. 10–16. *Belodella resima* (Philip). 10, Y. 1645 (Ct 263), antero-lateral view, ×90. 11, Y. 1646 (Ct 299), ×75. 12, Y. 1647 (Ct 255), ×75. 13, Y. 1648 (Ct 272), ×75. 14, Y. 1649 (Ct 411), ×90. 15, Y. 1650 (Ct 247), ×90. 16, Y. 1651 (Ct 415), ×90.
TELFORD, Belodella
are wide and shelf-like for almost the whole length of the unit but they are only prominent in the central region of small examples, narrowing rapidly towards the anterior and posterior extremities. They are asymmetrical with the inner flange being wider and often better developed on the posterior part of the bar. Their oral surfaces often have a gnarled or scalloped appearance, perhaps caused by abrasion. A large, laterally compressed cusp surmounts the crest of the arch and is variably inclined to the posterior. Its apex is broadly triangular in lateral view. Anterior and posterior parts of the bar contain seven to ten erect, short, broad denticles that are always less than half the size of the cusp. They are crowded but mostly discrete, and are laterally compressed although not as greatly as the cusp. The basal cavity is round and shallow, situated beneath the cusp. The sharp ridge marking the aboral margin of the unit divides to form a boundary about the cavity. On the outer side this boundary ridge is a distinct expanded lip, prominent only on small specimens that have small outer lateral flanges.

**Genus coelocerodontus** Ethington, 1959

*Type species.* *Coelocerodontus trigonius* Ethington, 1959 (p. 273, pl. 39, fig. 14) from the middle Ordovician Galena Formation of Iowa; by original designation.

**Diagnosis.** See Ethington (1959, p. 273).

*Coelocerodontus* is distinguished from other cone-like form genera by its thin walls and very deep basal cavity. *Belodella* Ethington is also thin-walled but has a denticulated posterior margin. Some examples of *Coelocerodontus* may also appear denticulated, although this is often due to erosion of the thin posterior edge and, as noted by Lindström (1964), it is possible that some pseudodenticulated Devonian specimens may have been confused with *Belodella*. Most of the present specimens of *Coelocerodontus* are from undoubtedly middle Devonian limestones of the Broken River Formation, and extension of the stratigraphic range of the genus was initially tentative because of the possibility that the specimens were reworked. However, they are delicate yet well-preserved forms, and quite widespread. Also Barnett *et al.* (1966), Clark and Ethington (1966), and Seddon (1970b) have reported definite upper Silurian and lower Devonian occurrences so it is likely that the genus could have ranged into middle Devonian time.

Occurrences of *Coelocerodontus* in limestones of the Broken River Embayment are spasmodic, and abundances too low for attempts at multi-element grouping.

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**Explanation of Plate 2**

Figs. 1–2. *Belodella triangularis* (Stauffer). 1, Y. 1652 (Ct 255), ×40. 2, Y. 1653 (Ct 255), ×40. Uncoated specimens showing basal cavity.

Figs. 3–4. *Belodella resina* (Philip). 3, Y. 1654 (Ct 255), ×40. 4, Y. 1655 (Ct 418), ×40. Uncoated specimens showing basal cavity.

Figs. 5–9, 11–12. *Neopanderodus aequabilis* sp. nov. 5, Y. 1533 (Ct 402), paratype, inner lateral view, ×70. 6, Y. 1533 (Ct 402), outer lateral view. 7, Y. 1656 (Ct 431), lateral view, ×50. 8, Y. 1532 (Ct 402), holotype, outer lateral view, ×90. 9, Y. 1532 (Ct 402), inner lateral view, ×90. 11, Y. 1533 (Ct 402), paratype, longitudinal ribs, ×400. 12, Y. 1533 (Ct 402), boundary between coarse and fine ribs, ×400.

Figs. 10, 13. *Neopanderodus* sp. 10, Y. 1657 (Ct 411), lateral view, ×100. 13, Y. 1657 (Ct 411), boundary between coarse and fine ribs, ×350.
TELFORD, Belodella
Coelocrodon dentus sp. nov.

Plate 3, figs. 1-3

Type material. Holotype: Y. 1529, Plate 3, fig. 3, from sample Ct 340. Paratypes: Y. 1530, Plate 3, fig. 2, from sample Ct 340; and Y. 1531, Plate 3, fig. 1, from sample Ct 410.

Type locality. Sample Ct 340, 9 m above base of Chinaman Creek Limestone Member, Broken River Formation; section at L. 3670, South Chinaman Creek, about 5.5 km north of 'Pandanus Creek'.

Diagnosis. A species of Coelocrodon consisting of a thin-walled cone, roughly triangular in cross-section, with keeled antero-lateral and posterior edges. The posterior keel may be eroded to form pseudodonticules. The apical part is sharply recurved and the deep basal cavity extends to the point of recurvature.

Description. The cone is bilaterally symmetrical and so sharply recurved that the apical part is at 90° to the remainder of the unit. Below the recurved portion the cone is approximately triangular in cross-section with a narrow posterior edge and wide, flat lateral and anterior faces. There is some variation in cross-section (distinctly triangular to narrowly quadrate). The antero-lateral margins and posterior edge are distinctly keeled; erosion of the posterior keel produces pseudodonticules. Some large specimens have a slightly broader posterior edge with a less prominent keel and little or no development of pseudodonticulation. Walls of the cone extremely thin, and translucent to transparent on well-preserved specimens, so that the outline of the basal cavity is visible. The cavity extends to the point of recurvature. On small specimens with a lesser degree of recurvature it reaches the apical tip. Surfaces of the cone are normally smooth but one specimen, with black, opaque walls, displays columnar surface patterns in the posterior third of each lateral face.

Comparison. Coelocrodon dentus sp. nov. is distinguished from the Ordovician C. trigoniun by the sharply recurved nature of its apical part, and its cross-section, which forms a narrow quadrant or isosceles rather than equilateral triangle. The variation shown by the cross-section takes it into the morphological range of another Ordovician form, C. tetragoniiun, which has a narrowly quadrate cross-section. However, C. dentus has only one central keel on the posterior face while C. tetragoniiun has a keel at each postero-lateral margin. The Silurian species, C. dyscrititus (Rexroad, 1967) is similar in general form to C. dentus and has a central posterior keel, but differs in also having keels at the postero-lateral margins.

EXPLANATION OF PLATE 3

Figs. 1-3. Coelocrodon dentus sp. nov. 1, Y. 1531 (Ct 410), paratype, cross-sectional view, ×180. 2, Y. 1530 (Ct 340), paratype, lateral view, ×60. 3, Y. 1529 (Ct 340), holotype, lateral view, ×60.

Figs. 4-7. Panderodus recurvatus (Rhodes). 4-5, Y. 1625 (Ct 255), inner and outer lateral views. 6, Y. 1626 (Ct 255), outer view. 7, Y. 1627 (Ct 255), outer view. All ×40.

Fig. 8. Drepanodus sp. A. Y. 1628 (Ct 345), lateral view, ×80.

Fig. 9. Drepanodus sp. B. Y. 1630 (Ct 407), lateral view, ×90.

Fig. 10. Panderodus unicostatus (Branson and Mehl) Y. 1631 (Ct 186), lateral view, ×45.

Fig. 11. Panderodus simplex (Branson and Mehl) Y. 1632 (Ct 196), lateral view, ×45.

Fig. 12. Panderodus gracilis (Branson and Mehl) Y. 1633 (Ct 208), postero-lateral view, ×100.

Figs. 13-15. Panderodus valbus (Philip) 13, Y. 1634 (Ct 304), inner lateral view, ×40. 14, Y. 1635 (Tentakulitenknollenkalk, West Germany), inner lateral view, ×80. 15, Y. 1636 (Ct 279), outer lateral view, ×80.
TELFORD, Coelocerodontus, Panderodus, Drepanodus
Genus Diplododella Bassler, 1925

1925 Diplododella Bassler, p. 219.
1926 Diplododella Bassler; Ulrich and Bassler, p. 41.
1945 Elsonella Youngquist, p. 358.
1956 Ellisia Müller, p. 822.
1968 Diplododella Bassler; Huddle, pp. 11–12.

Type species. Diplododella bilateralis Bassler, 1925 (p. 219) from the upper Devonian Chattanooga Shale of Alabama; by original designation. Holotype of type species illustrated by Huddle (1968, pl. 7, fig. 8).

Diagnosis. See Huddle (1968, p. 12).

The genus is distinguished from Hibbardella Bassler by its flattened, blade-like lateral processes and minute (or absent) basal cavity, and from Trichonodella Branson and Mehl by the presence of a denticulated posterior process. Multi-element relationships and nomenclatural problems associated with Diplododella and Hibbardella are considered in discussion of the latter genus.

Diplododella sp. A
Plate 16, fig. 14

Description. The unit consists of an anterior arch with a straight, posterior process extending at right angles from it. All specimens are broken although both lateral processes of the anterior arch are intact on one, and portions of the posterior process are present on the others. The lateral processes are slightly curved anteriorly and directed downwards at about 45° to the horizontal. They are blade-like, gradually increasing in depth towards their free ends. Their dentition is hindeodellid with partly confluent, rounded denticles; usually one or two small denticles separate the larger ones. A prominent cusp, roughly oval in cross-section, surmounts the crest of the arch, and beneath it is a very small basal cavity. The posterior process is not clear, but it appears to have been blade-like with hindeodellid dentition, perhaps less regular than that on the lateral processes.

Comparison. Because of the uncertain nature of the posterior process a more accurate assignment of this form is not possible. However, it may be distinguished from Diplododella perbona (Philip, 1966) by the hindeodellid dentition and curvature of the lateral processes. In these features Diplododella sp. A is comparable to Trichonodella symmetrica (Branson and Mehl, 1933) although the presence of a denticulated posterior process clearly separates it from that species. Such similarities indicate a possible phylogenetic relationship between forms of Diplododella and Trichonodella which is assessed more fully in description of the latter genus.

Diplododella sp. B
Plate 16, fig. 13

The single specimen is incomplete but in general form of the anterior arch and posterior process, and dentition of these processes, it is similar to Diplododella sp. A. A distinguishing feature, however, is the prominent central cusp, markedly triangular in cross-section with a flattened anterior face and sharp posterior edge.
Genus DREpanodus Pander, 1856

1856 Drepanodus Pander, p. 20.
1954 Drepanodus Pander; Lindström, p. 557.


Drepanodus sp. A

Plate 3, figs. 8–9

cf. 1966 Drepanodus sp. A of Philip, p. 444, pl. 1, figs. 4–5.

Description. The unit is a simple, symmetrical cone, slightly recurved close to the base, with the posterior margin meeting the base in a smooth curve. At midheight the cross-section of the cone is rounded or ovate but it becomes lenticular near the base where the posterior and anterior edges are sharper. The basal cavity is shallow with slightly flared lips, and in aboral view has an ovate outline. Columnar surface patterns are visible on well-preserved specimens.

Remarks. It has been questioned whether Devonian examples of Drepanodus are actually reworked fossils. However, preservation of Drepanodus sp. A is of comparable quality to associated and undoubtedly Devonian conodonts, and occurrences of the present specimens (Tables 2, 3) although at different localities, occupy equivalent stratigraphic positions. Also, Drepanodus sp. A of Philip (1966), which is very similar to the present form, is of approximately the same age (late early Devonian). Therefore it appears probable that Drepanodus sp. A is an authentic lower Devonian form-element.

Drepanodus sp. B

Plate 3, fig. 10

cf. 1966 Drepanodus sp. B of Philip, p. 444, pl. 1, figs. 6–7.

Description. The unit is a relatively short, erect cone. Above the basal part it is laterally flattened so that the cross-section is narrowly biconvex with sharp anterior and posterior edges. The basal cavity is shallow, with slightly flaring lips, and an ovate outline in aboral view.

Remarks. Poor quality of the specimens indicates that they could be reworked forms. They were recovered from a diverse middle Devonian conodont fauna in the upper part of the Lockup Well Limestone Member (Table 2), but compare closely with Drepanodus sp. B of Philip (1966) from the lower Devonian Murrindal Limestone, Buchan, Victoria.

Genus HIBbardella Bassler, 1925

1925 Hibbardella Bassler, p. 219.
1926 Hibbardella Bassler; Ulrich and Bassler, p. 37.
1941 *Hibbardella* Bassler; Branson and Mehl, pp. 175–176.
1953 *Roundya* Hass, pp. 88–89.
1956 *Hibbardella* Bassler; Müller, p. 825.

Type species. *Prioniodus angulatus* Hinde, 1879 (p. 360, pl. 15, fig. 17) from the upper Devonian Genesee Shale of New York State; by original designation.

*Diagnosis. See Huddle (1968, p. 13).*

The synonymy testifies to the repeated revision of *Hibbardella* and related form genera, mainly because of the once-uncertain character of the type species. Philip (1967) re-examined the holotype of the type species and confirmed the presence of a denticulated posterior process, which is the chief diagnostic feature of the genus. Also, Huddle (1968) described conodonts conspecific with the holotype of *Prioniodus angulatus* Hinde, and presumably from the same stratigraphic horizon, which had prominent posterior processes. Hence the taxonomic plan suggested by these authors is followed here; i.e. *Diplododella* Bassler, 1925 (syn. *Ellisonia* Müller, 1956), *Hibbardella* Bassler, 1925 (syn. *Roundya* Hass, 1953), and *Trichonodella* Branson and Mehl, 1948, are considered as separate, valid taxa. The main distinction between *Hibbardella* and *Diplododella* is that the former has a large basal cavity while the latter has no basal cavity or only a very small one, and usually has flattened, blade-like lateral processes.

*Hibbardella* cf. *wildungenensis* (Bischoff and Ziegler, 1957)

Plate 16, figs. 9–10

cf. 1957 *Roundya* *wildungenensis* Bischoff and Ziegler, pp. 112–113, pl. 11, figs. 9–12.

Only a single specimen is available so that precise identification is not possible. Denticles of the lateral processes making up the anterior arch are large and discrete. The basal cavity is a prominent triangular pit beneath the cusp extending as a groove along the aboral sides of the lateral and posterior processes. Specimens identified as *Hibbardella* cf. *wildungenensis* by Philip (1967, pl. 3, figs. 9–11) do not have aboral grooves on the lateral processes and have more slender denticles and lateral processes than the present specimen.

*Hibbardella* sp.

Plate 16, figs. 11–12

*Description.* This unit is highly arched with slender, bar-like, lateral processes and a long, denticulated, posterior process. The lateral processes are directed downward at angles of about 60° to the horizontal. The cusp at the crest of the anterior arch is very long and rounded. Three slender, rounded, discrete denticles occur on each lateral process and are sometimes separated by a single minute dentine. Dentition of the posterior process is hindeodellid. The basal cavity is a large pit beneath the
cusp, extending as a groove along the aboral side of the posterior process. Lamellae edges (lamellar scarps of Pierce and Langenheim 1970) are exposed in wide zones beneath the lateral processes.

*Comparison.* In its highly arched nature this form resembles *Hibbardella angulata* (Hinde, 1879), but the latter has a small basal cavity and greater numbers of denticles on the lateral processes. The present form is also distinguished from *H. wildungenensis* (Bischoff and Ziegler, 1957) by the character of the basal cavity and slender denticles and processes.

**Genus Hindeodella** Bassler, 1925

1925 *Hindeodella* Bassler, p. 219.
1926 *Hindeodella* Bassler; Ulrich and Bassler, pp. 38–39.
1968 *Hindeodella* Bassler; Huddle, p. 15.

*Type species.* *Hindeodella subtilis* Bassler, 1925 (p. 219) from the upper Devonian Gassaway Member of the Chattanooga Shale, Alabama; by original designation. Lectotype of type species illustrated by Huddle (1968, pl. 5, fig. 7).

*Hindeodella*-like forms are the most abundant components of Carboniferous natural assemblages (see Rhodes 1962, p. W73) and they are now commonly being employed in multi-element grouping of disjunct Devonian form-elements (e.g. Type I apparatuses of Klappper and Philip 1971). Their occurrence in such a wide variety of different apparatuses and assemblages led Klapper and Philip (1971) to consider *Hindeodella* as ‘a stable, taxonomically undiagnostic element in apparatus evolution’. However, the multi-element taxonomic work of Mashkova (1972), and detailed morphological examination of ramiform elements by Jeppsson (1972), indicates greater usefulness of *Hindeodella* in differentiation of multi-element groups.

*Hindeodella* cf. *priscilla* Stauffer, 1938

Plate 5, figs. 9–15

Fähraeus (1971) extended the range of variation of *Hindeodella priscilla* to include all species of *Hindeodella* described by Stauffer (1938). This has given *H. priscilla* such a general definition that the majority of lower Devonian hindeodellid forms may be identified as this species. However, as indicated by Mashkova (1972), slight differences between some forms are probably due to their occurrence in different multi-element groups. Therefore comprehensive taxonomic revision (from a form- or multi-element point of view) of lower Devonian representatives of *Hindeodella* is required before a satisfactory synonymy of *H. priscilla* can be assembled. Material from the Broken River Embayment was inadequate for this.

For identification of such form-elements *H. priscilla* was defined in a similar way to Walliser (1964). The specimens have a long, thin posterior bar, a short laterally bowed and sometimes downwardly deflected anterior bar, hindeodellid posterior dentition with two to six small denticles separating larger ones, and a small basal cavity. The variation suggests that more than one taxa may be present.
Hindeodella cf. equidentata Rhodes, 1953

Plate 5, fig. 8


The specimens are incomplete but have a close similarity to the distinctive form species Hindeodella equidentata. Both anterior and posterior processes are thick and robust. The cusp at the junction of the processes is large and rounded in cross-section, while denticles of both processes are discrete and of uniform size. The basal cavity beneath the cusp is large and on one specimen extends beneath the processes as a narrow groove.

Hindeodella sp.

Plate 5, fig. 7

The single specimen consists of a thick, long posterior bar and a short, sharply bowed anterior bar. A large cusp surmounts the junction of the bars. The posterior bar is incomplete but the remaining portion contains five large denticles separated by one or two much smaller ones. The anterior bar, almost at right angles to the other, is also broken and contains only two large discrete denticles. The basal cavity beneath the cusp is wide and relatively deep, and extends beneath the bars as a narrow groove. The specimen differs from Hindeodella equidentata in the presence of minute denticles separating the larger ones. It closely resembles forms identified as H. austiniensis Stauffer, 1940 by Bischoff and Ziegler (1957, pl. 7, figs. 8, 11; pl. 20, figs. 34–35) and Bultynck (1970, pl. 22, figs. 4–5).

Genus Icriodus Branson and Mehl, 1938

1938 Icriodus Branson and Mehl, p. 159.

Type species. Icriodus expansus Branson and Mehl, 1938 (p. 160, pl. 26, figs. 18–21) from the middle Devonian Mineola Limestone of Missouri; by original designation.

Diagnosis. See Branson and Mehl (1938, p. 159).

Icriodus-like forms constitute the platform (I) elements of Klapper and Philip's (1971) Type 4 apparatuses. Unlike other proposed Devonian multi-element groups (Jeppsson 1969; Klapper and Philip 1971), these apparatuses are believed to contain only two or three types of form-elements. Orientation of the elements within a group is not known. Elements of one Type 4 apparatus, Pedavis pesavis (Bischoff and Sannemann, 1958) sensu Klapper and Philip (1971, p. 450, text-fig. 14) were found in mutual association in faunas of the Martin's Well Limestone Member, Broken River Formation. They were also obtained by the author from the Chillagoe Formation and Etna Beds of Queensland.

Icriodus corniger Wittekindt, 1966

Plate 4, figs. 9–12

1966 Icriodus corniger Wittekindt, p. 629, pl. 1, figs. 9–12.
non 1969 Icriodus corniger Wittekindt; Carls and Gandl, p. 187, pl. 17, figs. 20–22; pl. 18, fig. 1.

Diagnosis. See Wittekindt (1966, p. 629).
Icriodus corniger shows variation in the number and arrangement of nodes on its oral surface, but it is distinguished by the spur-like inner lip of its basal excavation. I. nodosus (Huddle, 1934) is very similar although its definition was based on an incomplete specimen, the aboral surface of which was not illustrated. Most authors have interpreted I. nodosus as having an expanded basal trough with asymmetrical lips without a prominent spur-like projection. However, Boogaert (1967) and Seddon (1970b) described forms with aboral lips transitional in outline between those of I. corniger and I. nodosus. Revision of these species and re-examination of Huddle’s type specimen of I. nodosus is required. Considerable biostratigraphical value has been attributed to I. corniger, e.g. I. corniger Zone of Wittekindt (1966) and Ziegler (1971), but its importance is questionable until its relationship with I. nodosus is clarified.

Icriodus eslaensis Boogaert, 1967

Plate 4, figs. 7-8

1938 Icriodus cymbiformis? Branson and Mehl; Stauffer, p. 430, pl. 52, figs. 11, 13.
1940 Icriodus cymbiformis Branson and Mehl; Stauffer, p. 425, pl. 60, figs. 56–58, 68.
1940 Icriodus expansus Branson and Mehl; Stauffer, p. 425, pl. 60, figs. 59?, 64?, 70–71.
1967 Icriodus eslaensis Boogaert, pp. 180–181, pl. 1, figs. 9–12.

Diagnosis. See Boogaert (1967, p. 180).

Although only a single specimen was recovered, it is identical with forms described by Boogaert (1967) and can confidently be referred to as Icriodus eslaensis. This species is characterized by the large number of partly fused median nodes and only several widely spaced lateral nodes. I. cymbiformis Branson and Mehl, 1938 differs in having fewer median nodes that are mostly discrete.

