

EARLY DEVONIAN CONODONT FAUNAS FROM BUCHAN AND BINDI, VICTORIA, AUSTRALIA

by RUTH MAWSON

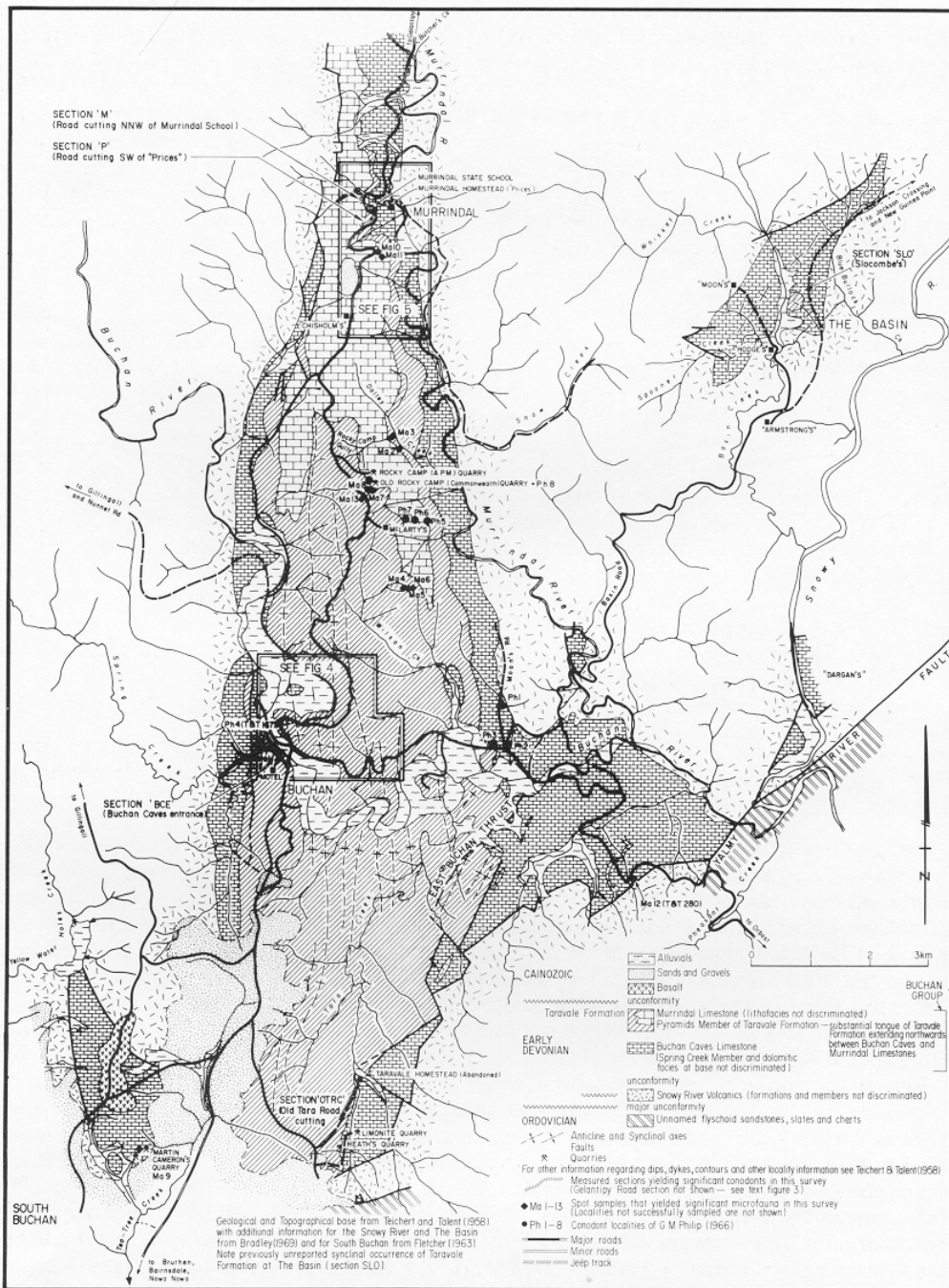
ABSTRACT. Conodont faunas of the Taravale Formation, in sections measured at Buchan and Bindi, Victoria (south-eastern Australia), contain polygnathid conodonts representative of the *dehiscens*, *perbonus/gronbergi*, *inversus*, and *serotinus* zones of the Early Devonian (late Pragian to middle Dalejan). New taxa described are *Polygnathus dehiscens abyssus*, *P. labiosus* and *P. pseudoserotinus* (both belonging to a lineage derived from *P. d. abyssus*), *P. nothoperbonus*, and *Ozarkodina prolata*. The ammonoid faunas of the Taravale Formation are shown to be restricted to the *dehiscens* and *perbonus* zones. Three species of goniatites, associated with two or more species of bactritids, occur within the *dehiscens* zone at Buchan and are thus among the oldest firmly dated ammonoids in the world.

STUDY of the sequence of conodont faunas at Buchan and Bindi, Victoria, had several objectives: to test the applicability in Australia of the zonal system developed mainly from northern hemisphere conodont sequences, paying special attention to the polygnathids; to commence development of a framework for the study of dactyloconarid biostratigraphy in this part of the world; and to provide more precise ages for the evolutionarily important Early Devonian ammonoids previously described (Teichert 1948; Erben 1964, 1965) from the Taravale Formation. As international correlation for the late Early Devonian has come to be based primarily on polygnathid conodonts (e.g. Klapper and Ziegler 1979; Klapper and Johnson 1980) the discussion of polygnathids given herein spreads wider than consideration of the polygnathids from the Buchan and Bindi areas. An account of the implications of the conodont work for ages of the Taravale ammonoids is given.

STRATIGRAPHY

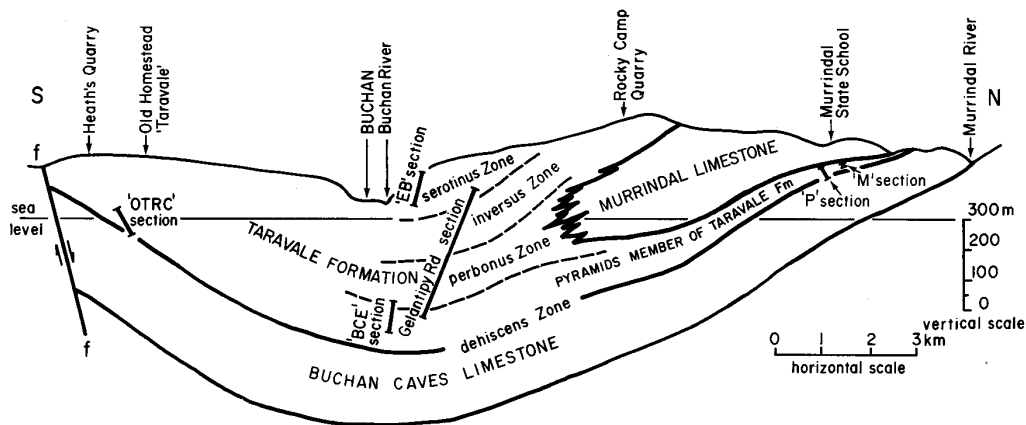
The Buchan Group of eastern Victoria is a sequence of carbonates and shales (maximum thickness *c.* 3,300 m) which outcrop in at least fifteen discrete areas to the north and east of their most extensive development in the Buchan-Murrindal area (text-figs. 1 and 2). Some occurrences are synclinal, as at Buchan and at The Basin, 12 km north-east of Buchan; others, such as that at Bindi and those at Jackson Crossing and in the headwaters of the Indi River and Limestone Creek, about 75 km to the north, and at Gillingall, 20 km to the north-north-west, owe their preservation to faulting. In all these occurrences, the basal unit of the Buchan Group, the Buchan Caves Limestone, rests disconformably or with minor unconformity on the Snowy River Volcanics (as at Buchan, The Basin, and at the junction of Dead Horse Creek and Limestone Creek in the headwaters of the Indi River); it is markedly unconformable at Bindi.

Lithologies of the Buchan Caves Limestone (maximum thickness *c.* 230 m at East Buchan, but up to 295 m at Bindi) have been described in some detail by Talent (1956) for the Buchan-Murrindal area. There is remarkable uniformity in lithologic and macro-faunal succession within the Buchan Caves Limestone throughout eastern Victoria, suggesting original deposition on a near-planar surface, termed the Buchan-Indi-Combiensbar Shelf by Talent (1965, 1969). A basal sequence of pale- to mid-grey dolomites (weathering to buff) is characteristic of all outcrop areas; it reaches a maximum thickness exceeding 40 m in the Back Creek area of East Buchan where it has been quarried commercially on a small scale. The remainder of the Buchan Caves Limestone consists predominantly of calcarenites, a fairly high frequency of algal pisolites, rare crinoidal limestones,



TEXT-FIG. 1. The Buchan Group in the Buchan-Murrindal-The Basin area, eastern Victoria.

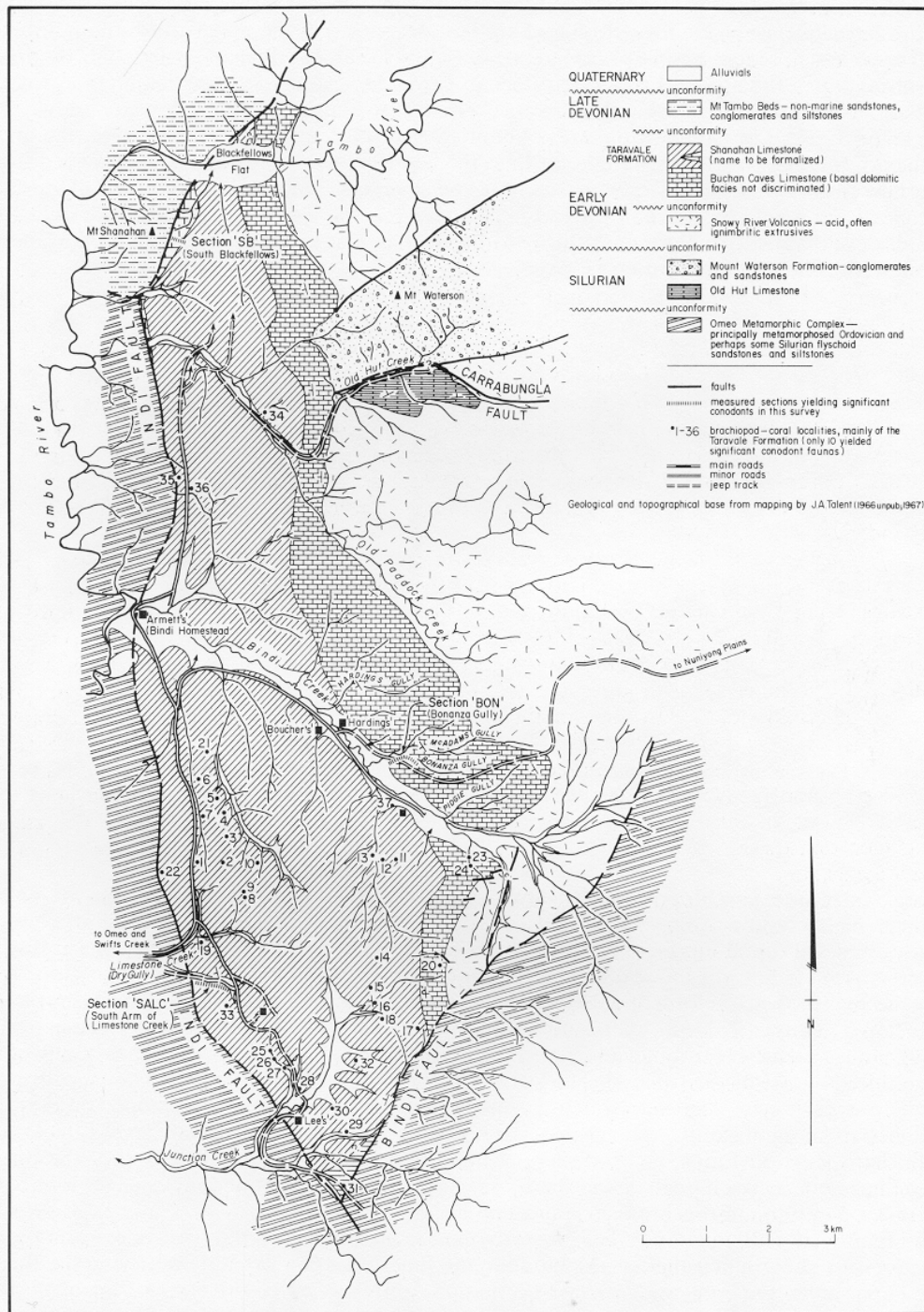
and, in the upper parts of the formation, micritic limestones (calclutites); the micrites aggregate 7–14 % of any sequence of the formation and are best developed in the upper third, though the last 15–30 m consists predominantly of calcarenites in all three areas (Buchan–Murrindal, Bindi, and The Basin) where the highest beds of the Buchan Caves Limestone occur in conjunction with the Taravale Formation. There are only three occurrences of non-carbonate sediments known from the Buchan Caves Limestone in the areas about Buchan (Talent 1956); one of these, the areally restricted Cameron Mudstone Member at East Buchan (loc. Ma12, text-fig. 1) has yielded dacryonarids consistent with a *kindlei* or perhaps *sulcatus* age and are therefore the oldest-dated sediments from within the Buchan Caves Limestone. At Bindi, impure carbonates and mudstones are well developed within the upper third of the Buchan Caves Limestone, outcropping best in Bonanza, McAdam's, and Harding's Gullies.



TEXT-FIG. 2. Diagrammatic north-south section of the Buchan–Murrindal area, eastern Victoria, showing relationship of stratigraphic units of the Buchan Group and position of stratigraphic sections relative to the stratigraphy.

Coral, ostracode, brachiopod, and bivalve faunas of the Buchan Caves Limestone are notable for their relatively low diversity (Hill 1950; Krömmelbein 1954; Talent 1956). Philip (1966) has already discussed conodonts from three spot-samples from the Buchan Caves Limestone at Buchan. The present study has not focused on the conodont faunas of the Buchan Caves Limestone apart from the highest beds at Murrindal (section 'P' sample 1.1 of Table 2) and The Basin (section 'SLO', lowest sample, Table 3), spot-sampling at Martin Cameron's Quarry, South Buchan (sample Ma 9), and a sequence through the upper Buchan Caves Limestone at Bonanza Gully, Bindi (section 'BON', text-fig. 3, Table 4). The last of these passes through an uncharacteristically richly fossiliferous carbonate sequence which Talent (1967), on the basis of brachiopod faunas, had concluded to be significantly younger than the highest horizons of the Buchan Caves Limestone in the Buchan–Murrindal area, i.e. that there was significant diachronism of the top of the Buchan Caves Limestone between Buchan and Bindi. As will be shown later, conodont evidence is in accord with this contention; the diachronism is substantial.

The main focus of this study has been the conodont faunas of the Taravale Formation, a sequence of nodular limestones, shales, and impure limestones conformably overlying the Buchan Caves Limestone. Outcrops of Taravale Formation are restricted to three areas: major developments at Buchan and Bindi, and a minor synclinal body (previously overlooked) occupying only a few hectares at The Basin. Presently available evidence suggests great differences in rates of



TEXT-FIG. 3. The Buchan Group at Bindi, eastern Victoria.

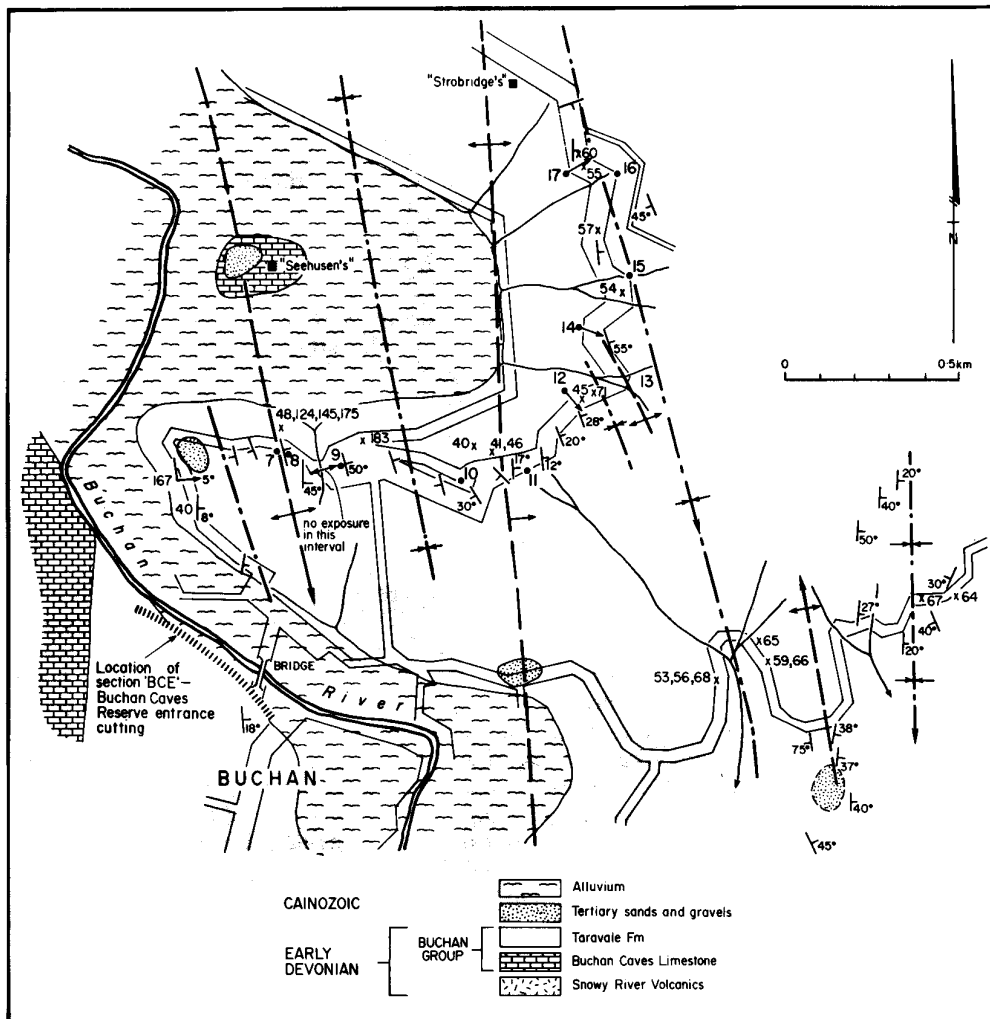
sedimentation between Bindi (c. 3,000 m of Taravale Formation and Shanahan Limestone—presumed to have been originally interdigitating southwards with the Taravale Formation—spanning from somewhere in the *perbonus* Zone to somewhere low in the *serotinus* Zone), Buchan (c. 700 m from somewhere presumed low in the *dehiscens* Zone to somewhere presumed low in the *serotinus* Zone), and The Basin where beds correlative with the *dehiscens* Zone aggregate a mere 60 m or so before being overlain by beds yielding *Polygnathus perbonus*.

In the Buchan area, the Taravale Formation grades northwards into the Murrindal Limestone. Teichert (in Teichert and Talent 1958) divided this unit of up to 250 m of limestones and subordinate mudstones into two members: well-bedded limestones were referred to as the McLarty Member and massive limestones, interpreted as being biohermal, were termed the Rocky Camp Member. The tongue of Taravale Formation lying between the Murrindal Limestone and the Buchan Caves Limestone to the north was designated the Pyramids Mudstone Member of the Taravale Formation. Some reservations have been voiced (Philip 1966) as to the utility of dividing the Murrindal Limestone into members in this way, but no lithofacies analysis subsequent to Teichert's work has yet been published. The Murrindal Limestone (up to 230 m in thickness) embraces a rich array of carbonate lithologies indicative of a wide range of environments: micrites to calcarenites and very minor rudites, algal limestones (including a very prominent biostromal marker horizon about 2 m thick, packed with dasycladacean algae, outcropping about 75 m above the base of the formation in the Rocky Camp-McLarty Ridge area), and intercalations of mudstones, calcareous mudstones, and nodular limestones; the last are best exposed in road cuttings 0.6 km south-south-west of the now-abandoned Murrindal State School.

