

# Treposeiidae (Beyrichiacea: Ostracoda) from the latest Devonian (Strunian) of the Bonaparte Basin, Western Australia

P.J. Jones<sup>1</sup>

Three new beyrichiacean genera are described from the type section of the Buttons beds, latest Devonian, along the eastern bank of the Ord River: *Notoscapha* gen. nov. (type species *N. oepiki* sp. nov.) from the lower part of the section below 120 m, *Paraboucheikius* gen. nov. (type species *P. martinsoni* sp. nov.) and *Katatona* gen. nov. (type species *K. romei* sp. nov.) both from the middle part of the section 120–200 m. They lack traces of a dolonoid closing mechanism, and are interpreted, within Martinsson's scheme of beyrichiacean phylogeny, as advanced treposeiids. The posterocentral site of a possible rudimentary crumina in a presumed female specimen of *Katatona romei* may indicate a

sylobial origin for the crumina in those genera having a similar type of dimorphism. This type of cruminal dimorphism is present in species from the Late Devonian of the European USSR that have been assigned to 'Aparchites' and to the related genera *Boucheikius*, *Copelandites*, and *Reversoscapha*. The distribution of species of *Katatona*, *Boucheikius*, and *Paraboucheikius* is discussed to evaluate their potential for long-distance correlation in the latest Devonian (ie., late Famennian and Strunian). At present, *Katatona* indicates a Strunian (Fa2d, Th1a) age, and its presence in the Buttons beds supports the age assignment recently proposed on miospore evidence.

## Introduction

The Treposeiidae, a relatively homogeneous beyrichiacean family, is characterised by females whose dimorphic pouch (crumina) is a ventral to posteroventral swelling that extends to incorporate part of the sylobium. As with all described Beyrichiacea, sexual maturity in the female dimorph is manifested only in the final moult stage, with the development of the crumina with its opening into the interior of the carapace. The male has no such dimorphic structure. This specialised and highly distinctive type of sexual dimorphism (cruminal dimorphism) is definitive of all Beyrichiacea (Martinsson, 1962; Henningsmoen, 1965; Kesling, 1969; Siveter, 1980).

The Treposeiidae, like other beyrichiacean families, is predominantly Silurian and Devonian in age, and many of its taxa are of local stratigraphical importance in the Middle Devonian of North America and Europe (Sanchez de Posada, 1977), and in the Upper Devonian of Europe, particularly in the Soviet Union (Gooday & Becker, 1979).

Pribyl (1962) recorded the first treposeiid in Australia, when he referred *Mastigobolbina socialis* Krömmelbein 1954 to *Kozłowskiella* Pribyl 1953. This species was originally described from the Bell Point Limestone of Waratah Bay, Victoria, a stratigraphical unit now regarded as Early Devonian (Zlichovian = early Emsian; Talent, 1956). However, as female specimens of *K. socialis* have yet to be found, the generic and even familial position of this species within the Beyrichiacea is still in doubt (Jones, 1974).

Previously, two treposeiid genera were recognised from the Upper Devonian (Famennian) of the Bonaparte Basin, northwestern Australia (Fig. 1), but, owing to insufficient material, they were left under open nomenclature (Treposeiine gen. A sp. A and Treposeiine gen. B sp. A of Jones, 1968). The specimens were recovered from ostracod samples of the Buttons beds collected from the type section in 1963, and from other sections in the Eight-Mile Creek area of the Burt Range (Figs. 2, 3) in 1965. Further treposeiid specimens were recovered when the type section was resampled by Dr Robert S. Nicoll and the writer in 1978, in an attempt to calibrate the provisional local ostracod zonation established for the Buttons beds (Jones, 1968, fig. 6) within the Famennian time scale by means of conodont biochronology. Results of a palynostratigraphic study of suitable samples have been presented by Playford (1982).

The two provisionally recognised genera and a third treposeiid genus are formally described herein. The material provides evidence of the possible sylobial origin of the crumina within

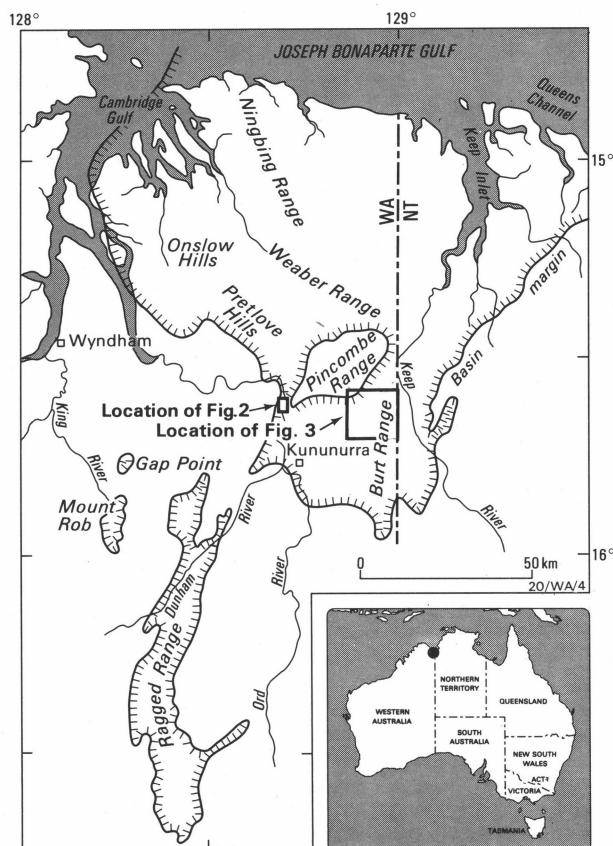


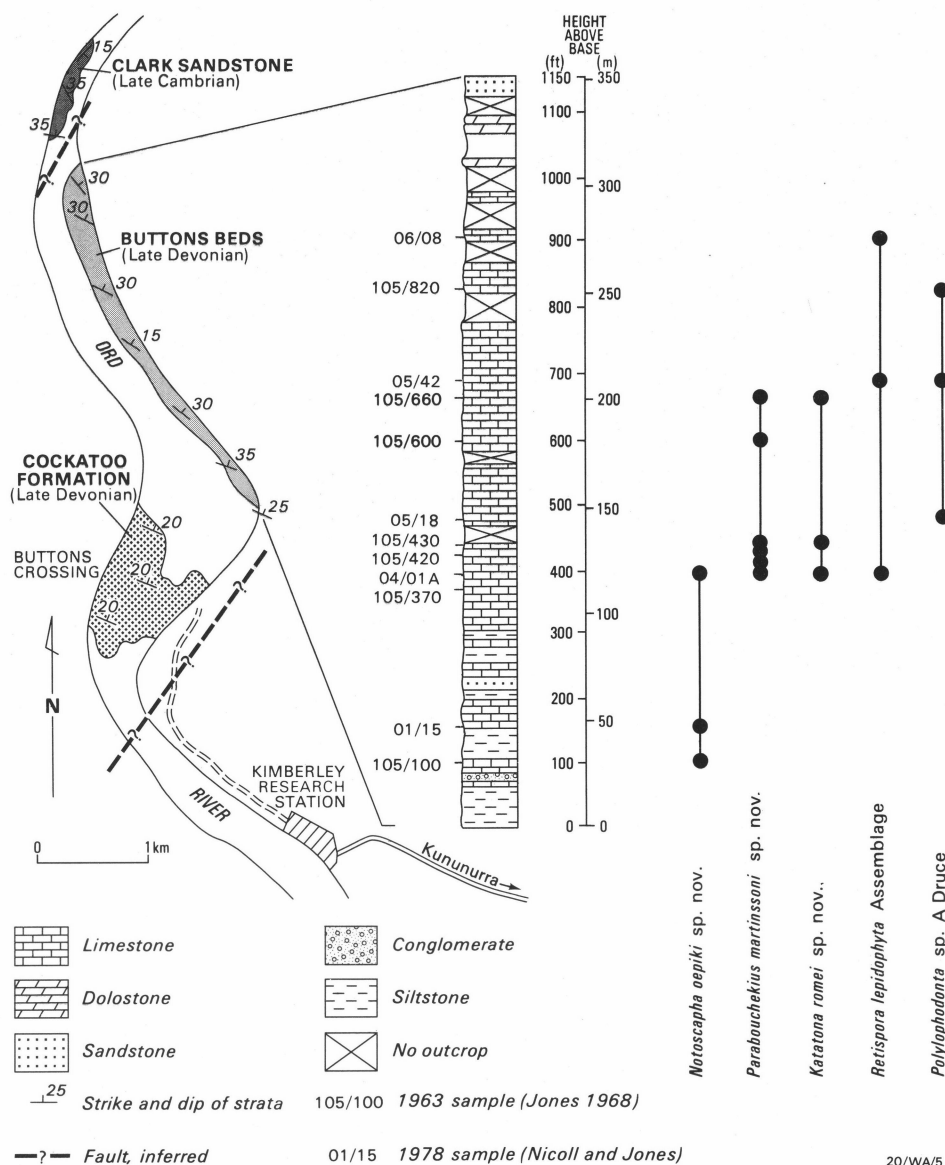
Figure 1. Locality map, Bonaparte Basin of Western Australia and Northern Territory. After Veevers & Roberts (1968, fig. 5).