Icriodus pesavis Bischoff and Sannemann, 1958

Plate 4, figs. 1–6; Plate 10, fig. 15

1958 Icriodus pesavis Bischoff and Sannemann, pp. 96–97, pl. 12, figs. 2, 3, 6, 7 only.
1972 1 element of Pedavis pesavis subsp. nov. A Klapper and Philip, p. 103.

Description. The unit comprises a central platform, two lateral processes, and a curved posterior process, giving an over-all ‘bird’s-foot-like’ shape. The lateral processes diverge antero-laterally from near the posterior end of the central platform and the posterior process, which is usually strongly curved, extends posteriorly from this point. Lateral processes are straight, approximately equal in size, and half to two-thirds the length of the central platform. They broaden anteriorly and the angle between each and the platform is about 45°. The straight or slightly curved posterior process varies in length according to the size of the whole specimen; it is broadest anteriorly, tapering to a pointed posterior tip. All processes and the central platform are ornamented by three longitudinal rows of nodes. Their development varies according to specimen size. On the central platform of small specimens the median row consists of low rounded nodes connected by thin ridges. Lateral rows consist of large bulbous nodes that are discrete or may be joined to an adjacent median node by a thin transverse ridge. While this general pattern persists, the arrangement of nodes on
lateral and posterior processes is more irregular. Often two, or all three, longitudinal rows may be fused, and a central trough often occurs on the inner lateral process. Large specimens, perhaps gerontic, have all lateral and median nodes strongly fused, forming an irregular system of very low transverse and longitudinal ridges. Anteriorly the central platform of all specimens is laterally compressed, forming a high blade-like structure. The length of this ‘blade’ increases with specimen size. Large specimens also have the anterior ends of the lateral processes similarly compressed. In aboral view the upper surface of the unit, along the posterior edge of the outer lateral process, appears to be folded downwards. Aboral surfaces of all specimens are deeply excavated, forming troughs that extend to extremities of the processes.

Remarks. Klapper and Philip (1972) defined two lower Devonian multi-element taxa (Pedavis pesavis pesavis, P. pesavis subsp. nov. A) characterized chiefly by their I elements which are variants of the form species Icriodus pesavis. Specimens referable to I. pesavis from the Broken River Embayment are similar to the I element of Pedavis pesavis subsp. nov. A as their posterior processes are straight or only slightly curved. Oral ornamentation of the specimens differs considerably, though much of this may be attributed to ontogenetic variation.

Icriodus has been used extensively in lower Devonian faunal zonation (Klapper 1969; Ziegler 1971) but its geographical and stratigraphical distribution is irregular. Hence the biostatigraphical significance of the species, when considered alone, is doubtful.

Icriodus cf. latericrescens latericrescens Branson and Mehl, 1938

Plate 4, figs. 13–14

cf. 1967 Icriodus latericrescens latericrescens Branson and Mehl; Klapper and Ziegler, pp. 74–75, pl. 10, figs. 4–9; pl. 11, figs. 1–5.

The specimen is a straight platform-like unit with a short lateral process at its posterior end. The oral surface is ornamented by three longitudinal rows of rounded, mainly discrete nodes; the median row consists of very small nodes set in a trough between the larger lateral nodes. Anteriorly the platform is laterally compressed, forming a blade-like structure made up of six fused denticles. The aboral surface is

EXPLANATION OF PLATE 4

All figures ×40 unless indicated otherwise.

Figs. 1–6. Icriodus pesavis Bischoff and Sannemann. 1–2, Y. 1703 (Ct 11), oral and aboral views, ×20.
3–4, Y. 1704 (Ct 214), oral and aboral views. 5–6, Y. 1705 (Etna Beds, Rockhampton), oral and aboral views, ×20.

Figs. 7–8. Icriodus eslaensis Boogaert. Y. 1706 (Ct 352), oral and aboral views.
Figs. 9–12. Icriodus corniger Wittekindt. 9–10, Y. 1707 (Ct 436), oral and aboral views. 11–12, Y. 1708 (Ct 436), oral and aboral views.

Figs. 15–18. Icriodus cf. symmetricus Branson and Mehl. 15–16, Y. 1710 (Ct 402), oral and aboral views.
17–18, Y. 1711 (Ct 358), oral and aboral views.
DEVO NIAN CONODONTS FROM QUEENSLAND

depthly excavated. In these features the specimen closely resembles *Icriodus latericrescens latericrescens*, especially an example illustrated by Klapper and Ziegler (1967, pl. 10, fig. 5) which has an anterior blade-like portion. Some characters of *I. l. latericrescens*, such as alignment, size, and ornamentation of the lateral process, are quite variable so that positive identification based on one specimen is not possible. However, the specimen may be distinguished clearly from *I. l. robustus* Orr, 1971 which has large median nodes.

*Icriodus* cf. *obliquimarginatus* Bischoff and Ziegler, 1957

Plate 4, figs. 19–20

cf. 1957  *Icriodus obliquimarginatus* Bischoff and Ziegler, pp. 62–63, pl. 6, fig. 14.
cf. 1970  *Icriodus obliquimarginatus* Bischoff and Ziegler; Seddon, pp. 54–55, pl. 4, figs. 15–18, 20.

The specimen is a long, slender, platform-like unit that is very shallowly curved in oral view. It is similar in oral and aboral surface features to *Icriodus obliquimarginatus*, particularly the examples described by Seddon (1970b). The oral surface bears three longitudinal rows of nodes. The median row, consisting of small nodes connected by narrow ridges, extends further, anteriorly and posteriorly, than the lateral rows. The five posterior-most median nodes are fused, making up a blade-like structure. Lateral nodes are large and may be joined to adjacent median ones by thin transverse ridges. The aboral surface is deeply excavated, forming a narrow trough that extends posteriorly and develops asymmetrical flaring lips. Seddon (1970b) considered his specimens to be intermediate between *I. obliquimarginatus* as originally described and *I. estaensis*, and proceeded to group the three forms into a single species. However, *I. estaensis* differs greatly from both Seddon’s and the present specimen by the larger number of small median nodes compared with the few, widely spaced lateral nodes.

*Icriodus* cf. *symmetricus* Branson and Mehl, 1934

Plate 4, figs. 15–18

cf. 1934  *Icriodus symmetricus* Branson and Mehl, p. 226, pl. 13, figs. 1–3.
cf. 1966  *Icriodus symmetricus* Branson and Mehl; Glenister and Klapper, pp. 805–806, pl. 95, figs. 4–5.

The specimens are of two types though both are comparable to *Icriodus symmetricus*. They are long platform-like units, slightly curved in oral view, and ornamented by three longitudinal rows of nodes. One type (Pl. 4, figs. 15–16) has a prominent median row with the nodes joined by narrow ridges, forming a carina-like structure. All lateral nodes are situated adjacent to a median node and, especially in the posterior half of the unit, they are connected to the median nodes by transverse ridges. The aboral surface is excavated with a deep trough that is expanded posteriorly. Lips of the expanded region are roughly symmetrical. This type resembles *I. symmetricus* as originally defined. The second type (Pl. 4, figs. 17–18) is more strongly curved in oral view and has the lateral nodes arranged subalternately to the median ones. These features indicate similarity to *I. curvatus* Branson and Mehl, 1938. Glenister and Klapper (1966) suppressed this species as a junior synonym of *I. symmetricus*, for they considered the differences in oral ornament of little consequence, and the asym-
metrical basal expansion in syntypes of *I. curvatus* to have resulted from poor preservation. Seddon (1970a) maintained the separation of these species for convenience in his biostratigraphic interpretations, but he noted that they seem to intergrade.

**Genus Ligonomina** Bassler, 1925

1925 *Ligonomina* Bassler, p. 218.
1931 *Hamulosodina* Cooper, p. 239.
1933 *Idiopriododus* Gunnell, p. 265.
1939 *Neocordylyodus* Cooper, p. 396.
1968 *Ligonomina* Bassler; Huddell, p. 18.

*Type species.* *Ligonomina pectinata* Bassler, 1925 (p. 218) from the upper Devonian Rhinestreet Shale Member of the West Falls Formation, New York State; by original designation. Lectotype of type species illustrated by Huddell (1968, p. 18).

**Ligonomina sp. A**  
Plate 5, figs. 3–6

*Description.* The specimens lack only the posterior extremities of the posterior processes. The unit is made up of a long, bar-like process with a large anterior cusp and short, downwardly and laterally deflected anterior process or anticusps. Dentition of the posterior process consists of a series of large discrete denticles separated by one or two much smaller ones. Between the cusp and the first of the larger denticles is a group of three smaller ones. The larger denticles increase in size posteriorly. The anticusps contain four or five large denticles directed almost perpendicular to those of the posterior process, but having similar posterior recurvature. The aboral margin of the posterior process is marked by a deep, wide groove. It broadens beneath the cusp to form a large basal cavity which continues along the lower margin of the anticusps.

*Comparison.* This form is characterized by the hindeodellid dentition of the posterior process and the short anticusps, with only a few large denticles. The posterior dentition is similar to *Ligonomina franconica* Sannemann, 1955, but that species has a much longer anticusps with numerous small denticles. *Ligonomina* sp. B of Pollock (1968, p. 432, pl. 62, fig. 21) partly resembles the present form but has longer, more slender posterior denticles and cusp.

**Ligonomina sp. B**  
Plate 5, figs. 1–2

*Description.* The specimens are incomplete but portions of the posterior process, as well as the anterior cusp and anticusps, are present. The posterior process is long and bar-like with short, thick, discrete denticles sometimes separated by a single smaller one. The anterior cusp is rounded in cross-section and evenly curved to the posterior. The anticusps is bowed at right angles to the posterior process and is curved aborally. It contains numerous, small, crowded denticles. The basal cavity is situated beneath
the cusp and extends anteriorly and posteriorly as a groove. Both cavity and groove have narrow ridge-like lips.

Comparison. These specimens most closely resemble *Ligonodina franconica* Sanne-
mann, 1955. They are also similar to *Ligonodina* sp. A of Philip (1967) from the middle
Devonian Moore Creek Limestone, New South Wales, which Philip compared with
specimens identified as *Ligonodina cf. franconica* by Bischoff and Ziegler (1957,
pl. 11, figs. 5, 8).

Genus LONCHODINA Bassler, 1925


Type species. *Lonchodina typicalis* Bassler, 1925 (p. 219) from the upper Devonian Rhinestreet Shale
Member of the West Falls Formation, New York State; by original designation. Lectotype of type species
illustrated by Huddle (1968, pl. 12, fig. 20).

Diagnosis. See Huddle (1968, p. 21).

*Lonchodina murrindalensis* Philip, 1966

Plate 6, fig. 11

1966 *Lonchodina murrindalensis* Philip, p. 446, pl. 4, figs. 9–14; text-fig. 4.

Diagnosis. See Philip (1966, p. 446).

Although only a small number of these specimens were obtained (Table 2) they
conform closely to the description and illustrations of *Lonchodina murrindalensis*
provided by Philip (1966). The species is distinguished by its very short processes and
deply excavated aboral surface. *L. walliseri* Ziegler, 1960 (see Walliser 1964, pl. 30,
figs. 26–33) has longer, more laterally flattened processes, but the two species are
generally similar and Philip (1966) suggested that they may be closely related.

*Lonchodina* sp.

Plate 6, fig. 10

One well-preserved specimen of this possibly new form was obtained. It is an
arched asymmetrical unit with laterally compressed and slightly bowed anterior and
posterior processes. A large cusp, oval in cross-section with a slightly flattened outer

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EXPLANATION OF PLATE 5

Figs. 1–2. *Ligonodina* sp. B. Y. 1591 (Ct 412), outer and inner lateral views, ×30.
Figs. 3–6. *Ligonodina* sp. A. 3. Y. 1592 (Ct 402), outer lateral view. 4. Y. 1592 (Ct 402), inner lateral view.
5. Y. 1593 (Ct 402), outer lateral view. 6. Y. 1593 (Ct 402), inner lateral view. All ×30.
Fig. 7. *Hindeodella* sp. Y. 1594 (Ct 400), inner lateral view, ×50.
Fig. 8. *Hindeodella* cf. *equidentata* Rhodes. Y. 1595 (Ct 222), inner lateral view, ×40.
views, ×50.
face, surmounts the junction of the processes. The anterior process is the longer, containing six discrete denticles decreasing in height towards the cusp. This process is sharply curved downwards while the posterior one extends almost horizontally from the cusp. Dentition of the posterior process is irregular, consisting of five discrete denticles of markedly differing sizes; one near the posterior end is almost the same size as the cusp itself. The aboral surface is excavated beneath the cusp to form a large basal cavity with small lips. The cavity continues as a groove beneath the processes.

**Genus Neopanderododus** Ziegler and Lindström, 1971


*Type species.* *Neopanderododus perlineatus* Ziegler and Lindström, 1971 (pp. 636, 638, pl. 1, figs. 1–7; pl. 2, figs. 5, 8) from the lower Eifelian Crinoidenkalk-Linse of West Germany; by original designation.

**Diagnosis.** See Ziegler and Lindström (1971, p. 633).

*Neopanderododus aequabilis* sp. nov.

Plate 2, figs. 5–9, 11–12

*Type material.* Holotype: Y. 1532, Plate 2, figs. 8–9, from sample Ct 402. Paratype: Y. 1533, Plate 2, figs. 5–6, 11–12, from sample Ct 402.

*Type locality.* Sample Ct 402, top of Lockup Well Limestone Member, Broken River Formation; section at L. 3673, about 13.5 km east of ‘Pandanus Creek’ on road to Lockup Well.

**Diagnosis.** A species of *Neopanderododus* consisting of a slender, asymmetrical, slightly recurved cone, with a deep basal cavity and antero-posteriorly expanded basal region. One lateral face is marked by a posteriorly situated longitudinal groove, and the entire surface of the cone is covered by a uniform columnar pattern.

**Description.** Specimens show little variation except in degree of recurvature, and infrequent lateral flexing. They are slender, elongate cones, that are clearly asymmetrical in their lower halves where a longitudinal groove is prominent on one lateral face. The groove is situated in the posterior third of the face. Anteriorly there is a low flange which may be better developed on large specimens and have a steep posterior edge. Also in the lower half, the cones are abruptly expanded, the posterior edge being extended as a blunt keel. Apically the groove and flange become indistinct and both

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**EXPLANATION OF PLATE 6**

Figs. 1–3. *Plectospathodus wulrathi* (Hibbard). 1, Y. 1580 (Ct 405), aboral view, × 50. 2, Y. 1581 (Ct 402), inner lateral view, × 50. 3, Y. 1579 (Ct 402), inner lateral view, × 50.  
Fig. 4. *Plectospathodus alternatus* Walliser. Y. 1574 (Ct 247), lateral view, × 75.  
Figs. 5–6. *Plectospathodus* sp. indet. 5, Y. 1583 (Ct 448), inner lateral view, × 50. 6, Y. 1582 (Ct 440), inner lateral view, × 50.  
Figs. 7–8. *Plectospathodus heterodentatus* (Stauffer). 7, Y. 1575 (Ct 400), inner lateral view, × 50. 8, Y. 1576 (Ct 437), inner lateral view, × 50.  
Fig. 9. *Lonchodina murrisdalensis* Philip. Y. 1585 (Ct 186), outer lateral view, × 50.  
Fig. 10. *Plectospathodus* sp. Y. 1578 (Ct 399), lateral view, × 30.  
Fig. 11. *Lonchodina* sp. Y. 1584 (Ct 333), inner lateral view, × 50.  
anterior and posterior faces are rounded. The cones have deep basal cavities and on some specimens an aboral extension of basal filling material is preserved. A uniform columnar pattern covers the entire external surface of the cones. The columns have flat outer faces, and extend to the basal regions where there is a narrow zone of fine ridges or wrinkles. At about midlength the columns average 10 microns in width but apically they converge and narrow. Slight flexing of cones gives the columns an apparent helical arrangement.

Remarks. Ziegler and Lindström (1971) defined two species, *Neopanderodus perlineatus* and *N. transisans*, but there seems little evidence for separation of these forms. They both differ from *N. aequabilis* sp. nov. by having a wider zone of fine ridges or wrinkles in the basal region, a smooth anterior face, and a less expanded base.

There has been no previous attempt to assign species of *Neopanderodus* to a multi-element group. In the present study yields of *N. aequabilis* were too irregular for deduction of any associations with other form species or for confidently instituting a multi-element group consisting of this form species alone.

*Neopanderodus* sp.

Plate 2, figs. 10, 13

The specimens are similar in most respects to *Neopanderodus aequabilis* sp. nov. but they are strongly recurved at midheight so that the apices are at 90° to the basal part of the cones. Antero-posterior expansion of the basal part ends abruptly at the point of recurvature, but the columnar surface pattern is continuous. Material recovered was insufficient to ascertain whether *N. aequabilis* and *Neopanderodus* sp. are connected by a morphological transition series. If *Neopanderodus* sp. is a separate form, it could be considered homeomorphic with *Panderodus recurvatus* (Rhodes, 1953), a similar strongly recurved form (differing only in absence of columnar pattern) that is a comparatively rare form species in Silurian and lower Devonian strata.

Genus *OZARKODINA* Branson and Mehl, 1933

1933 *Ozarkodina* Branson and Mehl, p. 51.
1934 *Subbryantodus* Branson and Mehl, p. 285.

*Type species.* *Ozarkodina typica* Branson and Mehl, 1933 (pp. 51–52, pl. 3, figs. 43–45) from the upper Silurian Bainbridge Formation of Missouri; by original designation.

*Diagnosis.* See Branson and Mehl (1933, p. 51).

*Discussion.* *Ozarkodina* is a long-ranging, widespread form genus characterized by its arched blade-like form, confluent denticles, and prominent central cusp. The type species, *O. typica*, has a small, central basal cavity. Various synonyms have been suggested; of these only *Subbryantodus* Branson and Mehl, 1934 appears to be in sufficiently close accord with the type description and illustrations. The most constant feature of recognized species of *Ozarkodina* from the Broken River Embayment is the central or subcentral position of the basal cavity. As suggested by Rhodes (1953), it is probably more useful to restrict usage of *Ozarkodina* to specimens with this character, giving less significance to arching or denticulation of the unit. This makes a clear distinction between *Ozarkodina* and *Bryantodina* Stauffer, 1935.
Multi-element relationships. Form species of Ozarkodina have been often employed in multi-element taxonomy, being delegated to many different genera. Bergström and Sweet (1966), Schopf (1966), and Webers (1966) proposed multi-element groups consisting entirely of such form species and hence, according to nomenclatural rules, referable to Ozarkodina. They also assembled seemingly unrelated groups that contained at least one Ozarkodina-like form. Similarly, Klapper and Philip (1971) included Ozarkodina-like elements in their various Devonian Type 1 apparatuses, often the same form-element being placed in different multi-element genera, e.g. the form species O. denckmanni Ziegler, 1956 is the O₁ element in groups representing the multi-element genera Ozarkodina, Polygnathus, and Eognathodus. In their Type 2 and 3 apparatuses Klapper and Philip (1971) replaced the O₁ element with an O₂ element typified by Prioniodina aversa Stauffer sensu Bischoff and Ziegler, 1957, pl. 20, fig. 24. This element still retains a general similarity to Ozarkodina. Thus an almost ubiquitous nature is proposed for Ozarkodina-like forms, suggesting that they were an important, perhaps essential, component of conodont skeletal structure.

Ozarkodina ballai Bischoff and Ziegler, 1957

Plate 11, figs. 14–15

1957 Ozarkodina ballai Bischoff and Ziegler, p. 74, pl. 13, figs. 1–2.

Diagnosis. See Bischoff and Ziegler (1957, p. 74).

Although only four specimens of this form were recovered they closely resemble the distinctive Ozarkodina ballai, whose definition by Bischoff and Sannemann (1958) and description by Bultynck (1970, p. 119, pl. 24, figs. 2, 4) are the only published records of the species. It is characterized by the sharp inward bend of the posterior process.

Ozarkodina denckmanni Ziegler, 1956

Plate 12, figs. 5–9

1952 Ozarkodina sp. of Graves, p. 610, pl. 80, fig. 14.
1956 Ozarkodina denckmanni Ziegler, p. 103, pl. 6, figs. 30–31; pl. 7, figs. 1–2.
1964 Ozarkodina typica denckmanni Ziegler; Walliser, p. 61, pl. 9, fig. 14; pl. 26, figs. 3–11.

Diagnosis. See Ziegler (1956, p. 103).

Description. The unit is a straight to shallowly arched blade with a central main cusp flanked anteriorly and posteriorly by numerous fused denticles. Present specimens show great diversity, varying from relatively short, high, laterally compressed blades to long, low, less-flattened blades. Other features vary in accord with this major trend. High blades have the cusp little larger than adjacent anterior denticles; posterior denticles are much smaller, decreasing further in size away from the cusp. Long, low blades have a more prominent cusp with the anterior denticles closer in size to, but still appreciably larger than, the posterior ones. Cusp and denticles of the low blades are less distinctly inclined. On all blade forms the numbers of anterior and posterior denticles are approximately equal, ranging from nine to twelve on high blades to ten to eighteen on long, low blades. All denticles are fused and germ (or suppressed) denticles are common. Transitions occur between the two basic blade forms and are
best illustrated by the changing character of the basal cavity. On high blades it is small with only narrow lips and is situated directly beneath the cusp. On slightly lower blades it develops more flaring, asymmetrical lips and the beginning of narrow anterior and posterior grooves. On the lowest blade forms the cavity is situated beneath the cusp or just posterior of this position. It is wide and deep with more prominent and markedly asymmetrical lips; grooves extending anteriorly and posteriorly are wider (usually wider anteriorly) and also have asymmetrical lips. Columnar surface patterns are conspicuous on the cusp and denticles of all blades, while lateral faces are smooth. Aboral zones of lamellae edges are distinct on specimens with larger basal cavities and grooves.