The Pyramids Member of the Taravale Formation outcrops poorly. The best exposures are by no means extensive and occur in road cuttings near the Murrindal State School (sections 'M' and 'P', text-figs. 2 and 5), in Dalley Creek downstream from its junction with Rocky Camp Gully (loc. Ma2, text-fig. 1), and in the gully east of 'Chisholm's' (text-fig. 5) where there are mudstones with limestone nodules and subordinate developments of flaggy or nodular argillaceous limestones. More typically, the Pyramids Member does not outcrop; areas underlain by this unit are normally represented by grassy slopes with occasional fist-sized or larger nodules bearing chonetid brachiopods (usually '*Chonetes australis* (M'Coy) or '*C. teichertii* Gill), and occasionally cephalopods.

Philip (1966) collected eight bulk samples for acid-leaching: three from the Buchan Caves Limestone, one from the Taravale Formation, and four from the Murrindal Limestone (text-fig. 1); all samples yielded conodonts. Using the information then available on northern hemisphere faunas, he concluded that the Murrindal Limestone was Early Emsian and the Buchan Caves Limestone youngest Siegenian.

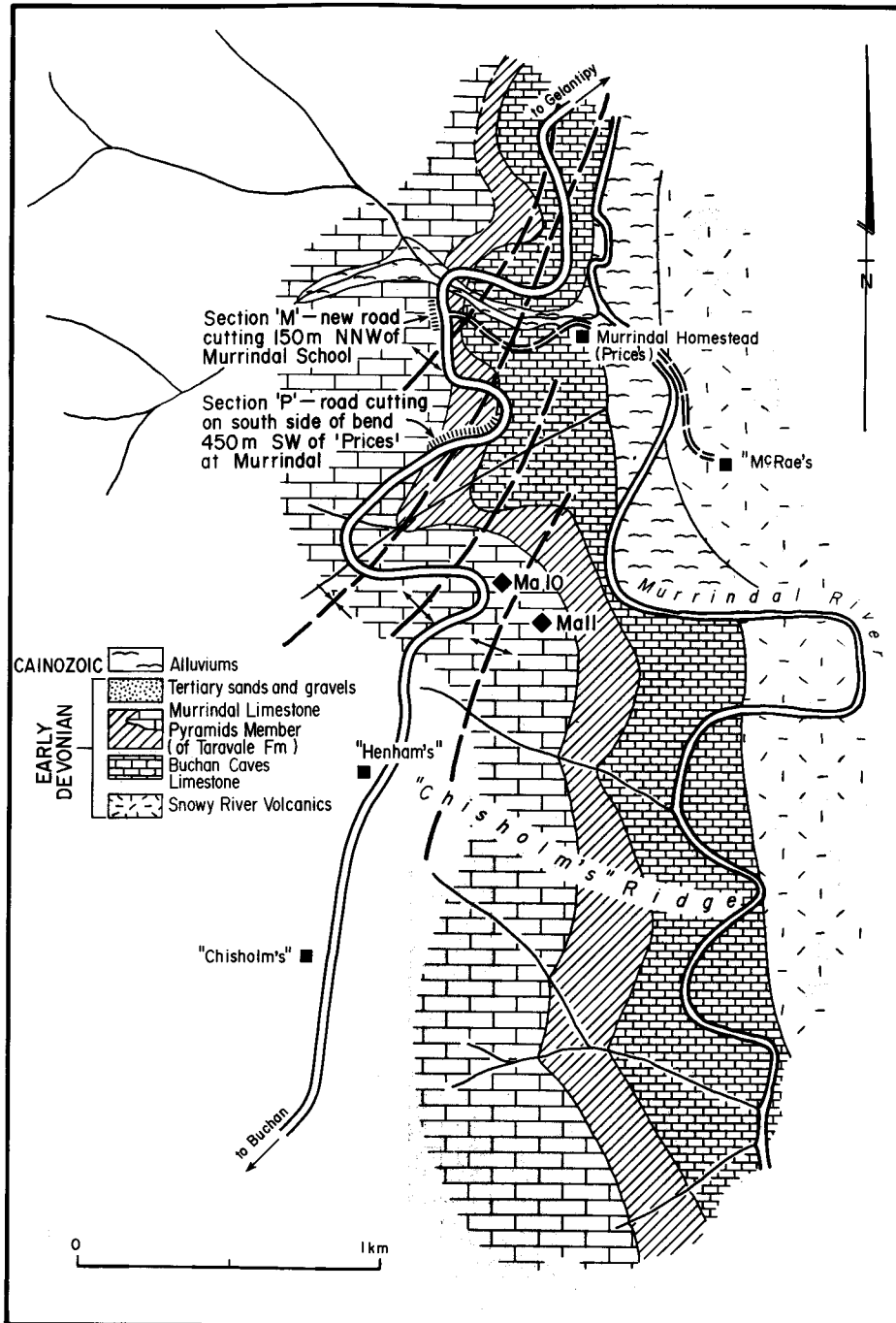
Because of its combination of ammonoids and dacroconarids and the assumed considerable time-equivalence of strata involved, the initial focus of the present study was the Taravale Formation. A cutting on the disused road to the old Tara homestead (top of Buchan Caves Limestone and lower beds of Taravale Formation in continuous outcrop), another at the entrance to the Buchan Caves Reserve (text-figs. 1 and 2) (type localities for *Teicherticeras desideratum* (Teichert) and *Talenticeras talenti* Erben), and, above all, a near-continuous suite of outcrops in road cuttings for 3.5 km along the Gelantipy Road north of Buchan (text-fig. 4) provided the basis for investigations which involved bed-by-bed collecting for conodonts, dacroconarids, and associated macrofauna. This work was supplemented by sampling of the basal beds of the Pyramids Member of the Taravale Formation at Murrindal near the abandoned Murrindal State School, and beds outcropping on the Buchan-Orbost road that are considered on structural grounds to be slightly higher stratigraphically than the highest beds exposed on the Gelantipy Road. There are few outcrops of the Taravale Formation away from road cuttings, so little additional sampling was carried out in the Buchan-Murrindal area. A previously unsuspected area of Taravale Formation was discovered in the core of the main syncline at The Basin, 12 km north-east of Buchan; poorly outcropping nodule horizons yielded excellently preserved conodonts. To supplement information gained from these sections, spot-samples were taken from key areas (text-fig. 1), for example at the top of the Murrindal Limestone along the access road to the old Rocky Camp (Commonwealth) Quarry,



TEXT-FIG. 4. Location of collecting sequence in Taravale Formation in road cutting along the Buchan-Gelantipy Road, eastern Victoria.

above and below the Murrindal Limestone on McLarty's Ridge, in and above McLarty's Landslip, and in the road cuttings about Teichert's localities 65 and 66 on the East Buchan Road.

The Taravale Formation at Bindi (text-fig. 3), 50 km north-north-west of Buchan appears to be homoclinal and, as previously mentioned, much thicker (*c.* 3,000 m) than at Buchan. This great thickness is puzzling. Exposures are admittedly very poor over most of Bindi, but among the scatter of outcrops along Old Paddock Creek no reversed facings were found, so isoclinal folding is not the answer. It is accordingly concluded that the sequence of Taravale Formation at Bindi is much thicker than at Buchan or The Basin. Some thirty-five spot-samples from restricted areas of outcrop (text-fig. 3) previously collected for macrofossils were sampled and some re-sampled; though not many of these yielded conodonts, none of the results (Table 4) suggests any reversal of sequence.



TEXT-FIG. 5. Location of stratigraphic sections and localities sampled at Murrindal, eastern Victoria.

Limestones in an appreciable section of what appear to be the highest beds outcropping along a rough road on the left flank of Limestone Creek (also known as Dry Gully) were sampled.

It has been suggested (Talent 1965, 1967) that the highest beds of the Buchan Caves Limestone at Bindi extend to horizons substantially younger than those at Buchan; to test this, a stratigraphic section was measured through these beds in the vicinity of McAdam's and Bonanza Gullies (text-fig. 3). An additional section was measured through the Shanahan Limestone, a previously overlooked but substantial (thickness *c.* 210 m) and well-exposed sliver of limestones, resembling the Murrindal Limestone of the Buchan-Murrindal area, outcropping adjacent to the Indi Fault north of Bindi. The conodont evidence adduced here, that it is correlative with the *perbonus* Zone, suggests that configurationally it was very similar to the Murrindal Limestone: interfingering southwards with the Taravale Formation (spanning from somewhere in the *perbonus* Zone into the *serotinus* Zone).

The Taravale Formation typically consists of impure limestone nodules and irregular, discontinuous limestone beds in mudstones. Because of the muddy nature of the limestone sampled, the conodont yield was only moderate (Tables 1-6) and the leaching process slow but, using generally large samples (*c.* 8-10 kg), sufficient yields have been obtained, in my opinion, to verify the proposed polygnathid lineages (text-fig. 6). The samples from the Buchan and Bindi areas yielded 5,131 conodonts from 1,581 kg of limestone, equivalent to 3.2 conodonts per kg.

EARLY DEVONIAN POLYGNATHID LINEAGES FROM EASTERN AUSTRALIA

The phylogeny of Early Devonian polygnathid conodonts has been greatly clarified since Klapper and Johnson (1975) illustrated, with faunas from the Early Devonian at Lone Mountain, Nevada, the evolutionary sequence from *Polygnathus dehiscens* to *P. laticostatus* and from *P. aff. P. perbonus* to *P. serotinus*, the latter sequence being characterized by an interval of stratigraphic overlap of *P. inversus* and *P. serotinus*.

Comparison of the Nevada and other Early Devonian faunas from the northern hemisphere (e.g. Carls and Gandl 1969; Klapper 1969; Uyeno in McGregor and Uyeno 1972; Perry *et al.* 1974; Al-Rawi 1977; Chatterton 1979; Lane and Ormiston 1979; and Uyeno and Klapper 1980) with those already known from Australia (e.g. Philip 1966; Philip and Jackson 1967; Telford 1975; Fordham 1976; Pickett 1978) indicates that the southern hemisphere polygnathid lineages for this period of time differ: The *P. gronbergi*-*P. laticostatus* lineage is not clearly present in Australian faunas and, moreover, the *P. aff. P. perbonus* lineage (herein described as the *P. nothoperbonus* lineage) appears to vary in detail in Australia compared with the same lineage in the northern hemisphere. From *P. dehiscens* Philip and Jackson, two lineages were identified by Klapper and Johnson (1975):

- (1) *P. gronbergi* Klapper and Johnson → *P. laticostatus* Klapper and Johnson;
- (2) *P. aff. P. perbonus* → *P. inversus* Klapper and Johnson → *P. serotinus* Telford.

Unlike the succession at Lone Mountain, Nevada, the Buchan and Bindi sequences in south-eastern Australia do not contain the *dehiscens* → *gronbergi* → *laticostatus* lineage but it appears that two different paths of evolution from *P. dehiscens* are represented:

- (1) a lineage very similar to the second lineage of Klapper and Johnson (1975);
- (2) a lineage not previously described.

Near the base of the sections measured at Buchan and at Bindi (text-figs. 1-3), the first polygnathid element in the sequence is *P. dehiscens* (Tables 5 and 6). In some smaller specimens of early *P. dehiscens* (see Pl. 32, figs. 1 and 2), the adcarinal grooves are only very slightly developed and ornamentation consists typically of nodes on very short ridges, consistent with evolution from *P. pireneae* Boersma (Boersma 1974; Klapper in Ziegler 1977). No specimens definitely identified as *P. pireneae* have been found. However, two subspecies of *P. dehiscens* can be distinguished: *P. dehiscens dehiscens* with a large basal cavity forming an open, flat, or very shallow trough posteriorly and *P. dehiscens abyssus* with a deeper, V-shaped basal cavity.

TABLE 5. Distribution of Pa elements of *Polygnathus* spp. at Buchan, eastern Victoria.

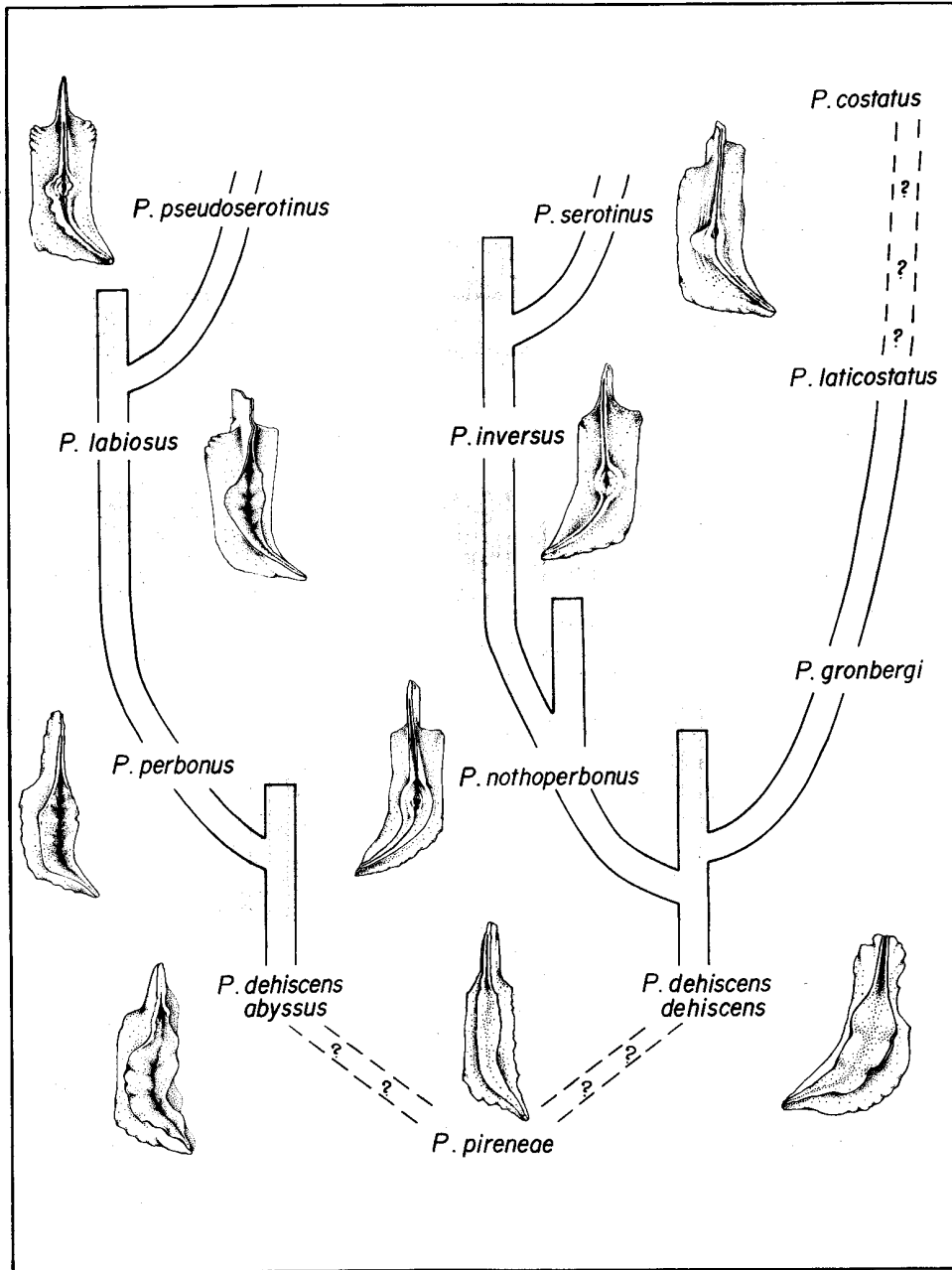
	OLD TARA ROAD CUTTING SECTION										GELANTIPY ROAD SECTION										BUCHAN CAVES ENTRANCE SECTION										GELANTIPY ROAD SECTION										EAST BUCHAN SECTION																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59
<i>P. dehiscens dehiscens</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Transitional to <i>P. nothoperbonus</i>																																																											
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<i>P. serotinus</i>																																																											
<i>P. dehiscens abyssus</i>	1	5																																																									
Transitional to <i>P. perbonus</i>	4																																																										
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Transitional to <i>P. pseudoserotinus</i>																																																											
<i>P. pseudoserotinus</i>																																																											

TABLE 6. Distribution of Pa elements of *Polygnathus* spp. at The Basin and Bindi, eastern Victoria.

	BONANZA GULLY SECTION						SALC 4 SOUTH ARM LIMSTONE 7 CK. SECTION			SLOCOMBES SECTION						SHANAHAN LIMSTONE SECTION								
	BON29-35	36-39	46-50	50-56	56-60.5	60.5-65	163-170	220-240	T3	T3	T3	Buchan Caves L/s at the Basin	SLO20	40	52	60	65	60-80	150	155	200	250	SBB	SBL
<i>P. dehiscens dehiscens</i>	1	5	3																					
Transitional to <i>P. nothoperbonus</i>		3	4																					
<i>P. nothoperbonus</i>		5	1				2															6	4	1
Transitional to <i>P. inversus</i>																								
<i>P. inversus</i>																								
Transitional to <i>P. serotinus</i>																								
<i>P. serotinus</i>																								
<i>P. dehiscens abyssus</i>	1	3	9		1	1					2	4	8	1	8									
Transitional to <i>P. perbonus</i>					1	1																		
<i>P. perbonus</i>					3	1																		
<i>P. labiosus</i>								3																
Transitional to <i>P. pseudoserotinus</i>																								
<i>P. pseudoserotinus</i>																								

are seen from *P. labiosus* to a form superficially similar to *P. serotinus*, herein described as *P. pseudoserotinus* sp. nov., where the small, subcircular, shelf-like protuberance is suspended (rather than supported by a bulge in the platform on the outer side of the pit as in *P. serotinus*), representing the vestigial lips of *P. labiosus*. The intermediate forms show development of the higher outer margin as the basal cavity 'seams up' asymmetrically leaving a lip on the outer margin of the pit. The reduction in size of the basal cavity in this lineage has resulted from the progressive 'seaming up' of the cavity (text-fig. 6).

Quo vadis polygnathids? Although the Buchan and Bindi samples have yielded no polygnathids younger than *P. serotinus*, faunas of the *serotinus* and younger zones are known from elsewhere in eastern Australia, notably from the Broken River (Telford 1975) and Timor, New South Wales (Pedder, Jackson and Ellenor 1970). The best sequences for scrutiny of *serotinus* and later zones spanning the Early Devonian–Middle Devonian boundary are to be found in the Broken River



TEXT-FIG. 6. Proposed lineages of Early Devonian *Polygnathus* in Australia; the right-hand branch is a northern hemisphere lineage.

area (Mawson *et al.* 1985), which includes the type locality for *P. serotinus* (Telford 1975). From examination of Telford's original material of *P. serotinus* and topotype material (Mawson *et al.* 1985), the lip adjacent to the basal pit is buttressed by shell material rather than being a free, ledge-like lip. Localities yielding *P. serotinus* also contain specimens intermediate between *P. labiosus* and *P. pseudoserotinus*.