*Katatona* and allied genera, and brings into question the validity of Rozhdestvenskaya's (1972) concept of the superfamily Aparchitacea. These small treposeiids are of significance in long-distance correlation (Australia to the European USSR and Belgium) of the late Famennian and Strunian. The new taxa described herein are part of the diverse benthic ostracod fauna of the Buttons beds, which will be fully described elsewhere.

## Buttons beds

The Buttons beds are part of a carbonate platform sequence that flanks the Precambrian Pincombe Range inlier, and consist of over 350 m of sandy and silty limestone with minor silty dolomite and sandstone (Veevers & Roberts, 1968, pp. 59–64). The type section (section 105 of Veevers & Roberts, 1968, p. 62, figs. 30, 35) is along the eastern bank of the Ord River, just north of Buttons Crossing (Fig. 2), but neither the base nor the top of

<sup>1</sup>Division of Continental Geology, BMR



**Figure 2. Map and stratigraphic column of the type section of the Buttons beds.** The column shows generalised lithologies and stratigraphical distribution of productive samples with treposellids, the *Retispora lepidophyta* miospore assemblage (Playford 1982), and the conodont *Polylophodonta* sp. A of Druce (Druce 1969; R.S. Nicoll, personal communication). Adapted from Veevers & Roberts (1968, figs. 30, 35).

the formation is exposed here. Other sections have been studied in the Eight-Mile Creek area (Fig. 3), where the Buttons beds are thought to be disconformably overlain by the Early Carboniferous (Tn1b) Burt Range Formation (Jones, 1968), and in the Sorby Hills, where the beds unconformably overlie Precambrian siltstone (Veevers & Roberts, 1968).

The Buttons beds are richly fossiliferous, and are thought to have been deposited in shallow warm lagoons on the landward side of a reef complex that now constitutes the Ningbing Limestone (Veevers, 1969). The fauna includes abundant ostracods (Jones, 1968) and calcareous algae (Veevers, 1970; Mamet & Roux, 1983), calcareous foraminifers (Mamet, personal communication), some brachiopods (Roberts, 1971), corals (Hill, 1954), bivalves, gastropods, stromatoporoids, and crinoids. Conodonts are low in numbers of individuals and types of elements, and are dominated by *Polylophodonta* sp. A of Druce 1969. The results of the 1978 collecting added little to the previous conodont knowledge (Druce, 1969), except that the stratigraphical range of *Polylophodonta* sp. A was determined in the type section between 120 m (395 feet, in sample 04/01A) and 250 m (sample 105/820 of Veevers & Roberts,

1968) above the base. This is a new conodont taxon, and has not been found in samples of the Famennian Ningbing Limestone in association with other conodont elements that are more diagnostic for age determination.

Floral remains in the Buttons beds include the plant *Lepidophloeum australe* (McCoy), and the recently reported microflora (Playford, 1982). This microflora belongs to the *Retispora lepidophyta* Assemblage that was originally defined by Playford (1976) from the lower part of the Fairfield Group of the Canning Basin, Western Australia. On this basis, Playford (1982) regarded the Buttons beds as latest Devonian in age, probably within the Strunian (Fa2d to Tn1a, or early Tn1b) Stage of the Belgian sequence (Conil & others, 1976). This is somewhat younger than previous, faunally based age assessments of the Buttons beds (eg., Jones, 1968; Druce, 1969; Roberts & others, 1967, 1972), which have suggested, a Famennian age (i.e., doII  $\beta$  - doIII; Falc Fa2b). The previous age assessments of the Buttons beds have been reviewed and discussed by Playford (1982), and studies of the entire ostracod fauna currently in progress generally support his assessment of a latest Devonian age.



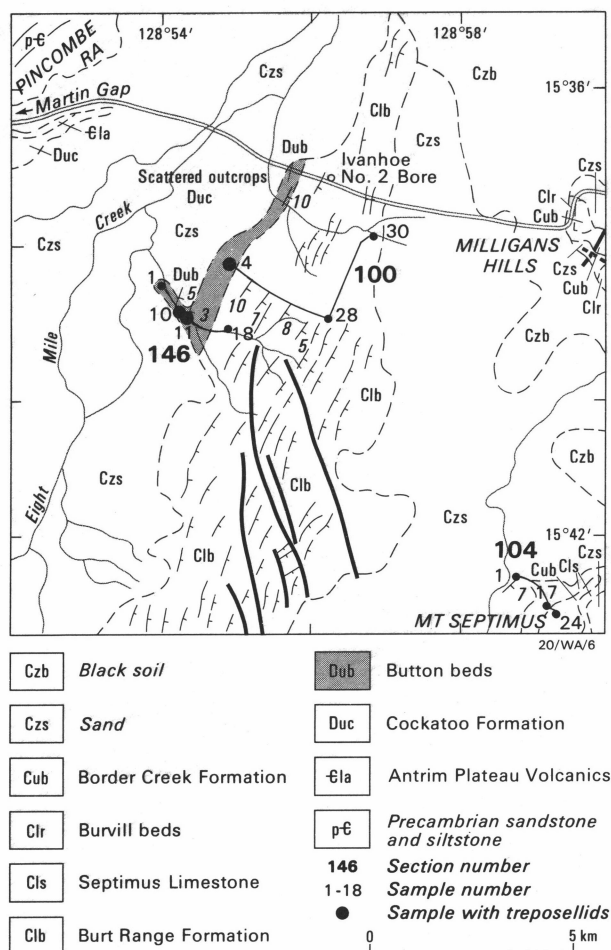


Figure 3. Treposellid localities in Eight-Mile Creek area of the Buttons beds. Adapted from Veevers & Roberts (1968, fig. 39).

## Material and methods

The original study of treposellids from the Buttons beds (Jones, 1968, pp. 16, 17; Fig. 6) was based on a collection recovered from six samples taken from the type section at 100, 370, 420, 600, and 660 feet above the base, and three samples from localities 100/4, 146/10, and 146/11 of Veevers & Roberts (1968) in the Eight-Mile Creek area. Further treposellid specimens were found in two samples collected in 1978 by Robert S. Nicoll and the writer (01/15, 04/01A) from 45 m (149 feet) and 120 m (395 feet) above the base, respectively, in the type section.

Adult specimens are no longer than 0.6 mm; thus, the treposellids are small in comparison with other ostracods in the Buttons beds, and are easily overlooked in washed residues. Treposellid individuals are rare, consisting of only 27 carapaces out of more than one thousand specimens recovered.

The morphological terminology follows Kesling (1951), Jaanusson (1957), Martinsson (1962), and Henningsmoen (1965). The following abbreviations are used in tables and systematic descriptions: L, length of carapace; H, height of carapace; W, width of carapace; Lh, length of hinge-line; H/L, height/length ratio; H/W, height/width ratio; Lh/L, length of hinge-line/length of carapace; C, carapace; l/r, left valve overlapping right valve; f, female; t, tecnomorph. All measurements are given in millimetres. All type and figured specimens are deposited in the Commonwealth Palaeontological Collection (prefix CPC), Bureau of Mineral Resources, Canberra.

## Systematic palaeontology

Class **Ostracoda** Latreille 1802  
 Order **Beyrichicopida** Pokorný 1953  
 Suborder **Palaeocopa** Henningsmoen 1953  
 Superfamily **Beyrichiacea** Matthew 1886.  
 Family **Treposeillidae** Henningsmoen 1954

**Diagnosis.** (after Siveter, 1980, p. 76) Beyrichiacea primarily with tubular structures in the velum, which may be reduced. An originally anteroventral crumina tending to incorporate, or incorporating, a large posterior part of the shell, particularly the syllobium. Dolonoid closing mechanism of the crumina sometimes clearly indicated, but in most cases obsolete.

**Discussion.** The Treposeillidae was originally introduced and later defined by Henningsmoen (1954, 1955) as a subfamily of the Beyrichiidae with a ventrally to posteroventrally situated crumina. The velum is mostly flange-like or reduced to a narrow ridge.

Martinsson (1963, 1965) implied that the Treposeillinae should be raised to family level when he identified three main developmental lines of the beyrichiacean crumina, viz. Craspedobolbinidae, Beyrichiidae, and Treposeillinae. On this basis, Siveter (1980) formally translated Treposeillinae into a family name.