Remarks. Type specimens of *Ozarkodina denckmanni* illustrated by Ziegler (1956) consisted of long, low-bladed forms only, but Walliser (1964) described greater variation of the species. In his upper Silurian faunas Walliser also found specimens with morphology transitional between *O. denckmanni* and *O. typica* and hence concluded that the former is a subspecies of the latter. More recent workers on lower Devonian faunas have reverted to giving *O. denckmanni* full specific status. The present study supports such a designation, as distinct differences between *O. denckmanni* and *O. typica* were observed. The latter does not display morphological variation trends, has equal-sized anterior and posterior denticles, and its central cusp is broader and more triangular in lateral view than the cusp of *O. denckmanni*. Usually *O. typica* is rare in lower Devonian faunas compared with *O. denckmanni*, and appears to have declined in abundance concomitantly with the advent of increasing numbers of the latter.

*Ozarkodina playfordi* sp. nov.

Plate 11, figs. 16–17

1957 *Ozarkodina congesta* Stauffer; Bischoff and Ziegler, pp. 75–76, pl. 12, figs. 18–20; pl. 13, fig. 4.

Type material. Holotype: Y. 1534, Plate 11, fig. 16, from sample Ct 402. Paratype: Y. 1535, Plate 11, fig. 17, from sample Ct 407.

Type locality. Sample Ct 402, top of Lockup Well Limestone Member, Broken River Formation; section at L. 3673, about 13.5 km east of 'Pandanus Creek' on road to Lockup Well.

Diagnosis. A species of *Ozarkodina* consisting of a prominently arched, laterally compressed blade with uniformly arranged anterior and posterior denticles and a small central basal cavity sometimes extended anteriorly and posteriorly as a very narrow groove.

Description. The unit is a strongly to moderately arched blade. It is laterally compressed with flattened denticles and a sharp aboral margin, but there is a low, lateral, flange-like expansion near the base of the denticles. A large cusp surmounts the crest of the arch. Anterior of the cusp are seven to nine, posteriorly inclined denticles; ten to thirteen erect denticles occur posterior of the cusp. All denticles are fused for about three-quarters of their length and they gradually decrease in size away from the cusp; the largest ones are equal to half the size of the cusp. The basal cavity beneath the cusp is small and shallow with slightly flaring lips. It extends anteriorly and posteriorly.
for short distances as a narrow groove. The groove usually gives way to an inverted aboral margin with exposed lamellae edges.

Comparison. Ozarkodina playfordi sp. nov., O. congesta Stauffer, 1940, and O. lata Bischoff and Ziegler, 1957 are similar in over-all appearance, differing only in the number and size of denticles and the size of the basal cavity. O. congesta has a large basal cavity, an excavated aboral margin, and, according to the description of the holotype by Stauffer (1940), about six denticles anterior of the cusp. O. lata has a small central basal cavity and numerous (up to fourteen slender denticles on the anterior and posterior processes. Specimens identified by Bischoff and Ziegler (1957) as O. congesta are referable to O. playfordi. Those authors placed more emphasis on similarities of dentition rather than differences in form of the basal cavity which is deemed herein to be a more significant feature.

Ozarkodina cf. jaegeri Walliser, 1964
Plate 11, fig. 12

cf. 1964 Ozarkodina jaegeri Walliser, pp. 57–58, pl. 9, fig. 16; pl. 25, figs. 11–18.

Three specimens resemble the forms designated as Ozarkodina jaegeri by Walliser (1964). They differ from typical low-bladed examples of O. denckmanni only in the more erect nature of the cusp and denticles.

Ozarkodina cf. kutscheri Bischoff and Ziegler, 1957
Plate 11, fig. 4

cf. 1957 Ozarkodina kutscheri Bischoff and Ziegler, p. 79, pl. 12, figs. 12, 14.

Only one specimen was obtained but it is comparable with Ozarkodina kutscheri and only its singular occurrence prevents more definite identification.

Ozarkodina cf. media Walliser, 1957
Plate 11, figs. 10–11

The considerable morphological variation envisaged by Walliser (1964) for Ozarkodina media allows assignment to this species of a number of widely differing forms. Subsequent workers (Philip 1966; Pedder et al. 1970b; Fåhraeus 1971; Rexroad and Craig 1971) have tended to restrict usage of the binomen to forms corresponding with Walliser's (1964) figures 25 and 33 of plate 26. These are similar to the type specimens described by Walliser (1957) and consist of a shallow, slightly arched to straight, laterally compressed blade with a central main cusp, numerous discrete denticles anterior and posterior of the cusp, and a small central basal cavity with asymmetrical flaring lips. Specimens with these characteristics were recovered from limestones of the Broken River Embayment but several dissimilar specimens that, according to Walliser (1964), could be related to O. media also were encountered. Additional material collected by the author from lower Devonian strata in other regions (Chillagoe Formation, Chillagoe and Etna Beds, Mount Etna, Queensland; Windellama Limestone, Windefflama, New South Wales) displays morphology
transitional between the specimens from the Broken River Embayment. Thus it appears that Walliser’s (1964) variation series may be valid, though the scarcity of the present specimens inhibits definite identification.

*Ozarkodina typica* Branson and Mehl, 1933

Plate 11, fig. 13

1933 *Ozarkodina typica* Branson and Mehl, p. 51, pl. 3, figs. 43-45.
1964 *Ozarkodina typica* Branson and Mehl; Walliser, pp. 61-62, pl. 9, fig. 21; pl. 25, figs. 20-21; pl. 26, figs. 1-2.
1970 *Ozarkodina jaegeri* Walliser; Duce, p. 40, pl. 6, fig. 6.

*Ozarkodina typica* is an uncommon species in lower Devonian conodont faunas although it was quite abundant during late Silurian time (Walliser 1964; Rexroad and Craig 1971), and Jeppsson (1969) included it in his multi-element species *Hindeodella confluens*. Its relationship with *O. denckmanni* was considered in description of the latter species.

**Genus Panderodus** Ethington, 1959

1959 *Panderodus* Ethington, p. 284.

*Type species.* *Paludoth unicostatus* Branson and Mehl, 1933 (p. 42, pl. 3, fig. 3) from the upper Silurian Bainbridge Formation of Missouri; by original designation.


Ethington (1959) defined *Panderodus* as a simple asymmetrical cone with a deep basal cavity and lateral faces ornamented by costae or grooves. He contended that the cross-section of the cone could be used for specific identification, but recent studies have shown that the grooves and costae of the lateral faces are equally important (Rexroad 1967; Rexroad and Craig 1971; Ziegler and Lindström 1971). Longitudinal striations on *Panderodus* were noted by Lindström (1964) but they were not considered in any taxonomic description of the genus until Ziegler and Lindström (1971), following scanning electron microscopic studies, emended the original diagnosis by including details of fine longitudinal ridges or wrinkles (forming columnar surface patterns). These are common in the basal parts of the cones and also in zones along the postero-lateral faces. The pattern frequently occurs on other cone-like form genera but the concentration of very fine ridges in the basal area is characteristic of *Panderodus*. Ziegler and Lindström (1971) used the presence or absence of the pattern in speciation, e.g. definition of *P. semicostatus*, but the validity of such discrimination is questionable. On specimens from the Broken River Embayment external patterns display varying development, often within the one form-element.

*Multi-element relationships.* Bergström and Sweet (1966) defined two Ordovician panderodid multi-element species: 1, *Panderodus panderi*, made up solely of the form-element *P. panderi* (Stauffer, 1940); and 2, *P. gracilis*, including the form-elements *P. compressus* (Branson and Mehl, 1933) and *P. gracilis* (Branson and Mehl, 1933). The form-element *P. panderi* is not represented in the Devonian faunas of the Broken River Embayment but *P. gracilis* and *P. simplex* (Branson and Mehl, 1933) (possibly
equivalent to *P. compressus*) are very common. Bergström and Sweet (1966) found these units occurring in a 2:1 ratio yet in the present faunas there are approximately equal numbers of them, at individual localities as well as in total. Therefore, while *P. gracilis* and *P. simplex* obviously have close associations during the early Devonian, further extension of the range of the Ordovician multi-element species is uncertain. Abundances of other panderodid form species in the Devonian faunas, i.e. *P. recurvatus* (Rhodes, 1953), *P. unicoostatus* (Branson and Mehl, 1933), and *P. valgus* (Philip, 1965), vary independently of each other and of the number of *P. gracilis* and *P. simplex*. They could possibly constitute separate multi-element groups comparable to the Ordovician *P. panderi*.

**Panderodus gracilis** (Branson and Mehl, 1933)

Plate 3, fig. 13

1933 *Paltodus gracilis* Branson and Mehl, p. 108, pl. 8, figs. 20–21.
1959 *Panderodus gracilis* Branson and Mehl; Ethington, p. 285, pl. 39, fig. 1.
1971 *Panderodus gracilis* Branson and Mehl; Rexroad and Craig, pp. 695–696, pl. 81, figs. 28–29.

**Emended diagnosis.** A species of *Panderodus* with a long slender cone, sometimes laterally flexed and slightly recurved at the tip, with a rounded anterior face and blunt to rounded posterior edge. One lateral face has a central longitudinal groove flanked anteriorly by a flange that is surmounted by a single costa. The other lateral face has a similar central flange and costa so that the unit approaches bilateral symmetry.

**Remarks.** Large (presumably adult) upper Silurian–lower Devonian specimens of *Panderodus gracilis*, *P. unicoostatus*, and *P. simplex* can be distinguished by their bicostate, unicostate, and acostate characters respectively. However, juvenile forms of these species are very similar. *P. simplex* differs slightly from the others as the cone appears to be laterally flattened with almost negligible flanges on the lateral faces, but specimens of *P. gracilis* and *P. unicoostatus*, on which lateral costa have not fully developed, are virtually inseparable. This had led to some confusion in previous interpretations of these form species and many identifications in the literature are doubtful. *P. gracilis*, especially, has been neglected by numerous authors, often being identified as *P. simplex* or *P. unicoostatus*.

Ziegler and Lindström (1971) defined a new species, *P. semicostatus*, on the basis of columnar surface patterns observed with a scanning electron microscope. Similar patterns have been found common to both *P. gracilis* and *P. unicoostatus*, indicating that such features are not diagnostic at specific level. *P. semicostatus* is probably referable to *P. gracilis*.

**Panderodus recurvatus** (Rhodes, 1953)

Plate 3, figs. 4–7

1953 *Paltodus recurvatus* Rhodes, p. 297, pl. 23, figs. 219–220.
1971 *Panderodus recurvatus* Rhodes; Rexroad and Craig, pp. 696–697, pl. 81, figs. 23–25.

**Diagnosis.** See Rhodes (1953, p. 297).

*Panderodus recurvatus* is distinguished from other cone-like, form-elements by its strong recurvature, expanded basal portion, and costate antero-lateral margins. It
is not common and indeed is far less abundant than other panderodid species in faunas from the Broken River Embayment (Tables 2, 3). Rexroad and Craig (1971) related Silurian examples of the species to the Ordovician *P. panderi* which Bergström and Sweet (1966) also found to be rare in their otherwise large faunas. Discovery of *P. recurvatus* in limestones of the Broken River Embayment extends the known upper limit of its stratigraphic range from upper Silurian to late lower Devonian.

*Panderodus simplex* (Branson and Mehl, 1933)

Plate 3, fig. 12

1933 *Paltodus simplex* Branson and Mehl, p. 42, pl. 3, fig. 4.
1966 *Panderodus acostatus* Branson and Mehl; Clark and Ethington, p. 682, pl. 82, fig. 10.
1966 *Panderodus compressus* Branson and Mehl; Philip, p. 447, pl. 1, figs. 13, 18.
1966 *Panderodus compressus* Branson and Mehl; Hamar, p. 65, pl. 1, figs. 1-4.
1971 *Panderodus compressus* Branson and Mehl; Fähraeus, p. 677, pl. 78, figs. 19-20.

*Emended diagnosis.* A species of *Panderodus* consisting of a moderately recurved cone with rounded anterior and posterior faces, and a longitudinal groove marking one lateral face. Costae or angular lateral flanges are absent.

*Remarks.* Nomenclatural problems concerning synonymy of *Panderodus simplex* and the paratypes of *P. acostatus* (Branson and Branson, 1947) were fully outlined by Clark and Ethington (1966) and Rexroad (1967); taxonomy adopted by these authors is followed herein. Large specimens of *P. simplex* are easily distinguishable by their evenly rounded anterior and posterior faces and lack of ornamentation. They are similar to *P. compressus* although Clark and Ethington (1966) considered this species to be a more strongly recurved form. Rexroad (1967) suggested that the Ordovician *P. compressus* could be the ancestor of Silurian–Devonian *P. simplex*.

*Panderodus unicostatus* (Branson and Mehl, 1933)

Plate 3, fig. 11

1933 *Paltodus unicostatus* Branson and Mehl, p. 42, pl. 3, fig. 3.
1959 *Panderodus unicostatus* Branson and Mehl; Sweet et al., p. 1057, pl. 131, fig. 3.
1967 *Panderodus unicostatus unicostatus* Branson and Mehl; Rexroad, p. 46, pl. 4, figs. 1-2.
1971 *Panderodus unicostatus* Branson and Mehl; Rexroad and Craig, pp. 697-698, pl. 81, figs. 30-34.

*Emended diagnosis.* A species of *Panderodus* consisting of a moderately recurved, laterally flexed cone with a rounded anterior face and sharp to rounded posterior edge. Lateral faces are mainly rounded; one is marked by a longitudinal groove, and the other contains a single costa close to the antero-lateral margin.

*Remarks.* *Panderodus unicostatus* is an extremely long-ranging form species, having been recorded from strata of Ordovician to middle Devonian age. The unicostate nature is sufficient to distinguish large specimens but, as discussed in regard to *P. gracilis*, small specimens may be confused with other panderodid species. To avoid misidentifications it is thus essential to have comprehensive collections, and many previous records of *P. unicostatus* must be considered questionable until recollected or re-examined.
DEVONIAN CONODONTS FROM QUEENSLAND

Panderodus valgus (Philip, 1965)

Plate 3, figs. 14–16

1965 Panderodus valgus Philip, p. 109, pl. 8, figs. 7–8; text-fig. 2b.
1966 Panderodus valgus Philip; Philip, p. 448, pl. 1, figs. 1–3.


Present material is identical with the forms described by Philip (1965, 1966). Although relatively common in faunas from the Broken River Embayment, Panderodus valgus has been reported infrequently from elsewhere in eastern Australia, and only two occurrences outside eastern Australia have been documented (Schönlau 1969; Seddon 1970b). Several examples of the species were also identified in material from the Tentakulitenkalk, Frankenwald, West Germany (kindly loaned by Dr. G. C. O. Bischoff).

Genus Pelekysgnathus Thomas, 1949

1949 Pelekysgnathus Thomas, p. 424.

Type species. Pelekysgnathus inclinatus Thomas, 1949 (pp. 424–425, pl. 2, fig. 10) from the upper Devonian Maple Mill Shale of Iowa; by original designation.

Diagnosis. See Thomas (1949, p. 424).

Pelekysgnathus sp.

Plate 10, fig. 1

The single specimen is a short, platform-like unit, straight in oral view, with a broad, antero-laterally directed process arising near its posterior end. The platform is ornamented by a row of seven rounded nodes that are connected by narrow, low ridges. Some nodes are expanded laterally, forming short transverse ridges. The lateral process, which is little more than an expansion of one side of the platform, is poorly ornamented by a low ridge. In lateral view the unit is shallowly arched with the crest at midlength. The aboral surface is deeply excavated.

Genus Plectospathodus Branson and Mehl, 1933

1933 Plectospathodus Branson and Mehl, p. 47.
1934 Angulodus Huddle, p. 76.
1938 Cervicornoides Stauffer, p. 424.

Type species. Plectospathodus flexuosus Branson and Mehl, 1933 (p. 47, pl. 3, figs. 31–32) from the upper Silurian Bainbridge Formation of Missouri; by original designation.

Emended diagnosis. Plectospathodus is an asymmetrical conodont form genus consisting of bar or blade-like anterior and posterior processes that are usually twisted, with their ends deflected aborally. The posterior process is the longer. A large curved cusp surmounts the junction between the processes. Dentition of the processes is variable; denticles may be rounded and discrete, or flattened and confluent, and several larger ones may be present at the ends of the processes. The basal cavity, small or slightly expanded with flaring lips, is situated beneath the cusp.
Discussion. The original definition of *Plectospathodus* (Branson and Mehl 1933, p. 47) was based on several incomplete specimens, but it has been followed by subsequent workers and its validity was confirmed by Rexroad and Craig (1971). A description by Huddle (1934, p. 76) of the genus *Angulodus* was very similar to the definition of *Plectospathodus*, yet little has been done to compare or clearly separate these genera. Indeed, the only commonly recorded major distinction is a stratigraphical rather than morphological one; *Plectospathodus* was considered to range from middle Silurian to early Devonian time while *Angulodus* has been recorded from strata of middle Devonian to early Carboniferous age. There are a number of morphological similarities; both are asymmetrical forms with anterior and posterior processes, a sub-central main cusp, irregular dentition, and ends of processes deflected aborally. Huddle (1934) described *Angulodus* as having a thick rounded bar and rounded denticles whereas *Plectospathodus* has been usually interpreted as blade-like with flattened denticles. However, these differences are probably not of generic significance and in fact have been used in other form genera as a specific distinction, for example *Hindeodella priscilla* and *H. equidentata* are laterally compressed and uncompressed bar-like forms respectively. Philip (1967) suggested possible relationships between species of *Plectospathodus* and *Angulodus*; notably *P. alternatus* and *A. walrathi*. Also, Klapper and Philip (1971) found that the angulodontan form-element of their proposed multi-element groups was the middle or late Devonian equivalent of Silurian and early Devonian plectospathodontan form-elements. Thus *Angulodus* should be considered a junior synonym of *Plectospathodus*, and the latter's definition and stratigraphic range have been emended herein.

Lindström (1964) installed *Plectospathodus* in a morphological transition series with *Trichonodella* Branson and Mehl, 1948, and Rexroad and Craig (1971) claimed that *Plectospathodus* is more closely related to *Trichonodella* than any other genus. However, an important difference between these genera is that *Trichonodella* is a symmetrical form-element and *Plectospathodus* is always markedly asymmetrical. They have been shown to occur within the same multi-element groups (Walliser 1964; Jeppsson 1969; Klapper and Philip 1971; Mashkova 1972), so the superficial similarities noted by Lindström (1964) and Rexroad and Craig (1971) could merely reflect this relationship. *Trichonodella* appears more closely related to the symmetrical form genus *Hibbardella* Bassler, 1925 (see p. 74).

*Plectospathodus alternatus* Walliser, 1964

Plate 6, fig. 4

1960 *Plectospathodus* cf. *extensus* Rhodes; Ziegler, p. 191, pl. 15, figs. 6-7.
1964 *Plectospathodus alternatus* Walliser, p. 64, pl. 9, fig. 17; pl. 30, figs. 23-35.

Diagnosis. See Walliser (1964, p. 64).

Specimens show great variety in size but retain similar general form and dentition (hindeodellid). This species is distinguished by its twisted processes, dentition, and small basal cavity. Philip (1967) suggested a relationship between it and *Plectospathodus walrathi* (Hibbard, 1927) but, although small specimens of the latter may
approach *P. alternatus*, normal specimens have thick bar-like processes and rounded discrete denticles.

*Plectospathodus heterodentatus* (Stauffer, 1938)

Plate 6, figs. 7–8

1938  *Cervicornoides heterodentatus* Stauffer, p. 424, pl. 51, fig. 1J.
1957  *Hindeodella adunca* Bischoff and Ziegler, pp. 57–58, pl. 7, figs. 11–13.
1967  *Plectospathodus heterodentatus* Stauffer; Philip, p. 157, pl. 3, figs. 19–22.


*Plectospathodus heterodentatus* has thick processes with irregular dentition, and a large basal cavity with an inwardly projecting lip. It has been recorded exclusively from middle Devonian strata although it is most similar to the lower Devonian species *P. extensus* Rhodes, 1953. As suggested by Philip (1967), *P. heterodentatus* could be a derivative of the earlier form.

*Plectospathodus walrathi* (Hibbard, 1927)

Plate 6, figs. 1–3

1927  *Hindeodella walrathi* Hibbard, p. 205, fig. 4a–b.
1934  *Hindeodella cataca* Huddle, p. 40, pl. 4, fig. 18.
1934  *Angulodus walrathi* (Hibbard); Huddle, pp. 77–78 (*Angulodus, nom. null.*), pl. 4, fig. 15; pl. 10, fig. 5.
1940  *Angulodus elongatus* Stauffer, pp. 419–420, pl. 58, figs. 1, 8, 21–22.
1943  *Hindeodella amplea* Cooper and Sloss, p. 173, pl. 23, fig. 20.
1968  *Hindeodina compressa* Huddle; Mound, p. 486, pl. 66, fig. 25.

*Emended diagnosis.* A species of *Plectospathodus* with thick, bar-like processes, sometimes laterally compressed; a small but prominent cusp and discrete denticles alternating in size; and a small basal cavity with slightly expanded lips.