Weddige and Ziegler (1979, fig. 1, p. 160), using material from the Rhenish Slate Mountains, proposed a 'tree' with three main branches to depict the evolution of polygnathids. All three branches, the *linguiformis* branch, the *robusticostatus* branch, and the *costatus* branch, are represented in Australian faunas, including the Broken River faunas of north Queensland (Telford 1975; Mawson *et al.* 1985). As Australian faunas do not contain the *dehiscens-gronbergi-laticostatus* lineage (see also Klapper and Johnson 1980), forms ancestral to the *costatus* main branch probably arrived in Australia towards the end of the Early Devonian when seaways were becoming less restricted (Charpentier 1984) and there was an increase in cosmopolitanism of conodont faunas (Telford 1972, 1979; Klapper and Johnson 1980; Charpentier 1984).

DACRYOCONARIDS OF THE TARAVALÉ FORMATION

Initially it was envisaged that this study would include a parallel zonation of dacryoconarids and conodonts of the Taravale Formation at Buchan. Although over two hundred horizons in the Gelantipy Road section and a further forty in the entrance to the Buchan Caves Road section have been sampled, washed, and picked and many dozens of thin sections prepared, the work has been hindered by the lack of complete specimens; most of the thousands of specimens picked from the samples lack the initial chamber, making identification, in many instances, impossible. Thin sectioning of the specimens contained within limestone nodules has not gone far towards solving the problem as the crystallinity of preservation of most material has, at high magnification, obscured structural details.

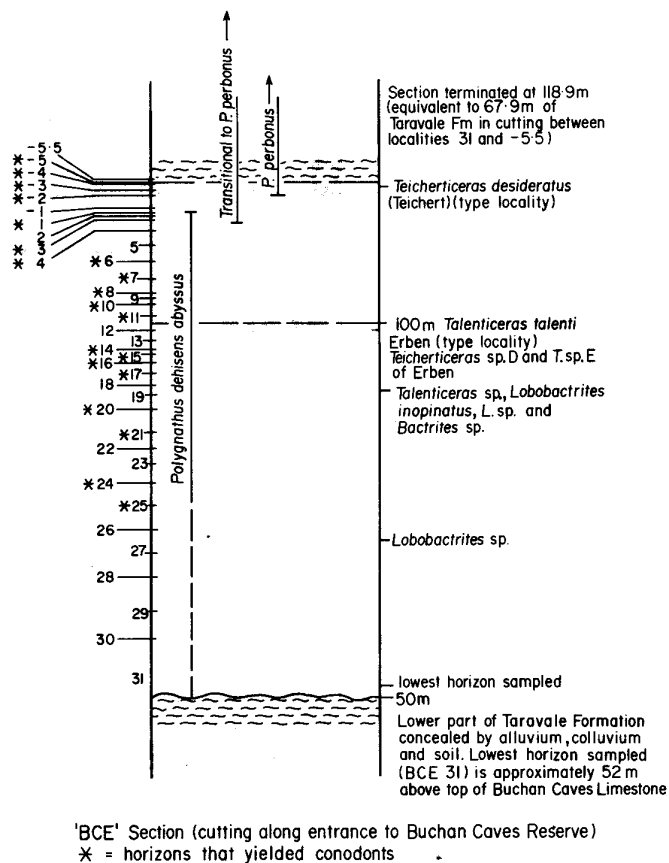
Some species of dacryoconarids from the Taravale Formation are new, and some similar to, if not the same as, undescribed species from La Grange, France, presently being studied by Professor Hubert Lardeux (pers. comm.). Work on the identification and zonation of the dacryoconarids will continue with a view to calibrating the conodont and dacryoconarid successions for the *dehiscens* to *serotinus* zones.

AGE OF AMMONOIDS PREVIOUSLY DESCRIBED FROM THE TARAVALÉ FORMATION

One of the objectives of the present investigation was to provide a firmer basis for dating the Taravale Formation goniatites and bactritids. When these were first recorded from Buchan by Teichert (1948), the association of *Gyroceratites* and *Lobobactrites* was taken to be indicative of an early Middle Devonian age. At that time there were very few records of ammonoids from horizons that were of indubitable late Early Devonian age; all of these, mostly poorly known and, in terms of modern stratigraphic imperatives, imprecisely located stratigraphically, were from Germany or Bohemia. The fauna was subsequently expanded by Erben (1964, 1965) who concluded that the Buchan ammonoids must be of late Emsian age; this was the view advocated by Chlupač (1976) in a review of the oldest goniatite faunas and their stratigraphic significance. Subsequently, House (1979) placed the two genera based on type species from the Taravale Formation, *Teicherticeras* and *Talenticeras*, doubtfully within the early but not earliest Emsian.

Conodont studies have vastly improved correlations of ammonoid-bearing units and time-ranges for many early ammonoids, thus providing a framework within which their early evolution can be more precisely understood. Among such studies is that of the Nandan facies of South China by Xian *et al.* (1980) who combined biostratigraphic studies of conodonts, dacryoconarids, ammonoids, trilobites, and tabulate corals. Interestingly, they documented the co-occurrence of *Anetoceras* and

Erbenoceras with *Polygnathus perbonus* and *Nowakia barrandei* Bouček and Prantl, but not with *P. dehiscentis*, though with the range of *Anetoceras* possibly extending down into an interval wherein *P. dehiscentis* may overlap with *P. perbonus*. The situation seems to be similar in the Bohemian where the earliest goniatites appear at the top of the Zlichov Limestone, again associated with *N. barrandei* and with *P. perbonus* or *P. ?perbonus* according to Chlupač *et al.* (1977). In a review of the Devonian biostratigraphy of Guangxi, Bai *et al.* (1980, p. 5, fig. 4) showed that the range of *Anetoceras* coincides with that of *P. dehiscentis* for approximately 8 m in the Chongzhou Formation. Bultynck and Hollard (1980, pp. 13-14, figs. 2 and 3) showed *A. advolvens* occurring with *P. gronbergi* (their Fauna III) and with *Icriodus bilatericrescens* (their Fauna II). The latter may be a pre-gronbergi-perbonus Zone ammonoid occurrence, but in an assemblage lacking polygnathids it is difficult to determine if Fauna II belongs to the upper *dehiscentis* Zone or to the lower *gronbergi* Zone because *I. bilatericrescens* spans both zones. There can be little doubt that the type localities for the oldest goniatites at Buchan occur within the *dehiscentis* Zone (text-fig. 7), within the upper part of the zone, in early rather than late Zlichovian.



TEXT-FIG. 7. Detail of Buchan Caves Entrance (BCE) section showing stratigraphic position of goniatites, bactritids, and polygnathid conodonts.

The conodont correlations for the various goniatites and bactritids from the Taravale Formation can be summarized as follows:

1. The type locality for *Talenticeras talenti* Erben and the horizons of *Teicherticeras* n. sp. D and n. sp. E of Erben (1965) fall well within the *dehiscens* Zone (text-fig. 7, Table 3).

2. The type locality of *Teicherticeras desideratum* (Teichert) occurs low in the *perbonus* Zone (text-fig. 7, Tables 3 and 5).

3. The type locality for *Lobobactrites inopinatus* Teichert (his loc. C, 1948), from beds in the centre of the anticline from which the Gelantipy Road stratigraphic section was commenced (text-fig. 7, Tables 1 and 5), is from the *dehiscens* Zone. The paratype, from Teichert's locality B, is not precisely located (confirmatory conodont evidence is not available), but is surely within the *perbonus* Zone. The best estimate of this horizon, taking into account the outcrops around the first hairpin bend on the Gelantipy Road north of Buchan, is that it is approximately equivalent to the sampled horizons 8.8.4.2 or 8.8.4.3 on the Gelantipy Road section, i.e. a few metres above the horizon of the holotype of *T. desideratum*. Teichert (1948) believed these two horizons to be the same; this may well be the case.

4. The localities for the holotype and paratypes of *Bactrites howitti* Teichert (locs. D and E of Teichert 1948) were not sampled for conodonts but were considered by Teichert to be approximately equivalent stratigraphically. Their position, about 90 m above the top of the Buchan Caves Limestone, suggests a horizon about the same as that of the type locality for *Talenticeras talenti* in the entrance cutting to the Buchan Caves Reserve, i.e. within the *dehiscens* Zone; but the suggestion of decreasing thickness of section north-eastward towards The Basin may indicate that these horizons are slightly younger, i.e. within the lower part of the *perbonus* Zone. Several as yet unidentified specimens of *Bactrites*, seemingly belonging to this species, have been collected from *dehiscens* horizons in the entrance cutting to the Buchan Caves Reserve.

In summary, the ammonoid faunas of the Taravale Formation are restricted to the *dehiscens* and *perbonus* zones, with at least three species of goniatites and one (possibly two) species of bactritids occurring in the *dehiscens* Zone, thus making them among the oldest firmly dated ammonoids in the world.

CONCLUSIONS

Basic data for evaluation of four of the Australian Early Devonian (*dehiscens* to *serotinus* zones) conodont faunas has been presented. There are, admittedly, a number of elements (some new) that at this stage appear to be endemic. Some endemism in Australian faunas has been pointed out previously (Telford 1972, 1979; Fåhraeus 1976; Klapper and Johnson 1980; Charpentier 1984), but its degree in Australian conodont faunas for the late Early Devonian is not sufficient to confound international correlation. The apparent extensions of range of some previously described species produce no profound discrepancies that would call into question significant parts of the present zonal scheme for this part of the Early Devonian. The present scheme has evolved rapidly, particularly over the past decade, and has been thoroughly reviewed and reworked recently (Klapper and Ziegler 1979; Klapper and Johnson 1980; Ziegler and Klapper 1985). The increased data presented here for at least four of the zones has reinforced the applicability of this zonal scheme to Australian faunas.

Dehiscens Zone

The key species of this zone, *Polygnathus dehiscens*, is found at the base of the Taravale Formation at Buchan (text-figs. 1 and 2; OTRC section) and high in the Buchan Caves Limestone at Bindi (text-fig. 3, BON section), confirming the diachronous nature of the top of the Buchan Caves Limestone between Buchan and Bindi. With *P. dehiscens dehiscens* occurs *P. d. abyssus* subsp. nov. (whose range is similar to that of *P. d. dehiscens*); *P. d. dehiscens* extends upwards to 105.6 m above the top of the Buchan Caves Limestone in the Taravale Formation at Buchan, and *P. d. abyssus* extends to 116 m above the base of the same section (Table 5). The type locality for *Talenticeras talenti* Erben lies between beds BCE12 and BCE11, 100 m above the base of the Buchan Caves

Limestone in the section at the entrance to the Buchan Caves, within the *dehiscens* Zone. Sixteen metres higher in the section, within bed BCE3, the type locality for *Teicherticeras desideratus* (Teichert) falls low in the *perbonus* Zone.

Elsewhere in Australia, conodont faunas of the *dehiscens* Zone have been documented from New South Wales at Ravine (Flood 1969) and Wee Jasper (Philip and Jackson 1967; Pedder, Jackson and Philip 1970).

Perbonus Zone

As the differences in the ranges of *P. perbonus* (from 116 m to 271 m above the base of the Buchan Caves Limestone) and *P. nothoperbonus* (from 119 m to 272 m) are not great in the Gelantipy Road section at Buchan (Table 5), they are taken to be approximate stratigraphical equivalents. Apart from at Buchan, Bindi, and The Basin, the *perbonus* Zone is known to occur in Australia at Wee Jasper (Philip and Jackson 1967; Pedder, Jackson and Philip 1970). Pickett (1980) reported a single specimen of *P. perbonus* from Cobar; the specimens referred to as '*P. perbonus* late form' by Pickett (1978) from Mount Frome, are probably *P. perbonus sensu stricto*.

Inversus Zone

P. inversus and *P. labiosus* seem to have broadly the same stratigraphic range, but *P. labiosus* arises 29 m lower in the Taravale Formation along the Gelantipy Road. *P. labiosus* overlaps considerably in range with *P. perbonus*, but in the Gelantipy Road section there is a gap of 3 m between the highest occurrence of *P. perbonus* and the first occurrence of *P. inversus*. Elsewhere in Australia, faunas of *inversus* zone age occur in Queensland at the Broken River (Telford 1975) and in the Nogoia anticline, Springsure, Queensland (Fordham 1976).

Serotinus Zone

P. pseudoserotinus, assumed to be broadly equivalent stratigraphically to *P. serotinus*, first appears in the Gelantipy Road section 419 m above the top of the Buchan Caves Limestone; the entry of *P. serotinus* is some 34 m higher (Table 5). At Bindi, in the SALC (south arm of Limestone Creek) section, both forms occur (Table 6). It is assumed that these occurrences represent very early forms of *P. serotinus* as they occur in sequence with or after *P. inversus*. Older forms of *P. serotinus* occur in the Jessey Springs section at the Broken River (Mawson *et al.* 1985); in this section, the upper boundary of the *serotinus* Zone is placed at last occurrence of *Pandorinellina exigua exigua* (Mawson *et al.* 1985). Key species of this zone have been reported from Wee Jasper, New South Wales (Philip and Jackson 1967; Pedder, Jackson and Philip 1970), Mount Frome, New South Wales (Pickett 1978), and the Nogoia anticline, Springsure, Queensland (Fordham 1976).

SYSTEMATIC PALAEOLOGY

As the purpose of this study was primarily biostratigraphic, and because the Pa elements of multielement assemblages show most obvious changes through time, only the Pa elements of the multi-element species of *Polygnathus*, *Oulodus*, *Pandorinellina*, and *Ozarkodina* found at Buchan and Bindi are described in detail. Other elements are illustrated but not discussed at length. Non-platform elements have not been differentiated for each of the polygnathid species. No multi-element reconstructions have been attempted for coniform elements that have been illustrated (Pl. 41) but not described. Type and figured specimens are housed in the collections of the National Museum of Victoria, Melbourne (NMVP) and the Australian Museum, Sydney (AMF). Precise horizon and locality data for each sample number can be obtained by reference to text-figs. 1-5 and tables 1-6.

Family HIBBARDELLIDAE Müller, 1956 Genus OULODUS Branson and Mehl, 1933

- 1933 *Oulodus* Branson and Mehl, p. 116.
1935a *Gyrognathus* Stauffer, p. 144.
1935b *Barbarodina* Stauffer, pp. 602-603.

- 1969 *Ligonodina* Bassler; Jeppsson, pp. 20–21.
 1971 *Delotaxis* Klapper and Philip, p. 446.

Type species. *Oulodus serratus* (Stauffer, 1930).

Remarks. For discussion of the genus and variation within it, see Mawson (1986).

Oulodus murrindalensis (Philip, 1966)

Plate 31, figs. 1–9

- 1966 *Lonchodina* n. sp. Philip, p. 446, pl. 3, fig. 24 (*non* figs. 19 and 20) [Pa element].
 1966 *Lonchodina murrindalensis* n. sp. Philip, p. 446, pl. 4, figs. 9–14 [Pb element].
 1966 *Plectospathodus extensus lacertus* n. subsp. Philip, p. 448, pl. 1, figs. 25–28 [M element].
 1966 *Trichonodella* sp. cf. *T. inconstans* Walliser; Philip, p. 451, pl. 4, figs. 24 and 25 [Sa element].
 1966 *Hindeodella equidentata* Rhodes; Philip, p. 445, pl. 3, fig. 1 [Sc element].

Holotype. Specimen 8850/32 (Philip 1966, pl. 4, figs. 9, 10, 12) from the Murrindal Limestone (Loc. 6 of Philip 1966, text-fig. 1; see also text-fig. 1 herein) of Buchan, Victoria.

Diagnosis. A species of *Oulodus* in which all elements are characterized by the irregularity in size and arrangement of denticles, and the deeply excavated basal cavity beneath each element.

Material. Six specimens of the Pa element from four localities; seventy-three non-platform elements from twenty-two localities (Tables 1–4).

Discussion. Except for the Sb element, all elements of *O. murrindalensis* were figured by Philip (1966) in his study of the conodont faunas from the Buchan Group. The Sb element is digyrate ('lonchodiniform') and, like the Sa element (alate—'trichonodelliform') and the Sc elements (bipennate—'ligonodiniform') of the symmetry transition series, has irregularly spaced denticles of varying sizes, some discrete and some tending to be fused at their bases. Specimens of *O. murrindalensis* collected by Philip (1966) were confined to the *perbonus* Zone. This study shows the highest occurrence of *O. murrindalensis* as bed 8.12 in the Gelantipy Road section within the *perbonus* Zone. The first occurrence is in bed OTRC 2, low in the Taravale Formation at Buchan, and in sample BON 25–27.5, high in the Buchan Caves Limestone at Bindi, confirming its presence also in the *dehiscens* Zone.

The irregularity of denticulation in *O. murrindalensis* clearly separates it from older species of *Oulodus* described from Windellama, New South Wales (Mawson 1986).

Family POLYGNATHIDAE Bassler, 1925

Genus POLYGNATHUS Hinde, 1879

Type species. *Polygnathus dubius* Hinde, 1879.

Discussion. See Klapper in Ziegler (1973) for discussion of the genus. Pa elements of *P. dehiscens*, *P. d. abyssus*, *P. perbonus*, *P. nothoperbonus*, *P. inversus*, *P. labiosus*, *P. serotinus*, and *P. pseudoserotinus* are described below in full. The non-platform elements (Klapper and Philip 1971; Klapper in Ziegler 1973) have been described previously (see Philip 1966) and are illustrated herein (Pl. 36, figs. 11–18). As the majority of conodonts for this study were recovered from the nodular limestone within the sequence of mudstones, shales, and impure limestones of the Taravale Formation at Buchan and Bindi, it is not surprising that the numbers of specimens, especially the less robust non-platform elements, are relatively low. It is surprising, however, that only seven specimens of the Sa (alate—'diplodellan'-type) element of the polygnathid apparatuses have been recovered from the 325 samples that yielded conodonts for this study. Philip (1966) recorded the presence of the Sa element, '*Roundya perbona*' from the Murrindal Limestone but not from the Buchan Caves Limestone at Buchan, negative evidence consistent with a pre-*dehiscens* Zone age for the faunas of the Buchan Caves Limestone at Buchan. As discussed earlier, the uppermost Buchan Caves Limestone at Bindi, containing both *P. dehiscens* and *P. perbonus*, is younger than the top of the Buchan

Caves Limestone at Buchan. From both high and low in the sections at Wee Jasper, New South Wales, rare occurrences of the Sa element, '*Hibbardella perbona*' have been reported (Pedder, Jackson and Philip 1970). Altogether 711 polygnathid Pa elements that can be speciated with certainty from ninety-eight localities (Tables 5 and 6), a further forty-three Pa elements that cannot be assigned with certainty because of preservation, juvenile forms, etc., and 459 non-platform elements from 105 localities (Tables 1-4) have been recovered from Buchan and Bindi localities.

Polygnathus dehiscens Philip and Jackson, 1967

Amended diagnosis. Pa elements have a large basal cavity occupying most of platform except for crimp. Cavity is V-shaped or flat or in form of extremely shallow trough at posterior end.

Discussion. This study shows that the profile of the basal cavity of *P. dehiscens* varies from flat to distinctly V-shaped, and on this basis two subspecies are distinguished: the nominate subspecies and *P. dehiscens abyssus* n. subsp.