### Genus *Notoscapha* nov.

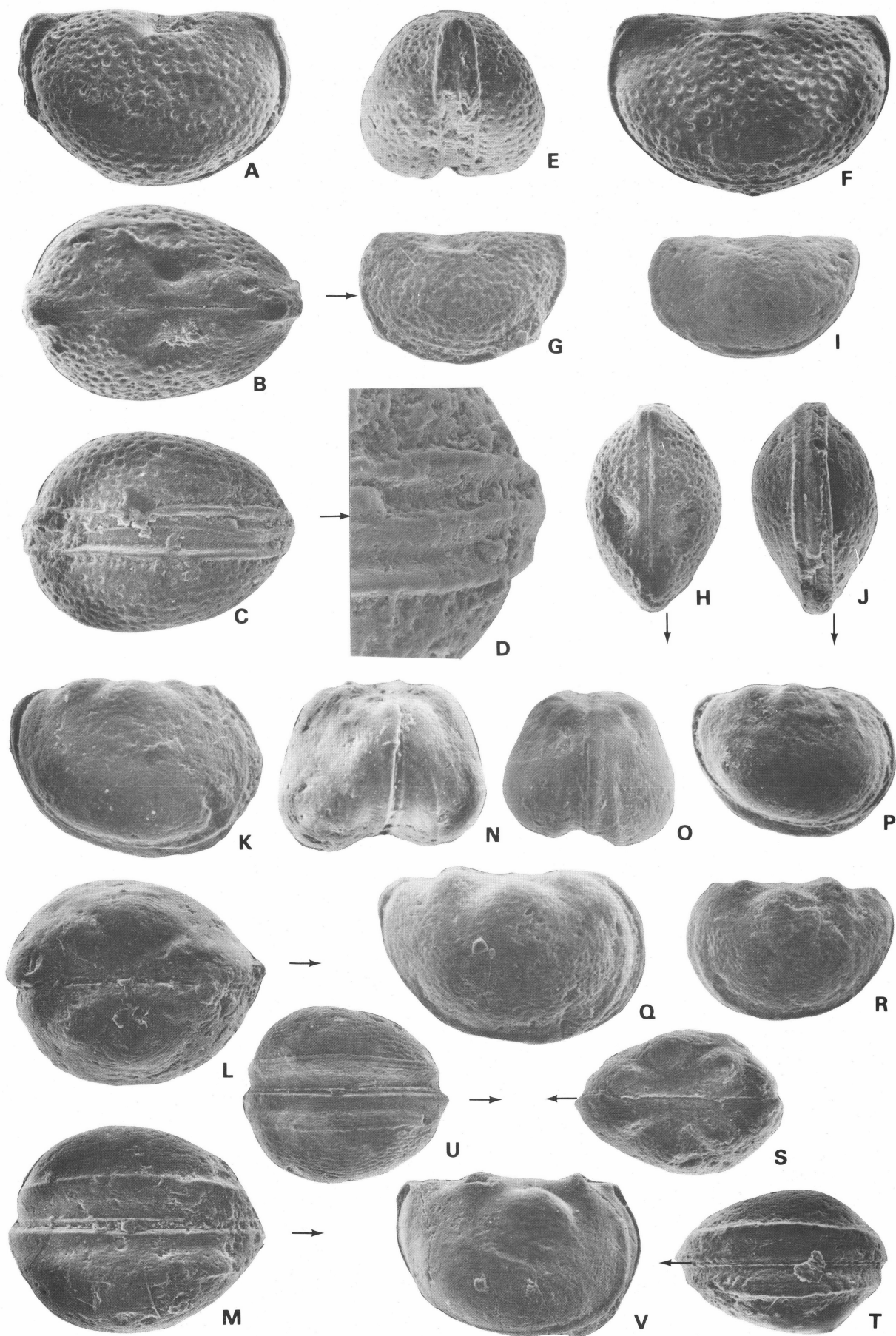
**Derivation of the name.** Greek *notos*, back and *skaphos*, hollowed out, scooped, referring to the pit on the dorsum.

**Type species.** *Notoscapha oepiki* sp. nov.

**Diagnosis.** Small, coarsely reticulate, non-lobate Treposeillidae with a pit just in front of mid-length near a broadly arched dorsum. Velar ridge smooth, narrow, somewhat wider at the anterior and posterior obtuse cardinal corners, complete, close, and parallel to marginal structure. Crumina mostly posteroventral, and laterally overhangs posteroventral part of the velar ridge.

**Discussion.** *Notoscapha* is a small monotypic genus with characters in common with the larger, Middle Devonian treposeillids, *Hibbardia* Kesling 1953, and *Parakozłowskiella* Adamczak 1968: a smooth, narrow, low velar ridge; a smooth, narrow, subvelar field; and coarse reticulation, except for a smooth area at the anterodorsal corner. The dolonoid scar and 'treposeilline bridges' that Martinsson (1962, p. 211) recognised in *Hibbardia*, are not apparent in *Parakozłowskiella* or *Notoscapha*, which appears to be close to *Parakozłowskiella*, but which is distinguished by the absence of an adductor sulcus (S2) and pointed postadductor lobe (L3), and by its small size.

The dorsal pit in *Notoscapha* appears to be a relict feature of a former adductor sulcus, and the genus may be interpreted as another example of lobal reduction in the Treposeillidae, part of the general simplification of the beyrichiacean carapace that took place in the phylogeny of the Beyrichiacea (Martinsson, 1963). The pit may represent the centre of a dorsal muscle-scar field that connected muscles to various appendages, as in many present-day Cyprididae (cf. Smith, 1965). It could hardly have served as the centre of an adductor muscle-scar field, as little mechanical advantage could have been gained from such a position (cf. Adamczak, 1976, pp. 306–309).



*Notoscapa oepiki* sp. nov.  
Figures 4A–J; 5A,B

1968 Treposelline Genus A sp. A Jones (*partim*), p. 16.

**Derivation of the name.** In honour of the late Professor Armin Aleksander Öpik (1898–1983; formerly of the Bureau of Mineral Resources, Canberra), for his contributions to the study of Palaeozoic ostracods in Estonia and Australia.

**Material.** 8C (5f; 3t). Holotype: f CPC24651 (Figs. 4A–E) from locality 04/01A, Buttons beds type section (105 of Veevers & Roberts, 1968), east bank of Ord River, 120 m above the base. Paratypes: f (Fig. 4F; destroyed during SEM photography), f CPC24652 (Fig. 5A) and t CPC24653 (Fig. 5B), t CPC24654 (Figs. 4G,H), and t CPC24655 (Figs. 4I,J), all from locality 04/01A. Other unfigured f adults at localities 105/100 and 01/15, Buttons beds type section, at 30 m and 45 m above the base, respectively.

**Diagnosis.** As for the genus.

**Description.** Lateral outline preplete in t, subamplete in f. End outline biconvex, heart-shaped, ventrally swollen in f; drop-shaped, dorsally swollen in t. Dorsal border gently sinuous in lateral view, consisting of a slight concavity in the vicinity of the median pit, and a low inflation behind. Hinge line straight, long (0.86–0.92L), slightly depressed in a shallow groove between a fine dorsal crista on each valve. Cardinal corners obtuse. Dorsum broadly arched in transverse section, separated from lateral surface by an obtuse bend at the base of the dorsomedian pit. Outline in dorsal and ventral views subelliptical, posteriorly swollen in f, subelliptical in t.

Velar ridge and crumina as in generic diagnosis; subvelar field narrow; no dolonoid scar or 'treposelline bridges'.

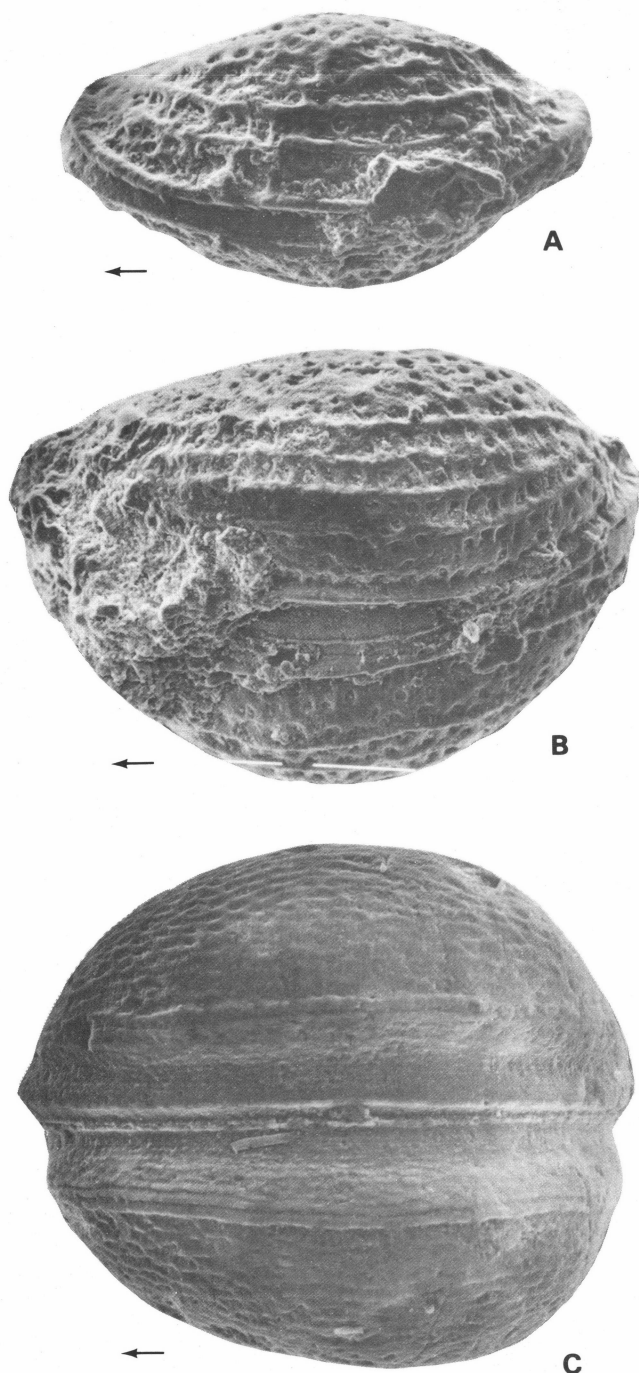
Surface reticulate except for smooth areas in the dorsal depression, anterodorsal region, velar ridge, and subvelar field. In addition to the fine crista on the dorsum, each valve bears three to four long fine cristae on the base of the crumina of f and two long cristae in the ventral region of t. Pore-like openings on each valve, irregularly distributed in the subvelar field and the supravelar field close to the velar ridge (Fig. 4D).