*Remarks.* *Plectospathodus walrathi* is a common, long-ranging form species, having been recorded from middle and upper Devonian strata of Europe, North America, and Australia. It is distinguished from other similarly occurring forms, e.g. *P. heterodentatus*, by its hindeodellid dentition and sometimes blade-like nature.

*Plectospathodus* sp.

Plate 6, fig. 9

*Description.* The unit is asymmetrical with thick, bar-like anterior and posterior processes; the posterior one is longer. Both processes are twisted and laterally bowed in opposite directions. Their free ends are deflected aborally, with the deflection of the posterior process being very prominent. The cusp is not distinct as it is of similar appearance to the other denticles which are very large, discrete, and rounded in cross-section. Only eleven denticles are actually present on the entire unit. The basal cavity is deep and wide with a thin lip on one (inner?) side. A shallow groove extends from the cavity along the aboral margin of the anterior process. Lamellae edges are exposed in a zone surrounding the cavity and groove, and including most of the aboral sides of the processes.
Comparison. The specimens closely resemble *Plectospathodus demissus* (Huddle) sensu Bischoff and Ziegler (1957, pl. 20, fig. 1), although the European example has a more prominent cusp and what appears to be a groove along the entire aboral margin.

**Genus Polygnathus** Hinde, 1879

1889  *Polygnathus* Hinde; Miller, p. 520.
1926  *Polygnathus* Hinde; Roundy in Roundy, Girty and Goldman, p. 13.
1939  *Macropolygnathus* Cooper, p. 392.
1957  *Ctenopolygnathus* Müller and Müller, p. 1048.
1964  *Polygnathus* Hinde; Ziegler et al., pp. 421–423.

*Type species.* *Polygnathus dubius* Hinde, 1879. The lectotype of *P. foliatus* Bryant, 1921 was chosen as neotype of *P. dubius* by Huddle (1970). The specimen is USNM 135038; figured by Bryant (1921, pl. 10, fig. 16), from the upper Devonian North Evans Limestone, New York State.


Ziegler et al. (1964) and Huddle (1970) have fully reviewed the nomenclatural problems concerning validity of present interpretations of *Polygnathus* and designation of its type species. Huddle’s (1970) proposal, that *P. dubius* Hinde, 1879 be retained as type species with the lectotype of *P. foliatus* as its neotype, has been generally accepted (Fähraeus 1971; Klapper and Philip 1971). *Polygnathus* is used extensively in Devonian conodont-based correlations (Ziegler 1962, 1971; Klapper et al. 1971). Species of the genus are abundant and diverse in eastern Australian faunas, often providing the sole means of correlation of these faunas. They dominate middle Devonian faunas of the Broken River Embayment but are of lesser importance in lower Devonian faunas in which *Spathognathodus* is the most common ‘platform’ genus.

**Polygnathus foveolatus** Philip and Jackson, 1967

Philip and Jackson (1967) restricted *Polygnathus foveolatus* (as *P. linguiformis foveolata*) to forms with an expanded central basal cavity extending as a groove to the anterior and posterior ends of the unit (Philip and Jackson 1967, text-fig. 2d–h). In addition they identified as *P. l. linguiformis* Hinde, 1879, forms with a small central basal cavity and anterior groove (ibid., text-fig. 2a–c). As noted by Klapper (1969, p. 13) these specimens are closer morphologically to *P. foveolatus* and should be referred to this species. Nevertheless, there is justification for making some taxonomic separation of these forms. Pedder et al. (1970b) demonstrated their sequential occurrence in the Taemas Limestone, New South Wales, and Klapper et al. (1971) described a similar situation in lower Devonian strata of Nevada, western North America. Thus, while they probably are related phylogenetically (text-fig. 4), the older form with an expanded basal cavity may be referred to as form $\alpha$, and the younger form with a small basal cavity may be designated as form $\beta$. Only specimens of form $\beta$ were obtained from limestones of the Broken River Formation but typical examples of form $\alpha$, from the Douglas Creek Limestone in central Queensland, are illustrated (Pl. 7, figs. 17–20). A third form of *P. foveolatus* also was recovered from
the Broken River Formation and, as described later, it is sufficiently distinct from the above-mentioned forms to be instituted as a new subspecies, *P. f. serotinus*.

*Polygnathus foveolatus foveolatus* Philip and Jackson, 1967, form β  
Plate 7, figs. 9–16

1967  *Polygnathus linguiformis linguiformis* Hinde; Philip and Jackson, p. 1265, text-fig. 2a–c.  
1969  *Polygnathus foveolatus* Philip; Klapper, pp. 13–14, pl. 6, figs. 24–26 only.  
1970b  *Polygnathus linguiformis linguiformis* Hinde; Pedder *et al.*, p. 216, pl. 40, figs. 6, 8–10.

**Diagnosis.** See Philip and Jackson (1967, p. 1265).

**Description.** The specimens vary with size, but the character of the basal cavity remains constant. The unit is slender and trough-shaped with a short, high anterior blade and a long roughly symmetrical platform that is deflected inwards and aborally at about midlength, forming a tongue-like posterior end. Degree of deflection increases from small to large specimens. The tongue of large specimens is ribbed by thin continuous transverse ridges. On such specimens, the central platform *carina*, which is a low ridge-like extension of the anterior blade, terminates immediately anterior of the tongue. Smaller specimens have progressively lesser development of the transverse ridges and extremely small forms have none. In these cases the central carina extends further posteriorly though it is usually degenerated into a series of discrete nodes. Undelected anterior platform margins are approximately parallel and as high as, or higher than, the carina. They are ornamented by short transverse ridges that are separated from the carina by shallow adcarinal grooves. The ridges are stronger towards the margins and, especially on small specimens, give the platform a crenate margin. The small basal cavity is situated beneath the central portion of the platform at the point of deflection, and continues to the anterior and posterior ends of the unit as gradually narrowing grooves. The cavity and grooves are bounded by a narrow zone of lamellae edges.

**Comparison.** *Polygnathus foveolatus foveolatus* form β has a similar over-all platform shape to *P. linguiformis* but differs in having a centrally sited basal cavity. *P. dehiscens* Philip and Jackson, 1967 exhibits similar variation in platform ornament, e.g. *P. l. dehiscens* of Pedder *et al.* (1970b, pl. 40, figs. 15–19, 21–22), but has a greatly expanded basal cavity and somewhat flattened oral surface. Probably *P. f. foveolatus* form β developed from *P. dehiscens* (through *P. f. foveolatus* form α) as they have been found, in sequence, in eastern Australia (Philip and Jackson 1967) and western North America (Klapper *et al.* 1971).

*Polygnathus foveolatus serotinus* subsp. nov.

Plate 7, figs. 1–8

1969  *Polygnathus foveolatus* Philip and Jackson; Klapper, pp. 13–14, pl. 6, figs. 22–23 only.  
1970b  *Polygnathus linguiformis foveolatus* Philip and Jackson; Pedder *et al.*, pp. 216–217, pl. 40, fig. 7 only.

**Type material.** Holotype: Y. 1537, Plate 7, figs. 5–6, from sample Ct 324. Paratype: Y. 1538, Plate 7, figs. 7–8, from sample Ct 324.

**Type locality.** Sample Ct 324, 372 m above base of Dip Creek Limestone Member, Broken River Formation; section at L., 3667, 150 m south of Dip Creek, about 6·4 km east of 'Pandanus Creek'.
**Diagnosis.** A subspecies of *Polygnathus foveolatus* having a restricted basal cavity with a projecting outer lip, situated slightly anterior of the point of deflection of the platform; the cavity is inverted posteriorly forming a keel, and continues anteriorly as a narrow groove.

**Remarks.** This subspecies exhibits similar morphological variation trends to *P. foveolatus foveolatus* form β and, in addition, the basal cavity shows minor variation from small to large specimens. It consists of a small pit immediately anterior to the deflection point of the platform and has a laterally projecting, semicircular outer lip and a thin ridge-like inner lip. On small specimens the cavity continues anteriorly as a distinct but narrow groove while posteriorly there is a low median keel caused by inversion of the aboral surface. Larger specimens have a more restricted aboral excavation, sometimes without an anterior groove, and posteriorly they have a more prominent median keel.

As in western North America (Dr. G. Klapper, personal communication), *P. f. serotinus* was found in association with *P. f. foveolatus* form β, but it is easily distinguished by the prominent outer lip of the basal cavity. A simplified phylogeny of these late early and middle Devonian polygnathids is illustrated (text-fig. 4).

*Polygnathus linguiformis* Hinde, 1879

Recognized subspecies of *Polygnathus linguiformis* include *P. l. linguiformis*, *P. l. cooperi* Klapper, 1971, *P. l. mucronatus* Wittekindt, 1966, and *P. l. transversus* Wittekindt, 1966. Three morphotypes of *P. l. linguiformis* were designated by Bultynck (1970) and, although corresponding forms were observed in the present faunas, they showed intergradation and have been described together as *P. l. linguiformis*.

*Polygnathus linguiformis cooperi* Klapper, 1971

Plate 8, figs. 6–15

1971 *Polygnathus linguiformis cooperi* Klapper, p. 64, pl. 1, figs. 17–22; pl. 2, fig. 21.

**Diagnosis.** See Klapper (1971, p. 64).

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**EXPLANATION OF PLATE 7**

All figures × 40.

Figs. 1–8. *Polygnathus foveolatus serotinus* subsp. nov. 1–2, Y. 1713 (Ct 326), aboral and oral views. 3–4, Y. 1714 (Ct 326), aboral and oral views. 5–6, Y. 1537 (Ct 324), holotype, oral and aboral views. 7–8, Y. 1538 (Ct 324), paratype, aboral and oral views.

Figs. 9–16. *Polygnathus foveolatus foveolatus* Philip and Jackson, form β. 9–10, Y. 1715 (Ct 290), oral and aboral views. 11–12, Y. 1716 (Ct 345), oral and aboral views. 13–14, Y. 1717 (Ct 378), oral and aboral views. 15–16, Y. 1718 (Ct 345), oral and aboral views.

Figs. 17–20. *Polygnathus foveolatus foveolatus* Philip and Jackson, form α. 17–18, Y. 1719, oral and aboral views. 19–20, Y. 1720, oral and aboral views (both specimens from Douglas Creek Limestone, Clermont, central Queensland).

Figs. 21–24. *Polygnathus cf. costatus costatus* Klapper. 21–22, Y. 1721 (Ct 436), juvenile specimen, oral and aboral views. 23–24, Y. 1722 (Ct 436), adult specimen, aboral and oral views.

TELFORD, Polygnathus

Specimens show a variety of sizes, presumably indicating juvenile to adult forms, but generally they conform morphologically to the definition of the subspecies. Several large specimens have high outer platform margins (e.g. Pl. 18, fig. 14). This departs

EXPLANATION OF PLATE 8

All figures $\times 40$.

Figs. 1–5. Polygnathus linguiformis linguiformis Hinde. 1–2, Y. 1724 (Ct 348), oral and aboral views. 3–4, Y. 1725 (Ct 349), oral and aboral views. 5, Y. 1726 (Ct 435), oral view.

Figs. 6–15. Polygnathus linguiformis cooperi Klapper. 6–7, Y. 1727 (Ct 412), aboral and oral views. 8–9, Y. 1728 (Ct 412), aboral and oral views. 10–11, Y. 1729 (Ct 414), oral and aboral views. 12–13, Y. 1730 (Ct 412), oral and aboral views. 14–15, Y. 1731 (Ct 412), oral and aboral views.
TELFORD, Polygnathus
somewhat from Klapper’s (1971) diagnosis, but in all other features these specimens are similar to *P. linguiformis cooperi* and they may constitute geronic forms.

*Polygnathus linguiformis linguiformis* Hinde, 1879

Plate 8, figs. 1–5; Plate 9, figs. 13–14

1879 *Polygnathus linguiformis* Hinde, p. 367, pl. 17, fig. 15.
1879 *Polygnathus? simplex* Hinde, pp. 367–368, pl. 17, fig. 17.
1928 *Polygnathus simplex* Hinde; Holmes, pp. 18–19, pl. 7, fig. 5.
1938 *Polygnathus sanduskiensis* Stauffer, p. 438, pl. 53, figs. 27, 36, 37.
1966 *Polygnathus linguiformis linguiformis* Hinde; Wittekindt, p. 635, pl. 2, figs. 10–12.
1967 *Polygnathus linguiformis linguiformis* Hinde; Boogaert, p. 184, pl. 2, fig. 44 (*non* pl. 3, fig. 1 = *P. cf. dehiscens* Philip and Jackson, 1967).
1967 *Polygnathus linguiformis linguiformis* Hinde; Philip and Jackson, p. 1264, text-figs. 2a–c, 3c (*= P. foveolatus* Philip and Jackson, 1967).
1970 *Polygnathus linguiformis linguiformis* Hinde; Bultynck, pp. 125–127, pl. 9, figs. 1–7; pl. 10, figs. 1–8; pl. 11, figs. 1–6; pl. 12, figs. 1–7 (*non* pl. 9, figs. 8–11 = *P. linguiformis cooperi* Klapper, 1971).
1971 *Polygnathus linguiformis linguiformis* Hinde γ morphotype Bultynck; Klapper, p. 64, pl. 2, figs. 18, 19, 22–40; pl. 3, figs. 13–15.


A transversely ribbed, posterior tongue and high, sharply geniculated outer margin distinguish *Polygnathus linguiformis linguiformis* from the other subspecies. Both *P. dehiscens* and *P. foveolatus* have similar platforms but they differ in position of the basal cavity. *P. webbi* lacks a posterior tongue, having the carina extending the full length of the platform. Bultynck (1970) separated α, β, and γ morphotypes according to platform symmetry and height of the outer platform margin. Both characters are variable on present specimens, and, although the three morphotypes can be identified, forms transitional between them also occur. Bultynck’s subdivision was stratigraphically useful in the Couvinian type section but possibly the scheme is not correlative worldwide. An analogous case is Seddon’s (1970a) separation, for stratigraphic purposes, of *Icriodus symmetricus*, *I. curvatus*, and *I. alternatus* from the upper Devonian of the Canning Basin, Western Australia. He recognized that the species intergrade and the subdivision may be valid only in certain facies-controlled situations.

*Polygnathus linguiformis* cf. *mucronatus* Wittekindt, 1966

Plate 7, figs. 25–26


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**Explanation of Plate 9**

All figures × 40.

Figs. 1–12. *Polygnathus pseudofoliatus* Wittekindt. 1–2, Y. 1732 (Ct 400), oral and aboral views. 3–4, Y. 1733 (Ct 402), oral and aboral view. 5–6, Y. 1734 (Ct 402), oral and oral views. 7–8, Y. 1735 (Ct 402), oral and aboral views. 9–10, Y. 1736 (Ct 399), oral and aboral views. 11–12, Y. 1737 (Ct 402), oral and aboral views.

Only one specimen was obtained but it could be likened to *Polygnathus linguiformis mucronatus* because of its short platform terminating anterior of the posterior end of the unit. This subspecies lacks the characteristic ribbed posterior tongue of the *P. linguiformis* group, but additional features, viz. size of anterior blade, position and size of basal cavity, and high outer platform margin, are indicative of its affinity with *P. linguiformis*. *P. angusticostatus* Wittekindt, 1966 has a similarly short platform, though it tapers gradually towards the posterior and has a large, anteriorly situated basal cavity.

*Polygnathus pseudofoliatus* Wittekindt, 1966

Plate 9, figs. 1-12

For synonymy and diagnosis see Klapper (1971, p. 63).

*Description.* Several morphological variants are included in this species. They range from small, presumably juvenile specimens, to intermediate-sized ones with slender inner and outer platforms, to large forms with a markedly expanded outer platform. The unit consists of a broad posterior platform and a long, straight anterior blade usually constituting about half the length of the unit; on small specimens the blade is only about one-third of the total length. The posterior third of the platform is slightly bowed laterally (small specimens have completely straight platforms and bowing increases with specimen size). Asymmetry of the inner and outer sides of the platform varies. Small specimens have a slender almost symmetrical platform. With increase in specimen size the platform becomes relatively broader, the outer side being slightly larger than the inner. On very large specimens the outer side is greatly expanded, the widest point lying at about midlength of the platform. Anterior constriction of the platform also appears to vary with specimen size. There is little or no constriction on small specimens but the expanded platform of large specimens rapidly narrows anteriorly, forming high, parallel, ridge-like margins. The platform has a central carina of discrete rounded nodes that extends to the posterior tip. On small specimens the carina is prominent for its entire length, but in the posterior third of larger specimens the nodes are lower and more widely spaced. On all specimens the carina is flanked by shallow adcarinal grooves. These are sometimes deeper anteriorly, especially where platform constriction is greater. Other platform ornament consists of lateral nodes which expand with increase in platform size to form transverse ridges. In the posterior third of large platforms the ridges are more irregular, consisting only of rows of transversely aligned nodes, and often, on greatly expanded platforms, the posterior ornament is made up entirely of small randomly arranged nodes.

The basal cavity varies in position according to specimen size. It is situated beneath the anterior end of the platform of small specimens but gradually moves to a point midway between midlength and the anterior end of the platform of large specimens. The cavity is small, shallow, oval in outline, and bounded by low ridge-like lips. Median keels extend anteriorly and posteriorly from it; the posterior one reaches the posterior end of the platform while the anterior one, which is centrally grooved, continues to about midlength of the anterior blade. All specimens have a wide zone of lamellae edges surrounding the cavity and keels.
Remarks. *Polygnathus pseudofoliatus* is characterized by its long anterior blade and slender to expanded platform having smoothly rounded margins. Its separation from *P. eiffius* Bischoff and Ziegler, 1957 is difficult to accept. Bischoff and Ziegler (1957) and Klapper (1971) advocated distinction of *P. eiffius* by the presence of rostral ridges together with a greatly expanded outer platform. Specimens with prominent rostral ridges have been illustrated, e.g. Philip (1967, pl. 1, figs. 5–6); Bultynck (1970, pl. 14, fig. 4), but they are apparently rare. Klapper (1971) did not locate any in his large New York collections, and no definite examples were extracted from limestones of the Broken River Embayment (several specimens were found with anterior platform ridges but these are marginal ridges formed by the strong anterior constriction of the platform).

As indicated by the present material, and also noted by Klapper (1971), platform outline of *P. pseudofoliatus* shows great variation, some types being greatly expanded and having the finely nodose ornament that is supposedly typical of *P. eiffius*. These types (= *Polygnathus* aff. *eiffius* of Klapper (1971, pl. 2, figs. 14, 15, 20) and Pl. 9, figs. 9, 11 herein) are clearly referable to *P. pseudofoliatus* as they lack rostral ridges. Occurrence of such forms and the rarity of specimens with unquestionable rostral ridges suggests that separation of *P. pseudofoliatus* and *P. eiffius* may not be necessary or valid. Placing them in synonymy would not disrupt any proposed zonal schemes as the two species have been shown to have almost identical time ranges (Bischoff and Ziegler 1957, table 4; Wittekindt 1966, table 1; Bultynck 1970, pl. 38).

*Polygnathus cf. costatus costatus* Klapper, 1971

Plate 7, figs. 21–24


Klapper (1971) distinguished two subspecies of *Polygnathus costatus*, *P. costatus costatus* and *P. c. patulus*. Several specimens from lens Dmb closely resemble the former but their fragmentary nature prevents positive identification.

Genus Sagittodontus Rhodes, 1953

*Type species*. *Sagittodontus robustus* Rhodes, 1953 (p. 311, pl. 21, figs. 141–142) from the upper Ordovician Gelli-Grin Limestone of Wales; by original designation.

*Diagnosis*. See Rhodes (1953, p. 310).

*Sagittodontus* is characterized by its barb-like or pyramidal appearance, concave faces, deeply excavated base, and faint denticulation. The three species informally designated herein display a wide range of morphology but all have a basic subpyramidal structure. They constitute the first described lower Devonian species of *Sagittodontus*, although Klapper and Philip (1971, 1972) noted the presence of sagittodontan elements in their upper Silurian and lower Devonian Type 4 multi-element apparatuses.

*Sagittodontus* sp. A

Plate 10, figs. 9–10

*Description*. The unit is short and subpyramidal, having a cross-sectional outline approximately in the form of an isosceles triangle. The posterior face forms the short
side of the triangle. Posterior and antero-lateral faces are shallowly concave and smooth. Postero-lateral edges are sharp while the long anterior edge is bluntly rounded; none has denticles or other irregularities. The apex is inclined posteriorly but slightly twisted laterally giving the unit some degree of asymmetry. The aboral surface appears deeply excavated, though on all specimens this cavity contains basal filling material.

**Comparison.** *Sagittodontus* sp. A is distinguished from other lower Devonian species of *Sagittodontus* by its smooth faces and undentictuated edges. It is similar to the Ordovician *S. robustus* Rhodes, 1953 but the latter is less basally expanded and has a short anterior edge.

**Sagittodontus** sp. B

Plate 10, figs. 11-12

1971  Genus and species indet. A. Fähraeus, p. 681, pl. 78, fig. 18.

**Description.** The unit is low, widely expanded, and has a roughly triangular cross-section. Antero-lateral and posterior faces are shallowly concave while the anterior edge is broadly rounded. The apical part is offset laterally from the anterior-posterior plane of the unit and is postero-laterally inclined. Posterior-lateral edges contain two to six denticles that vary in size and are irregularly arranged. Thin randomly distributed longitudinal costae occur on all faces and sometimes occur along the anterior edge and near the base of denticles. The aboral surface is deeply excavated.