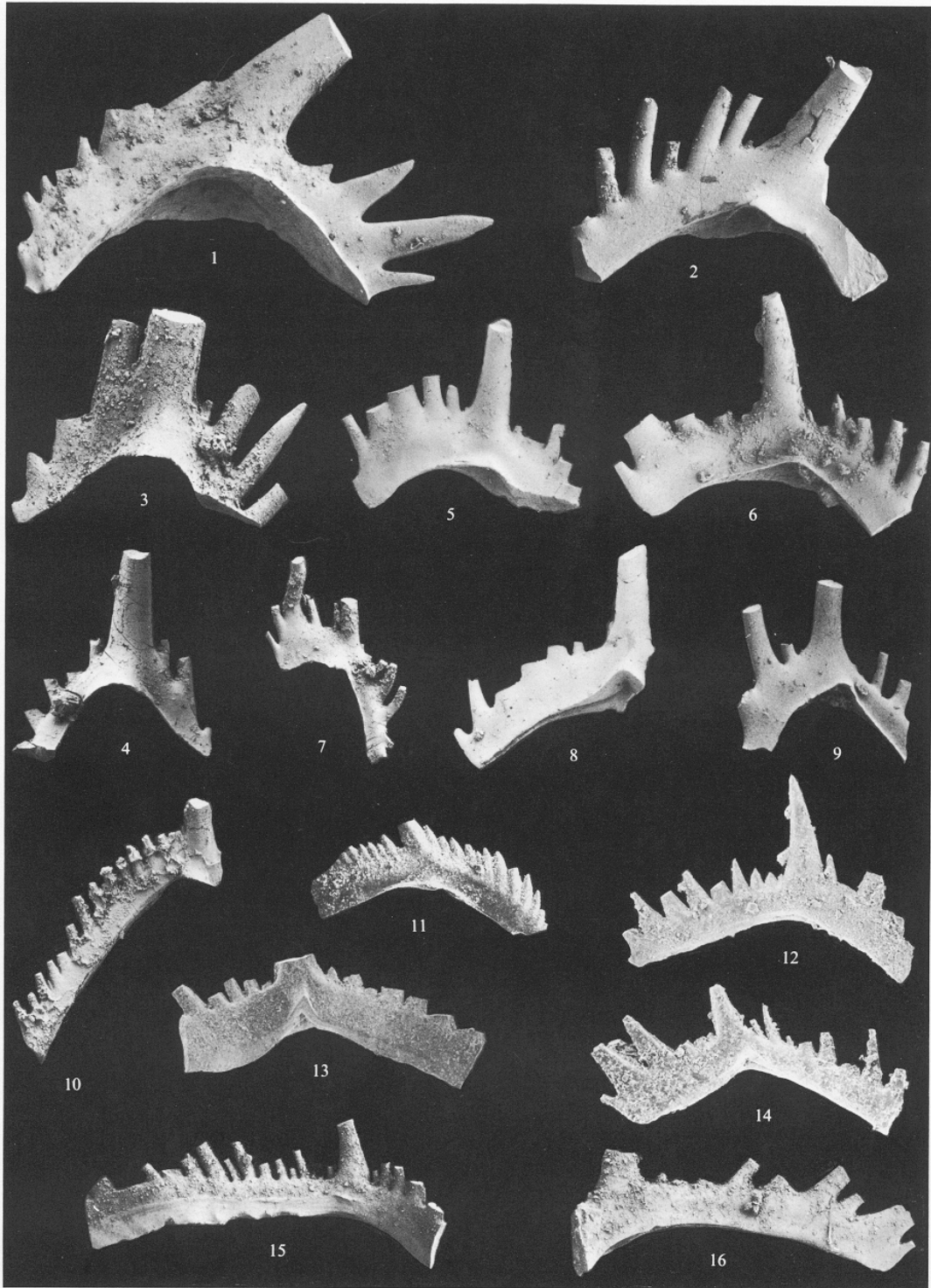
Polygnathus dehiscens dehiscens Philip and Jackson, 1967

Plate 32, figs. 1-10; Plate 36, fig. 6

- 1967 *Polygnathus linguiformis linguiformis* Hinde; Adrichem Boogaert, p. 184, pl. 3, fig. 1.
 1967 *Polygnathus linguiformis dehiscens* n. subsp. Philip and Jackson, p. 1265, figs. 2i-k (listed incorrectly as h-j in figure caption), 3a.
 1969 *Polygnathus lenzi* n. sp. Klapper, pp. 14-15, pl. 6, figs. 9-18.
 1969 *Polygnathus webbi excavata* n. subsp. Carls and Gandl, pp. 193-195, pl. 18, figs. 9-13.
 1969 *Polygnathus linguiformis foveolata* Philip and Jackson; Carls and Gandl, p. 196, pl. 18, figs. 14-19, 22.
 1970 *Polygnathus linguiformis dehiscens* Philip and Jackson; Philip and Jackson in Pedder, Jackson and Philip, p. 216, pl. 40, figs. 18, 20.
 1971 *Polygnathus dehiscens* Philip and Jackson; Fåhraeus, pp. 677-678, pl. 77, figs. 1-12.
 1972 *Polygnathus lenzi* Klapper; Uyeno in McGregor and Uyeno, p. 14, pl. 5, figs. 10-12.
 1974 *Polygnathus dehiscens* Philip and Jackson; Klapper in Perry *et al.*, p. 1087.
 1975 *Polygnathus dehiscens* Philip and Jackson; Klapper and Johnson, pp. 72, 73, pl. 1, figs. 1-8, 13-16.
 1976 *Polygnathus dehiscens* Philip and Jackson; Lane and Ormiston, pl. 1, figs. 17-20.
 1976 *Polygnathus dehiscens* Philip and Jackson; Bultynck, pl. 11, figs. 1-15.
 1977 *Polygnathus dehiscens* Philip and Jackson; Klapper in Ziegler, pp. 447-448, *Polygnathus* pl. 8, figs. 7 and 8.
 1977 *Polygnathus dehiscens* Philip and Jackson; Savage, pl. 1, figs. 29-36.
 1978 *Polygnathus dehiscens* Philip and Jackson; Apekina and Mashkova, pl. 74, figs. 1, 9; pl. 75, figs. 1 and 2.
 1979 *Polygnathus dehiscens* Philip and Jackson; Lane and Ormiston, pl. 5, figs. 24-26, 35, 36.

EXPLANATION OF PLATE 31

- Figs. 1-9. *Oulodus murrindalensis* (Philip). Pa elements: 1, NMVP 99075, sample SLO 200, ×45. 2, NMVP 99076, sample SLO 60, ×45. Pb elements: 3, NMVP 99077, sample OTRC 2, ×60. 4, NMVP 99078, sample OTRC 2, ×60. M element: 7, NMVP 99079, sample OTRC 2, ×45. Sa elements: 8, NMVP 99080, sample SLO 130, ×45; 9, NMVP 99081, sample SLO 10, ×45. Sb elements: 5, NMVP 99082, sample SLO 60; 6, NMVP 99083, sample SLO 52, ×45.
 Figs. 10-16. *Ozarkodina excavata excavata* (Branson and Mehl). Pa element: 11, NMVP 99084, sample 8.10, ×45. Pb element: 12, NMVP 99085, sample BON 25-27.5, ×45. M element: 10, NMVP 99086, sample OTRC 1, ×45. Sb elements: 13, NMVP 99087, sample BCE-4, ×45; 14, NMVP 99088, sample BON 25-27.5, ×45. Sc elements: 15, NMVP 99089, sample Forrest Motel, ×45; 16, NMVP 99090, sample SLO 60, ×45.



MAWSON, *Oulodus*, *Ozarkodina*

- 1980 *Polygnathus dehiscens* Philip and Jackson; Bultynck and Hollard, pl. 2, fig. 5.
 1980 *Polygnathus dehiscens* Philip and Jackson; Uyeno and Klapper, pl. 8.1, figs. 1-4.
 1980 *Polygnathus dehiscens* Philip and Jackson; Xiong in Xian *et al.*, pl. 22, figs. 1-4, 9-12, 19, 20.

Diagnosis. 'Representative Pa elements of *Polygnathus dehiscens dehiscens* have a large basal cavity occupying most of platform except for crimp. Cavity is flat or in form of extremely shallow trough at posterior end.' (Klapper in Ziegler 1977, p. 447.)

Material. Twenty-seven specimens from eleven localities; twenty-eight specimens transitional between *P. dehiscens dehiscens* and *P. nothoperbonus* from seventeen localities (Tables 5 and 6).

Discussion. In the material examined from Buchan and Bindi, two clusters of specimens can be distinguished: one in which specimens have a flat basal cavity, and one in which specimens have a deep V-shaped basal cavity. As a polygnathid lineage arises from each of these forms, the configuration of the basal cavity is taken as a sufficient criterion on which to base two subspecies, forms with the deeper cavity being discriminated as a new subspecies, *P. dehiscens abyssus*, described below.

Polygnathus dehiscens abyssus subsp. nov.

Plate 34, figs. 1-7; Plate 36, fig. 1

- 1969 *Polygnathus linguiformis dehiscens* Philip and Jackson; Flood, p. 9, pl. 2, figs. 1-6.
 1970 *Polygnathus linguiformis dehiscens* Philip and Jackson; Philip and Jackson in Pedder, Jackson and Philip, pl. 40, figs. 21 and 23.
 1978 *Polygnathus lenzi* Klapper; Wang and Wang, pp. 340-341, pl. 41, figs. 1-3, 7-9, 24-26.

Derivation of name. *abyssus* (Lat.) = deep, in reference to the deep, V-shaped basal cavity.

Holotype. AMF 66031 (Pl. 34, figs. 3 and 4) from the Buchan Caves Limestone, 11.4 to 12.3 m above the base of the BON section (sample BON 36-39) at Bindi, Victoria.

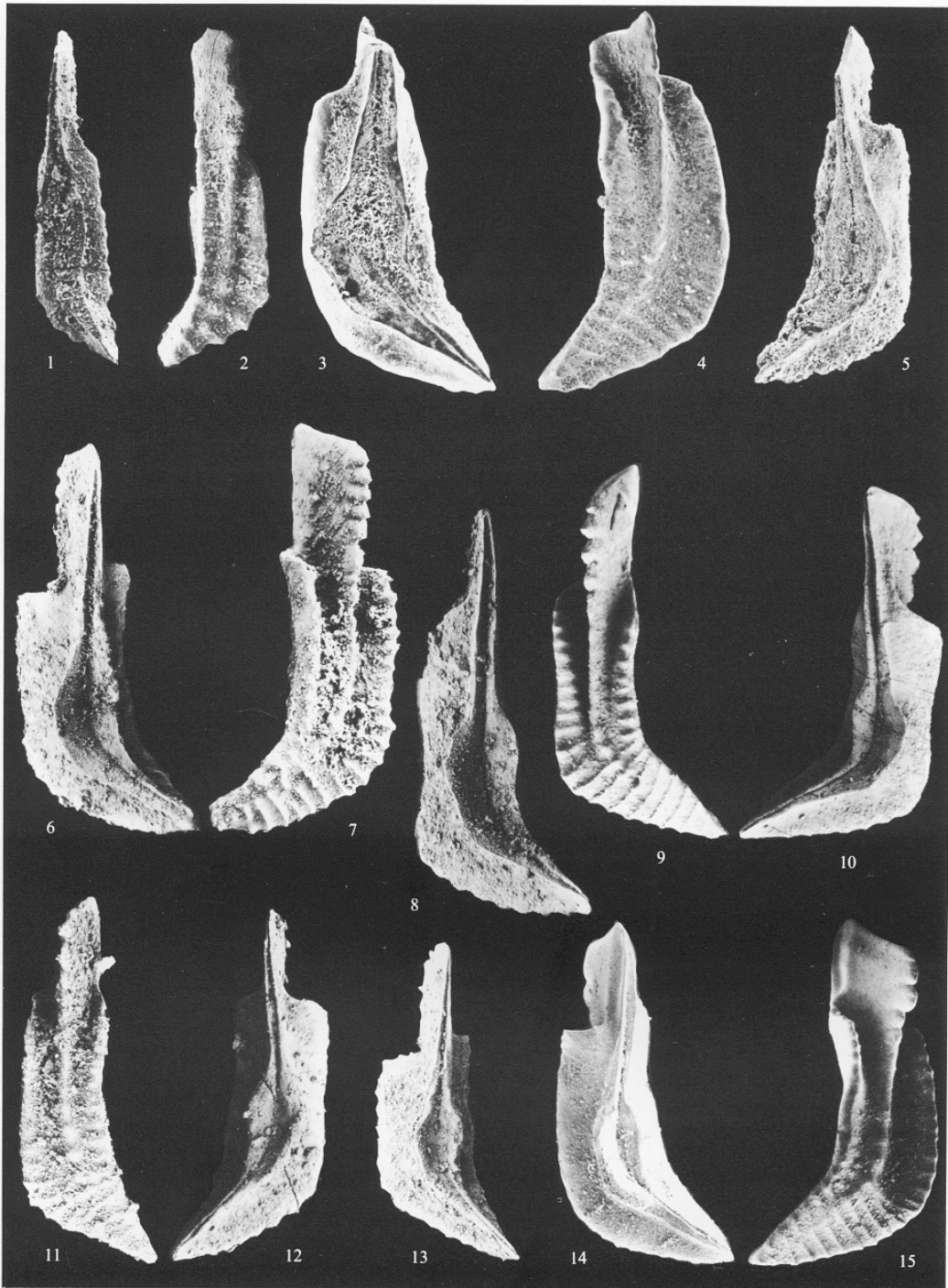
Material. Seventy-eight specimens from twenty-four localities; thirty-three specimens transitional between *P. dehiscens abyssus* and *P. perbonus* from nineteen localities (Tables 5 and 6).

Diagnosis. Pa elements have basal cavity occupying most of the platform except for the crimp with lips of the basal cavity forming a V-shaped profile in cross section.

Discussion. Specimens previously designated *P. dehiscens* from the Lick Hole Limestone at Ravine, New South Wales have a deeper basal cavity than specimens illustrated from Taemas, New South Wales; compare specimens from Ravine (Flood 1969, pl. 11, figs. 5 and 6; Philip and Jackson in Pedder, Jackson and Philip 1970, pl. 40, fig. 23) with material from the Cavan Limestone, Taemas (Ibid. pl. 40, fig. 20—aboral view of holotype). Collections made by Flood and Philip and Jackson from Ravine, and by Philip and Jackson from Taemas, were examined at Sydney University and New England University, Armidale in order to confirm the above.

EXPLANATION OF PLATE 32

- Figs. 1-10. *Polygnathus dehiscens dehiscens* Philip and Jackson. 1 and 2, lower and upper views of AMF 66007, sample 7.17, a specimen transitional between *P. pirenae* and *P. d. dehiscens*, $\times 60$. 3 and 4, lower and upper views of AMF 66008, sample OTRC 5, $\times 60$. 5, lower view of AMF 66009, sample OTRC 5, $\times 60$. 6-10, specimens transitional between *P. d. dehiscens* and *P. nothoperbonus*. 6 and 7, lower and upper views of AMF 66013, sample 8.10.2, $\times 60$; 8, lower view of AMF 66010, sample 8.9, $\times 75$; 9 and 10, upper and lower views of AMF 66011, sample Ma7, $\times 60$.
 Figs. 11-15. *P. nothoperbonus* sp. nov. 11 and 12, upper and lower views of AMF 66016, sample BON 46-50, $\times 60$. 13, lower view of AMF 66015, sample OTRC 16, $\times 60$. 14 and 15, lower and upper views of AMF 66018, sample 8.9.2, $\times 45$.



MAWSON, *Polygnathus*

Polygnathus inversus Klapper and Johnson, 1975

Plate 33, figs. 3-8; Plate 36, figs. 8 and 9

Synonymy. See Klapper and Johnson (1975, p. 73; 1980, p. 453).

Material. Seventy-eight specimens from thirteen localities; forty-one specimens transitional between *P. inversus* and *P. serotinus* from nine localities (Tables 5 and 6).

Discussion. Specimens of *P. inversus* from Buchan and Bindi show the same range of variation as the Nevada material (Klapper and Johnson 1975), from *P. inversus s. s.* to forms transitional to *P. serotinus* in which an incipient bulge surmounted by a lip is noticeable on the outer side of the basal pit, but the height of the inner and outer margin on the oral surface anterior of the angular deflection of the platform is still the same. The pit, anterior groove, and posterior keel area are bounded by narrow bands of lamellae edge (inverted area) indicative of the plane of attachment of the basal body.

Polygnathus labiosus sp. nov.

Plate 35, figs. 1-9; Plate 36, figs. 3 and 4

Derivation of name. *labiosus* (Lat.) = large-lipped, in reference to the flared nature of the flanks of the basal cavity.

Holotype. AMF 66043 (Pl. 35, figs. 5 and 6) from the Taravale Formation, 340.5 m above the base of the Gelantipy Road section (sample 15.2) at Buchan, Victoria.

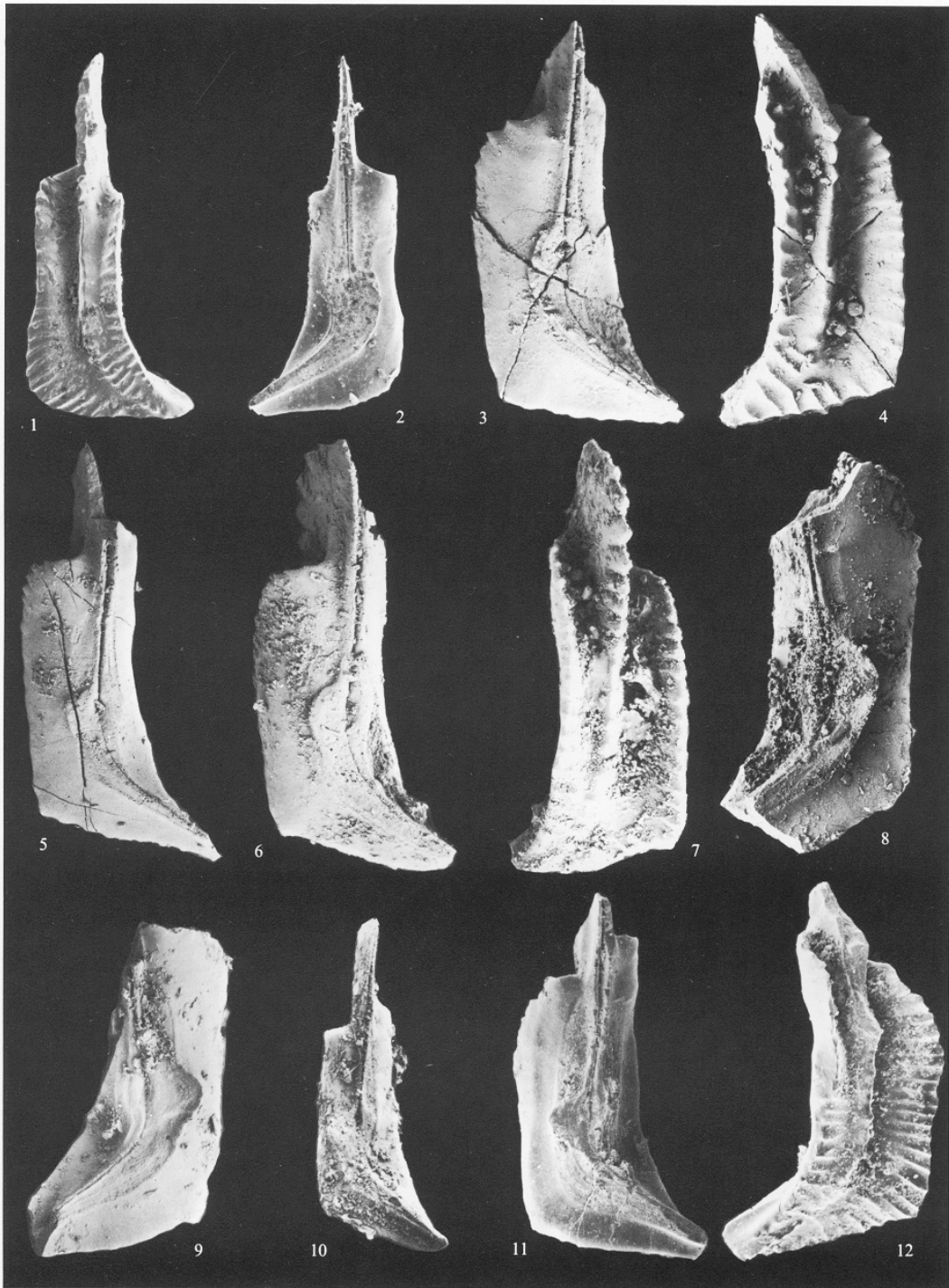
Diagnosis. Pa elements have a basal cavity with large flaring lips in the centre of the unit anterior to the inward deflection of platform. Cavity is joined posterior of lips and extends as groove anterior of lips. Transverse ridges cross posterior third of platform and can be either complete or interrupted.

