14

STUDIES ON WESTERN AUSTRALIAN PERMIAN BRACHIOPODS

1. THE FAMILY ANOPLIIDAE (CHONETIDINA)

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ABSTRACT: The Family Anopliidae is reviewed and divided into two subfamilies: Anopliinae Muir-Wood and Caenanopliinae subfam. nov. New representatives of the family from the Permian sequences of the Carnarvon Basin, Western Australia, are *Tornquistia occidentalis* sp. nov., *Tornquistia magna* sp. nov., *Tornquistia* sp. aff. *tropicalis* Grant and *Demonedys granti* sp. nov.

INTRODUCTION

A study of Permian chonetid brachiopods from Western Australia has revealed representatives of the Anopliidae belonging to *Tornquistia* and *Demonedys*. These plus the several new genera since Muir-Wood's (1962) monograph on the Chonetidina have led to a review of the phylogeny of the group.

The new species described herein from Western Australia come from the Carnarvon Basin. The Permian stratigraphic succession of the Carnarvon Basin has been elucidated and reviewed by Condon (1967) and Playford *et al.* (1975), with some changes in nomenclature by van de Graaff *et al.* (1977). It is not proposed to review the stratigraphic sequence further here.

COLLECTIONS

Registered number prefixes refer to the following institutions: CPC — Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Geology and Geophysics; GSWA — Geological Survey of Western Australia; MUGD — University of Melbourne, Department of Geology.

TERMINOLOGY

Terminology applied to the Chonetidina in this paper follows Muir-Wood (1962, 1965). Internal structures of the dorsal valve of anopliid brachiopods are critical to their correct generic placement. The important criteria are the presence or absence, in varying combinations, of three structures, namely: 1. the lateral septa (Muir-Wood 1962, p. 21, or anderidia of Sadlick 1965, p. 157-159), 2. the accessory septa, 3. the median septum. Additional septa and rows of papillae may also be present in the dorsal valve.

PHYLOGENY

The inferred phylogeny and generic ranges of the Family Anopliidae are shown in Fig. 1. Detailed generic morphology is reviewed under 'Systematic Palaeontology'. It is considered that the family includes two basic stocks (herein defined as subfamilies) one being characterized by smooth shells, the other by costate shells. Variations in external shell shape between genera is probably related to environmental factors and hence similar gross morphologies developed in each stock at different times. Examples of such heterochronous homeomorphy are: 1. a distinct ventral sulcus in *Chonetina* (smooth shell, Late Carboniferous) and in 'New Genus' (costate shell, Late Artinskian); 2. a distinct ventral fold in *Demonedys* (smooth shell, Late Artinskian) and a possible new genus typified by *Chonetella dubia* Loczy, 1897, p.69, text-fig. 16 (costate shell, Late Carboniferous).

The inferred phylogeny for Silurian to Early Middle Devonian anopliids is based largely, on that suggested by Boucot and Harper (1968, p.146) with the addition of *Austronoplia* Isaacson 1977. The author is unaware of any members of the family having been recorded from Eifelian or Givetian deposits. However the costate stock reappears in the Frasnian with the genus *Corbicularia* Lyashenko from the Russian Platform, and a representative of *Globosochonetes* (*G. mathesonensis*, Roberts 1971, p.74, pl.8, figs.1-10) from northwestern Australia, while the smooth stock reappears in the Famennian with specimens referred to *Tornquistia* by Gallwitz (1932, pl. 8, figs. 8-10). Gallwitz also figures at least one costate specimen (pl. 8, fig. 11).