**Comparison.** *Sagittodontus* sp. B is distinguished by its irregularly denticulated postero-lateral edges. Klapper and Philip (1971, text-fig. 14) illustrated a similar form in their multi-element species *Pedavis pesavis*. Other form-elements of this species are *Icriodus pesavis* Bischoff and Sannemann, 1958 and a striate cone probably referable to *Scolopodus erectus* sp. nov. described here. All studied specimens of *Sagittodontus* sp. B occurred in association with these form-elements.

**Sagittodontus** sp. C

Plate 10, figs. 13-14

**Description.** The unit is elongated antero-posteriorly, having a narrowly triangular cross-section, and is almost blade-like in appearance. Aboral margins are expanded

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**EXPLANATION OF PLATE 10**

Fig. 1. *Pelekysgnathus* sp. Y. 1695 (Ct 466), oral view, ×40.

Figs. 2-7. *Scolopodus erectus* sp. nov. 2, Y. 1539 (Ct 218), holotype, postero-lateral view, ×80. 3, Y. 1539 (Ct 218), lateral view, ×80. 4, Y. 1696 (Ct 187), lateral view, ×70. 5, Y. 1540 (Ct 186), paratype, lateral view, ×70. 6, Y. 1541 (Ct 187), paratype, lateral view, ×70. 7, Y. 1697 (Ct 261), lateral view, ×110.

Fig. 8. *Scolopodus devonicus* Bischoff and Sannemann. Y. 1698 (Ct 361), lateral view, ×50.

Figs. 9-10. *Sagittodontus* sp. A. Y. 1699 (Ct 261), lateral and oral views, ×50.

Figs. 11-12. *Sagittodontus* sp. B. Y. 1700 (Ct 218), posterior and oral views, ×50.


Fig. 15. *Icriodus pesavis* Bischoff and Sannemann. Y. 1702 (Ct 218), oral view, ×25.
TELFORD, *Pelekysgnathus, Scolopodus, Sagittodontus, Icriodus*
and rounded but orally the unit becomes laterally flattened. The apex is posteriorly inclined and shows only slight lateral twisting. The anterior edge contains four to six denticles that increase in height towards the apex. Postero-lateral edges are virtually indistinguishable as the posterior portion of the unit is rounded. All faces are ornamented by thin longitudinal costae but these are more strongly developed on the rounded posterior portion. All specimens contain a cone of black basal filling material with similar cross-sectional outline to the aboral margin of the conodont, and projecting aborally for a distance equal to one-quarter of the height of the total unit.

Comparison. Sagittodontus sp. C is distinguished by its laterally flattened appearance, denticulated anterior edge, and costate ornament. Of the three lower Devonian species it departs furthest from the original definition of Sagittodontus, and the almost blade-like appearance and central row of denticles suggest relationship with Pelekysgnathus Thomas, 1949. However, the character of the apex and surface ornament is similar to that of Sagittodontus sp. B, an undoubted sagittodontid form, so that Sagittodontus sp. C probably represents an extreme variant of the genus. It also was associated invariably with specimens of Icriodus pesavis and Scolopodus erectus.

Genus SCOLOPODUS Pander, 1859

1965 Scolopodus Pander; Harris and Harris, p. 36.

Type species. Scolopodus sublaevis Pander, 1856 (pp. 25–26, pl. 2, fig. 3) from the lower Ordovician Glaukonitsand of Estonia, U.S.S.R.; by subsequent designation (first species) of Holmes (1928, p. 22, pl. 2, fig. 11).

Rare Ordovician examples of Scolopodus were described by Bergström and Sweet (1966) in a multi-element group composed entirely of these simple cone-like forms. Klapper and Philip (1971) proposed a much different taxonomic position for such forms, assigning one example of a striate cone to their Devonian Type 4 apparatus Pedavis pesavis. This striate cone (termed the M2 element) is very similar to variants of S. erectus sp. nov. described herein. Moreover, S. erectus was found in all samples from the Broken River Embayment from which Icriodus pesavis was recovered.

Scolopodus devonicus Bischoff and Sannemann, 1958

Plate 10, fig. 8

1958 Scolopodus devonicus Bischoff and Sannemann, p. 103, pl. 15, fig. 19.
1970 Scolopodus devonicus Bischoff and Sannemann; Bultynck, pp. 132–133, pl. 27, figs. 1–3.


Scolopodus devonicus is a rare Devonian form-element. Bischoff and Sannemann (1958) based the species on only two specimens. Likewise, Bultynck (1970) described only a small collection of them. The species is distinguished by its slight recurrature, elliptical cross-section, costate ornament, and deep basal cavity. Differentiation from S. erectus sp. nov. is considered in description of that species.
Scolopodus erectus sp. nov.

Plate 10, figs. 2–7

Type material. Holotype: Y. 1539, Plate 10, figs. 2–3, from sample Ct 218. Paratypes: Y. 1540, Plate 10, fig. 5, from sample Ct 186; and Y. 1541, Plate 10, fig. 6, from sample Ct 187.

Type locality. Sample Ct 218, 30 m above base of Martin’s Well Limestone Member, Broken River Formation; section at L. 3662 about 1200 m south-east of Martin’s Well, ‘Pandanus Creek’.

Diagnosis. A species of Scolopodus consisting of a short erect cone with a broad base in lateral view; the surface ornamented by numerous prominent costae; large specimens bear one or two small accessory denticles near the posterior basal margin.

Description. The specimens vary with size. The unit is a simple, short erect cone with an abruptly expanded basal portion. The amount of basal expansion increases with specimen size; small specimens, which have a broad basal part in lateral view, decrease in thickness towards the apex. Large specimens may also show slight posterior inclination. All specimens are ornamented by several thin, but prominent, costae converging towards the apex. On large specimens one posterior costa forms a low, sharp-edged keel. On some specimens the lower part of the keel crossing the expanded portion of the cone is modified to form one or two short rounded denticles. Several stages of modification were observed on a sequence of specimens.

Remarks. Scolopodus erectus sp. nov. may be separated from S. devonicus by its erect nature and the development of accessory denticles. The species commonly occurs with Icriodus pesavis and Sagittodontus sp. B or Sagittodontus sp. C, thus complying with the Type 4 multi-element association proposed by Klapper and Philip (1971).

Genus Spathognathodus Branson and Mehl, 1941

1856 Ctenognathus Pander, p. 32.
1933 Spathodus Branson and Mehl, p. 46.
1941 Spathognathodus Branson and Mehl, p. 98.
1945 Mehlina Youngquist, p. 363.
1959 Ctenognathodus Fay, p. 195.

Type species. Ctenognathodus murchisoni Pander, 1856 (p. 32, pl. 4, fig. 17; pl. 6, fig. 18) from the upper Silurian limestone of Rootsikulle, Estonia, U.S.S.R.; by subsequent designation of Gross (1954).

Diagnosis. See Branson and Mehl (1933, p. 46).

Spathognathodus is the most diversely represented conodont form genus in faunas of the Broken River Embayment. It has wide application in biostratigraphic studies (e.g. Klapper et al. 1971) and is especially important in correlation of eastern Australian lower Devonian sequences (Telford 1972). Its representatives display considerable infraspecific variation which is emphasized in the following descriptions.

Spathognathodus bidentatus Bischoff and Ziegler, 1957

Plate 12, fig. 8

1957 Spathognathodus bidentatus Bischoff and Ziegler, pp. 114–115, pl. 6, figs. 8–13.
1966 Spathognathodus bidentatus bidentatus Bischoff and Ziegler; Bultynck, p. 200, pl. 2, figs. 11–12.

Diagnosis. See Bischoff and Ziegler (1957, p. 114).
Description. The specimens are incomplete. They consist of straight, blade-like forms with a symmetrical, heart-shaped basal cavity beneath the posterior end; the cavity tapers posteriorly. The oral edge contains denticles of two sizes; above the basal cavity are four to six broad, fused denticles while anterior of these are about twelve smaller denticles that are also fused for most of their length.

Remarks. The specimens are referred to Spathognathodus bidentatus because of the two sizes of denticles, and the position and shape of the basal cavity.

*Spathognathodus brevis* Bischoff and Ziegler, 1957
Plate 11, fig. 1

1957 *Spathognathodus*? sp., Rhodes and Dineley, p. 367, pl. 37, fig. 11.
1966 *Spathognathodus brevis* Bischoff and Ziegler; Wittekindt, p. 643, pl. 3, figs. 23–24.
1969 *Pelekysgnathus*? sp., Seddon, p. 27.

Diagnosis. See Bischoff and Ziegler (1957, p. 117).

Occurrences of *Spathognathodus brevis* in the Broken River Embayment have some stratigraphic significance as Bischoff and Ziegler (1957), Wittekindt (1966), and Seddon (1970a) have shown the species to have a restricted range (late middle Devonian–early upper Devonian). The species is distinguished by the basal cavity which is posteriorly situated and bears asymmetrical flaring lips.

*Spathognathodus eosteinhornensis* Walliser, 1964
Plate 12, figs. 9–11

1964 *Spathognathodus steinhornensis eosteinhornensis* Walliser, pp. 85–86, pl. 9, fig. 15; pl. 20, figs. 7–16, 19–25.
1971 *Spathognathodus eosteinhornensis* Walliser; Rexroad and Nicoll, pl. 2, figs. 1–3, 6, 7.

Diagnosis. See Walliser (1964, p. 85).

*Spathognathodus eosteinhornensis* is the only conodont form species occurring in the Graveyard Creek Formation that is useful for correlation of the unit. It is dis-
TELFORD, Spathognathodus, Ozarkodina
tinguished from other late Silurian–early Devonian representatives of Spathognathodus, especially S. steinhornensis Ziegler, 1956, by its uniformly sized denticles.

_Spathognathodus exiguis_ Philip, 1966

Plate 14, figs. 10–18

1966 _Spathognathodus frankenwaldensis_ Bischoff and Sannemann; Clark and Ethington, pp. 685-686, pl. 82, figs. 15, 21.
1966 _Spathognathodus exiguis_ Philip, pp. 449–450, pl. 3, figs. 26–37; text-fig. 7.
1966 _Spathognathodus steinhornensis buchanensis_ Philip, pp. 450–451, pl. 2, figs. 14, 22 only (figs. 1-13, 15–21, 23–28 = _S. optimus_).
1969 _Spathognathodus exiguis philipi_ Klapper, pp. 16–18, pl. 4, figs. 30–38.
1970a _Spathognathodus steinhornensis exiguis_ Philip; Pedder _et al._, pp. 217–218, pl. 38, fig. 13.
1970b _Spathognathodus steinhornensis optimus_ Moskalenko; Pedder _et al._, pp. 217–218, pl. 38, figs. 7, 11 only (figs. 4–6, 8, 10, 12 = _S. optimus_).
1971 _Spathognathodus exiguis_ Philip; Fähraeus, pp. 678–679, pl. 77, figs. 25–30, 32.
1971 _Spathognathodus optimus_ Moskalenko; Fähraeus, pp. 679–680, pl. 77, figs. 19–20 only (figs. 15–18, 21, 23, 24, 31 = _S. optimus_).

_Emended diagnosis._ A species of _Spathognathodus_ with strongly enlarged denticles at the anterior end, and a deep basal cavity with markedly asymmetrical, flaring lips; the cavity is restricted to the central third of the unit or variably expanded towards the posterior as a narrow groove.

_Description._ Several variants of _Spathognathodus exiguis_ are present but they can be related through transitional forms. In the following descriptions, features that are constant among the variants are documented first and then the morphological variation trends are outlined. The unit is a deep blade, essentially straight in oral view, with three or four enlarged denticles at the anterior end. The posterior denticle is always the largest; the others decrease in height anteriorly. The remaining posterior denticles are about half the height of the large anterior one, and are strongly fused. They are subequal although small germ denticles are common and there may be two or three minute denticles at the posterior end of the blade. The basal cavity is deep, situated beneath the posterior third of the blade, and bounded by asymmetrical, widely flaring lips. In lateral view, the outer margin of the larger lip always protrudes below the main aboral margin of the blase. The flared parts of the lips terminate anteriorly at

_EXPLINATION OF PLATE 12_

All figures are lateral views and × 40 unless indicated otherwise.

Figs. 1–4. _Spathognathodus sulcatus_ (Philip). 1, Y. 1670 (Ct 403). 2, Y. 1670 (Ct 403), oral view. 3, Y. 1671 (Ct 403). 4, Y. 1671 (Ct 403), oral view. Small, basal cavity forms.

Figs. 5–7. _Spathognathodus sulcatus_ (Philip). 5, Y. 1672 (Ct 189). 6, Y. 1672 (Ct 189), oral view. 7, Y. 1673 (Ct 259), oral view. Large, basal cavity forms.

Fig. 8. _Spathognathodus bidentatus_ Bischoff and Ziegler. Y. 1674 (Ct 414).

Figs. 9–11. _Spathognathodus eosteinhornensis_ Walliser. 9, Y. 1675 (Ct 445). 10, Y. 1676 (Ct 445). 11, Y. 1676 (Ct 445), oral view.

Figs. 12–14. _Spathognathodus sp._ Y. 1677 (Ct 261). 13, Y. 1678 (Ct 204). 14, Y. 1678 (Ct 204), oral view.

Figs. 15–20. _Spathognathodus n._ sp. A. 15, Y. 1547 (Ct 403). 16, Y. 1547 (Ct 403), aboral view. 17, Y. 1548 (Ct 405). 18, Y. 1548 (Ct 405), aboral view. 19, Y. 1549 (Ct 405). 20, Y. 1549 (Ct 405), aboral view.
a point directly below the posterior edge of the posteriormost enlarged denticle. The aboral margin anterior of the basal cavity is convex in lateral view while posterior of the cavity it is straight to shallowly concave.

Three variation trends occur (text-fig. 5). The posterior margin of the basal cavity ranges from being abruptly truncated to being extended to the posterior end of the blade as a slightly expanded groove. Transitional forms show the cavity extending for varying distances towards the posterior end. Accompanying expansion of the cavity is a gradual shortening and shallow arching of the entire unit. Also, the enlarged anterior denticles show an increasingly right-handed offset from the vertical plane of the posterior denticles. Forms with restricted cavities dominate early faunas, like that of the Martin’s Well Limestone Member, but all other varieties are also present. Younger faunas, like those of the Dip Creek Limestone Member, have a greater proportion of forms with posteriorly expanded cavities.

TEXT-FIG. 5. Morphological variation in *Spathognathodus exiguis* Philip.

**Remarks.** *Spathognathodus exiguis* is identified generally by its ‘constant’ features, number and arrangement of enlarged anterior denticles, aborally projecting lip of basal cavity, anterior termination of cavity. None the less, considerable confusion exists in regard to distinguishing this species from *S. optimus*, as well as separation of them both from ‘European’ forms such as *S. steinhornensis*, *S. remscheidensis* Ziegler, 1960, and *S. frankenwaldensis* Bischoff and Sannemann, 1958 (Philip 1966; Klapper 1969; Pedder et al. 1970b; Fähraeus 1971). Thus the different infraspecific morphological variation series in the Broken River Embayment are compared, and a discussion follows the description of *S. optimus*.

*Spathognathodus? intermedius* Bultynck, 1970

Plate 13, figs. 14–15

1957 *Polygnathus kockeliana* juv.? of Bischoff and Ziegler, pp. 91–92, pl. 2, figs. 14–15.
1966 *Spathognathodus bidentatus transitans* Bultynck, pp. 201–202, pl. 1, figs. 7–10.
1970 *Spathognathodus intermedius* Bultynck, pp. 133–134, pl. 18, figs. 2–6.
1971 *Polygnathus intermedius* (Bultynck); Klapper, pp. 65–66, pl. 3, fig. 26.

**Diagnosis.** See Bultynck (1966, p. 202).

**Description.** The unit is large (up to 2.5 mm in length) and robust, consisting of a high blade whose posterior third is slightly curved in oral view and may be deflected downwards. The anterior half of the blade contains about ten long, slender denticles,
rounded in cross-section and fused for most of their length. They are uniformly sized although sometimes there are two or three larger anterior denticles. Posteriorly there is a similar number of broader, less laterally compressed denticles, which are not as closely set as, and markedly shorter than, the anterior denticles, and they decrease in height towards the posterior end of the blade. The basal cavity is about midway between midlength and the posterior end of the blade. It is shallow and elongated antero-posteriorly without flaring lateral lips, although the blade is thickened near the cavity. In lateral view the aboral margin bends sharply upward at the beginning of the cavity. The bend is less noticeable on specimens with strong downward deflection of the posterior part of the blade. Anterior of the bend the aboral edge is sharp, while posterior of the cavity it is somewhat flattened and may bear a narrow median groove.

Remarks. Except for slight thickening of the blade above the basal cavity, there is no evidence of the characteristic platform expansions of *Polygnathus*, and therefore the species is referable to *Spathognathodus*.

*Spathognathodus* n. sp. A

Plate 12, figs. 15–20

1972 *Spathognathodus* n. sp. A of McGregor and Uyeno, pl. 5, figs. 19–21, 30–32.

Description. The unit is a short blade, straight in oral view and very shallowly arched in lateral view, that displays little variation from small to large examples. Three or four enlarged denticles occur at the anterior end of the blade; the posteriormost of these may be slightly higher than the others. Posterior denticles are short, subequal, and strongly fused; germ denticles are rare. The posterior two-thirds of the aboral surface is excavated, forming a long basal cavity. Expanded lips of the cavity are almost symmetrical, widest anteriorly, and taper gradually to the posterior end of the blade. The anterior end of the cavity is directly below the posteriormost enlarged anterior denticle. The aboral margin anterior of the cavity is convex.

Comparison. *Spathognathodus* n. sp. A is distinguished by its posteriorly extended basal cavity. *S. philipi* Druce, 1970b is very similar, differing only in the rapid posterior shallowing of the blade and unevenly tapered basal cavity lips. *S. exigus* is similar in its dentition, anterior aboral margin, and anterior termination of the basal cavity, but has only a posterior aboral groove rather than an extended basal cavity.

*Spathognathodus optimus* Moskalenko, 1966

Plate 14, figs. 1–9

1966 *Spathognathodus optimus* Moskalenko, pp. 88–89, pl. 11, figs. 12–15.
1966 *Spathognathodus steinhornensis buchanensis* Philip, pp. 450–451, pl. 2, figs. 1–13, 15–21, 23–28 (*non* figs. 14, 22 = *S. exigus*).
1967 *Spathognathodus frankenwaldensis* Bischoff and Sannemann; Huddle in Churkin and Brabb, pl. 5, figs. 1–3, 7, 4, 5.
1969 *Spathognathodus remschiedensis* Ziegler; Klapper, pp. 21–22, pl. 4, figs. 4–12 only (*figs. 1–3 = *S. remschiedensis*).
1969 *Spathognathodus steinhornensis optimus* Moskalenko; Flood, pl. 2, figs. 7–10.
1970b *Spathognathodus steinhornensis optimus* Moskalenko; Pedder et al., p. 218, pl. 38, figs. 4–6, 8, 10, 12 (non figs. 7, 11 = *S. exiguis*).

1970 *Spathognathodus remscheldensis* Ziegler; Druce, pp. 43–44, pl. 7, fig. 6a–c.

1970 *Spathognathodus steinhornensis steinhornensis* Ziegler; Druce, p. 45, pl. 7, figs. 7a–8c (non pl. 8, fig. 1).

1971 *Spathognathodus optimus* Moskalenko; Fähraeus, pp. 679–680, pl. 77, figs. 15–18, 21, 23, 24, 31 (non figs. 19–20 = *S. exiguis*).

**Emended diagnosis.** *Spathognathodus* with enlarged denticles at the anterior end, and a centrally sited basal cavity with asymmetrical, flaring lips; the cavity is restricted to midlength of the unit, its anterior margin lying some distance posterior of the enlarged anterior denticles; there is sometimes a slightly enlarged denticle above the basal cavity.

**Description.** *Spathognathodus optimus* varies in several features. Constant features are described first, followed by variable infraspecific characters. The unit consists of a deep blade, straight in oral view, having at least four to six enlarged denticles at the anterior end. The basal cavity, bounded by asymmetrical, flaring lips, is at midlength of the unit. There is always a gap between the anterior edge of the cavity and the point on the aboral margin directly below the posterior most of the enlarged anterior denticles. The aboral margin anterior and posterior of the cavity is generally straight; the posterior portion of the unit may slope slightly downwards but its aboral margin is straight.

Arrangement and relative size of the enlarged anterior denticles are the most variable characters. The denticles may be equal or unequal, and the largest denticle(s) may be posterior or central within the group. These variations occur randomly, but other variables are more continuous. Some forms have an enlarged denticle above the basal cavity with varying degrees of prominence; decrease in prominence corresponds with a decrease in the size difference between the posterior and enlarged anterior denticles; occasionally the anterior denticles are barely distinguishable from a series of uniform posterior ones. Such evenly denticulated forms usually lack germ denticles which also are rare on other variants. Many specimens have no decrease in prominence of the anterior denticles but their posterior denticles are uniformly arranged. This suggests that two lineages of *S. optimus* may be present in the faunas, both having end-members with uniform posterior dentition, but which differ anteriorly.

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**Explanation of Plate 13**

All figures × 40.

Figs. 1–10. *Spathognathodus palethorpei* sp. nov. 3, 6, Y. 1543 (Ct 299), paratype, lateral and oral views. 2, 7, Y. 1544 (Ct 299), paratype, lateral and oral views. 1, 8, Y. 1545 (Ct 299), paratype, lateral and oral views. 4, 9, Y. 1546 (Ct 299), paratype, lateral and oral views. 5, 10, Y. 1542 (Ct 299), holotype, lateral and oral views.