Material. Forty-two specimens from twelve localities; twenty-eight specimens transitional between *P. labiosus* and *P. pseudoserotinus* from nine localities (Tables 5 and 6).

Discussion. The strong inwardly deflected posterior platform of *P. labiosus* shows the same variation in arrangement of transverse ridges as in *P. perbonus*. The parallel striations of lamellae bounding the posterior keel and cavity in *P. inversus* are not developed in *P. labiosus* as the basal body material is restricted to the interior of the lips of the basal cavity and does not extend to the posterior as in *P. inversus*. The flaring lips of *P. labiosus* are accentuated in specimens where basal body material is preserved (Pl. 35, fig. 2) but is clearly differentiated from the extended lips of *P. labiosus* by the manner of attachment, composition, and colour. There is a gradation from *P. perbonus* to *P. labiosus*, but the latter can be easily distinguished by the extended lips of the basal cavity.

EXPLANATION OF PLATE 33

- Figs. 1 and 2. *Polygnathus nothoperbonus* sp. nov. Upper and lower views of AMF 66020, sample T3, a specimen transitional between *P. nothoperbonus* and *P. inversus*, $\times 60$.
 Figs. 3-8. *P. inversus* Klapper and Johnson. 3 and 4, lower and upper views of AMF 66033, sample T3, $\times 75$. 5, lower view of AMF 66021, sample T2, $\times 75$. 6-8, specimens transitional between *P. inversus* and *P. serotinus*. 6 and 7, lower and upper views of AMF 66024, sample T3, $\times 90$; 8, lower view of AMF 66026, sample T3, $\times 90$.
 Figs. 9-12. *P. serotinus* 'delta morphotype' Telford. 9, lower view of AMF 66027, sample EB 3, $\times 75$. 10, lower view of AMF 66028, sample T3, $\times 45$. 11 and 12, lower and upper views of AMF 66029, sample T2, $\times 90$.



MAWSON, *Polygnathus*

Polygnathus nothoperbonus sp. nov.

Plate 32, figs. 11-15; Plate 33, figs. 1 and 2; Plate 36, fig. 7

- 1975 *Polygnathus* aff. *P. perbonus* (Philip); Klapper and Johnson, p. 74, pl. 2, figs. 1-10.
 1979 *Polygnathus* aff. *P. perbonus* (Philip); Lane and Ormiston, p. 62, pl. 8, figs. 26 and 27.
 1980 *Polygnathus* aff. *P. perbonus* (Philip); Uyeno and Klapper, pl. 8.1, figs. 5 and 6; pl. 8.3, figs. 11 and 12.

Derivation of name. *notho* (Gr.) = spurious, bastard, in reference to its superficial similarity to *P. perbonus*.

Holotype. University of Iowa 38018 (Klapper and Johnson 1975, pl. 2, figs. 7 and 8) from the Baratine Member of McColley Canyon Formation at Lone Mountain, Nevada (J-30-73, 172 m above formation base at loc. 1 of Klapper and Johnson 1975, fig. 2).

Diagnosis. Representative Pa elements of *P. nothoperbonus* have a medium-sized basal cavity expanded beneath the central part of the platform anterior of the sharp, inward deflection of the platform, inverted posteriorly, and extended anteriorly as a narrow groove. The cavity is flat or shallow. Transverse ridges crossing posterior third of oral platform usually interrupted. Anterior outer platform margin at about same height as inner margin.

Material. Ninety-four specimens from thirty-two localities; thirty-one specimens transitional between *P. nothoperbonus* and *P. inversus* from thirteen localities (Tables 5 and 6).

Discussion. *P. aff. P. perbonus* (*sensu* Klapper and Johnson 1975) is here given specific status for the following reasons: it can be clearly separated from *P. perbonus* by its shallow basal cavity, the lips (or lateral flanks) of which are only slightly V-shaped, and by the clear inversion of the posterior portion of the cavity; and it completes the *P. serotinus* lineage. In their original description and diagnosis of *P. perbonus*, Philip and Jackson (1967, p. 1265) made no special mention of the oral ornamentation, although Klapper and Johnson (1975), in an amended diagnosis of the form, stated that 'Transverse ridges cross [the] posterior third of the platform'. They remarked that although *P. perbonus* had not been found in Nevada, *P. aff. P. perbonus* had, the latter having a shallower basal cavity and showing some variation in the posterior transverse ridges compared with *P. perbonus* 'in which the transverse ridges are not interrupted'.

From a study of polygnathid faunas from Buchan, and especially from collections of topotype material from the Murrindal Limestone (Hyland and Mawson, in prep.), it appears that *P. perbonus* exhibits variation in arrangement of the posterior transverse ridges on its oral surface. Text-fig. 8 compares oral views of the holotype of *P. linguiformis foveolata* Philip and Jackson (= *P. perbonus*) and specimens of *P. aff. P. perbonus* from Nevada. It appears that the variation in the transverse ridges in *P. aff. P. perbonus* falls within the range of variation shown by *P. perbonus*. The difference then between *P. perbonus* and *P. aff. P. perbonus* (*sensu* Klapper and Johnson 1975) is the depth of the basal cavity, and it is on the basis of this feature that *P. nothoperbonus* sp. nov. is herein erected to include *P. aff. P. perbonus*.

From the Buchan and Bindi material it is clear that *P. nothoperbonus* is intermediate between *P. dehiscens dehiscens* and *P. inversus*, the latter showing complete inversion of the basal cavity posterior to the cavity pit. The oral ornamentation of *P. nothoperbonus* shows the same variation as *P. inversus*. The occurrence of *P. nothoperbonus* elsewhere (e.g. Sor Fiord, Ellesmere Island; see Uyeno and Klapper 1980, p. 85), entirely below the first occurrence of *P. inversus* and occurring together with *P. inversus* (e.g. Blue Fiord, Ellesmere Island; Uyeno and Klapper 1980), lends support to the reality of the *dehiscens dehiscens* → *serotinus* lineage occurring both in the northern hemisphere and in Australia.

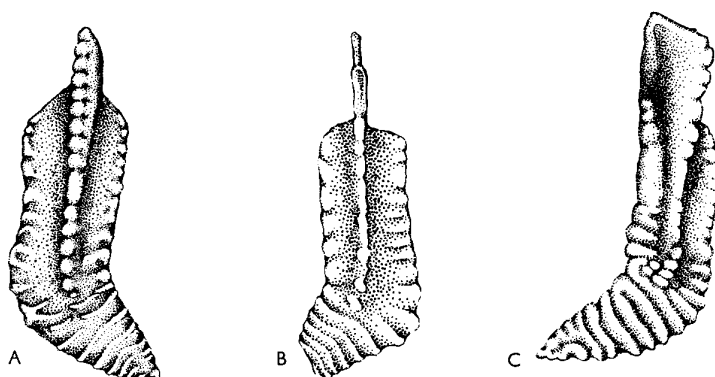
Polygnathus perbonus (Philip, 1966)

Plate 34, figs. 8-13; Plate 36, fig. 2

Synonymy. See Klapper and Johnson (1975, p. 74; 1980, p. 454).

Material. 159 specimens from thirty-three localities (Tables 5 and 6).

Discussion. *P. perbonus* is characterized by a medium-sized, V-shaped basal cavity expanded beneath the central part of the platform anterior of the sharp inward deflection of the platform and continuing posteriorly as a keel, where the basal cavity has 'seamed' together. There appear to be no parallel striations flanking the keel as basal body material is restricted to the inner portion of the cavity. Although Philip (1966, p. 448) noted that 'deflected posterior portion of platform bears transverse ridges', he illustrated (1966, pl. 2, figs. 35, 36, 39) specimens where these transverse ridges are not continuous; the specimen he illustrated as pl. 2, fig. 36 was later chosen as the holotype for *P. foveolatus* (= *P. perbonus*) by Philip and Jackson (1967). The posterior portion of the platform of *P. perbonus*, therefore, is characterized by transverse ridges which are not always continuous (see above, in discussion of oral ornamentation of *P. nothoperbonus*).



TEXT-FIG. 8. Line-drawing comparison of *Polygnathus* aff. *P. perbonus* of Klapper and Johnson (1980) and the holotype of *P. foveolata* = *P. perbonus* (Philip). A, *P. aff. P. perbonus* (Klapper and Johnson 1975, pl. 2, fig. 7). B, *P. aff. P. perbonus* (Klapper and Johnson 1975, pl. 2, fig. 1). C, *P. perbonus* (Philip 1966, pl. 2, fig. 39); note transverse lines not continuous across posterior third of platform.

Polygnathus pseudoserotinus sp. nov.

Plate 35, figs. 10-12; Plate 36, fig. 5

1979 *Polygnathus serotinus* alpha morphotype Telford; Lane and Ormiston, p. 63, pl. 7, figs. 13 and 37.

Derivation of name. *pseudo* (Gr. *pseudes*) = false, in reference to superficial similarity to *P. serotinus* Telford.

Holotype. AMF 66049 (Pl. 35, figs. 11 and 12) from the Taravale Formation, 371 m above the base of the East Buchan section (sample EB 3) at Buchan, Victoria.

Diagnosis. Pa elements have small pit located slightly anterior of inward deflection of platform. On outer side of pit, a small, subcircular, shelf-like protuberance is suspended above platform. Cavity is entirely joined posterior of pit and extends anteriorly of pit as shallow groove. Anterior outer margin is higher and wider than inner margin.

Material. Thirteen specimens from seven localities (Tables 5 and 6).

Discussion. Although there is a superficial similarity between *P. pseudoserotinus* and *P. serotinus*, the main difference lies in the nature and mode of formation of the tiny lip on the outer side of

the basal pit. In *P. pseudoserotinus* the lip is suspended above the platform rather than supported by a solid buttress of platform material, as occurs in *P. serotinus*. Plate 35, fig. 11 shows the lack of exposed edges of lamellae in the zone parallel to the keel in *P. pseudoserotinus* compared with the clear development of this zone in *P. serotinus* (Pl. 33, figs. 9 and 11). Lane (*in* Lane and Ormiston 1979) noted this difference when distinguishing two of his three morphotypes of *P. serotinus* in the Salmontrout River area, Alaska. Unfortunately, his collections did not include sufficient material to see how each evolved from *P. dehiscens*: one by inversion of the basal cavity (*sensu* Lindström 1964), the other by seaming-up of the basal cavity. It could be that specimens described by Wang (1979) as *P. declinatus*, and later assigned by Uyeno and Klapper (1980) to *P. inversus* transitional to *P. serotinus*, belong to the new species *P. pseudoserotinus*. Wang's description (1979, p. 407) fits that of *P. pseudoserotinus* but it is not clear from his pl. 1, figs. 12-22 whether the 'flange-like anterior outer margin' has resulted from inversion or 'seaming-up' of the basal cavity. His line drawing (Wang 1979, fig. 3, p. 402) appears to indicate some inversion; if this is so, his specimens should remain assigned to *P. inversus* transitional to *P. serotinus*, but if not, *P. declinatus* has priority over *P. pseudoserotinus*.

Polygnathus serotinus Telford, 1975

Discussion. Occurring in most instances with *P. inversus*, the specimens of *P. serotinus* recovered from Buchan and Bindi are the 'early' form and match very closely with Telford's type material from the Dip Creek Limestone Member of the Broken River Formation, north Queensland (Telford 1975, pl. 7, figs. 5-8). Lane (*in* Lane and Ormiston 1979, p. 63) recognized three morphotypes of *P. serotinus*: 'alpha morph' in which 'the protuberance on the lower side usually is formed as a shelf-like extension of the basal pit . . .'; 'delta morph' in which 'the protuberance is formed as a shelf-like extension of the basal pit that is supported in its entire extent by a solid shaft . . .'; and 'gamma morph' with its rounded or quadrate outline and a protuberance consisting of 'both a bulge in the platform proper and a remnant shelf-like extension of the basal pit'. Lane and Ormiston's (1979) 'alpha morph' has been described herein as *P. pseudoserotinus* as it belongs to a different lineage to *P. serotinus s. s.*, having evolved from the *dehiscens abyssus* stock by the 'seaming up', rather than inversion, of the basal cavity.

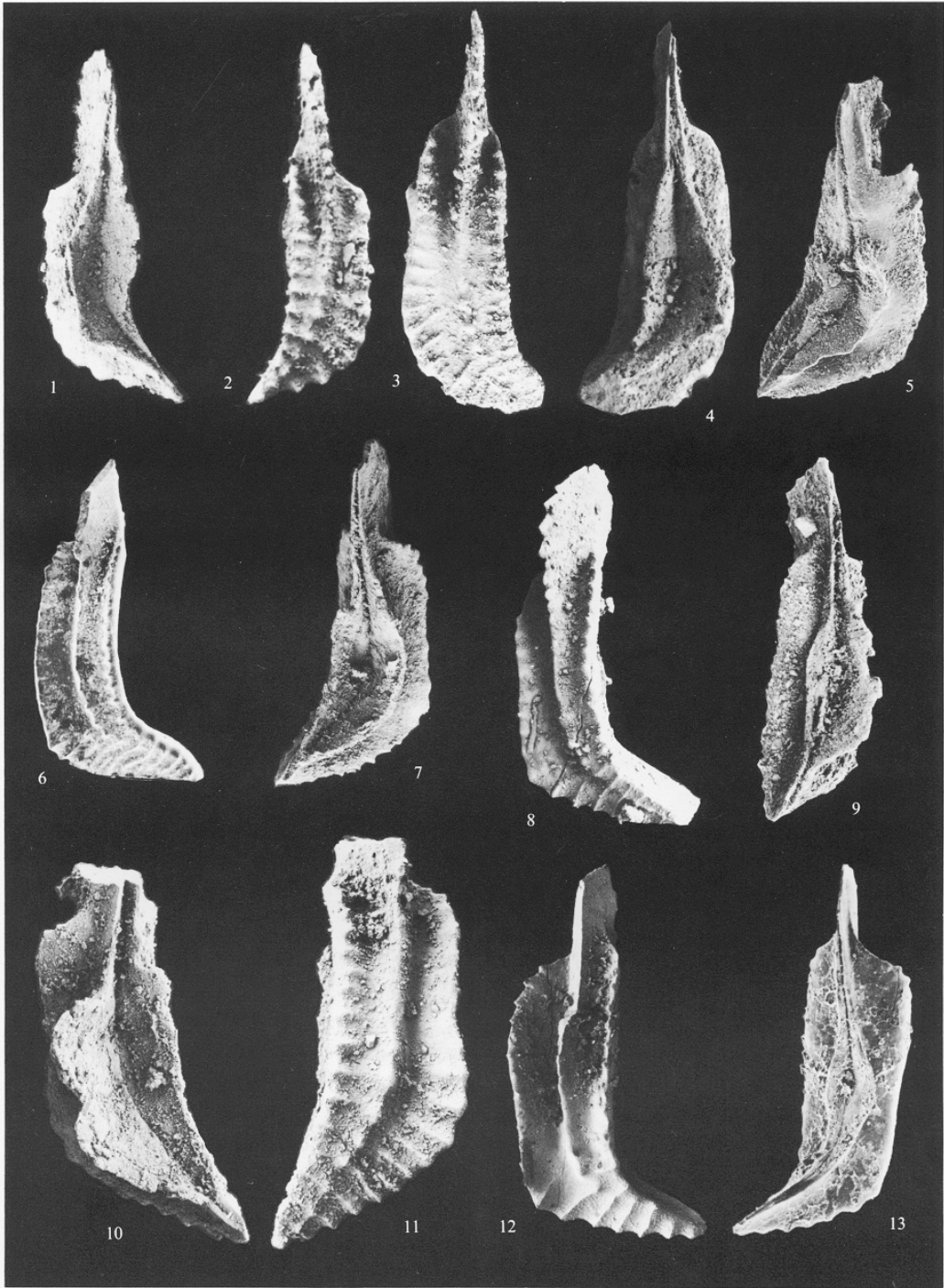
'gamma morphotype'

- 1978 *Polygnathus serotinus* Telford; Klapper *et al.*, pl. 1, figs. 9 and 10 [Pa element].
 1978 *Polygnathus serotinus* Telford; Apekina and Mashkova, pl. 77, fig. 6 (*non* figs. 1 and 2).
 1979 *Polygnathus serotinus* gamma morphotype Telford; Lane and Ormiston, p. 63, pl. 8, figs. 2, 6, 13-16, 19-22, 32, 33 [Pa elements].
 1980 *Polygnathus serotinus* Telford; Xiong, pp. 97-98, pl. 25, figs. 17-20 [Pa element].

Diagnosis. A morphotype of *P. serotinus* characterized by 'a rounded or quadrate outer margin at the point of junction of the small posterior platform and the main platform. On the lower surface, the protuberance consists of both a bulge in the platform proper and a remnant shelf-like extension of the basal pit' (Lane and Ormiston 1979).

EXPLANATION OF PLATE 34

- Figs. 1-7. *Polygnathus dehiscens abyssus* subsp. nov. 1 and 2, lower and upper views of AMF 66030, sample BON 36-39, $\times 75$. 3 and 4, upper and lower views of AMF 66031, sample BON 36-39, holotype, $\times 60$. 5, lower view of AMF 66032, sample OTRC 5, $\times 60$. 6 and 7, specimen transitional between *P. d. abyssus* and *P. perbonus*, upper and lower views of AMF 66034, sample OTRC 5, $\times 60$.
 Figs. 8-13. *P. perbonus* (Philip). 8 and 9, upper and lower views of AMF 66035, sample BON 46-50, $\times 60$. 10 and 11, lower and upper views of AMF 66036, sample BCE 20, $\times 60$. 12 and 13, upper and lower views of AMF 66037, sample 15.2, $\times 90$.



MAWSON, *Polygnathus*

Discussion. As no specimens of *P. serotinus* 'gamma morph' have been found in association with *P. serotinus* 'delta morph' in the Buchan and Bindi region, it may be that the former is found only in the upper part of the *serotinus* Zone. If this can be proved, a subdivision of the *serotinus* Zone may be possible. Until further sampling is carried out, both in Victoria and in areas such as the Broken River region, the potential for this remains uncertain. Specimens illustrated by Xiong (1980) from south China show the typical rounded posterior margin of this morphotype. In his discussion of *P. serotinus*, Xiong suggested that specimens having a rounded posterior margin should perhaps be separated from those with a straight posterior margin; he did not, however, indicate at what level this separation should be regarded—morphotype, subspecies, or species.