Internal features of valves not known.

**Dimensions.**

		L	H	W	H/L	H/W	Figs.
Holotype	f CPC24651	0.60	0.39	0.45	0.65	0.87	4A–E
Paratype	f destroyed	0.61	0.39	0.45	0.64	0.87	4F
Paratype	f CPC24652	0.58	0.38	0.48	0.66	0.79	5A
Paratype	t CPC24653	0.50	0.30	0.27	0.60	0.90	5B
Paratype	t CPC24654	0.48	0.30	0.29	0.63	0.97	4G,H
Paratype	t CPC24655	0.45	0.29	0.28	0.64	0.97	4I,J

**Remarks.** The presence or absence of cruminal cristae appears to be a factor of preservation. The pore-like openings may be the external openings of normal pore canals, but this cannot be proved without an examination of the internal surface of single valves.



**Figure 5. Treposellidae from the Buttons beds (type section):**

A,B, *Notoscapa oepiki* sp. nov., to show cristae; C, *Parabouchekius martinsoni* sp. nov. to show pore-like openings; arrows indicate anterior end.

*Notoscapa oepiki* sp. nov.: A, tecnomorph carapace CPC24653, ventral view, tilted (x140); B, f carapace CPC24652, ventral view, tilted (x140).

*Parabouchekius martinsoni* sp. nov.: C, f carapace CPC24657, ventral view (x170); same specimen as illustrated in Fig. 4U).

**Figure 4. Treposellidae from the Buttons beds (type section):**

A–J, *Notoscapa oepiki* sp. nov.; K–V, *Parabouchekius martinsoni* sp. nov. Magnification x80, unless otherwise indicated; arrows indicate anterior end in dorsal and ventral views.

*Notoscapa oepiki* sp. nov. A–E, Holotype f carapace CPC24651, right lateral, dorsal and ventral views, ventral view of anterior end, showing pore-like openings (x200), and posterior view; F, f carapace (destroyed during SEM photography), left lateral view; G,H, tecnomorph carapace CPC24654, left lateral and dorsal views; I,J, tecnomorph carapace CPC24655, right lateral and ventral views.

*Parabouchekius martinsoni* sp. nov. K–N, Holotype f carapace CPC24656, right lateral, dorsal, ventral, and posterior views; O,P, f carapace CPC7056, anterior and right lateral views (previously illustrated by Jones 1968, pl. 1, figs. 10a–c); Q–T, tecnomorph carapace CPC24658, right lateral (x100), left lateral, dorsal and ventral views; U, f carapace CPC24657, ventral view; V, f carapace CPC24663, right lateral view.

All specimens previously recorded from locality 105/100 (Jones 1968, Fig. 6) under the open name *Treposeiline* gen. A sp. A are now included in this species. Thus, *Notoscapha oepiki* is known to range over the lower part of the Buttons beds, from 30 to 120 m above the base of the type section.

#### Genus *Parabouchekius* nov.

**Derivation of the name.** Greek *para*, near, and *Bouchekius*, referring to the morphological relationship to the genus *Bouchekius* Rozhdestvenskaya 1972.

**Type species.** *Parabouchekius martinssoni* sp. nov.

**Diagnosis.** Small, finely reticulate Treposeillidae with a wide, flattened, weakly lobate dorsum that merges imperceptibly into the lateral surface of the crumina. Lobation consists of a broad dorsocentral lobe just below the hinge line, a low cuspidate posterior lobe, and a smaller anterior cusp both projecting slightly above the hinge line. Velar ridge smooth, narrow, complete, traceable from the posterodorsal corner, along the base of the crumina to the anterior cusp. Crumina tumid, located in ventral part of the carapace without obscuring the velar ridge in lateral view; subvelar field of crumina wide, striate, and contains a row of pore-like openings.

**Discussion.** The type species of the monotypic *Parabouchekius* is morphologically similar to the type species of *Bouchekius* Rozhdestvenskaya 1972, *B. rotundus* Rozhdestvenskaya, 1972. Both species are small and the f carapaces possess strongly inflated and ventrally located cruminae, so that the width of the carapace exceeds the height, and forms a subcircular outline in dorsal and ventral views. Other similarities are the slight l/r overlap, and somewhat rounded cardinal corners.

*Bouchekius* and *Parabouchekius* differ in the venter, dorsum, and surface microsculpture. In *Bouchekius* the velar ridge is close and parallel to the marginal structure, whereas in *Parabouchekius* the velar ridge is slightly bowed and delimits a wider subvelar field. The dorsum of *Bouchekius* is narrow, slightly channelled, and non-lobate, whereas the dorsum of *Parabouchekius* is wide, almost flattened, and weakly lobate. The broad dorsocentral lobe in *Parabouchekius* may be a highly inflated preadductor lobe (L2) that has completely effaced the adductor sulcus (S2). *Parabouchekius* has also a longer hinge-line and a shorter carapace height ( $Lh/L > 0.73$ ;  $H/L < 0.79$ ) than *Bouchekius* ( $Lh/L < 0.64$ ;  $H/L > 0.79$ ). *Parabouchekius* is finely reticulate; *Bouchekius* is smooth.

#### *Parabouchekius martinssoni* sp. nov. Figures 4K–V; 5C

1968 Treposeiline Genus A sp. A Jones, p.16, pl. 1 figs. 10a–c, not 11a, b (= *Katatona romei* sp. nov. t)

**Derivation of the name.** In honour of the late Professor Anders Martinsson (1930–1983; formerly of the University of Uppsala, Sweden), who originally pointed out to the author the treposeiline affinities of this species.

**Material.** 11 C (8 f; 3 t) Holotype: f CPC24656 (Figs. 4K–N) from locality 04/01A, Buttons beds type section (105 of Veevers & Roberts 1968), east bank of the Ord River, 120 m above the base. Paratypes: t CPC24658 (Figs. 4Q–T from locality 04/01A, f CPC7056 (Figs. 4O,P; previously illustrated by Jones 1968, pl. 1, figs. 10a–c) from locality 105/430, Buttons beds type section, 430 feet (131 m) above the base, f CPC24657 (Figs. 4U, 5C) from locality 105/660, 660 feet (200 m) above the base, and f CPC24663 (Fig. 4V) from locality 105/370, 370 feet (113 m)

above the base. Unfigured C occur in 105/660, and at other levels in the type section of the Buttons beds at 105/600 and 105/420, and in the Eight-Mile Creek area, Burt Range at 100/4.

**Diagnosis.** As for the genus.

**Description.** Lateral outline subovate, preplete in t and f. End outline heart-shaped ventrally swollen with a broad orthoclinal dorsum; more inflated in f. Cardinal corners rounded. Hinge-line straight, moderately long (0.73–0.86L). Lobation weakly developed, consisting of three low broad swellings along the dorsal border (see generic diagnosis). The broad dorsocentral lobe (?L2) merges into the syllobium, which in turn, is widened by the expansion of the crumina in the ventral region. Outline in dorsal and ventral views, subelliptical, centrally swollen to subcircular in f, subelliptical in t.

Velar ridge smooth, parallel to free margin, not obscured by the crumina in lateral view. Subvelar field wide, depressed, bearing fine parallel striae, and one or two (?) row(s) of pore-like openings on each valve; no dolonoid scar or 'treposeiline bridges'. Free margin a smooth narrow ridge.

Lateral (supravelar) surface of carapace finely reticulate.

Internal features of valves not known.

#### Dimensions.

		L	H	W	H/L	H/W	Figs.
Holotype	f CPC24656	0.55	0.40	0.46	0.73	0.87	4K–N
Paratype	f CPC24657	0.48	0.38	0.41	0.79	0.93	4U,5C
Paratype	f CPC7056	0.46	0.35	0.39	0.76	0.90	4O,P
Paratype	t CPC24658	0.45	0.31	0.33	0.69	0.94	4Q–T
Paratype	f CPC24663	0.56	0.40	0.45	0.71	0.89	4V

**Remarks.** The muri that define the reticulae appear highly susceptible to abrasion, a process that may account for the patches devoid of reticulae on some carapaces. It is not known whether the pore-like openings (Fig. 5C) are the external openings of normal pore canals, because the corresponding openings on the internal surface of the shell cannot be determined without examining single valves.