Figs. 11–13. *Spathognathodus* cf. *bipennatus* Bischoff and Ziegler. 11, Y. 1679 (Ct 365), lateral view. 13, Y. 1679 (Ct 365), oral view. 12, Y. 1680 (Ct 359), oral view.

TELFORD, *Spathognathodus*
Remarks. *Spathognathodus optimus* may be distinguished by its ‘constant’ features, such as the central position of the basal cavity and number of enlarged anterior denticles. However, some varieties show strong similarity to other species:

(a) Forms having slightly irregular posterior dentition, and on which the posterior-most of the enlarged anterior denticles is the largest, resemble the variety of *S. exiguus* which has a restricted basal cavity (text-fig. 6a). These forms differ in the position of the basal cavity which, on *S. exiguus*, terminates below the posterior-most of the enlarged anterior denticles. Also, the aboral margin of *S. exiguus*, anterior of the cavity, is convex while that of *S. optimus* is straight.

(b) Forms with an enlarged denticle above the basal cavity, as well as enlarged denticles, are partially similar to *S. remschiedensis* and *S. steinhornensis* (text-fig. 6b). However, *S. steinhornensis* differs from *S. optimus* in the posterior position of its basal cavity. Also, there are usually only two enlarged anterior denticles and the oral surfaces of the cavity lips may be ornamented by a single node or denticle. *S. remschiedensis* is more difficult to separate from the similar variant of *S. optimus*. In the initial description of *S. remschiedensis*, Ziegler (1960) noted that the species has symmetrical or almost symmetrical basal cavity lips. In a comprehensive study of *S. remschiedensis* from the northern Appalachians of eastern North America Barnett (1971) found that most specimens had almost symmetrical basal cavity lips. Walliser (1964) broadened the definition to include forms with markedly asymmetrical lips although this was probably to include *S. canadensis* Walliser, 1960, from Devon Island, Canada, in *S. remschiedensis*. *S. canadensis* may actually represent a small variant of *S. optimus* so that the definition of *S. remschiedensis* need not be altered. Klapper (1969) identified a number of specimens from Yukon Territory, Canada, as *S. remschiedensis* but he recognized that they have markedly asymmetrical basal cavity lips and are possibly transitional between *S. remschiedensis* and *S. optimus*. These forms correspond to *S. optimus* as defined herein. Thus, *S. remschiedensis* Ziegler, 1960 may be distinguished from *S. optimus* by having symmetrical or nearly symmetrical basal cavity lips, only two enlarged anterior denticles, and a horizontal aboral margin posterior of the basal cavity.

(c) Forms of *S. optimus* with prominently enlarged anterior denticles, and very uniform posterior denticles, show some similarity to *S. frankenwaldensis* (text-fig. 6c). However, the latter has only two enlarged anterior denticles and its aboral margin anterior of the basal cavity is distinctly convex. As illustrated (text-fig. 6c), *S. exiguus* has a convex anterior margin but it contains a greater number of enlarged anterior denticles and its basal cavity is more anteriorly situated than in *S. frankenwaldensis*.

**Explanation of Plate 14**

All figures are lateral views and ×40 unless indicated otherwise.

Figs. 1–9. *Spathognathodus optimus* Moskalenko. 1, Y. 1683 (Ct 408). 2, Y. 1684 (Ct 252). 3, Y. 1684 (Ct 252), aboral view. 4, Y. 1685 (Ct 346). 5, Y. 1685 (Ct 346), aboral view. 6, Y. 1686 (Ct 410). 7, Y. 1686 (Ct 410), aboral view. 8, Y. 1687 (Ct 410). 9, Y. 1688 (Ct 308).

Figs. 10–18. *Spathognathodus exiguus* Philip. 10, Y. 1689 (Ct 282). 11, Y. 1690 (Ct 246). 12, Y. 1692 (Ct 255). 13, Y. 1692 (Ct 265). 14, Y. 1692 (Ct 265), aboral view showing posteriorly restricted basal cavity. 15, Y. 1693 (Ct 409). 16, Y. 1693 (Ct 409), aboral view showing transitional basal cavity. 17, Y. 1694 (Ct 410). 18, Y. 1694 (Ct 410), aboral view showing posteriorly extended basal cavity.
TELFORD, *Spathognathodus*
Specimens definitely referable to *S. steinhornensis*, *S. remscheidensis*, and *S. frankenwaldensis* are rare in eastern Australian lower Devonian faunas. Philip (1965) described *S. steinhornensis* from the Cooper's Creek Formation, Tyers, Victoria, and Druce (1970a) made dubious assignment of several specimens from the Mount Holly Beds, Raglan, Queensland, to *S. frankenwaldensis*, *S. remscheidensis*, and *S. steinhornensis*. These species are also rare or absent in lower Devonian faunas of western North America. Specimens identified as *S. remscheidensis* (Klapper, 1969) and *S. frankenwaldensis* (Huddle in Churkin and Brabb 1967) have been shown above to resemble variants of *S. optimus*; even *S. canadensis* could be a variant of *S. optimus*. Conversely, *S. exigus* and *S. optimus* have not been reported from European Lower Devonian faunas in which the other species are common. Hence, it seems that two major groups of spathognathodid conodonts evolved separately during the Early Devonian, indicating that some faunal provincialism probably existed at this time.
Faunas of a ‘Pacific province’ contained *S. exiguis*–*S. optimus* stocks while a ‘European province’ held faunas containing *S. frankenwaldensis*–*S. remschoidensis*–*S. steinhornensis* stocks.

**Spathognathodus palethorpe**i sp. nov.

*Plate 13, figs. 1–10*

**Type material.** Holotype: Y. 1542, Plate 13, figs. 5, 10, from sample Ct 299. Paratypes: Y. 1543–1546, Plate 13, figs. 1–4, 6–9, from Ct 299.

**Type locality.** Sample Ct 299, 204 m above base of Dip Creek Limestone Member, Broken River Formation; section at L. 3666, 600 m east of ‘Pandanus Creek’–Martin’s Well road crossing of Gray Creek, about 7 km north-east of ‘Pandanus Creek’, north Queensland.

**Diagnosis.** A species of *Spathognathodus* with strongly enlarged anterior denticles, a centrally to slightly anteriorly situated basal cavity, and posterior dentition of two thin rows of rounded nodes or low denticles separated by a thin median ridge.

**Description.** Recovered specimens illustrate a distinct ontogenetic series. The unit is a shallowly arched blade with three or four enlarged denticles at the anterior end; the posteriormost of these is the largest, and the remainder decrease in height anteriorly. In oral view the posterior half of the blade is gently curved, the curvature increasing with specimen size. Also, the enlarged anterior denticles have a distinct right-handed offset from the vertical plane of the posterior part of the blade.

Posterior dentition shows greatest variation. On juvenile specimens it is a single row of short, fused denticles connected by a very faint median ridge. These denticles increase in width posteriorly but remain equal in height so that, in lateral view, the central and to a lesser extent, the posterior oral edge is remarkably flat. On progressively more mature specimens the median ridge becomes more prominent, and eventually divides the posterior denticles into two rows of rounded, node-like structures. They are better developed in the posterior half of the unit and are often connected to the median ridge by short, narrow transverse ridges. Four to six posterior denticles, lying immediately posterior of the enlarged anterior denticles, are markedly smaller than the others, and only on large specimens are they divided by the median ridge.

The basal cavity is centrally or slightly anteriorly situated. It is wide and deep with asymmetrical, tongue-like, flaring lips; the outer lip is the larger and it protrudes below the main aboral margin of the unit. The cavity extends for a short distance anteriorly, and to the posterior end of the unit, as a narrow groove. The aboral margin of the unit anterior of the cavity is convex while posterior of the cavity it is shallowly concave.

**Remarks.** *Spathognathodus palethorpe* i sp. nov. is easily distinguished by its posterior dentition. Other lower and middle Devonian, ‘double-rowed’ spathognathodid conodonts, e.g. *S. sulcatus* (Philip, 1965) and *S. bipennatus* Bischoff and Ziegler, 1957, normally have a trough, rather than a prominent ridge, separating the dentine rows. Upper Devonian forms such as *S. costatus* (Branson, 1934) also lack a median ridge and have less node-like denticles. In fact the node-like posterior denticles and system of median and transverse ridges of *S. palethorpe* i resemble the oral ornament
of some forms of *Icriodus*. The enlarged anterior denticles and basal cavity of *S. palethorpei* are very similar to *S. exiguis*. Indeed, separation of juvenile forms of *S. palethorpei* from *S. exiguis* is difficult unless the faint median ridge is present. Whether these similarities indicate an evolutionary development is questionable, and no large forms with transitional morphology have been found.

Lower Devonian ‘double-rowed’ spathognathodids such as *S. palethorpei* and *S. sulcatus* (see later) are relatively common in eastern Australia and western North America, but they are rare or absent from European faunas. Such a distribution reinforces the separation of lower Devonian conodonts into European and Pacific provinces.

*Spathognathodus sulcatus* (Philip, 1965)

Plate 12, figs. 1–7

1965 *Eognathodus sulcatus* Philip, p. 100, pl. 10, figs. 17, 18, 20, 21, 24, 25; text-fig. 1.
1966 *Spathognathodus bipennatus nevadensis* Clark and Ethington, p. 687, pl. 84, figs. 1, 6, 8, 10, 11.
1969 *Spathognathodus sulcatus* (Philip); Klapper, pp. 22–23, pl. 2, figs. 35–37, 42–47; pl. 3, figs. 1–21.

**Diagnosis.** See Klapper (1969, p. 22).

Two different types of *Spathognathodus sulcatus* were first defined by Klapper (1969) who found that the form with a small basal cavity dominated the upper range of the species, while the other (containing a large basal cavity) dominated the lower part. *S. sulcatus* is comparatively rare in faunas of the Broken River Embayment (Table 2). Nevertheless, both morphological types were found; the ‘small form’ occurs in seemingly younger strata (lower part of the Lockup Well Limestone Member) than the ‘large form’ (Martin’s Well Limestone Member). *S. linearis* (Philip, 1966), which has a similar basal cavity to the early form of *S. sulcatus*, is distinguished by having only a single row of denticles.

*Spathognathodus cf. bipennatus* Bischoff and Ziegler, 1957

Plate 13, figs. 11–13

1966 *Spathognathodus cf. bipennatus* Bischoff and Ziegler; Bultynck, p. 202, pl. 2, figs. 4–8.
1970 *Spathognathodus cf. bipennatus* Bischoff and Ziegler; Bultynck, p. 134, pl. 18, fig. 9; pl. 19, figs. 1–5.

Poor preservation of the specimens prevents accurate identification. They closely resemble forms tentatively assigned to *S. bipennatus* by Bultynck (1966, 1970). They are not reworked forms of *S. palethorpei* as their basal cavities are small and centrally situated.

*Spathognathodus cf. inclinatus* (Rhodes, 1953)

Plate 11, figs. 2–3


*Spathognathodus inclinatus* has a world-wide distribution in middle Silurian to lower Devonian strata and is distinguished by a long low bar with uniformly sized denticles, and a narrow basal cavity lacking flared lips. The small number of present specimens (Table 1) prevents accurate assignment.
Short blade length, indistinct posterior denticles, and a very large anterior denticle indicate close similarity with *Spathognathodus boucoti* Klapper, 1969. However, Klapper’s specimens have a somewhat anteriorly sited basal cavity, in contrast to the central position of the cavity on the present specimens.

**Genus Synprioniodina** Bassler, 1925

1925 *Synprioniodina* Bassler, p. 219.
1925 *Euprioniodina* Bassler, p. 219.
1926 *Synprioniodina* Bassler; Ulrich and Bassler, p. 42.
1956 *Neoprioniodus* Rhodes and Müller, p. 698.
1968 *Synprioniodina* Bassler; Huddle, p. 45.

*Type species.* *Synprioniodina alternata* Bassler, 1925 (p. 219) from the Gassaway Member of the Chattanooga Shale, Alabama; by original designation. Holotype of type species illustrated by Huddle (1968, pl. 6, fig. 5).

*Emended diagnosis.* Posterior bar arched and bowed with anteriorly directed, closely spaced, discrete or fused denticles; terminal cusp and denticulated or nondenticulated anticusp present. The posterior bar and anticusp form an acute aboral angle in most species. Basal cavity beneath the cusp expanded on the inner side (emended after Huddle, 1968, p. 45).

*Discussion.* *Synprioniodina* is characterized by its pick-shaped appearance and prominent, denticulated anticusp. Nevertheless, there has been confusion over its validity and relationships with the genera *Prioniodus* Pander, 1956, *Neoprioniodus* Rhodes and Müller, 1956, *Prioniodina* Bassler, 1925, and *Euprioniodina* Bassler, 1925. All of these were accepted as distinct by Hass (1962), but they have been variously grouped by other authors. *Neoprioniodus* and *Euprioniodina* are also pick-shaped units with an anticusp rather than-anterior process and, together with *Synprioniodina*, may be easily separated from *Prioniodus*, which has a central cusp and a lateral process as well as anterior and posterior processes. *Prioniodina* has only a short anterior process but, as seen on the type species *P. subcurvata* Bassler (Huddle, 1968, p. 44, pl. 1, figs. 1–8), this is obviously a separately developed process and not a mere prolongation of the cusp.

The problem remains of the possible synonymy of the pick-shaped forms. Huddle (1968) could find no distinction between *Euprioniodina* and *Synprioniodina* and hence suppressed the former as a junior synonym. Although this differs from the views of previous authors (Lindström 1954, 1964; Sannemann 1955; Hass 1962) it seems to be a reasonable interpretation. Huddle (1968, p. 25) distinguished *Neoprioniodus* from *Synprioniodina* solely by its nondenticulated anticusp, yet he also noted (pp. 24–25) that some species of *Neoprioniodus* may have a few denticles on the anticusp. Rhodes and Müller (1956) originally established *Neoprioniodus* for pick-shaped forms excluded from *Prioniodus* by Lindström (1954). In their diagnosis, Rhodes and Müller stated that the anterior edge of the anticusp may or may not be denticulated. They did not, however, compare the denticulated examples with *Synprioniodina*, into whose morphological range such forms extend. Presumably, Rhodes and Müller
assumed that Synprioniodina was a synonym of Prioniodina which they did consider in comparison with Neoprioniodus, and which they distinguished by its well-developed denticulated anterior process. In fact it is this character that was used above to separate Synprioniodina and Prioniodina.

The situation that has thus developed is that some species with nondentihcated anticusps are referable to Neoprioniodus and others with strongly developed anterior denticles are placed in Synprioniodina, but a third group, whose anticusps contain only a few small denticles or which vary from nondentihcated to denticulated, may be assigned to either genus. The confusion is demonstrated by the upper Silurian-lower Devonian form-element Neoprioniodus bicurvatus (Branson and Mehl) sensu Walliser (1964, pp. 46–47, pl. 29, figs. 27–33). One of Walliser’s specimens (pl. 29, fig. 30) contains several distinct anterior denticles. The anticusps of other examples appear to be nondentihcated although Rexroad and Craig (1971) doubtfully assigned figures 27 and 28 to Synprioniodina. Following Walliser (1964), numerous other authors, e.g. Philip (1966), Schulze (1968), Fähraeus (1969), have included denticulated and nondentihcated forms in N. bicurvatus.

Multi-element studies also suggest a close relationship between Neoprioniodus and Synprioniodina. An N element is present in Klapper and Philip’s (1971) Types 1, 2, and 3 apparatuses and it is represented by either a Neoprioniodus-like or Synprioniodina-like form. Jeppson (1971) deduced particular positions for pick-shaped forms within assemblages, indicating that over-all symmetry is a more important criterion than dentition. Therefore, as a convenience to form taxonomy, and in accordance with possibly natural relationships defined by multi-element grouping, Neoprioniodus and Synprioniodina should be considered synonymous; according to rules of priority, Synprioniodina becomes the senior synonym.

**Synprioniodina bicurvata** (Branson and Mehl, 1933)

Plate 15, figs. 6–11

1933 *Prioniodus bicurvatus* Branson and Mehl, p. 44, pl. 3, figs. 9–12.
1956 *Prioniodina tropa* (Stauffer); Ziegler, p. 104, pl. 6, fig. 29; pl. 7, fig. 29.
1957 *Prioniodina bicurvata* (Branson and Mehl); Walliser, p. 46, pl. 2, fig. 18 (non fig. 19).
1960 *Prioniodina bicurvata pronoides* Walliser, p. 33, pl. 8, figs. 8–9 (non fig. 10).

**EXPLANATION OF PLATE 15**

All figures are ×40 unless indicated otherwise.

Figs. 1–5. *Synprioniodina scalena* sp. nov. 1. Y. 1551 (Ct 212), paratype, inner lateral view. ×75. 2. Y. 1550 (Ct 410), holotype, inner lateral view. 3. Y. 1550 (Ct 410), outer lateral view. 4. Y. 1552 (Ct 417), paratype, inner lateral view. 5. Y. 1552 (Ct 417), outer lateral view.

Figs. 6–11. *Synprioniodina bicurvata* (Branson and Mehl). 6. Y. 1603 (Ct 240), inner lateral view. ×55. 7. Y. 1604 (Ct 199), outer lateral view. ×75. 8. Y. 1605 (Ct 202), inner lateral view. ×75. 9. Y. 1606 (Ct 204), inner lateral view. ×55. 10. Y. 1607 (Ct 256), outer lateral view. ×75. 11. Y. 1608 (Ct 256), inner lateral view. ×75.


Fig. 15. *Synprioniodina cf. alternata* Bassler. Y. 1611 (Ct 407), inner lateral view.

Figs. 16–18. *Synprioniodina cf. armata* (Hinde). 16. Y. 1612 (Ct 403), outer lateral view. 17. Y. 1612 (Ct 403), inner lateral view. 18. Y. 1613 (Ct 402), inner lateral view.
TELFORD, *Synprioniodina*
Emended diagnosis. A species of Synprioniodina with a long posterior process containing partially fused, anteriorly inclined denticles of uniform size; the anticusp is nondenticulated or bears several small denticles; the basal cavity beneath the cusp has an inwardly flaring lip.

Remarks. Jeppsson (1969) pointed out that most of the specimens ascribed to Neoprioniodus (= Synprioniodina) bicurvatus by Walliser (1964) do not appear to correspond exactly with the type specimens of Branson and Mehl (1933) from the Bainbridge Formation, Missouri. Also, in their restudy of conodonts from the Bainbridge Formation, Rexroad and Craig (1971) proposed a more restricted definition of S. bicurvata than had been followed by Walliser (1964) and subsequent authors. According to this definition the posterior process has uniformly sized denticles rather than denticles alternating in size, and they must be at least partly fused. Thus up to three different species may be represented by Walliser's (1964) material; one of them is equivalent to S. bicurvata and another is described below as a new species, S. scalena.

Synprioniodina scalena sp. nov.

Plate 15, figs. 1-5

1960 Prioniodina bicurvata pronoides Walliser; Ziegler, p. 193, pl. 15, fig. 9.
1964 Neoprioniodus bicurvatus (Branson and Mehl); Walliser, p. 46, pl. 29, figs. 28-29 (non figs. 27, 30-33).
1966 Neoprioniodus bicurvatus (Branson and Mehl); Philip, p. 446, pl. 4, fig. 13.
1968 Neoprioniodus bicurvatus (Branson and Mehl); Schulze, p. 200, pl. 18, fig. 9.
1969 Neoprioniodus bicurvatus (Branson and Mehl); Fähraeus, pl. 2, figs. 9-10.
1970 Neoprioniodus bicurvatus (Branson and Mehl); Seddon, pl. 3, fig. 12.
1970 Synprioniodina bicurvata (Branson and Mehl); Pollock, Rexroad and Nicoll, p. 762, pl. 114, figs. 16-17.

Type material. Holotype: Y. 1550, Plate 15, figs. 2-3, from sample Ct 410. Paratypes: Y. 1551, Plate 15, fig. 1, from sample Ct 212; and Y. 1552, Plate 15, figs. 4-5, from sample Ct 417.

Type locality. Sample Ct 410, limestone lens at L. 3675 doubtfully assigned to the Lockup Well Limestone Member, Broken River Formation; Lockup Well, about 17.5 km east-north-east of 'Pandanus Creek'.

Diagnosis. A species of Synprioniodina with a long posterior process bearing discrete or partly fused denticles that alternate in size; the anticusp is nondenticulated or has several minute denticles; the basal cavity beneath the cusp has an inwardly flaring lip.

Description. The unit is pick-shaped, consisting of a long, bar-like posterior process that curves downward from a large terminal cusp and short anticusp. The posterior process is narrowly triangular in cross-section and may be laterally bowed. Dentine of slender, discrete or partly fused denticles that alternate in size; the small denticles are usually less than one-third of the size of the larger ones. Near the cusp are three or four strongly fused, equal denticles. All denticles are subparallel to the
cusp, which is erect and laterally flattened, with sharp anterior and posterior edges. The cusp extends aborally to form a short anticusp which may be nondenticulated or may bear several minute, fused denticles. Beneath the cusp is a wide basal cavity with a prominent inwardly flaring lip. The cavity extends as a narrow groove beneath the posterior process. Columnar surface patterns cover the cusp and denticles but the remainder of the unit is smooth.

Remarks. Synprioniodina scalena sp. nov. is distinguished by its posterior dentition and nondenticulated to weakly denticulated anticusp. Assignment of this form to S. bicurvata by a number of authors was considered in description of the latter species.