'delta morphotype'

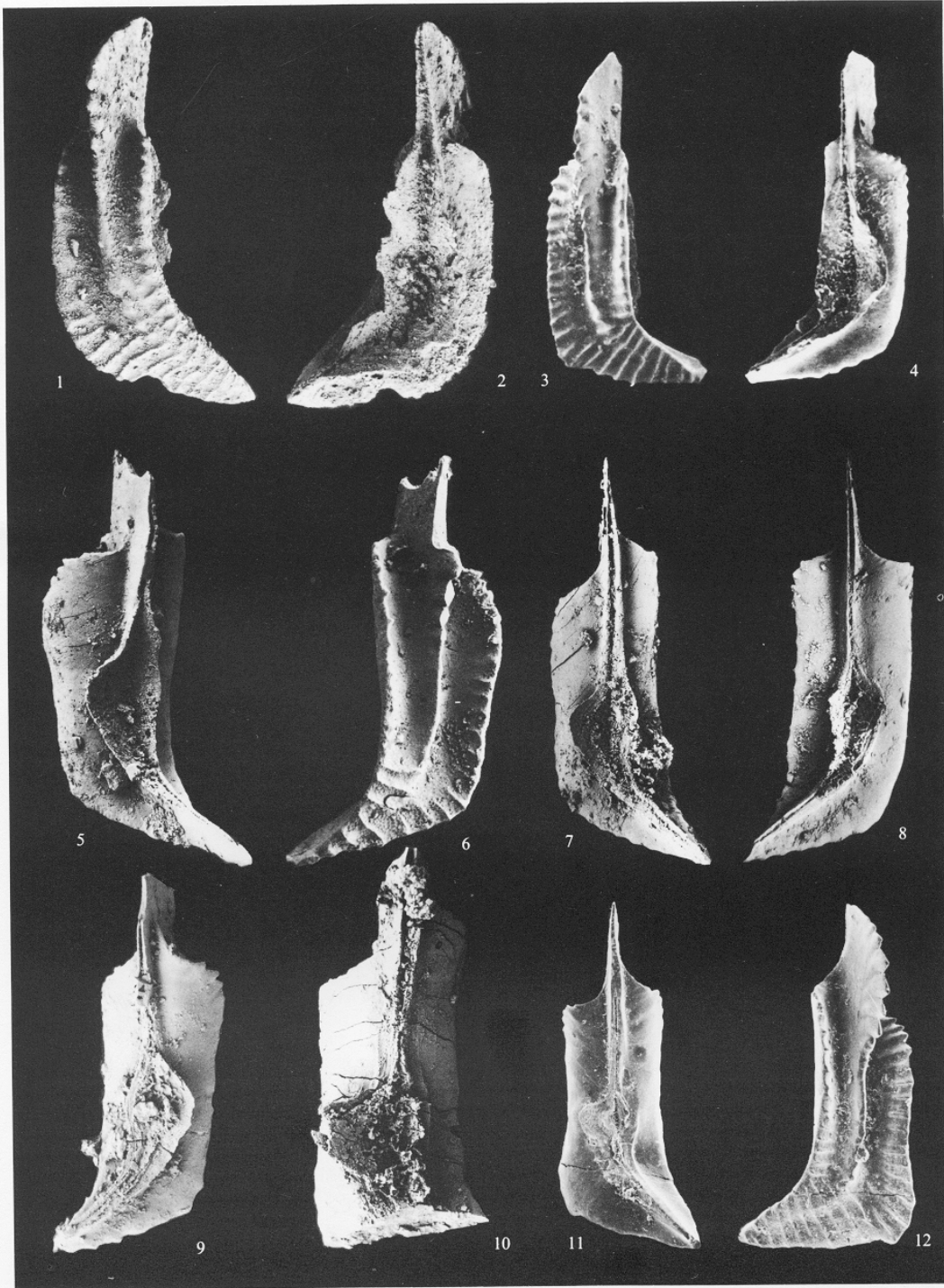
Plate 33, figs. 9–12; Plate 36, fig. 10

- 1967 *Polygnathus linguiformis linguiformis* Hinde; Philip and Jackson, pp. 13–14, text-fig. 2a (*non* 2b, 2c).
 1970 *Polygnathus linguiformis linguiformis* Hinde; Philip and Jackson in Pedder, Jackson and Philip, pp. 216–217, pl. 40, figs. 6 and 8 (*non* figs. 9 and 10).
 1974 *Polygnathus perbonus* n. subsp. D, Klapper in Perry *et al.*, pp. 1089 and 1091, pl. 8, figs. 9–13, 15, 16.
 1975 *Polygnathus* sp. nov. D, Klapper and Johnson, pp. 74, 75, pl. 3, figs. 1, 2, 8–10.
 1975 *Polygnathus foveolatus serotinus* subsp. nov. Telford, pp. 43 and 44, pl. 7, figs. 5–8 (*non* figs. 1–4).
 1975 *Polygnathus totensis* sp. nov. Snigireva, p. 27, pl. 4, figs. 3 and 4.
 1976 *Polygnathus serotinus* Telford; Bultynck, pl. 10, fig. 23; pl. 11, fig. 21.
 1976 *Polygnathus foveolatus* Telford; Fordham, pl. 5, figs. 5–8, 15, 16, 29, 30, 34 (*non* figs. 9, 10, 13, 14, 31, 33).
 1977 *Polygnathus serotinus* Telford; Weddige, pp. 319–320, pl. 4, figs. 77–79.
 1977 *Polygnathus serotinus* Telford; Klapper in Ziegler, pp. 495–496, *Polygnathus* pl. 9, figs. 4 and 5.
 1978 *Polygnathus serotinus* Telford; Pickett, pl. 1, figs. 23–25; pl. 2, fig. 18.
 1978 *Polygnathus serotinus* Telford; Klapper *et al.*, pl. 1, figs. 30 and 31 (*non* figs. 9 and 10).
 1978 *Polygnathus serotinus* Telford; Apekina and Mashkova, pl. 76, fig. 9; pl. 77, figs. 1 and 2 (*non* fig. 6).
 1979 *Polygnathus serotinus* delta morphotype Telford; Lane and Ormiston, p. 63, pl. 8, figs. 8–10, 34, 35.
 1980 *Polygnathus serotinus* Telford; Xiong, pp. 97–98, pl. 23, figs. 1–8; pl. 25, figs. 5–16, 23, 24, 26, 27 [Pa elements].

Amended diagnosis (modified from Klapper in Ziegler 1977 and Lane and Ormiston 1979). Pa elements have a small pit located just anterior to the sharp inward deflection of the keel. Small, subcircular, shelf-like protuberance, supported in its entire extent by a solid shaft from the main platform's lower surface, occurs on the outer side of the pit. Cavity entirely inverted posterior of pit. Flange-like anterior outer margin is distinctly higher than carina and inner margin, and separated from carina by wide, deep, adcarinal trough.

EXPLANATION OF PLATE 35

- Figs. 1–9. *Polygnathus labiosus* sp. nov. 1 and 2, upper and lower views of AMF 66041, sample BON 46-50, × 60. 3 and 4, upper and lower views of AMF 66044, sample 15.2, × 60. 5 and 6, lower and upper views of AMF 66043, holotype, sample 15.2, × 90. 7–9, specimens transitional between *P. labiosus* and *P. pseudoserotinus*. 7, lower view of AMF 66045, sample 15.06, × 90; 8, lower view of AMF 66046, sample 16.01, × 90; 9, lower view of AMF 66047, sample EB 5, × 90.
 Figs. 10–12. *P. pseudoserotinus* sp. nov. 10, lower view of AMF 66048, sample 15.01, × 75. 11 and 12, lower and upper views of AMF 66049, sample EB 3, holotype, × 90.



MAWSON, *Polygnathus*

Material. Fifteen specimens from five localities (Tables 5 and 6).

Discussion. Most specimens from Buchan and Bindi, Victoria, and the Broken River, north Queensland, belong to Lane's 'delta morphotype'; a small number of specimens fitting Lane's 'gamma morphotype' definition are found in Broken River. Forms transitional between *P. inversus* and *P. serotinus* occur with *P. serotinus* delta morph low in the section at Jessey Springs; they are included with the latter because they share more characteristics diagnostic of *P. serotinus* than *P. inversus*. On their upper surface the outer margin is somewhat higher than the inner margin and the carina, and a deep adcarinal trough is developed between the carina and the outer margin, reminiscent of *P. serotinus*. Posterior to the pit on the lower surface, however, the cavity is not completely inverted, and the distinctive lip of *P. serotinus* is not fully developed.

Genus OZARKODINA Branson and Mehl, 1933

Type species. *Ozarkodina typica* Branson and Mehl, 1933.

Discussion. The multi-element composition of *Ozarkodina* is as follows: Pa element is carminate ('spathognathodontan'); Pb element is angulate ('ozarkodinan'); M element is dolabrate (commonly 'neoprioniodontan' or less commonly 'synprioniodontan'); Sa element is alate ('trichonodellan'); Sb element is bipennate ('hindeodellan'); Sc element is digyrate ('plectospathodontan'). The only basis for differentiating *Pandorinellina* and *Ozarkodina* is the Sa element: in *Ozarkodina* the posterior process is expressed only by a slight swelling on the posterior base of the cusp ('trichonodellan' element) whereas in *Pandorinellina* the posterior process is well developed ('diplodellan' element) (Klapper and Philip 1971; Klapper in Ziegler 1973). *Pandorinellina* n. sp. O of Klapper (1977) is referred to *Ozarkodina* because there is a dearth of 'diplodellan' elements in the conodont faunas at Buchan and Bindi, and, moreover, a 'trichonodellan' form that conforms with the symmetry transition series is available.

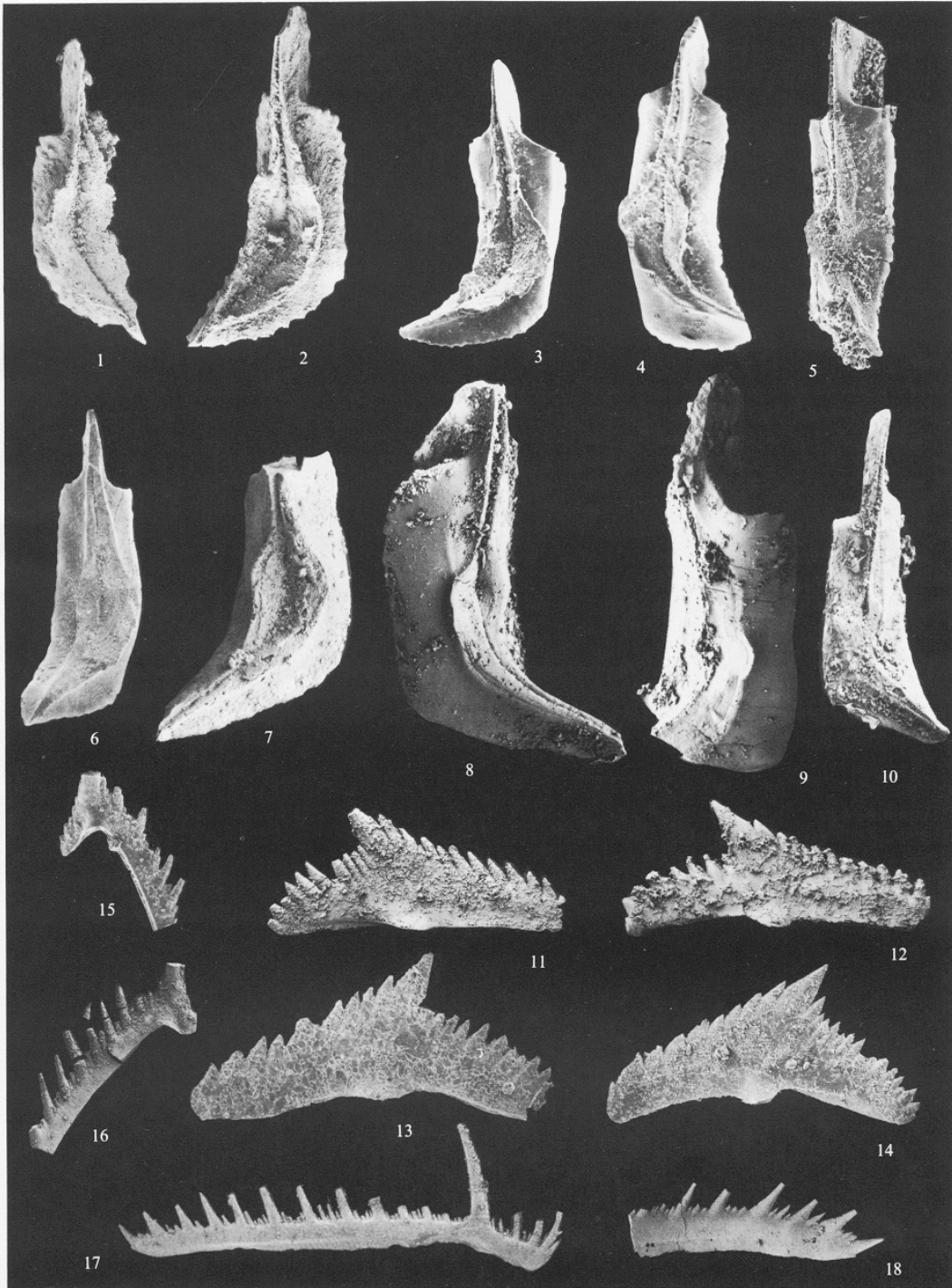
Ozarkodina buchanensis (Philip, 1966)

Plate 37

- 1966 *Spathognathodus steinhornensis buchanensis* n. subsp. Philip, pp. 450–451, pl. 2, figs. 1–15 (non figs. 16–28) [Pa element].
 1966 *Ozarkodina denckmanni* Ziegler; Philip, pp. 446–447, pl. 4, figs. 16 and 17 (non figs. 15, 18–20) [Pb element].
 1966 *Neoprioniodus bicurvatus* (Branson and Mehl); Philip, p. 446, pl. 3, figs. 14–16 (non figs. 12 and 13) [M element].

EXPLANATION OF PLATE 36

- Fig. 1. *Polygnathus dehiscens abyssus* subsp. nov., lower view of NMVP 99001, sample SLO 60, × 45.
 Fig. 2. *P. perbonus* (Philip), lower view of NMVP 99002, sample OTRC 5, × 60.
 Figs. 3 and 4. *P. labiosus* sp. nov. 3, lower view of NMVP 99003, sample 15.2, × 45. 4, lower view of specimen transitional between *P. labiosus* and *P. pseudoserotinus*, NMVP 99004, sample 15.2, × 60.
 Fig. 5. *P. pseudoserotinus* sp. nov., lower view of NMVP 99005, sample SALC 6, × 60.
 Fig. 6. *P. dehiscens dehiscens* Philip and Jackson, lower view of NMVP 99006, sample OTRC 5, × 45.
 Fig. 7. *P. nothoperbonus* sp. nov., lower view of NMVP 99007, sample BON 60.5–65, × 60.
 Figs. 8 and 9. *P. inversus* Klapper and Johnson. 8, lower view of NMVP 99008, sample T3, × 90. 9, lower view of specimen transitional between *P. inversus* and *P. serotinus*, NMVP 99009, sample EB 3, × 45.
 Fig. 10. *P. serotinus* 'delta morphotype' Telford, lower view of NMVP 99010, sample T3, × 45.
 Figs. 11–18. *P.* spp. Pb elements: 11, NMVP 99011, sample OTRC 1, × 45; 12, NMVP 99012, sample OTRC 1, × 45; 13, NMVP 99013, sample OTRC 1, × 45; 14, NMVP 99014, sample SLO 60, × 45. M elements: 15, NMVP 99015, sample Ma 10, × 45; 16, NMVP 99016, sample Ma 10, × 45. Sb element: 18, NMVP 99018, sample SB40–60, × 45. Sc element: 17, NMVP 99017, sample Ma 2, × 45.



MAWSON, *Polygnathus*

- 1966 *Trichonodella symmetrica pinnula* n. subsp. Philip, pp. 452-453, pl. 4, figs. 1-6 [Sa element].
 1966 *Plectospathodus alternatus* Walliser; Philip, p. 448, pl. 3, figs. 10, 17, 21, 25 [Sb elements].
 1966 *Hindeodella priscilla* Stauffer; Philip, p. 445, pl. 3, figs. 2, 7, 9 (*non* figs. 6, 8, 11, 18) [Sc elements].
 1970 *Spathognathodus steinhornensis optimus* Moskalenko; Pedder, Jackson and Philip, p. 218, pl. 38, figs. 4-6 (*non* figs. 7, 10-12) [Pa element].
 1971 *Ozarkodina buchanensis* (Philip); Klapper and Philip, p. 448, fig. 10 [Pa, Pb, M, Sa, Sb, Sc elements].
 1973 *Ozarkodina buchanensis* (Philip); Klapper *in* Ziegler, pp. 215-216, *Ozarkodina* pl. 1, figs. P, O, N, A1, A2, A3 [Pa, Pb, M, Sa, Sb, Sc elements].
 1973 *Spathognathodus steinhornensis* cf. *buchanensis* Philip; Cooper, p. 80, pl. 2, figs. 8, 9, 12; pl. 3, figs. 2-5 [Pa element].
 1979 *Ozarkodina buchanensis* (Philip); Lane and Ormiston, pp. 54-55, pl. 2, figs. 32 and 35; pl. 3, fig. 13 [M, Sa, Pa elements].

Material. 385 specimens of the Pa element from sixty localities; 183 non-platform elements from fifty-four localities (Tables 1 and 4).

Discussion. This apparatus, a Type 1 apparatus of Klapper and Philip (1972), was first illustrated from material collected from the top of the Buchan Caves Limestone (Philip 1966). Material from a stratigraphically similar locality, both above and below the contact of the Buchan Caves Limestone and the Taravale Formation at Murrindal ('P' section; text-figs. 1 and 5), has yielded a similar fauna with Pa, Pb, and Sc elements represented. In faunas from the basal Taravale Formation at Slocombes (SLO section; text-fig. 1) all elements are present. The highest occurrence of *O. buchanensis* is in bed 7.14.4 in the Gelantipy Road section at Buchan (text-figs. 1 and 4) showing that, at Buchan at least, it does not range higher than the *dehiscens* Zone.