#### Genus *Katatona* nov.

**Derivation of the name.** Greek *katatonos*, broader than high, referring to the width of the adult female carapace.

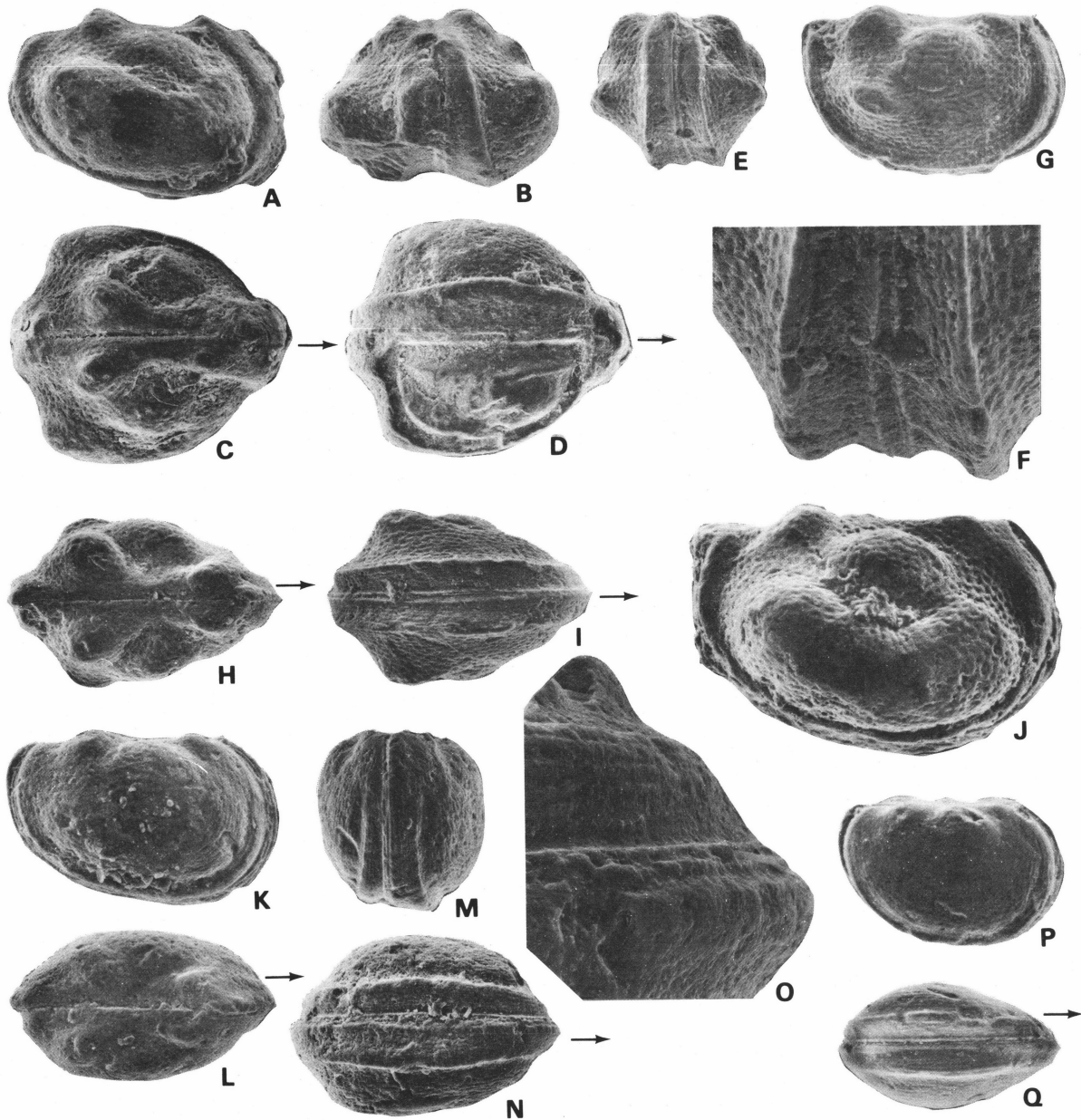
**Type species.** *Katatona romei* sp. nov.

**Other species.** *Kegelites acutilobatus* Rome 1971; Tn1a, Feluy, Namur Synclitorium, Belgium.

**Diagnosis.** Small, finely reticulate Treposeillidae with a dorsal lobation set off from the crumina by a distinct syllobial sulcule. Lobation consists of a broad dorsocentral node below the hinge line, a cuspidate posterior lobe, and a smaller anterior cusp projecting slightly above the hinge line. Velar ridge smooth, narrow, complete, traceable from the posterodorsal corner, along the base of the crumina to the anterior cusp. Crumina laterally tumid in posteroventral part of the syllobium, without obscuring the velar ridge; width considerably exceeds the height of the carapace; subvelar field striate; wide in f, narrow in t.

**Discussion.** The type species closely resembles *Kegelites acutilobatus* Rome 1971, described from the Feluy section in the Namur Synclitorium, Belgium. Rome (1971, p.11, Figs. 1,2,6,7) described and indicated a 'kirkbyid' pit in his drawings of the type specimens, and Becker & Bless (1974, fig. 20), who referred the species to *Kelletina* Swartz 1936 (Kellettinidae Sohn 1954;





**Figure 6. Treposellidae from the Buttons beds (type section):**

*Katatona romei* sp. nov. Magnification x80, unless otherwise indicated; arrows indicate anterior end in dorsal and ventral views.

A-D, Holotype f carapace CPC7058, right lateral, posterior, dorsal, and ventral views (previously illustrated by Jones 1968, pl. 1, figs. 13a,b); E-I f carapace CPC24660 with rudimentary crumina, posterior view, posterior view of subvelar field (x240), right lateral, dorsal and ventral views; J, f carapace (destroyed during SEM photography), right lateral view (x100); K-O, tecnomorph carapace CPC 24659, right lateral, dorsal, anterior, and ventral views, and detail of anterior end of venter (x400); P,Q, tecnomorph carapace CPC7057, right lateral and ventral views (previously illustrated by Jones 1968, pl. 1, figs 11a,b).

Kirkbyacea Ulrich & Bassler 1908), showed a smaller subcentral (S2) pit in their drawings of the species. It is difficult to see such a pit in the excellent photographs of this species provided by Becker & Bless (*in* Becker & others, 1974, pl. 14, figs. 1-5), unless it is obscured within part of the syllobial sulcule. However, these illustrations and those originally provided by Rome (1971) demonstrate to my satisfaction, that 'K'. *acutilobatus* has cruminal dimorphism and belongs to the Beyrichiacea not the Kirkbyacea, a superfamily that has no known dimorphism. Moreover, 'K'. *acutilobatus* is a treposellid, because its crumina is incorporated into the syllobium. Presumably, Becker & Bless (*in* Becker & others, 1974) referred 'Kegelites' *acutilobatus* Rome 1971 to *Kellettina* because of the lack of a well-defined 'kirkbyid' pit, a definitive

character of the Kellettinidae. Adductor pits are also known to be present in the Beyrichiacea; for example in the craspedobolbinid genus *Bolbineossia* Kesling, Heany, Kauffman & Oden 1958.

*Katatona* superficially resembles *Schweyerina* Zaspelova 1952 (type species *S. ovata* Zaspelova 1952; Upper Devonian, Frasnian, Russian Platform) in that both are small and reticulate, and have a generally similar outline in lateral view, a velar ridge, and cuspidate posterodorsal lobe. However, *Katatona* possesses cruminal dimorphism and a broad dorsocentral node, whereas *Schweyerina*, has no known dimorphism and is more laterally compressed when compared to tecnomorphs of *Katatona*.

*Katatona romei* sp. nov.

Figure 6A–Q

1968 Treposelline Genus B sp. A Jones, p. 17, pl. 1, figs. 13a, b; text fig. 8 (= f)

1968 Treposelline Genus A sp. A Jones (*partim*), p. 16, pl. 1, figs 11a, b (= t); not figs 10a–c (= *Parabouchekius martinssoni* sp. nov.).

**Derivation of the name.** In honour of the late Dr Dom Remacle Rome O.S.B. (1893–1974; formerly of the University of Louvain, Belgium) for his contribution to the study of Tournaisian ostracods.

**Material.** 9C (5 f; 3 t). Holotype: f CPC7058 (Figs. 6A–D; previously illustrated by Jones 1968, pl. 1, Figs. 13a,b) from locality 105/430, Buttons beds, type section (105 of Veevers & Roberts, 1968), east bank of Ord River, 430 feet (131 m) above the base. Paratypes: f (Fig. 6J; destroyed during SEM photography), an abnormal f CPC24660 (Figs 6E–I), and t CPC 24659 (Figs. 6K–O), all from locality 04/01A, Buttons beds, type section 120 m above the base; t CPC7057 (Figs. 6P–Q; previously illustrated by Jones 1968, pl.1, figs. 11a,b) from locality 105/660, Buttons beds 660 feet (200 m) above the base of the type section; unfigured f CPC24661 from locality 146/11, CPC24662 from locality 146/10; and two from locality 100/4, all from the Buttons beds, Eight-Mile Creek, in the Burt Range area.

**Diagnosis.** *Katatona* with arrow-head-shaped outline in dorsal and ventral views, posterior end of crumina wide and subangulate, velar ridge slightly arched along base of crumina, cristae absent.