**Synprioniodina cf. alternata** Bassler, 1925

Plate 15, fig. 15

cf. 1968 *Synprioniodina alternata* Bassler; Huddle, pp. 45–46, pl. 6, figs. 3–5, 12.

The specimens are incomplete but they resemble *Synprioniodina alternata* Bassler (Huddle 1968, pp. 45–46, pl. 6, figs. 3–5, 12), especially in the robust nature of the posterior bar and outward twisting of the anticusp. Assignment to this species is somewhat doubtful because of the unusual short terminal cusp, as well as the low number of specimens (Table 2).

**Synprioniodina cf. armata** (Hinde, 1879)

Plate 15, figs. 16–18

cf. 1968 *Neoproniodus armatus* (Hinde); Huddle, pp. 25–26, pl. 6, fig. 11; pl. 7, figs. 1, 4.

Huddle (1968) noted that *Synprioniodina armata* (Hinde, 1879) has a small basal cavity, which contrasts with the deep aboral excavations of the present specimens. However, in most other features, especially the large flattened cusp and denticulation of the anticusp and posterior process, the specimens are comparable to *S. armata*.

**Synprioniodina cf. falx** (Huddle, 1934)

Plate 15, figs. 12–14

cf. 1934 *Euproniodina falx* Huddle, p. 53, pl. 11, fig. 9.

The specimens closely resemble *Synprioniodina falx* (Huddle, 1934) which is characterized by its alternating posterior denticles and antero-aborally directed, denticulated anticusp.

**Genus TRICHONODELLA** Branson and Mehl, 1948

1933 *Trichognathus* Branson and Mehl, p. 36 (homonym of *Trichognathus* Berthod, 1827).
1947 *Trichonodella* Branson and Branson, pp. 551–552 (nom. nud.).
1948 *Trichonodella* Branson and Mehl, p. 527.
1953 *Trichonodella* Branson and Mehl; Hass, pp. 89–90.
1968 *Trichonodella* Branson and Mehl; Huddle, p. 47.

*Type species.* *Trichognathus prima* Branson and Mehl, 1933 (p. 36, pl. 1, fig. 32) from the middle Ordovician Harding Sandstone of Colorado; by original designation.
Discussion. Nomenclatural problems involving definition of *Trichonodella* have bearing on the validity of several conodont taxa. Hass (1953) placed arched bar forms lacking a denticulated posterior process into *Trichonodella* and forms having such a process into a new genus, *Roundya* (shown earlier in this paper to accord with part of *Hibbardella* Bassler), although his emended diagnosis of *Trichonodella* did not differ greatly from Branson and Mehl’s original one. Lindström (1954, 1964) and Philip (1965) also believed that forms with a denticulated posterior process should not be included in *Trichonodella*. Ordovician conodont workers encountered more complexities. Sweet *et al.* (1959) considered that as *Trichonodella* lacked a denticulated posterior process and had a large basal cavity extending beneath the lateral processes, and *Roundya* had a denticulated posterior process but a smaller basal cavity confined to an area beneath the cusp, then forms common in their faunas, which had both denticulated posterior processes and large basal cavities, did not properly correspond to either of these form genera. Sweet *et al.* (1959) then assumed denticles of the posterior process to have only minor taxonomic significance and declared that the character of the basal cavity has greater importance. Consequently they included their symmetrical arched conodonts in *Trichonodella*. Rather than support such an uncertain assignation, Rexroad (1967) suggested that a new genus be erected for these problematical forms, but in the light of recent revisions of *Hibbardella* (Philip 1967; Huddleston 1968; this paper) it seems more probable that they should be referred to the latter.

*Multi-element relationships.* A useful consequence of recent multi-element taxonomic studies is that relationships between form-elements of various symmetry types may be more easily explained. As stated earlier, some authors (Lindström 1964; Rexroad and Craig 1971) considered the form genera *Plectospathodus* and *Trichonodella* to be closely related. However, these two forms have markedly different symmetry, and reconstruction of multi-element assemblages by Jeppsson (1971) indicates their different ‘life’ positions. Symmetrically *Trichonodella* is comparable to *Diplododella* and *Hibbardella*, differing from these genera only in the absence of a denticulated posterior process. For instance, *T. symmetrica* (Branson and Mehl, 1933) has flattened, blade-like, lateral processes and a relatively small basal cavity, as do *D. aurita* (Sannemann, 1955), *D. perbona* (Philip, 1966), and *Diplododella* sp. A (this paper) which also possess denticulated posterior processes. Another lower Devonian trichonodellid form, *T. inconstans* Walliser, 1957, has an excavated basal cavity and bar-like lateral processes identical with some middle Devonian hibbardellid forms, e.g. *H. devonica* (Stauffer, 1938), *H. triangularis* (Bischoff and Ziegler, 1957), *H. wiedenrenensis* (Bischoff and Ziegler, 1957).

Klapper and Philip (1971) found diplododellid and hibbardellid elements occupying equivalent positions in middle and upper Devonian Type 1 apparatuses, to trichonodellid elements in lower Devonian apparatuses, and suggested an evolutionary relationship between these forms. Jeppsson (1971) placed these symmetrical elements in similar positions within his multi-element assemblages.

Arched symmetrical form-elements were not prolific in conodont faunas of the Broken River Embayment, but occurrences of *Trichonodella* were confined to the lower Devonian limestones while diplododellid and hibbardellid forms ranged throughout
strata of early and middle Devonian age. Elsewhere a similar situation prevails; *Trichonodella* is rarely recorded from middle Devonian strata but quite common in older strata, while the distribution of *Diploiodella* and *Hibbardella* is the reverse. Thus form-element morphology, multi-element taxonomy, and stratigraphic distribution all point to a major phylogenetic trend, at least during Devonian time, of the arched symmetrical conodont units. From two main trichonodellid stocks, diploiodellid and hibbardellid forms have evolved, by addition of a denticulated posterior process.

*Trichonodella excavata* (Branson and Mehl, 1933)

Plate 16, figs. 1–3

1933 *Trichognathus excavata* Branson and Mehl, p. 51, pl. 3, figs. 35–36.
1952 *Trichonodella excavata* (Branson and Mehl); Fay, p. 198.
1953 *Trichonodella symmertica* (Branson and Mehl); Rhodes, pp. 315–316, pl. 23, fig. 232 (non fig. 246).
1957 *Trichonodella cf. excavata* sp. a of Walliser, p. 50, pl. 3, fig. 5.
1957 *Trichonodella cf. excavata* sp. b of Walliser, p. 50, pl. 3, fig. 9.
1957 *Trichonodella* sp. of Gross, p. 81, text-fig. Im.
1970 *Trichonodella symmertica* (Branson and Mehl); Druce, pp. 47–48, pl. 9, figs. 7–8.


Walliser (1964) emphasized the great variability in forms of *Trichonodella excavata*. It is similar in process arrangement and denticulation to *T. symmertica* but may be distinguished by a prominent extension of the basal cavity, varying distances (perhaps governed by specimen maturity) up the posterior face of the cusp. Micro-ornament of poorly developed columnar patterns is present on the cusp and denticles.

*Trichonodella inconstans* Walliser, 1957

Plate 16, figs. 7–8

1957 *Trichonodella inconstans* Walliser, pp. 50–51, pl. 3, figs. 10–17.
1962 *Trichonodella cf. inconstans* Walliser; Jentzsch, p. 947, pl. 3, figs. 5, 7.
1970 *Trichonodella cf. T. inconstans* Walliser; Druce, p. 48, pl. 9, fig. 4.

*Diagnosis.* See Walliser (1957, p. 50).

*Trichonodella inconstans* is characterized by its bar-like lateral processes and discrete denticles. The basal cavity, in its fully developed form, is distinctive in lacking a boundary ridge such as displayed by *T. excavata*. *T. blanda* (Stauffer, 1940) can be separated from *T. inconstans* by its short lateral processes containing only three or four denticles. Extreme variation displayed by *T. inconstans* according to specimen size is probably the reason for attempts to subdivide the species, e.g. Fähraeus (1971, p. 681).

*Trichonodella pinnula* Philip, 1966

Plate 16, figs. 5–6

1966 *Trichonodella symmertica pinnula* Philip, pp. 452, 454, pl. 4, figs. 1–6; text-fig. 9.

*Diagnosis.* See Philip (1966, p. 452).
Although only one specimen was obtained, it was clearly identifiable as *Trichonodella pinnula* by the distinctive, laterally flattened cusp. This character separates the species from *T. symmetrica* which has a thick cusp of triangular cross-section.

*Trichonodella symmetrica* (Branson and Mehl, 1933)

Plate 16, fig. 4

1933 *Trichognathus symmetrica* Branson and Mehl, p. 50, pl. 3, figs. 33–34.
1952 *Trichonodella symmetrica* (Branson and Mehl); Fay, p. 199.
1953 *Trichonodella symmetrica* (Branson and Mehl); Rhodes, pp. 315–316, pl. 23, fig. 246 only (fig. 232 = *T. excavata*).
1960 *Trichonodella n. sp. aff. symmetrica* (Branson and Mehl); Ziegler, pp. 197–198, pl. 15, figs. 1–2.
1962 *Trichonodella aff. symmetrica* Ziegler [sic]; Jentzsch, pp. 974–975, pl. 3, fig. 11.
1970 *Trichonodella symmetrica* (Branson and Mehl); Druce, pp. 47–48, pl. 9, figs. 7–8.

*Diagnosis.* See Philip (1965, pp. 112–113).

*Trichonodella symmetrica* is distinguished by its anteriorly flattened cusp, deep blade-like lateral processes, and very small basal cavity. These features cause *T. symmetrica* to resemble closely the anterior arches of the lower Devonian *Diplododella perbona* (Philip, 1966), *Diplododella* sp. A (this paper), and the very similar middle–upper Devonian form, *D. aurita* (Sannemann, 1955). Addition to *T. symmetrica* of a denticulated posterior process, perhaps by increased development of the basal posterior expansion of the cusp, would produce these diplododellid species. *D. zeravshanica* (Moskalenko, 1966) could represent a transitional form between *T. symmetrica* and the later diplododellid forms, as it is described as having a very short posterior process with only two or three denticles. Illustrated examples of *D. aurita* also show variation in length of the posterior process, e.g. compare Glenister and Klapper (1966, pl. 96, fig. 18) and Mound (1968, pl. 66, figs. 4–5).

**THE CONODONT FAUNAS**

Eosteinhornensis fauna. Limestone lenses within the Graveyard Creek Formation generally contain poor conodont faunas with few diagnostic species (Tables 1, 5). Only *Spathognathodus eosteinhornensis*, occurring in the Jack Limestone Member,

**EXPLANATION OF PLATE 16**

Figs. 1–3. *Trichonodella excavata* (Branson and Mehl). 1, Y. 1553 (Ct 464), posterior view, ×100. 2, Y. 1554 (Ct 441), posterior view, ×50. 3, Y. 1555 (Ct 220), posterior view, ×50.

Fig. 4. *Trichonodella symmetrica* (Branson and Mehl). Y. 1562 (Ct 257), posterior view, ×50.

Figs. 5–6. *Trichonodella pinnula* Philip. 5, Y. 1563 (Ct 272), aboral view, ×250. 6, Y. 1563 (Ct 272), posterior view, ×75.

Figs. 7–8. *Trichonodella inconstans* Walliser. 7, Y. 1558 (Ct 192), posterior view, ×50. 8, Y. 1556 (Ct 262), posterior view, ×50.

Figs. 9–10. *Hibbardella cf. wildungenensis* (Bischoff and Ziegler). 9, Y. 1568 (Ct 348), postero-aboral view, ×150. 10, Y. 1568 (Ct 348), posterior view, ×50.

Figs. 11–12. *Hibbardella sp. 11*. Y. 1570 (Ct 402), posterior view, ×50. 12, Y. 1569 (Ct 423), lateral view, ×50.

Fig. 13. *Diplododella sp.* B. Y. 1564 (Ct 402), lateral view, ×75.

Fig. 14. *Diplododella sp.* A. Y. 1567 (Ct 246), posterior view, ×75.
TELFORD, Trichonodella, Hibbardella, Diplododella
and an unnamed lense east of Jessey's Springs (L. 3683 on text-fig. 2) probably equivalent to the Jack Limestone, was found to be restricted to faunas of the Graveyard Creek Formation. Small collections from two other small lenses of the Graveyard Creek Formation (L. 3685 and L. 3686, text-fig. 2) did not contain *S. eosteinhornensis*, but nor were there any species typical of the succeeding faunas in the Broken River Formation. Hence these collections are tentatively included in the *eosteinhornensis* fauna.

At present, *S. eosteinhornensis* has been recorded from only one locality in eastern Australia outside the Broken River Embayment. This was in undifferentiated Siluro-Devonian rocks of the Craigiee Anticline, east-central Queensland (Hill et al. 1969).

**Pesavis and exiguis faunas.** Conodons are more consistently abundant in the Martin's Well Limestone Member of the Broken River Formation than in other rock units of the Broken River Embayment, and most species, including *Spathognathodus exiguis* and *S. optimus*, range throughout the member. However, several species (*Icriodus pesavis*, *Sagittodontus* sp. B, *Scolopodus erectus* and an early form of *Spathognathodus sulcatus*) occurred only in the lower part of the member in most sections. Hence two faunal divisions could be established: a lower one characterized by the above species, together with *Spathognathodus exiguis* and *S. optimus*, and an upper one containing *S. exiguis* and *S. optimus* in the absence of the other forms. The *exiguis* fauna could be distinguished from the succeeding *foveolatus-palethorpei* fauna (which contains the same spathognathodid form species) by the absence of *Polygnathus foveolatus* and *S. palethorpei*, the greater proportion of variants of *S. exiguis* with restricted basal cavities, and abundance of high-bladed variants of *Ozarkodina denckmanni*.

Distribution of the *pesavis* fauna may be the result of particular environmental or facies conditions. No samples from section L. 3664 (text-fig. 2) contain the diagnostic elements of the fauna. This section through the Martin’s Well Limestone was some distance east of the other four sections, in a part of the member consisting mainly of massively bedded limestone. In the other sections the member consisted of thinly
TABLE 4. Upper Silurian to middle Devonian conodont faunas in the Broken River Embayment.

<table>
<thead>
<tr>
<th>FAUNA</th>
<th>KEY SPECIES</th>
<th>DISTRIBUTION</th>
<th>AGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>brevis</td>
<td><em>Spathognathodus brevis</em>, <em>S. cf. bipennatus</em></td>
<td>Upper third Chinaman Creek Lst. Mbr., Broken River Fm.</td>
<td>Givetian</td>
</tr>
<tr>
<td>pseudofoliatuas</td>
<td><em>Ozarkodina playfordi</em>, <em>Polygnathus linguiformis linguiformis</em>, <em>P. pseudofoliatuas</em>, <em>Spathognathodus intermedius</em>, <em>S. cf. bipennatus</em></td>
<td>Upper part Lookup Well Lst. Mbr., middle third Chinaman Creek Lst. Mbr., upper part lens Dmb&lt;sub&gt;E&lt;/sub&gt;, Broken River Fm.</td>
<td>late Couvinian early Givetian</td>
</tr>
<tr>
<td>linguiformis cooperi</td>
<td><em>Icriodus corniger</em>, <em>Polygnathus linguiformis cooperi</em>, <em>P. linguiformis linguiformis</em>, <em>P. cf. costatus costatus</em>, <em>Spathognathodus bidentatus</em></td>
<td>middle part Lookup Well Lst. Mbr., middle part lens Dmb&lt;sub&gt;E&lt;/sub&gt;, upper 150 m lens Dmb&lt;sub&gt;F&lt;/sub&gt;, Broken River Fm.</td>
<td>early Couvinian</td>
</tr>
<tr>
<td>foveolatus - palethorpe</td>
<td><em>Neopanderodus equebilis</em>, <em>Polygnathus foveolatus foveolatus form B</em>, <em>P. foveolatus serotinus</em>, <em>Spathognathodus palæthorpe</em></td>
<td>Dip Creek Lst. Mbr., lower third Chinaman Creek Lst. Mbr., lower-middle part Lookup Well Lst. Mbr., lower part lens Dmb&lt;sub&gt;E&lt;/sub&gt;, lower 200 m lens Dmb&lt;sub&gt;F&lt;/sub&gt;, Broken River Fm.</td>
<td>late Emsian</td>
</tr>
<tr>
<td>Spathognathodus n. sp.</td>
<td><em>Spathognathodus n. sp.</em>, <em>S. sulcatus</em> (late form)</td>
<td>? lower part Lookup Well Lst. Mbr., Broken River Fm.</td>
<td>early Emsian</td>
</tr>
<tr>
<td>exigus</td>
<td><em>Spathognathodus exigus</em>, <em>S. optimus</em></td>
<td>unnamed lens (at L3684) in upper part of Graveyard Creek Fm.; upper half Martin's Well Lst. Mbr., 1st. at Lookup Well (L3675), Broken River Fm.</td>
<td>middle - late</td>
</tr>
<tr>
<td>pesavis</td>
<td><em>Icriodus pesavis</em>, <em>Sagittodontus sp B</em>, <em>Scopododus erectus</em>, <em>Spathognathodus exigus</em>, <em>S. optimus</em>, <em>S. sulcatus</em> (early form)</td>
<td>unnamed lens (L3657) near base of Broken River Fm., lower half Martin's Well Lst. Mbr., Broken River Fm.</td>
<td>Siegenian</td>
</tr>
<tr>
<td>eosteinornensis</td>
<td><em>Spathognathodus eosteinornensis</em></td>
<td>Jack Lst. Mbr., Graveyard Creek Fm.</td>
<td>Ludlovian</td>
</tr>
</tbody>
</table>

TEXT-FIG. 8. Distribution of the *pesavis* and *exigus* faunas in the Martin's Well Limestone Member.
bedded detrital limestones with numerous shale intercalations, suggesting more shallow-water conditions than in the east. Thus, in attempting interbasinal correlations and age assignments, the *pesavis* and *exiguus* faunas are considered as one unit.

Elements of these faunas are widespread in eastern Australia and have been used in the zonal scheme of Philip and Pedder (1967b). Apparent sequential occurrence of the early form of *Spathognathodus sulcatus* and *Icriodus pesavis* prompted these authors to assign them to separate zones. This is not supported by more recent data which shows the two species occurring together in the Martin's Well Limestone Member and lower part of the Garra Formation, Wellington, New South Wales (Druce 1970b). Klapper (1969) defined the early and late variants of *S. sulcatus*, implying that the separation was an evolutionary trend. It is preferable to use this relationship in lower Devonian correlations, independently of the somewhat erratic appearances of *I. pesavis*. Recent multi-element taxonomic studies (Klapper and Philip 1972) also indicate uncertainty in the biostratigraphic use of *I. pesavis* (as a form-element), for the apparatus containing this element shows considerable variability.

A number of rock units in eastern Australia that are evidently coeval, as correlated by conodonts, with the Martin's Well Limestone, are indicated on Table 6. The documented conodont fauna from the Buchan Caves Limestone, Victoria (Philip 1966) also has an *exiguus* faunal aspect. However, conodonts from this unit were obtained by reconnaissance only (Philip 1966, text-fig. 2) and other faunal evidence suggests a significantly younger age (Thomson and Campbell 1971).

*Spathognathodus n. sp. fauna*. This small distinct fauna was obtained from section L. 3674 (text-fig. 2) in the lowermost exposed beds of the Lockup Well Limestone Member. The two key species (Table 4) have not been found elsewhere in the Broken River Embayment. *Spathognathodus n. sp.* possibly evolved from *S. exigus* and, as mentioned above, the late form of *S. sulcatus* probably developed from the early form recorded in the *pesavis* fauna. Therefore, the *Spathognathodus n. sp.* fauna is assumed to post-date the *exiguus* and *pesavis* faunas. It precedes the *foveolatus–palethorpei* fauna which occurs stratigraphically higher in the Lockup Well Limestone (text-fig. 9).

The key species have a restricted distribution in eastern Australia outside the Broken River Embayment. The late form of *S. sulcatus* has been obtained by the author only from lower Devonian limestones of the Chillagoe Formation, north Queensland. *Spathognathodus n. sp.* was recognized by the present author in the Dunstable Formation, central Queensland, but it occurred with *Polygnathus lingiformis lingiformis* which is typical of much younger faunas in the Broken River Embayment (Table 4).

*Foveolatus–palethorpei* fauna. This fauna is the most widespread in the Broken River Embayment (Table 4), and is the oldest Devonian fauna in the Jessey's Springs and Broken River areas (text-fig. 9). It has considerable significance in eastern Australian and intercontinental correlations, as it contains the first polygnathid forms to appear in the embayment's marine sequence. The distinctive new double-rowed spathognathoid form *Spathognathodus palethorpei* is useful for intrabasinal correlations, but there is no record of the species elsewhere in eastern Australia. Variants of
TABLE 5. Distribution of form species among recognized conodont faunas of the Broken River Embayment.

S. exiguus and S. optimus are prominent in the foveolatus-pale thorpei fauna, although their importance is diminished by the abundance of S. pale thorpei and two subspecies of Polygnathus foveolatus. The appearance of Neopanderodus aequabilis in this fauna follows the pattern suggested by Ziegler and Lindström (1971) whereby multistriate simple cones are thought to have developed from early lower Devonian panderodid forms.