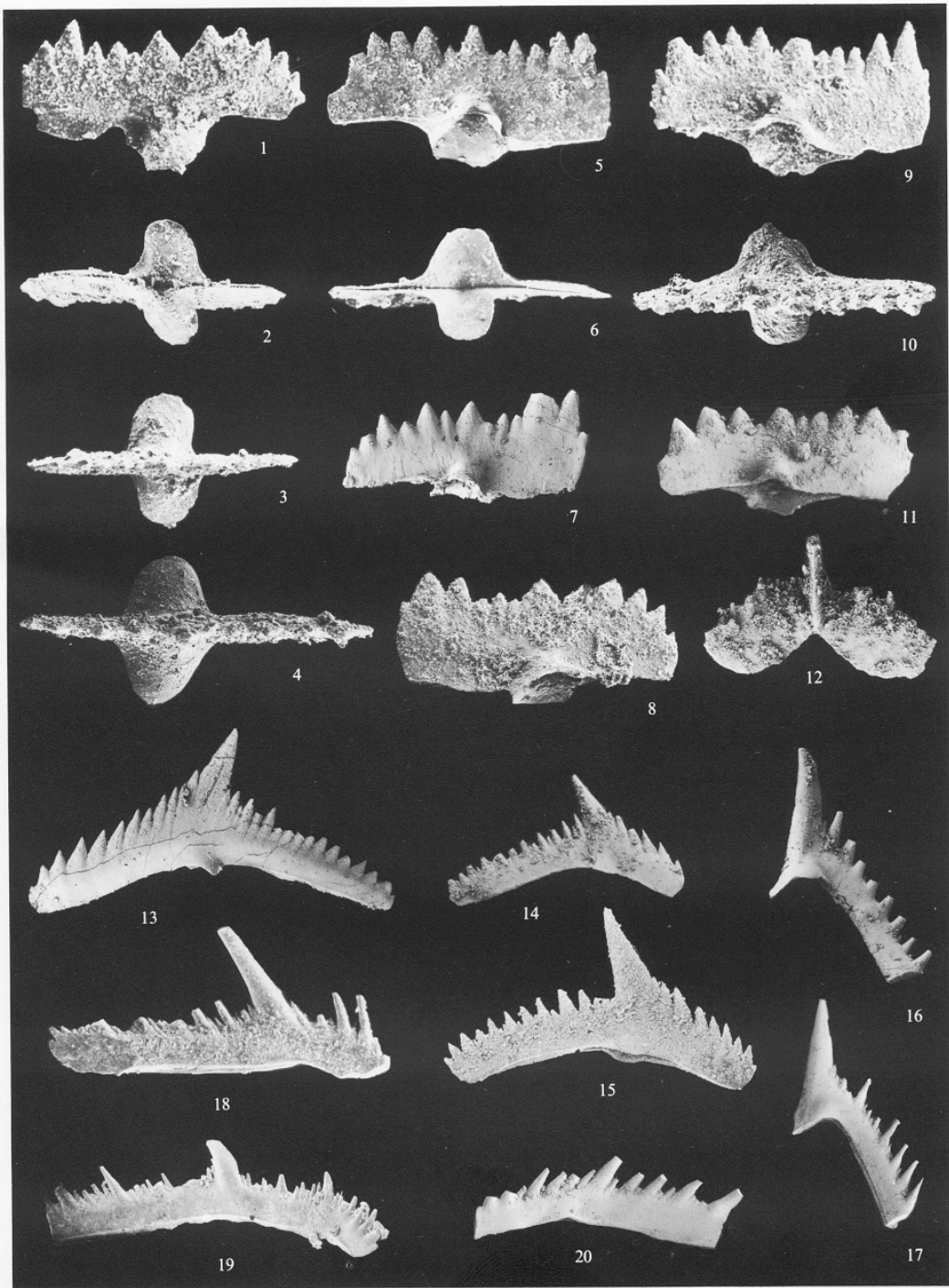
The older species *O. remscheidensis remscheidensis* closely resembles *O. buchanensis* but they can be differentiated by the more strongly recurved lateral processes, smaller pit, and more compressed cusp of the Sa element of the latter (Klapper *in* Ziegler 1975, p. 215), and by the shorter, higher blade and the more centrally positioned basal cavity of the Pa element. *O. remscheidensis repetitor* also resembles *O. buchanensis*, but the lack of symmetry in the arrangement of the denticles of the latter separates the two. *O. buchanensis* is younger than the two subspecies of *O. remscheidensis*, the highest occurrence of *O. r. remscheidensis* being in the *delta* Zone (Klapper and Johnson 1980, p. 416) and the highest occurrence of *O. r. repetitor* in the *pesavis* Zone (Klapper and Johnson 1980, p. 417) (text-fig. 9).

Bed-by-bed sampling of the Buchan Caves Limestone at Buchan, Bindi, and The Basin is in progress; this should provide more precision for the lower limit of the range of *O. buchanensis*. The fauna from Loyola, Victoria (Cooper 1973), incidentally, contains thirty-six specimens of *O. buchanensis* occurring with *Polygnathus pireneae* Boermsa (identified by Cooper as *Spathognathodus trilinearis* sp. nov. and *P. sp.*, respectively). The occurrence of these forms together is indicative of the *kindlei* Zone (Klapper and Johnson 1980, p. 418).

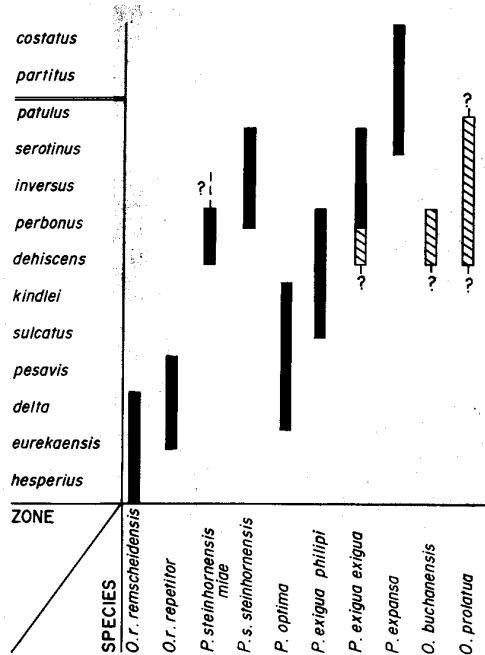
EXPLANATION OF PLATE 37

Figs. 1-20. *Ozarkodina buchanensis* (Philip). Pa elements: 1-3, lateral, lower, and upper views of NMVP 99019, sample P 6.1; 4, upper view of NMVP 99020, sample P 6.1; 5 and 6, lateral and lower views of NMVP 99021, sample P 6.1; 7, lateral view of NMVP 99022, sample SLO 40-60; 8, lateral view of NMVP 99023, sample P 7.1; 9 and 10, lateral and lower views of NMVP 99024, sample P 4.1; 11, lateral view of NMVP 99025, sample SLO 60. Pb elements: 13, NMVP 99027, sample Ma 10; 14, NMVP 99028, sample SLO 250; 15, NMVP 99029, sample Ma 2. M elements: 16, NMVP 99030, sample Taravale Fm. below SB 1; 17, NMVP 99031, sample SLO 60. Sa element: 12, NMVP 99026, sample SLO 130. Sb element: 19, NMVP 99033, sample OTRC 2. Sc elements: 18, NMVP 99032, sample 8.5.2; 20, NMVP 99034, sample SLO 60.

All × 60.



MAWSON, *Ozarkodina*



TEXT-FIG. 9. Range chart of a selection of spathognathodontan (Pa) elements occurring in the Early Devonian. Conodont zones are after Klapper and Johnson (1980) with the Early Devonian–Middle Devonian boundary between *patulus* and *partitus* zones as determined by the International Subcommittee on Devonian Stratigraphy in 1980 (Ziegler and Klapper 1985). Ranges shown as a solid bar are taken from Klapper and Johnson (1980); those with diagonal shading are additional information derived from this study (Tables 1–6).

Ozarkodina excavata excavata (Branson and Mehl, 1933)

Plate 31, figs. 10–16

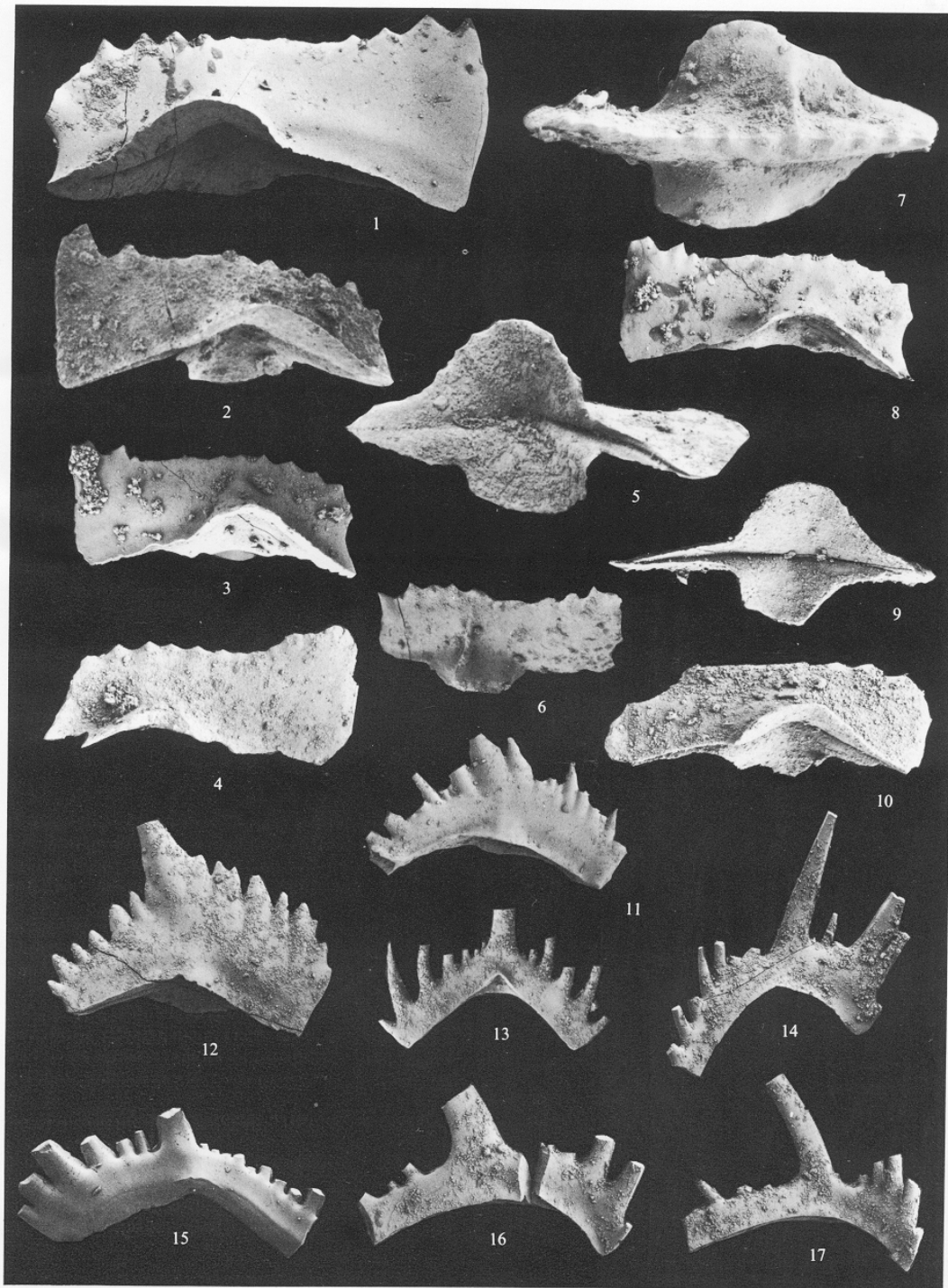
Synonymy. See Jeppsson (1974, pp. 19–20), Klapper (*in* Ziegler 1975, pp. 225–226), Klapper and Murphy (1975, pp. 34–37), Barrick and Klapper (1976, pp. 78–79), and Klapper and Johnson (1980, p. 450).

Material. Nineteen specimens of the Pa element from seven localities; nineteen non-Pa elements from thirteen localities (Tables 1 and 4).

Discussion. *O. e. excavata* occurs low in the sections at Buchan and Bindi (*dehiscens* and low *perbonus* zones). Apart from the Sa element, all elements (Pa, Pb, M, Sb, Sc) are represented. Philip (1966) identified '*S. inclinatus inclinatus* (Rhodes) [Pa element], '*O. media* Walliser [Pb element], and '*Trichonodella excavata* (Branson and Mehl) [Sa element] from McLarty's ridge (Loc. 6), about the middle of the Murrindal Limestone (text-fig. 1). He also identified '*Hindeodella equi-dentata* Rhodes [Sc element] from the same locality and from the top of the Buchan Caves Limestone (Loc. 3), as well as '*Neoprioniodus bicurvatus* (Branson and Mehl) [M element] from his Loc. 6, higher in

EXPLANATION OF PLATE 38

Figs. 1–17. *Ozarkodina linearis* (Philip). Pa elements: 1, lateral view of NMVP 99035, sample Shanahan Ls., ×45; 2, lateral view of NMVP 99036, sample BON 25–27.5, ×45; 3, lateral view of NMVP 99037, sample BON 60.5–65, ×45; 4, lateral view of NMVP 99038, sample SLO 60, ×45; 5, lower view of NMVP 99039, sample BON 36–39, ×45; 6, lateral view of NMVP 99040, sample SLO 220, ×45; 7, upper view of NMVP 99041, sample SLO 60, ×45; 8, lateral view of NMVP 99042, sample BON 60.5–65, ×60; 9 and 10, lower and lateral views of NMVP 99043, sample BON 60.5–65, ×60. Pb elements: 11, NMVP 99044, sample SLO 60, ×45; 12, NMVP 99045, sample Ma 10, ×45. M element: 14, NMVP 99046, sample Ma 10, ×45. Sa element: 13, NMVP 99047, sample Ma 10, ×45. Sb element: 15, NMVP 99048, sample Forrest Motel, ×45. Sc elements: 16, NMVP 99049, sample Ma 10, ×45; 17, NMVP 99050, sample Ma 10, ×45.



MAWSON, *Ozarkodina*

the Murrindal Limestone at his Locs. 7 and 8, and from the top of the Buchan Caves Limestone at his Locs. 2 and 3. Klapper and Johnson (1980, table 5, p. 419) concluded that *O. e. excavata* persists as high as the *perbonus* Zone at Wee Jasper, New South Wales. Its occurrence at Buchan in the *perbonus* Zone is therefore not surprising.

Ozarkodina linearis (Philip, 1966)

Plate 38

- 1966 *Eognathodus linearis* n. sp. Philip, pp. 444–445, pl. 4, figs. 33–36; text-fig. 3 [Pa element].
 1966 *Ozarkodina* sp. cf. *O. jaegeri* Walliser; Philip, p. 447, pl. 4, figs. 31 and 32 [Pb element].
 1966 *Trichonodella inconstans* Walliser; Philip, p. 451, pl. 4, figs. 21, 23, 27 (*non* fig. 30) [Sa element].
 1966 *Lonchodina* n. sp. Philip, p. 446, pl. 3, fig. 19 (*non* figs. 20 and 24) [Sb element].
 1966 *Lonchodina* n. sp. Philip, p. 446, pl. 3, fig. 20 (*non* figs. 19 and 24) [M element].
 1969 *Spathognathodus linearis* (Philip); Flood, pl. 2, fig. 12 [Pa element].
 1969 *Ozarkodina typica australis* Philip and Jackson; Flood, pl. 1, fig. 4 [Pb element].
 1969 *Lonchodina* n. sp. Philip; Flood, pl. 1, fig. 8 [M element].
 1969 *Ligonodina salopia* Rhodes; Flood, pl. 1, fig. 9 [Sc element].
 1970 *Spathognathodus linearis* (Philip); Philip and Jackson *in* Pedder, Jackson and Philip, p. 217, pl. 38, figs. 16–21 [Pa element].
 1970 *Ozarkodina typica australis* n. subsp. Philip and Jackson *in* Pedder, Jackson and Philip, p. 215, pl. 39, figs. 1–4, 11–15 [Pb element].
 1970 *Ligonodina salopia* Rhodes; Philip and Jackson *in* Pedder, Jackson and Philip, p. 213, pl. 40, figs. 1, 3, 4 [Sc element].
 1970 *Lonchodina greilingi* Walliser; Philip and Jackson *in* Pedder, Jackson and Philip, pl. 37, fig. 18 (*non* figs. 14 and 15) [M element].
 1970 *Lonchodina* sp. B, Philip and Jackson *in* Pedder, Jackson and Philip, p. 213, pl. 37, fig. 27 [Sb element].
 1970 *Trichonodella inconstans* Walliser; Philip and Jackson *in* Pedder, Jackson and Philip, p. 218, pl. 37, figs. 17, 19, 21 [Sa element].
 1971 *Spathognathodus linearis* (Philip); Fähræus, p. 679, pl. 77, fig. 39 [Pa element].

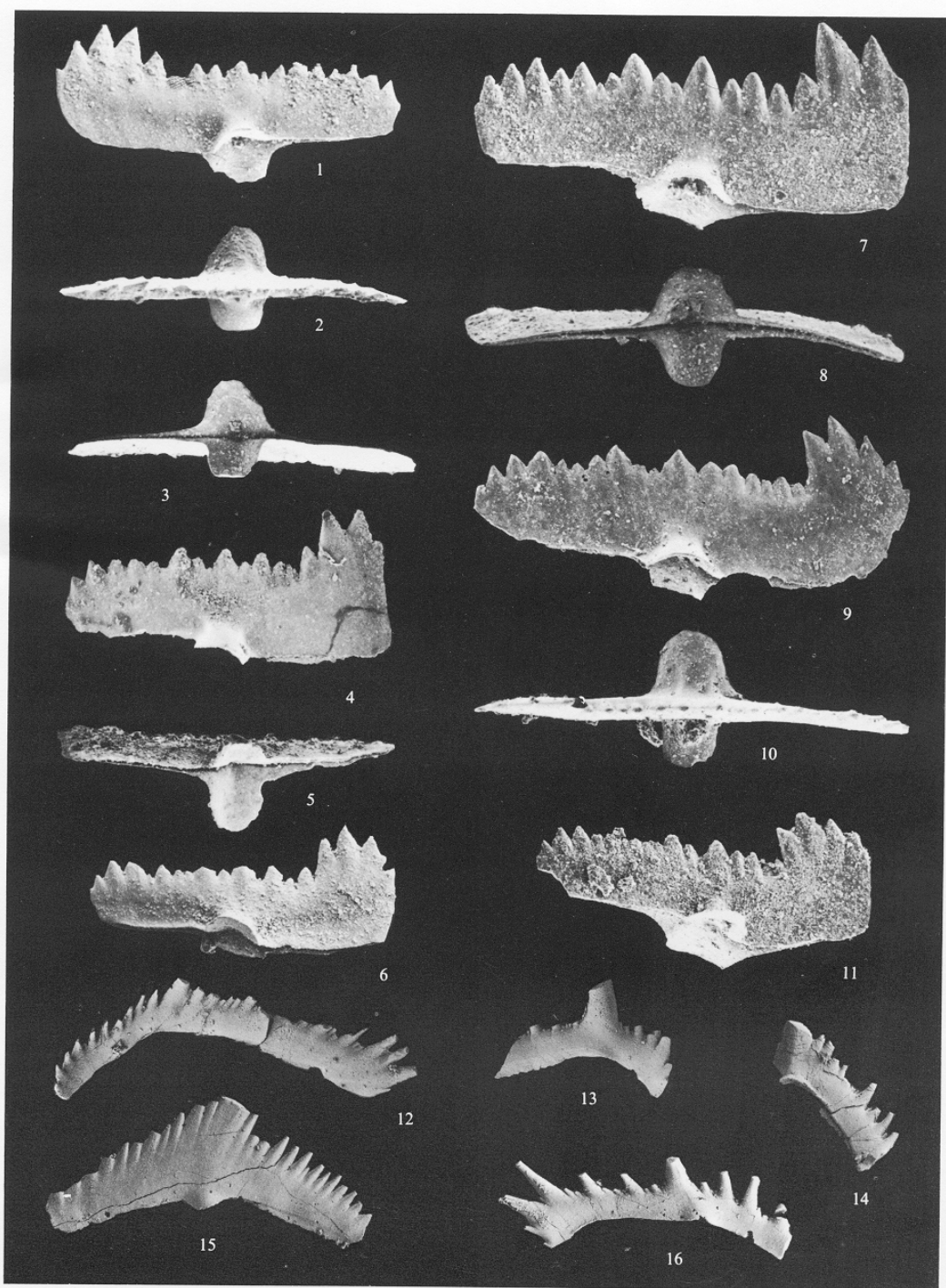
Amended diagnosis. Pa elements have a subrectangular blade, slightly convex anteriorly and concave posteriorly in lateral view. Denticles short and stubby; basal cavity with widely flaring sub-symmetrical lobes.

Material. Forty-three specimens of the Pa element from twenty-two localities; sixteen non-platform elements from thirteen localities (Tables 1–4).