**Description.** Lateral outline subelongate preplete in t and f. End outline subquadrate in t, and laterally globose in f. Hinge line straight, moderately long (0.78–0.88L), slightly depressed in a shallow groove. Cardinal corners subobtuse, rather than rounded. Lobation moderately developed (see generic diagnosis and discussion). The dorsocentral (?L2) and posterior (?L3) lobes pass imperceptibly into the central part of the carapace in t, and are separated from the crumina by a distinct syllobial sulcule in f. Outline in dorsal and ventral views, arrow-head-shaped in f, subelliptical in t.

Velar ridge and crumina as in generic diagnosis; subvelar field wide, depressed, bearing fine parallel striae and some pore-like openings; no dolonoid scar or 'treposelline bridges'. Free margin a smooth narrow ridge.

Lateral (supravelar) surface of carapace finely reticulate.

Internal features of valves not known.

**Interrupted cruminal metamorphosis.** Specimen CPC24660 (Figs.6E–I) bears a uniformly developed calcarine-like protuberance in the posterocentral area of each valve, which is absent in t specimens (eg, CPC24659, Figs 6K–O; CPC7057, Figs. 6P,Q). The bilateral symmetry of the valves indicates that the specimen is not a monstrosity, and there is no evidence of mechanical injury. The posterocentral structure corresponds to the point of maximum swelling in cruminate specimens, and it seems reasonable to regard it as an aborted crumina. The crumina is very small, and is abnormal only in the sense that its development was arrested at an early stage. The animal calcified its soft cuticle before the crumina had completely developed, perhaps as a result of a harmful chromosome mutation. The significance of the type of specimen for the construction of morphogenetic and phylogenetic models is discussed below.

**Dimensions.**

		L	H	W	H/L	H/W	Figs.
Holotype	f CPC7058	0.55	0.35	0.45	0.64	0.78	6A–D
Paratype	f destroyed	0.55	0.36	0.45	0.65	0.80	6J
Paratype	f CPC24659	0.49	0.29	0.30	0.59	0.97	6K–O
Paratype	f CPC24660	0.47	0.30	0.32	0.64	0.94	6E–I
Paratype	f CPC24661	0.48	0.34	0.37	0.71	0.87	–
Paratype	f CPC24662	0.45	0.30	0.32	0.67	0.94	–
Paratype	f CPC7057	0.41	0.27	0.29	0.66	0.93	6P,Q

**Comparisons.** The characters that *K. romei* have in common with *K. acutilobata* are given in the generic diagnosis; those that distinguish *K. acutilobata* are given below. The pore-like openings may be the external openings of normal pore canals, but this cannot be proved without an examination of the internal surface of single valves.

*Katatona acutilobata* (Rome 1971)

1971 *Kegelites acutilobata* Rome, p.11–13, figs. 1–10.

1974 *Kelletina acutilobata* (Rome 1971); Becker & Bless, p. 17, figs. 19,20

1974 *Kelletina acutilobata* (Rome 1971); Becker & Bless (*in* Becker & others 1974), pl. 14, figs. 1–5.

1982 *Kelletina acutilobata* (Rome 1971); Lethiers, p. 236, table 6, planche hors-texte 1.

1983 *Kelletina acutilobata* (Rome 1971); Bless, p. 32, Fig. 5.15.

**Differential diagnosis.** *Katatona* with subcircular outline in dorsal and ventral views, posterior end of crumina broadly rounded, velar ridge straight along base of crumina, crumina with 2 or 3 cristae.

**Lectotype.** f (Rome 1971, Figs. 1–5; depository and registered number not given<sup>1</sup>).

**Paralectotype.** t (Rome 1971, Figs. 6–10; depository and registered number not given<sup>1</sup>).

**Dimensions.**

		L	H	W	H/L	H/W	Figs.
Lectotype	f 0.67	0.42	0.48	0.63	0.87		
Paralectotype	t 0.65	0.39	0.30	0.60	1.30		
FE4a–21	f 0.60	0.34	0.50	0.57	0.68		Becker & Bless pl.14, fig. 1
FE4a–22	f 0.54	0.35	0.41	0.65	0.85		fig. 2
FE4a–15	t 0.58	0.37	0.35	0.64	1.06		fig. 3
FE4a–16	t 0.38	0.22	–	0.58	–		fig. 4
FE4a–17	t 0.56	0.35	0.31	0.62	1.13		fig. 5

**Remarks.** Becker & Bless (1974, p.17) studied some 30 specimens, mostly complete carapaces, '... and all belonging to a smaller instar than Rome's specimens', from the Feluy and Onoz sections in the Namur Synclinorium. However, the recognition of sexual dimorphism in the 5 specimens figured by them (*in* Becker & others, 1974, p.66, pl. 14, figs. 1–5) indicates that the adult size is more variable than Rome originally thought. The dimensions of these specimens have been calculated from the figures and their stated magnifications, as these data are not available in the original source. Unfortunately, I was unable to study topotype specimens, as samples collected by Dr Eric Groessens (Service Geologique de Belgique) and myself (27.8.75) from the type locality at Feluy (FE4 and FE3 of Becker & Bless 1974, p.16, Fig. 19) failed to yield ostracods. Other remarks on this species are included above (see generic discussion).

<sup>1</sup>Now known to be deposited in the Laboratoire de Paleontologie, Institut de Geologie, Université Catholique de Louvain, Louvain-la-Neuve, Belgium (Dr. M. Coen, personal communication, 17 May 1984).

## Discussion

### Origin of the crumina

The abrupt morphological change in the carapace of the female beyrichiacean from the penultimate to the final moult stage, without transitional forms, does not demonstrate how the crumina was developed. Martinsson (1960, 1962) proposed a possible solution to this problem in a remarkably detailed study of some extremely rare female valves that had calcified before the crumina had completely developed (examples of 'interrupted cruminal metamorphosis'). The incomplete cruminae of these craspedobolbinid valves formed a graded morphogenetic series, which Martinsson regarded as ontogenetic evidence in support of a dolon origin for the crumina and descentance of the Beyrichiacea (with crumina opening internally) from the Eurychilinaea (with dolon opening externally).

Kesling (1969, p. 284) discussed Martinsson's cases of 'interrupted cruminal metamorphosis', and concurred that those females with aborted cruminae died before completion of the final 'metamorphosis'. However, the fact that they were found at all shows that the development of the cruminae was arrested when the ostracods were alive and able to produce a new, and final carapace (cf. pathological pygidium of *Glyptagnostus stolidotus*; Opik 1967, p. 168). If these ostracods had died in the critical stages of moulting, the epidermal cells of the outer lamellae would not have calcified their valves (Turpen & Angell, 1971; Okada 1982). Thus, there is no reason to suppose that the beyrichiacean females showing 'interrupted cruminal metamorphosis' did not enter the adult stage and live as long as their sisters with normal cruminae. Martinsson (1962 p. 124, fig. 40G) found that 'pathological and teratological manifestations are extremely rare in the fossil parts of the beyrichiids' and did not regard his examples of 'interrupted cruminal metamorphosis' as pathological deformities.

When Martinsson (1965, p.117) summarised his views on beyrichiacean phylogeny, cruminal development in craspedobolbinids and beyrichiids had been demonstrated, based on females with aborted cruminae, but no such treposellid specimens had been found. The carapace CPC24660 of the treposellid *Katatona romei* possibly shows a rudimentary crumina on the syllobium, as described above. Thus, the crumina in *Katatona* may have had a syllobial rather than a velar origin. The proliferation of epidermal cells in the proecdysis period may have been insufficient to produce a normal-sized crumina, perhaps because of a harmful chromosome mutation. Traces of dolonoid scars or 'treposelline bridges' connecting velum and crumina, are absent in *Notoscapha*, *Parabouchekius*, and *Katatona*. However, there does appear to be a relationship between the width of the subvelar field and the degree of cruminal inflation (Fig. 7). In *Notoscapha*, the subvelar field is narrow, and the crumina is swollen posteroventrally, so that it overhangs the velar ridge. In *Parabouchekius*, and to a greater degree in *Katatona*, the subvelar field is wider, as the crumina tends to expand laterally, without overhanging the velar ridge.