The existence of three forms of P. foveolatus, viz. P. f. foveolatus form \( \alpha \), P. f. foveolatus form \( \beta \), and P. f. serotinus was described previously. Pedder et al. (1970b) illustrated sequential forms from the Taemas Limestone, New South Wales; P. f. foveolatus form \( \alpha \) was present in the lower part and the other two forms occurred together in the upper part of the unit. Klapper (1969) showed a similar situation in the Royal Creek sequence, Yukon Territory. P. f. foveolatus form \( \beta \) and P. f. serotinus are associated in the foveolatus-pale thorpei fauna (Table 4) which is therefore correlative with the upper fauna of the Taemas Limestone (= Fauna F of Philip and Pedder 1967b). The absence from the Broken River Embayment of P. f. foveolatus form \( \alpha \), and the even older P. dehiscens Philip and Jackson, may be explained by the great thickness (about 600 m) of unfossiliferous clastic sediments that separate the Martin’s Well Limestone Member from the Dip Creek Limestone Member which contains the earliest polygnathids (text-figs. 2, 9).

Other significant occurrences of P. f. foveolatus in eastern Australia, e.g. Murrindal Limestone, Victoria (Philip 1966), Douglas Creek Limestone, central Queensland (Philip and Pedder 1967c; this paper), are of form \( \alpha \) types and are representative of Fauna E of Philip and Pedder (1967b).

Linguiformis cooperi fauna. Few eastern Australian middle Devonian conodont faunas have been documented. Hence, biostatigraphical application of the linguiformis cooperi fauna, the earliest definite middle Devonian fauna in the Broken River Embayment (Table 4), is limited at present. Only the Timor Limestone, Murrurundi, New South Wales contains comparable faunas, from which Pedder et al. (1970a) described a form species, Polygnathus sp. cf. webbi Stauffer, which appears similar to P. linguiformis cooperi (Klapper 1971 noted that most pre-upper Devonian examples of P. webbi are incorrectly identified). Accompanying ‘P. sp. cf. webbi’, which occurs in the lower part of the Timor Limestone, is Icriodus corniger, another key species of the linguiformis cooperi fauna (Table 4). Pedder et al. (1970a) included these conodonts in their Lower Eifelian corniger microfossil assemblage (= Fauna G of Philip and Pedder 1967b).

Spathognathodus bidentatus also occurs in the linguiformis cooperi fauna but in the Timor Limestone it was restricted to the middle Eifelian australis assemblage (Pedder et al. 1970a), which contains forms more typical of the pseudofoliatus fauna in the Broken River Embayment (Table 4). The earlier appearance of S. bidentatus in north Queensland may indicate a longer time range for this species than has been formerly thought (Ziegler 1971).

Pseudofoliatus fauna. Large robust form-elements characterize this fauna, which is fairly widespread geographically but somewhat restricted stratigraphically. In the Lockup Well Limestone Member it occurs within thinly bedded, crinoidal limestone which constitutes the upper 5 m of the unit. There is only a single occurrence of the fauna in a similar lithology, forming the top bed of lens Dmb\(_E\) (text-figs. 2, 9). It
appears to occupy the middle third (about 150 m thick) of the Chinaman Creek Limestone Member but the collections are sparse (Table 2). Nevertheless, the *pseudofoliatus* fauna is distinctive, and is the most diverse fauna described here (Table 5).

Key species of this fauna have been recorded from the Moore Creek Limestone, Attunga, New South Wales (Philip 1967) and the Timor Limestone (Pedder et al. 1970a). In the latter, *Polygnathus pseudofofoliatus* and *Spathognathodus? intermedius* (= *S. bidentatus transitans* of Pedder *et al.*) are restricted to the middle Eifelian *australis* assemblage. Except for *P. eifius* Bischoff and Ziegler which is similar to *P. pseudofofoliatus* (Klapper, 1971; this paper), the younger *kockelianus-robusticostatus* assemblage in the Timor Limestone contains no platform-type conodonts that are also common to the *pseudofofoliatus* fauna. However, in the Moore Creek Limestone, definite examples of *P. pseudofofoliatus* occur with elements of the *kockelianus-robusticostatus* assemblage (Philip 1967). Because of this somewhat irregular distribution of *P. pseudofofoliatus*, and the absence of the index forms *P. kockelianus australis* Jackson and *P. k. kockelianus* Bischoff and Ziegler from limestones of the Broken River Embayment, precise correlation of the *pseudofofoliatus* fauna and the New South Wales assemblages is not possible. None the less, the common occurrence in these faunas of such form species as *P. linguiformis linguiformis*, *Spathognathodus? intermedius*, and *Spathognathodus* sp. cf. *S. bipennatus*, suggests that they lie within comparable age limits.

**Brevis fauna.** Collections from the upper third of the Chinaman Creek Limestone Member were meagre, but several occurring species are unique to this part of the sequence (Table 5). *Polygnathus linguiformis linguiformis* again is relatively common while *Spathognathodus cf. bipennatus* is more abundant than in the preceding *pseudofofoliatus* fauna. Similarly to the *linguiformis cooperi* fauna, the only reported occurrence of the *brevis* fauna in eastern Australia, apart from the Broken River Embayment, is in the Timor Limestone (Pedder *et al.* 1970a). *S. brevis*, a key species of the present fauna (Table 4), was considered to be one of several form species characterizing the *varcus* assemblage in the upper part of the unit. The others include *P. varcus* Stauffer and *P. l. transversus* Wittekindt, which have not been found in limestones of the Broken River Embayment. However, coral faunas assist in correlation of the *brevis* fauna and *varcus* assemblage, for example the distinctive coral *Endophyllum schlueri* Etheridge occurs in the upper Timor Limestone (Philip and Pedder 1967b), and in Wyatt and Jell’s (1967) ‘Upper Fauna’ of the Chinaman Creek Limestone Member.

**INTERCONTINENTAL CORRELATION**

**Limitations of present faunal zonations.** Because of the strong facies dependency of most fossil groups, a detailed and widely based faunal zonation scheme of the European lower and middle Devonian type sequences (the Eifel and Ardennes sequences) has not been firmly established. Graptolites, goniatites, trilobites, brachiopods, and conodonts have been used (Erben and Zagora 1967, fig. 3), but correlation of faunas from regions such as eastern Australia and North America with those of the European type sequences can rarely be made by direct comparisons. It is usually necessary to relate the overseas faunas to similar faunas elsewhere in Europe; the strata containing the latter may then be correlated with the type sequences using other data.
This procedure may involve comparisons of strata within Europe whose stratigraphic relationships are not clearly understood, or which may belong to different sedimentary facies, such as the Rhenish or Hercynian magnafacies (Erben 1962).

Ziegler (1971) claimed conodonts to be the only group of marine fossils with some degree of facies independency. Seddon (1970a), Barnett (1971), Ferrigno (1971), and Seddon and Sweet (1971) have demonstrated sedimentological and environmental controls on Devonian conodont evolution and distribution; but conodonts appear less restricted than other invertebrate groups. However, they are still rare throughout much of the Ardennes and Eifel sequences, especially the lower Devonian parts (Ziegler 1971). Little information has been published concerning conodont faunas of any age in the Barrandian Basin sequence of Czechoslovakia (Chlupac 1967), which, because of its extensive limestone development, is potentially suitable for delineation of a continuous faunal succession.

Some attempts have been made to institute a conodont-based zonal scheme of the European lower Devonian using data from several sequences (Walliser 1962; Ziegler 1971). While they may be valid and useful within Europe, it is not yet possible to correlate the tentatively defined zones and faunas world-wide. Philip and Pedder (1967b) and Klapper et al. (1971) proposed lower Devonian zonations for eastern Australia and North America respectively, but the composition and time ranges of their faunal units differ from the European examples.

Middle Devonian parts of the Ardennes sequence, and several sequences in the Rhenish Schiefergebirge (e.g. Siegerland-Sauerland and Giessen-Kellerwald sequences of Brinkmann 1969), certain abundant conodont faunas that have been described in some detail (Bischoff and Ziegler 1957; Wittekindt 1966; Bullynck 1970). Nevertheless, there are differences between the middle Devonian zonation schemes proposed by Wittekindt in the Giessen-Kellerwald area (modified subsequently by Ziegler 1971) and Bullynck in the Ardennes, due to variable ranges of some conodont species. This indicates the difficulty at present of obtaining precise correlation between eastern Australian middle Devonian faunal zones (e.g. Philip and Pedder 1967b; Pedder et al. 1970a) and the European schemes, although the discrepancies are not as great as in the lower Devonian.

Since lower and middle Devonian biostratigraphy has such fundamental problems, it is not surprising that conflicts have arisen regarding precise age assignments of various eastern Australian rock units, e.g. Cavan and Taemas Limestones, Wee Jasper, New South Wales (Pedder, Jackson and Philip 1970; Thomson and Campbell 1971). This problem has been compounded by the fact that conflicting age assignments have usually been added from the distribution of different invertebrate groups. Therefore in biochronological evaluation of conodont faunas of the Broken River Embayment, data from other fossil groups is considered when available. This additional information is mostly from rugose and tabulate corals (Hill 1943; Philip and Pedder 1967b–c; Strusz 1967). Ammonoids, brachiopods, graptolites, and trilobites have not yet proved to be as useful, although they are important in certain regions (Teichert 1948; Talent 1956; Chatterton 1971).

*Early Devonian conodont provincialism.* Difficulties in correlation of invertebrate faunas from the European Rhenish and Hercynian magnafacies reflect faunal com-
TEXT-FIG. 9. Diagrammatical representation of the upper Silurian–Devonian sequence in the Broken River Embayment showing the stratigraphic distribution of conodont faunas.
munity differences caused by local environmental variation. As type areas are involved, the consequences are considerable for inter-continental Devonian correlation. However, faunal provincialism may also be a significant factor, and may provide further explanation for the differences between faunas and faunal zonations of various regions. Provincialism of several early Devonian fossil groups has been described (Boucot et al. 1967; Talent 1972). Telford (in Talent 1972) proposed a possible faunal segregation of conodonts, mainly based on the distribution of the genera Polygnathus and Icriodus. The latter was shown by Seddon (1970a) and Seddon and Sweet (1971) to be subject to strong environmental controls but, even allowing for this factor, the world-wide early Devonian distribution of Icriodus was quite irregular. Its species were abundant in Europe (Carls 1969; Ziegler 1971), only moderately abundant in western North America (Klapper 1969), and rare in eastern North America (Klapper and Ziegler 1967; Klapper et al. 1971) and eastern Australia.

Distribution of Spathognathodus was not used previously in consideration of conodont provincialism, but the occurrences of several spathognathodid form species reveal significant inhomogeneities. ‘Double-rowed’ forms such as S. sulcatus and S. paletorpe are absent or very rare in European faunas. The former has been recorded extensively in eastern Australian and western North American lower Devonian sequences (Philip 1965; Philip and Pedder 1967c; Klapper 1969), while the latter is very abundant in presumed Emsian (see later) faunas of the Broken River Embayment. As described earlier, there are two main stocks of ‘single-rowed’ spathognathodid conodonts in eastern Australian lower Devonian faunas, represented by S. exigus and S. optimus. Similar forms have been described from western North America (Walliser 1960; Klapper 1969; Fähraeus 1971) and south-central Asia (Moskalenko 1966). However, different stocks have been identified in European faunas, for example S. frankenwaldensis Bischoff and Sannemann, S. remscheidensis Ziegler, and S. steinhornensis Ziegler.

Thus lower Devonian conodont faunas can be separated into two main geographical regions, informally designated as the European and Pacific provinces, with the latter encompassing eastern Australia and western North America. Eastern North American conodont faunas cannot be related precisely to this scheme as there seems to be a mixture of European and Pacific features, for example Barnett (1971) reported the widespread occurrence of the European S. remscheidensis but, as previously mentioned, species of Icriodus are uncommon.

Global distribution of middle Devonian conodont faunas is more homogeneous. Pedder et al. (1970a) described a similar faunal sequence in the Timor Limestone to that outlined in Europe by Ziegler (1971). Klapper (1971) found close relationships between New York early middle Devonian faunas and those from the Ardennes sequence (Bultynck 1970). Some difficulties in middle Devonian inter-continental correlation still remain, but these are mainly due to slight differences in certain specific ranges between various regions (Klapper et al. 1971).

Ages of the Broken River Embayment conodont faunas

Eosteinhorntenesis fauna. The key species of this fauna, Spathognathodus eosteinhorntenesis, was used by Walliser (1964) to define his uppermost Silurian eosteinhorntenesis Zone in the Carnic Alps, Europe. Mashkova (1967) confirmed this age
assignment in recovering *S. eostinhornensis* from the Skala Horizon, Podolia, which is overlain by strata containing *Icriodus woschmidtii* Ziegler, a diagnostic Gedinnian form species (Ziegler 1971). Also, Rexroad and Craig (1971) recorded *S. eostinhornensis* from the upper Silurian Bainbridge Formation, Missouri, although they indicated that the form species may be less restricted stratigraphically than is suggested by its occurrence in the Carnic Alps. Walliser (1971) noted that while its lower age limit is somewhat uncertain, *S. eostinhornensis* is a definite pre-Devonian form. Thus the *eostinhornensis* fauna from limestones of the Broken River Embayment, and especially the Jack Limestone Member, may be considered Ludlow in age.

Pesavis and *exiguus* faunas. Because of the apparent provinciality of lower Devonian form species of *Spathognathodus, Icriodus pesavis* is the only conodont of the *pesavis* or *exiguus* faunas, other than long-ranging cone and bar types, that bears some relationship to European faunas; however, the precise time-range of this form species is not known. Bischoff and Sannemann (1958) first described the form from the basal part of the Tentakulitenkollenkalk, Frankenwald, West Germany and gave it a questionable Siegenian age. Since then *I. pesavis* has been recorded from localities with a variety of ages, e.g. Carls (1969)—early Gedinnian, Ziegler (1971)—late Gedinnian. In North America the species occurs in the Caballos Novaculite (Graves 1952) and Pillar Bluff Limestone (Seddon 1970b) in Texas, and limestones of Royal Creek, Yukon Territory (Klapper 1969) and Eureka County, Nevada (Klapper et al. 1971). In contrast with the European assignments, these occurrences have been given an early Siegenian age. Thus a confident age assessment of eastern Australian limestones based on the appearance of *I. pesavis* is not yet possible.

As explained above (p. 80) *S. sulcatus* is more reliable in correlation within eastern Australia and, together with *S. exiguis*, enables correlation of the eastern Australian and western North American faunal successions. *S. sulcatus* ranges through Faunas 5 and 6 of Klapper et al. (1971) in both Nevada and the Yukon (the 'early' form occurs in Fauna 5 and the 'late' form in Fauna 6). The variant of *S. exiguis* with a restricted basal cavity (*S. exiguis philipi* of Klapper 1969), which is abundant in the *exiguus* fauna, is present in Fauna 5. Faunas 5 and 6 of Klapper et al. (1971) correspond to the Spinopalasia and Trematospira brachiopod zones, which have been dated as middle and late Siegenian respectively (Johnson et al. 1967). Consequently, a middle to late Siegenian age is possible for the combined *pesavis* and *exiguus* faunas of the Broken River Embayment. This is not in complete accord with proposed ages of associated coral faunas. Jell (1968) assigned a late Emsian age to corals of the Martin’s Well Limestone Member, and Strusz’s (1967) eastern Australian faunal association comprising corals from the Garra Formation, Etna Beds, and limestones of the Silverwood Group (Table 6) which all contain the *exiguus* fauna, was considered to be Emsian in age. The main reason for these discrepancies is the uncertainty in relating both the conodont and coral faunas to the European type sequences, which necessitates faunal comparisons with regions in which both fossil groups may not be adequately known.

*Spathognathodus* *n. sp.* fauna. The age of this fauna can be based only on the appearance of *Spathognathodus sulcatus* ('late form'). As noted above, this form species occurs in Fauna 6 of Klapper et al. (1971) which has been assigned a late
Siegenian or questionable early Emsian age (Lenz 1967). Within the Broken River Embayment the *Spathognathodus* n. sp. fauna closely precedes the distinct late Emsian (see below) *foveolatus-palethorpei* fauna in the Lockup Well Limestone Member (text-fig. 9) so that an early Emsian age is possible.

**Foveolatus-palethorpei fauna.** The age of this fauna is less equivocal, since it is based mainly on the appearance of the widely distributed polygonthid forms *Polygnathus foveolatus foveolatus* and *P. f. serotinus*. These conodonts have been used extensively in European and North American zonation schemes, and their occurrences have often been related to the distribution of other fossil groups. For instance, Ziegler (1971) included *P. foveolatus* in the European *Icriodus bilatericrescens*–*S. steinhornensis–Polygnathus* fauna to which he assigned a late early Emsian to late Emsian age range. Similar conodont faunas were described by Stoppel (1961) from limestones in the Kellerwald that were dated as late Emsian by means of associated goniatites.

In western North America *P. foveolatus* occurs in Fauna 9 of Klapper et al. (1971) which is stratigraphically equivalent to the upper part of the *Eurekaspiret pinyonensis* Zone of Johnson et al. (1967). According to the brachiopods, this zone appears to range from lower to upper Emsian. The known distribution of *P. foveolatus* was refined further by Klapper et al. (1971), in noting the presence of morphologically distinct early and late variants (designated herein as *P. f. foveolatus* forms α and β, and *P. f. serotinus*). These suggest a possible subdivision of Fauna 9. As noted earlier, Pedder et al. (1970b) described a similar sequential occurrence of the subspecies in the Taemas Limestone, Wee Jasper, dating this rock unit as Emsian on the basis of both conodont and coral information. The fauna from the upper part of the Taemas Limestone (= Fauna F of Philip and Pedder 1967b), containing *P. f. foveolatus* form β and *P. f. serotinus*, was shown to be correlative with the
foveolatus–palethorpei fauna of the Broken River Embayment, which therefore may be assigned a late Emsian age.

Linguiformis cooperi fauna. Less uncertainty is attached to the inter-continental correlation of middle Devonian conodont faunas. Index species of European middle Devonian faunal zones, proposed by Wittekindt (1966) and subsequently modified by Ziegler (1971), are found world-wide. Also Bultynck (1970) described in great detail the conodont succession of the type Couvinian sequence in the Ardennes, Belgium. Hence almost direct comparison of eastern Australian conodont faunas with faunas in this important sequence may be performed. Klapper (1971) has already established relationships between the Ardennes sequence and the New York State lower middle Devonian (Onondaga Limestone and Marcellus Formation).

The middle Devonian aspect of the linguiformis cooperi fauna is indicated clearly by the appearance of *P. linguiformis linguiformis* which is not known definitely from pre-middle Devonian strata. Other platform elements in the linguiformis cooperi fauna, e.g. *Icriodus corniger*, *P. l. cooperi*, are typical of Ziegler’s (1971) lower Eifelian *I. corniger* Zone and Klapper’s (1971) lower Couvinian *P. costatus patulus–P. l. cooperi* fauna. *S. bidentatus*, which is a rare component of the linguiformis cooperi fauna, is actually a characteristic member of Ziegler’s middle Eifelian *S. bidentatus* Zone, occurring in association with *P. angusticostatus* Wittekindt and *P. eiflusi* Bischoff and Ziegler. Neither of these polygnathids is known in limestones of the Broken River Embayment, and the biostratigraphic importance of *S. bidentatus* in the linguiformis cooperi fauna is uncertain.

In the Ardennes sequence *P. l. cooperi* is restricted to Co2b (Klapper 1971); *I. corniger* ranges from Co1 to Co2b. Thus, an early Couvinian age seems likely for the linguiformis cooperi fauna. Assignment to the Ardennes stage is preferred, as Ziegler’s (1971) zones are not based exactly on the Eifel type sequences.

Pseudofoliatius fauna. Although this fauna is easily recognized and apparently restricted stratigraphically in the Broken River Embayment (text-fig. 9), its key species generally are not indicative of a narrow time-range. *Polygnathus linguiformis linguiformis* ranges throughout the middle Devonian (Ziegler 1971); *Ozarkodina playfordi* has various Eifelian occurrences; *Spathognathodus* sp. cf. *S. bipennatus* ranges from late Couvinian through Givetian time (Bultynck 1970; Philip 1967).

*P. pseudofoliatius* and *S.? intermedius* may enable more precise age determination. In the Ardennes sequence both range from Co2c R/IV to Co2c V (Bultynck 1970, pl. 38). However, Ziegler (1971) indicated much wider age limits for *P. pseudofoliatius*, and Klapper (1971) found *S.? intermedius* extending lower than *P. pseudofoliatius* in the New York State sequence. Thus, only a tentative late Couvinian–early Givetian age may be attributed to the pseudofoliatius fauna in the Broken River Embayment. Nevertheless, this accords, in part, with late Eifelian ages given to similar conodont faunas, and associated corals, of the Moore Creek Limestone (Philip 1967) and the australis assemblage of the Timor Limestone (Pedder, Jackson and Ellenor 1970).

Brevis fauna. This fauna contains few stratigraphically significant conodont form species. *Polygnathus linguiformis linguiformis* is common, but it ranges throughout the middle Devonian. *Spathognathodus* cf. *bipennatus* is more abundant in the brevis
fauna than the *pseudofoliatus* fauna, but again it is a long-ranging form. The only other species of importance is *S. brevis*. In Europe it is restricted to the upper Givetian *P. varcus* Zone (Ziegler 1971), and it is a characteristic form of the Givetian *varcus* assemblage in the Timor Limestone (Pedder et al. 1970a). Thus a broad Givetian age is assumed for the *brevis* fauna. Supporting this is the associated occurrence of the brachiopod *Stringocephalus*, reported by Wyatt and Jell (1967), a diagnostic Givetian fossil.

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APPENDIX

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