Discussion. Philip (1966) recovered elements of *O. linearis* from the top of the Buchan Caves Limestone at Buchan (*dehiscens* Zone), but the present study has shown them to occur in small numbers high in the *perbonus* Zone, e.g. in bed 12.1 in the Gelantipy Road section (Table 1). The Pa element of *O. linearis* can be distinguished from the Pa element of *O. druceana* from Cobar, New South Wales (Pickett 1980) by being more rectangular in lateral view, rather than decreasing dramatically posteriorly. The basal cavity of *O. eurekaensis* from the Roberts Mountains, Nevada,

EXPLANATION OF PLATE 39

Figs. 1–16. *Ozarkodina prolata* sp. nov. Pa elements: 1–3, lateral, upper, and lower views of NMVP 99051, holotype, sample 8.8.10, × 60; 4, lateral view of NMVP 99052, sample BON 50-60, × 90; 5 and 6, lower and lateral views of NMVP 99053, sample 8.8.10, × 60; 7 and 8, lateral and lower views of NMVP 99054, sample Forrest Motel, × 90; 9 and 10, lateral and upper views of NMVP 99055, BON 65-70, × 90; 11, lateral view of NMVP 99056, sample BON 15-19.5, × 60. Pb element: 15, NMVP 99057, sample SB 40-60, × 90. M element: 14, NMVP 99058, sample SB 40-60, × 90. Sb element: 16, NMVP 99059, sample SB 40-60, × 90. Sc elements: 12, NMVP 99060, sample Taravale Fm. below SB 1, × 90; 13, NMVP 99061, sample SB 40-60, × 90.



MAWSON, *Ozarkodina*

is much narrower than that of *O. linearis* and does not expand rapidly to maximum width midway along the blade. The Pb, M, and symmetry transition elements of *O. linearis*, unlike those of *O. druceana*, are conventionally assigned to the genus *Ozarkodina*; those assigned to *O. druceana* by Pickett (1980) belong to a species of *Amydrotaxis*, possibly a morphotype of *A. johnsoni* Klapper and Murphy.

Ozarkodina prolata sp. nov.

Plate 39

- 1966 *Spathognathodus steinhornensis buchanensis* n. subsp. Philip, pp. 450–451, pl. 2, figs. 16–21, 24–28 (non figs. 1–15, 22, 23), text-fig. 8b, 8c [Pa element].
 1971 *Spathognathodus optimus* Moskalenko; Fähræus, pp. 679–680, pl. 77, figs. 15–18, 23, 24, 31 (non figs. 19–21) [Pa element].
 1976 *Ozarkodina remscheidensis* (Ziegler); Savage, p. 1182, pl. 1, figs. 1–12 (non figs. 13–15) [Pa, Pb, M, Sa, Sb, Sc elements].
 1977 *Pandorinellina* cf. *P. optima* (Moskalenko); Savage *et al.*, p. 2934, pl. 2, figs. 11–14 [Pa element].
 1980 *Pandorinellina* n. sp. O, Klapper and Johnson, p. 451.

Derivation of name. *prolatus* (Lat.) = extended, elongated, in reference to the long, relatively narrow blade of the Pa element.

Holotype. NMV P99051 (Pl. 39, figs. 1–3) from the Taravale Formation, 51.2 m above the base of the Gelantipy Road section (sample 8.8.10) at Buchan, Victoria.

Diagnosis. Pa elements have a long, relatively narrow, straight or slightly curved blade with numerous, irregular, moderately small, triangular denticles increasing in size towards the anterior. Widely flaring, rounded lobes of basal cavity are situated medially, taper anteriorly, and continue posteriorly as a groove.

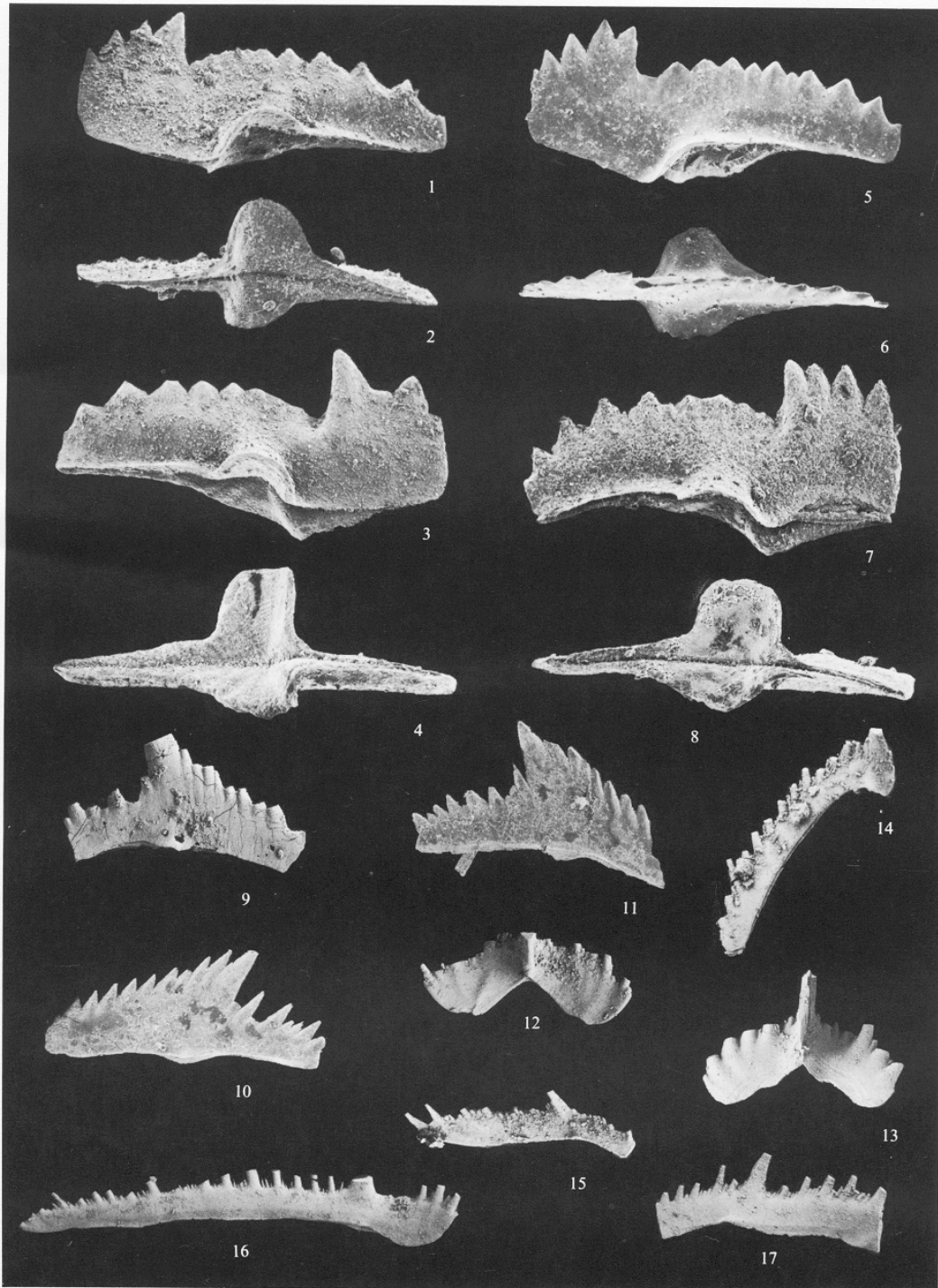
Material. 1,128 specimens of the Pa element from 104 localities; 460 non-platform elements from seventy-four localities (Tables 1–4).

Discussion. Klapper and Johnson (1980, p. 451) assigned this species to *Pandorinellina*, a genus that differs from *Ozarkodina* by the Sa element being ‘diplodellan’ rather than ‘trichonodellan’ in form (Klapper in Ziegler 1975, p. 317). The *prolata* apparatus is placed in *Ozarkodina* on two grounds: there is no ‘diplodellan’ element that will ‘fit’ the reconstruction; and, from an evolutionary viewpoint, it seems that the *prolata* line belongs to the ozarkodinids (see below).

The Pa element of *O. prolata* was first illustrated from Buchan by Philip (1966) who assigned it to *Spathognathodus eosteinhornensis buchanensis*, a form recovered from samples of older strata in the Buchan Caves Limestone. The following features of *O. prolata* separate the two: the longer blade; the slightly smaller denticles and their more uniform size (except anteriorly where two or three are clearly larger and higher); and the more centrally situated basal cavity that tapers anteriorly. Although these features separate the two species, it is clear that *O. buchanensis* is the

EXPLANATION OF PLATE 40

Figs. 1–17. *Pandorinellina exigua exigua* (Philip). Pa elements: 1 and 2, lateral and lower views of NMVP 99062, sample BON 13.5–15, × 60; 3 and 4, lateral and lower views of NMVP 99063, sample BON 50–60, × 60; 5 and 6, lateral and upper views of NMVP 99064, sample Ma 4, × 60; 7 and 8, lateral and lower views of NMVP 99065, sample BON 220–240, × 60. Pb elements: 9, NMVP 99066, sample SB 40–60, × 45; 10, NMVP 99067, sample OTRC 1, × 45; 11, NMVP 99068, sample OTRC 1, × 45. M element: 14, NMVP 99069, sample SLO 60, × 45. Sa elements: 12, NMVP 99070, sample Buchan Caves Ls. at The Basin, × 45; 13, NMVP 99071, sample Taravale Fm. below SB 1, × 45. Sb elements: 15, NMVP 99072, sample SLO 85, × 45; 17, NMVP 99074, sample SLO 250, × 45. Sc element: 16, NMVP 99073, sample Ma 10, × 45.



MAWSON, *Pandorinellina*

precursor of *O. prolata* and, in Australia at least, probably replaces the *remscheidensis repetitor* → *steinhornensis miae* transition of Bultynck (1971). The ranges so far established for the above (text-fig. 9) support this conclusion.

Specimens of *O. prolata* have been recovered from a section at La Grange, France (P. Bultynck, pers. comm.) where they occur in the same sample (A8/10) with *P. steinhornensis steinhornensis*. The Pa element of the older *P. optima* (Moskalenko) illustrated by Moskalenko (1966) has a much wider blade and a more anteriorly located basal cavity than *O. prolata*. An interesting study of the Pa element of *P. exigua midudenta* Wang and Ziegler has been made by Bai (1985). Forms referred to by Bai as 'alpha' and 'beta' morphotypes of *P. midudenta* may be synonymous with *O. buchanensis* and *O. prolata* respectively but, without information regarding the Sa element of the apparatuses, it is unwise to synonymize them.

Genus PANDORINELLINA Müller and Müller, 1957

Type species. Pandorinellina insita Stauffer, 1940

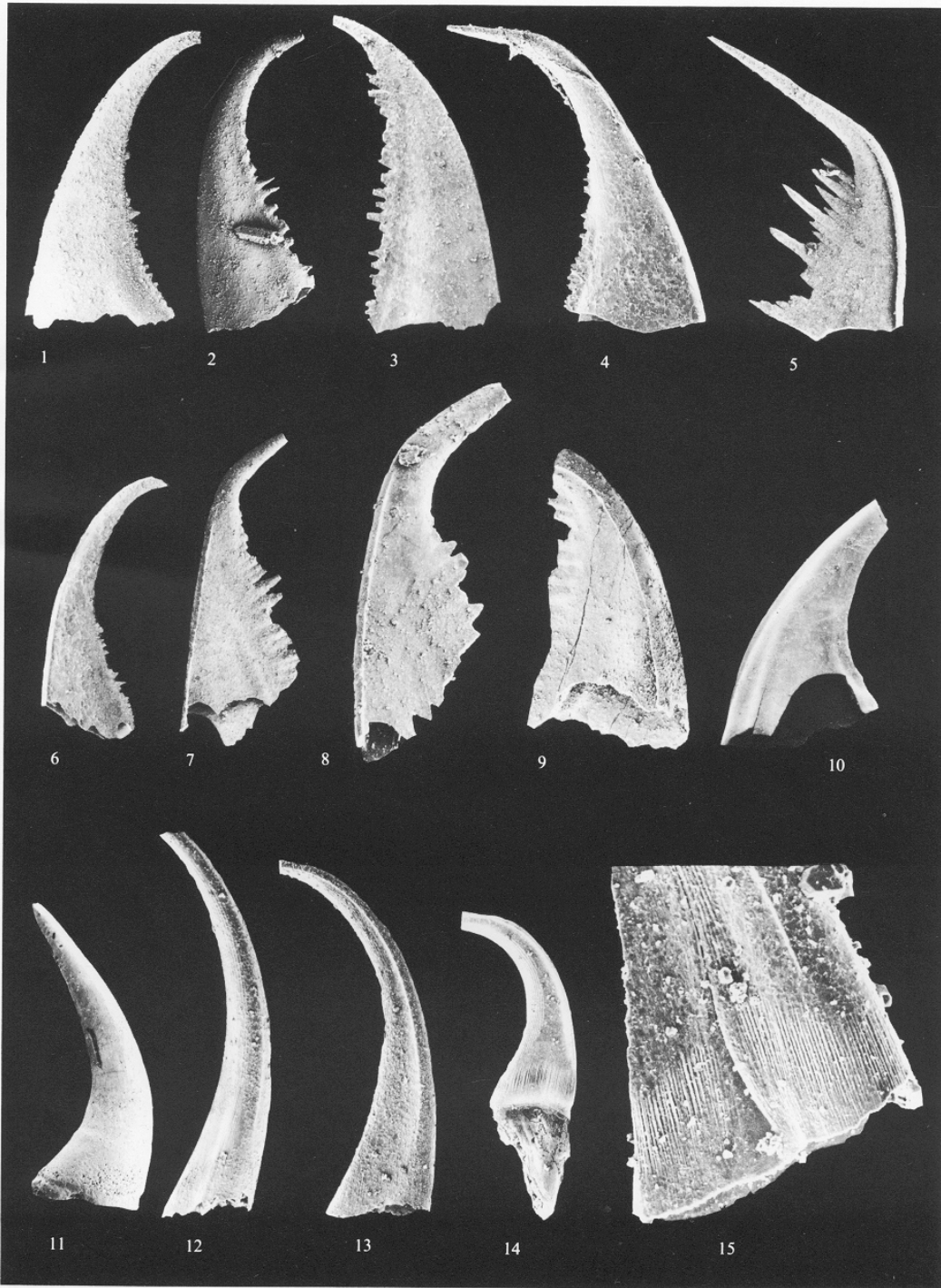
Pandorinellina exigua exigua (Philip, 1966)

Plate 40

- 1966 *Spathognathodus exigua* n. sp. Philip, pp. 449–450, pl. 3, figs. 26–37, text-fig. 7 [Pa element].
 1966 *Neoprioniodus bicurvatus* (Branson and Mehl); Philip, p. 446, pl. 3, fig. 13 (*non* figs. 12, 14–16) [M element].
 1966 *Spathognathodus frankenwaldensis* Bischoff and Sannemann; Clark and Ethington, pp. 685–686, pl. 82, figs. 15 and 21 [Pa element].
 1970 *Spathognathodus steinhornensis exiguus* Philip; Philip and Jackson in Pedder, Jackson and Philip, pp. 217–218, pl. 38, figs. 7, 8, 10, 11, 13 [Pa element].
 1971 *Spathognathodus optimus* Moskalenko; Fähræus, pp. 679–680, pl. 77, figs. 19 and 20 (*non* figs. 15–18, 21, 24, 31) [Pa element].
 1971 *Spathognathodus exiguus* Philip; Fähræus, pp. 678–679, pl. 77, figs. 25–30, 32 [Pa element].
 1972 *Spathognathodus* n. sp. A, Uyeno in McGregor and Uyeno, p. 13, pl. 5, figs. 19–21, 30–32 [Pa element].
 1972 *Ozarkodina* n. sp. A, Uyeno in McGregor and Uyeno, p. 13, pl. 5, figs. 4 and 5 [Pb element].
 1973 *Pandorinellina exigua exigua* (Philip); Klapper in Ziegler, p. 319, pl. 2, fig. 2 [Pa element].
 1974 *Pandorinellina exigua exigua* (Philip); Klapper in Perry *et al.*, pp. 1086–1087, pl. 6, figs. 12 and 13 [Pa element].
 1975 *Spathognathodus exiguus* Philip; Weyant, pl. 1, figs. 1–8 [Pa element].
 1975 *Spathognathodus exiguus* Philip; Telford, pp. 58 and 60, pl. 14, figs. 10–18 [Pa element].
 1978 *Ozarkodina* sp. Pickett, p. 100, pl. 1, figs. 8–11 (*non* figs. 12–16, 26, 27) [Pa element].
 1979 *Pandorinellina exigua* (Philip); Lane and Ormiston, pp. 58 and 59, pl. 6, figs. 15, 20, 24 (*non* figs. 25 and 26) [Pa element].

EXPLANATION OF PLATE 41

- Figs. 1–4. *Belodella devonica* (Stauffer). 1, NMVP 99091, sample Ma 7, × 60. 2, NMVP 99092, sample Ma 7, × 60. 3, NMVP 99093, sample OTRC top 1 m, × 60. 4, NMVP 99094, sample Ma 7, × 60.
 Figs. 5–8. *B. resima* (Philip). 5, NMVP 99095, sample Ma 7, × 60. 6, NMVP 99096, sample Ma 7, × 60. 7, NMVP 99097, sample Ma 8, × 60. 8, NMVP 99098, sample Ma 7, × 60.
 Fig. 9. *B. triangularis* (Stauffer), NMVP 99099, sample Ma 7, × 60.
 Fig. 10. *Panderodus valgus* (Philip), NMVP 99100, sample Ma 7, × 60.
 Fig. 11. *Drepanodus* sp., NMVP 99101, sample Ma 7, × 60.
 Figs. 12 and 13. *P. unicostatus* (Branson and Mehl). 12, NMVP 99102, sample Ma 7, × 60. 13, NMVP 99103, sample Ma 7, × 60.
 Figs. 14 and 15. *P. recurvatus* (Rhodes). 14, NMVP 99104, sample Ma 7, × 60. 15, NMVP 99105, sample Ma 7, × 300.



MAWSON, *Belodella*, *Panderodus*, *Drepanodus*

- 1979 *Ozarkodina denckmanni* Ziegler; Lane and Ormiston, pl. 6, fig. 23 [Pb element].
 1980 *Pandorinellina exigua exigua* (Philip); Uyeno and Klapper, pl. 8.1, figs. 25-27 [Pa element].

Material. 608 specimens of the Pa element from eighty-six localities; 281 non-platform elements from fifty-one localities (Tables 1-4).

Discussion. The Pa element of *P. e. exigua* first occurs at Buchan and Bindi together with *Polygnathus dehiscens*. Although *Pandorinellina exigua philipi* does not accompany *P. e. exigua* in any of these samples, transitional forms between them are found low in the *dehiscens* Zone; these have a very narrowly expanded basal cavity posterior to the lobes, so narrow as to be almost a groove like that found in *P. e. philipi*. Similar transitional forms from high in the section at Royal Creek, Yukon Territory, have been illustrated by Klapper (1969, pl. 5, figs. 1-5). Towards the top of the section at Buchan, the basal cavity of specimens of *P. e. exigua* tends to taper more evenly, with less constriction at the posterior of the basal cavity lobes than in specimens recovered from lower levels. These forms appear to be transitional between *P. e. exigua* and *P. expansa* Uyeno and Mason, a form that shares with *P. e. exigua* a characteristic blade with a high anterior third somewhat offset from the remaining, gently arched two-thirds. Pickett (1978) discussed specimens he referred to '*Ozarkodina*' sp. from the Mount Frome Limestone, New South Wales, recovered from beds below the first occurrence of *P. expansa s. s.* It appears from the shape of the basal cavity that the Pa elements figured by Pickett (1978, pl. 1, figs. 8-11) are similarly a form transitional between *P. e. exigua* and *P. expansa*, rather than juveniles of *P. palethorpei*. The Pb element of *P. e. exigua* has a short, narrow posterior blade (Pl. 40, fig. 10), a characteristic developed to an even greater degree in *P. expansa*; this further supports the phylogenetic relationship of the two. From the Ogilvie Formation, Northern Yukon, Perry *et al.* (1974) documented the presence of *P. e. exigua* in faunas containing *P. perbonus*, with *P. expansa* occurring higher in the sequence accompanied by *P. serotinus*.

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RUTH MAWSON
School of Earth Sciences
Macquarie University
New South Wales 2109
Australia