### Suprageneric classification

The three new genera described herein can be accommodated within Martinsson's (1962, p.4) phylogeny in that the Treposellidae 'had originally an anteroventral crumina which is in most forms only the anterior end of a voluminous mainly posteroventral cruminal swelling'. Phylogenetically, the three genera are advanced treposellids; the crumina is incorporated into the posteroventral part of the carapace in *Notoscapha* and *Katatona*, and in the ventral part of the carapace in

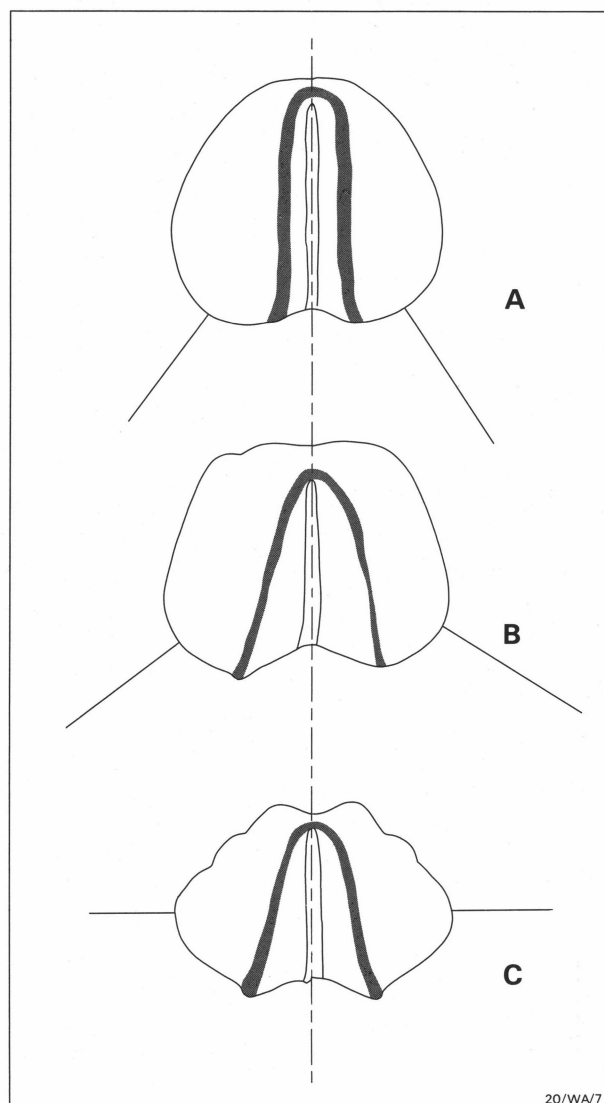


Figure 7. Schematic diagrams of the posterior ends of the females of (A) *Notoscapha oepiki* sp. nov., (B) *Parabouchekius martinssoni* sp. nov., and (C) *Katatona romei* sp. nov., (x80), showing the main direction of development of the crumina from its presumed point of origin, in relation to the width of the subvelar field.

*Parabouchekius*. In *Katatona*, the crumina is clearly defined and separated from the dorsal cusp by a syllobial sulcule (or semisulcus *sensu* Henningsmoen 1953, p. 188), but in *Notoscapha* and *Parabouchekius* it merges imperceptibly into the dorsal surface. The velum is a smooth narrow ridge that passes under the crumina without change in position or structure, and does not appear to participate in its formation. As with the treposellid genera *Phlyctiscapha* Kesling 1953, *Kozłowskiella* Pribyl 1953 and *Parakozłowskiella* Adamczak 1968, the new genera lack traces of dolonoid closing mechanisms that suggest in other treposellids a velar origin for the crumina (eg., the 'treposelline bridges' in *Strepula* Jones & Holl 1886, *Garniella* Martinsson 1962, *Bolbiprimitia* Kay 1940, *Retisacculus* Martinsson 1962 and *Prisculella* Martinsson 1966; Martinsson 1962, fig. 89; 1966, figs. 3, 4B; also *Treposella* Ulrich & Bassler 1908, and *Hibbardia* Kesling 1953; Martinsson 1962, fig. 97). The last two mentioned genera clearly show the external traces of the anteroventral origin of the cruminal development (Martinsson, 1962, p. 211).

Rozhdestvenskaya (1972) recognised the same type of cruminal dimorphism (as is here described for the new treposellids) in several relatively small, smooth, non-lobate, non-sulcate





The small dimorphic species described from the Upper Devonian of the USSR under *Aparchites* (e.g., *A. crassus* Polenova 1953, *A. volgensis* Rozhdestvenskaya & Netchaeva 1972) should be removed from the genus. Swartz (1969) showed that the lack of preserved marginal ornament in the holotype of *A. whiteavesi* reduced the value of the use of adventral structures for assessing the concepts of the genus and family. The holotype, the only known specimen, is a mostly exfoliated steinkern that appears to have a channelled free margin on both valves. The marginal grooves on the internal mould are the impressions of internal thickenings of the edges of the valves (Swartz, 1969, pl. 145, figs. 3,5), and are not homologous with the channelled free margins on the external surfaces of the carapaces of *A. crassus* and *A. volgensis*. These species, however, possess many features in common with the type species of *Boucchekius* Rozhdestvenskaya 1972 (*B. rotundus* Rozhdestvenskaya 1972): a small, highly tumid, balloon-like, non-lobate carapace with ventral crumina and velar ridges that are only superficially similar to the internal thickening on the exfoliated venter of the holotype of *Aparchites whiteavesi*. I suggest that these species should be referred to *Boucchekius*.

Other apparently dimorphic species from the Upper Devonian of the European USSR described under *Aparchites* Jones 1889 (e.g., *A. asymmetricus* Tschigova 1963; *A. elegans* Gurevitch 1972; *A. nimius* Tschigova 1977; *A. globulus* Posner 1979) are probably also incorrectly assigned to this genus. For example the holotype of *A. asymmetricus* Tschigova (1963, pl. 1, figs. 1a, b) appears to be very similar to the tectomorph paratype of *Reversoscapha jaanussoni* Rozhdestvenskaya (1972 pl. 10, figs. 1 pr, s,z,d). The latter figures may be compared, in turn, with the specimen figured by Rozhdestvenskaya (1972, pl. 5, figs. 3 pr,z) as *Aparchites asymmetricus* Tschigova. Therefore, the new combination *Reversoscapha asymmetrica* (Tschigova 1963) is suggested, with *R. jaanussoni* Rozhdestvenskaya, 1972 as a possible junior synonym.

To conclude, *Boucchekius*, *Reversoscapha*, and *Copelandites*, and the new Australian genera proposed in this paper are characterised by treposelline cruminae, the metamorphosis of which may be syllobial in origin. They have lost all trace of the dolonoid scars that indicated the anteroventral and velar origin

of the crumina in their craspedobolbinid and earlier treposellid ancestors. Therefore, I regard these genera and *Phlyctiscapha* Kesling 1953 (the genus selected by Ivanova as an example of so-called 'aparchitid dimorphism') not as *Aparchitacea* (*sensu* Rozhdestvenskaya 1972), but as treposellids in a late phase of their phylogeny.

This type of dimorphism is an evolutionary advanced type of cruminal dimorphism (= beyrichiid *sensu* Ivanova 1979); the site of origin of the crumina has possibly shifted from the velum to the syllobium, but it is still fundamentally cruminal in nature. It does not appear to be sufficiently distinctive to warrant a separate name, and Ivanova's (1979) term 'aparchitid dimorphism' is misleading and should be rejected because of the questionable status of the type species of *Aparchites*, and its holotype.

#### Age and correlation (Fig. 8)

The potential value of some of these small treposellids for long distance correlations during the latest Devonian (i.e., late Famennian and Strunian) is exemplified by the distribution of *Katatona*, *Boucchekius*, and the related genus *Paraboucchekius*.

In Belgium, *Katatona acutilobata* (Rome 1971) is present in the lower part of the Hastarian-Strunian sequence of Feluy and Onoz, on the northern flank of the Namur Synclinorium (Rome 1971; Becker & Bless 1974). This species appears to be confined to the Strunian, notwithstanding the question as to whether the Namur Synclinorium contains the lateral equivalent of the Calcaire d'Etroeungt (Tn1a) (Conil, 1959; Coen-Aubert & others, 1981), or whether it is present at all (Streel, 1977; *in* Austin & others, 1970). Adopting Streel's (*in* Austin & others, 1970) opinion, Rome (1971, 1977), regarded the ostracod fauna that he described from Feluy and Onoz as entirely Hastarian (Tn1b) in age; unfortunately he did not provide a chart of the ranges of the taxa within the sections, and the evidence of a Tn1b age, based on the TE spore zone, was confined to the upper parts of these sections. Becker & Bless (1974, p.17) have shown, however, that the ostracods *Kelletina* (i.e. *Katatona* in this paper), *Glyptolichwinella*, and the eridostracan *Cryptophyllus* are restricted to the lower parts of

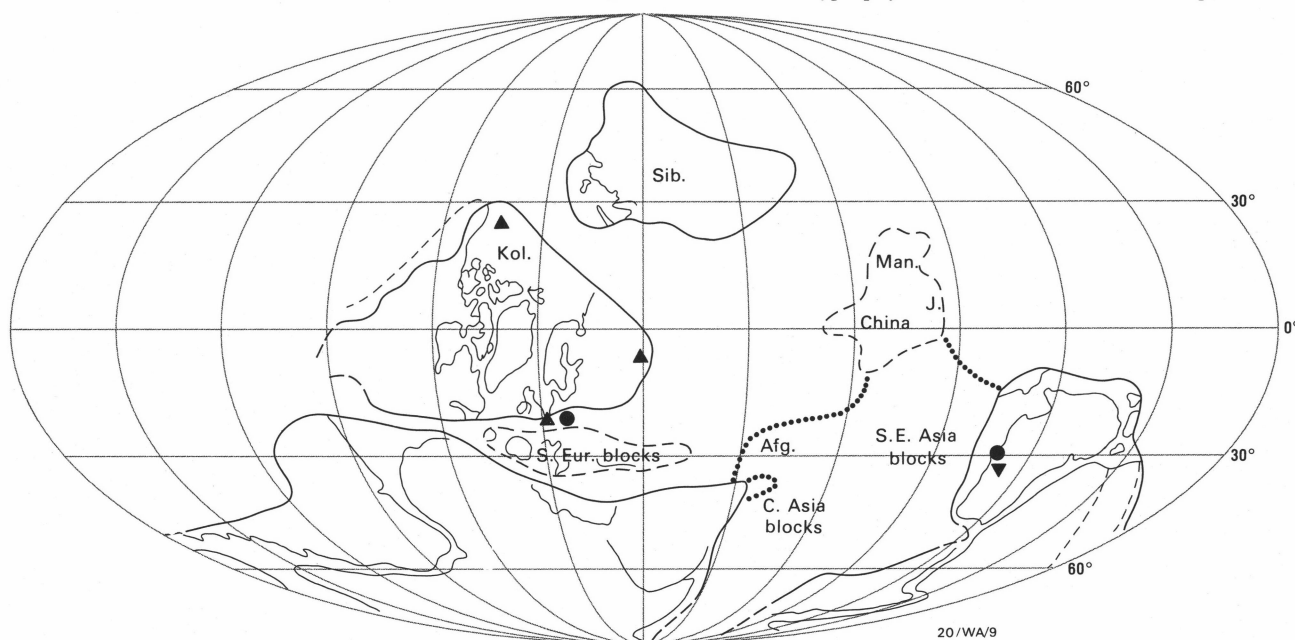


Figure 9. Distribution of the treposellid genera *Boucchekius* (triangles) during the Famennian, and *Paraboucchekius* (inverted triangles) and *Katatona* (circles) during the Strunian (Fa2d–Tn1a), plotted on Tarling's (1980, fig. 6) reconstruction of the continental blocks for the Early Carboniferous.

Afg. = Afghanistan, J = Japan, Kol = Koloyma Block, Man. = Manchurian Block, Sib. = Siberian Block, and S. Eur. = Southern European Blocks.

the Feluy and Onoz sections, and have confirmed the correlation proposed by Conil (1959) and his interpretation of a Tn1a age. The presence of *Katatona romei* within the range of the *Retispora lepidophyta* microfloral assemblage in the Buttons beds of northwestern Australia (Playford, 1982) provides further support for Conil's interpretation of a Tn1a age for the lower parts of the Feluy and Onoz sections, and suggests that they may even be as old as Fa2d. This interpretation has a bearing on the new benthic zonation, recently proposed by Lethiers (1982, table 6) for the Upper Devonian of the Ardenne and the Boulonnais. Thus, accepting Conil's (1959) original (Tn1a) correlation for the lower parts of the Feluy and Onoz sections, *Katatona acutilobata* (Rome, 1971), *Paracavellina coela* Rome 1971 and other species described by Rome (1977) from those localities, characterise not Zone CTO1 (Tn1b), but Zone DSO 8 superieure (Tn1a) instead. Furthermore, accepting a Fa2d age, these taxa may even represent the lower DSO 8 Zone.

In European USSR, *Boučekius rotundus* Rozhdestvenskaya 1972 is reported from the Dankov and lower Zavolsk (ie., Fa2c, Fa2d) strata of Bashkiria, Tataria, and the Orensburg and Voronezh regions of the southeastern margin of the Russian Platform (Rozhdestvenskaya, 1972). A species of *Boučekius* has been recognised in Belgium by Becker & Bless (in Becker & others, 1974, pl. 7, figs 3a,b) as *B. cf. rotundus*, in the Ourthe Valley of the eastern Dinant Synclinorium at their localities at Flagotier (FL42), Chanxhe (CH 11) and Montfort (M0 38) in the Fa2c  $\beta$  level of the Evieux Formation. This species was also found at Comblain-la-Tour (CT16) in a sample of the same age, collected by Dr M.J.M. Bless and myself (23.8.75). Dr V.A. Tschigova (1979, p.259) has also reported the presence of *Boučekius* aff. *rotundus* in the lower (members I and II) part of the Pereval'ny Suite of the Omolon Massif (Kolyma Block), northeastern Siberia. This stratigraphical level is correlated, on the basis of conodonts (Gagiev, 1979), with the upper *velifer* Zone; thus the representative from the Kolyma Block is slightly older (Fa2b) than those from Europe.

Other species of *Boučekius* described from the European USSR, which may be stratigraphically useful, include some formerly referred to '*Aparchites*' (eg., '*A. crassus* Polenova 1953; '*A. volgaensis* Rozhdestvenskaya & Netchaeva 1972). From the stratigraphical ranges given by Tschigova (1977, table 4), it would appear that *Boučekius volgaensis* is confined to the Lebedyan beds (Fa2b), and that the zone of overlap between the upper part of the range of *B. crassus*, and the lower part of the range of *B. rotundus* corresponds to the early Dankov (ie., early Fa2c).

Tarling's (1980, fig. 6) schematic reconstruction, based on palaeomagnetic studies, of the distribution of the continental blocks during the Early Carboniferous is selected here (Fig. 9) as a base to show the geographical distribution of *Boučekius* (Famennian), *Paraboučekius* and *Katatona* (Strunian). In this reconstruction, the Kolyma Block forms the northern margin of the supercontinent of Laurentia, which joined with the Canadian Shield during the Early Devonian and remained there until the opening of the present Canadian Arctic Ocean in the Jurassic. Thus, in Famennian time, species of *Boučekius* were distributed on the northern, eastern, and southern margins of Laurentia. During the Strunian, species of *Katatona* were present on the southern margin of Laurentia and on the northwestern margin of 'Eastern' Gondwanaland, where they were joined by a species of *Paraboučekius*.

To conclude, *Paraboučekius* and *Notoscapha* are at present monotypic and unrecorded outside the Bonaparte Basin, whereas *Boučekius* is represented by several species (eg., *B. crassus*, *B. rotundus*, *B. volgaensis*) of potential stratigraphic value for the Famennian of the Laurentian supercontinent, and

*Katatona* is represented by two species (*K. acutilobata*, *K. romei*) that may be of value for long-distance correlation of the Strunian rocks of Laurentia and 'Eastern' Gondwanaland. The stratigraphical value of these species may be limited by the low number of specimens recovered and their small size. Nevertheless, the recognition of *Katatona acutilobata* in Belgium in rocks of Strunian (Fa2d?-Tn1a) age, and of *K. romei* in the Bonaparte Basin in the Buttons beds, is consistent with the Strunian age for this unit recently suggested on palynostratigraphic evidence (Playford, 1982).

## Acknowledgements

It is a pleasure and privilege to contribute this paper to the memory of the late Professor A.A. Öpik FAA. Although his international reputation was based on his work on the geology and the trilobites of the Cambrian System, his many contributions to the knowledge of other groups of organisms, such as brachiopods, ostracods and conodonts, should not be forgotten. Ostracod workers will remember that he described a rare occurrence of ostracods in the Old Red Sandstone facies of the Middle Devonian in Estonia (Öpik 1935a). The major achievement of Öpik's European career as an ostracod worker was the laying of a firm taxonomic foundation for the Ordovician ostracods of Estonia (Öpik 1935b, 1937), a foundation that his former students Valdar Jaanusson (1957) and Lembit Sarv (1959) later built upon to establish their own eminent reputations as palaeontologists and biostratigraphers.

In Australia, Öpik (1953) made a significant contribution towards the little-known subject of the Silurian ostracods of this continent in his study of the fauna from the Lower Silurian '*Illaenus* Band' in the Heathcote area, Victoria. However, the major contribution of his Australian career, to an ostracod worker, was probably his study of the Cambrian Bradoriida (Öpik 1968). That paper is a major reference in the literature of bradoriid and crustacean origins, and was the culmination of his work on the neozoological and palaeontological affinities of a group of Crustacea that he never accepted as Ostracoda.

The methodology and philosophy of Öpik's approach to his studies were always meticulously explained in his publications. I cannot read such detailed explanations, for example, in his '*Mindyallan Bulletin*' (Öpik 1967, pp. 47-52), without a sense of awe for the breadth and depth of his knowledge, and his clarity of thought and expression. These qualities, and his friendly approachable manner, made him a source of inspiration to his BMR colleagues. He was an individualist and not a consensus man as far as scientific questions were concerned. To Öpik, these could only be answered, not by committees, but by individuals. On such questions, I remember him saying that '...in a committee decision, a minority of one may be closer to the 'true' answer'.

Armin Aleksander Öpik will be remembered as the father figure of BMR palaeontology, a distinguished geologist, an erudite teacher and a respected friend.

It is a pleasure also to record my thanks to Drs. D.J. Siveter (University of Leicester), M.J. Copeland (Geological Survey of Canada, Ottawa), K.G. McKenzie (Riverina College of Advanced Education, Wagga Wagga), and G.C. Young (BMR), who all contributed valuable time and valued criticism to an earlier draft of this paper. I also thank A.T. Wilson and P.W. Davies for scanning electron microscope photography and printing in the preparation of Figures 4 to 6.

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