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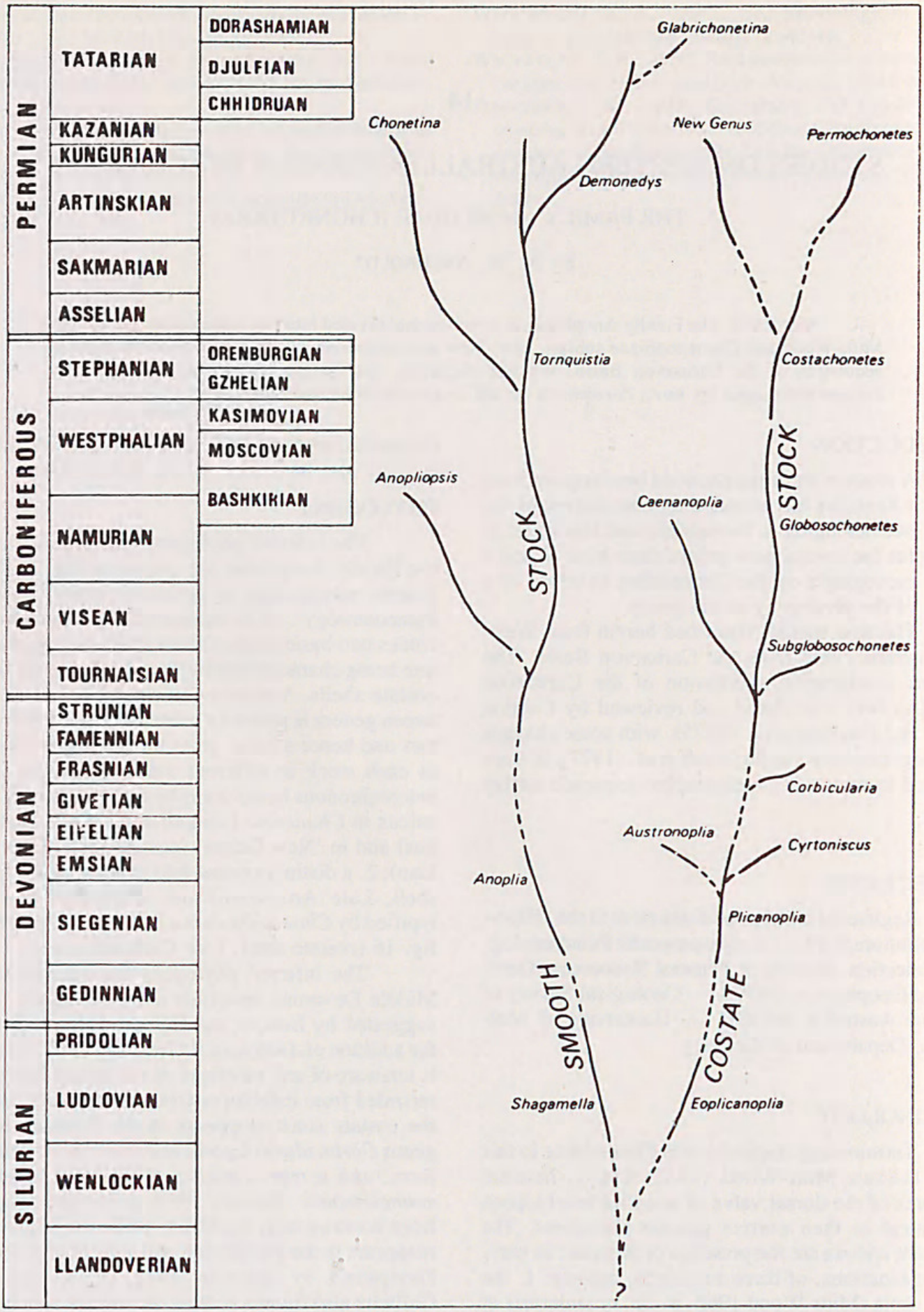

FIG. 1 — Inferred phylogeny of the Family Anopliidae Muir-Wood. The time-scale is used as a reference; no comment on a preferable Late Palaeozoic Stage nomenclature or stage duration is intended. Stages are shown as being of varying duration; for the Permian these will require alteration as more radioactive decay dates become available (see Waterhouse 1978b for a recent review of available data). Horizontal distances between genera do not imply degree of similarity. However, broken lines do indicate intermediate morphologies yet to be found.

In the costate stock, *Globosochonetes* Brunton ranges from Famennian into the Moscovian (Winkler-Prins 1970, p. 39). Arising from *Globosochonetes* in the Early Carboniferous are the forms *Caenanoplia* Carter and *Subglobosochonetes* Afanas'yeva, by modification of the internal dorsal structures. *Costachonetes* Waterhouse appears to arise in the Moscovian (Chao 1928, Rakovec 1932, Ivanov & Ivanova 1936) with the development of a weak, posteriorly developed, ventral sulcus. It ranges into the Early Permian (Yanagida 1967). More varied genera arise later in the Permian: *Permochonetes* Afanas'yeva and 'New Genus' (illustrated by Grant 1976 pl. 12, figs. 1-9). An additional development (not shown in Fig. 1), possibly from *Globosochonetes* is indicated by a form illustrated by Loczy (1897, p. 67, text fig. 16) as *Chonetella dubia*. This form, traditionally placed in the synonomy of *Costachonetes pygmaeus* (Loczy), see Chao (1928, p. 19), possesses a well developed ventral fold and hence, in external morphology, is a homeomorph of the smooth genus *Demonedys* Grant. It should be noted, as Chao (1928, p. 21) clearly described, that in a given population of anopiliids considerable variation can occur in the morphology of the ventral valve; this feature is also noted herein for the population of *Tornquistia occidentalis* sp. nov. However, all of Chao's illustrations of ventral valves of *Costachonetes pygmaeus* (Chao 1928, pl. 1, fig. 11a; pl. 2, figs. 1c and 2a) exhibit, a very weak, posteriorly developed, ventral sulcus as do illustrations of the species by Rakovec (1932, pl. 3, figs. 11 and 14), Ivanov and Ivanova (1936, pl. 2, figs. 14-16) and Yanagida (1967, p. 87, pl. 20, fig. 2). The occurrence of *Chonetes pygmaeus* in horizons of Gzhelian age of the Kuibyshev region reported by Semenova (1963, pp. 73-74, pl. 9, fig. 1), if correct, indicates a form with a well developed sulcus. On the other hand Loczy's figures of *Chonetella dubia* do not indicate any development of a ventral sulcus. A similar form is the *Chonetes pygmaeus* var. *asinuata* of Yungerman (1948, p. 40, pl. 1, fig. 4) from Late Carboniferous strata of the Donetz Basin.

The smooth stock reappeared in the Famennian with *Tornquistia* Paeckelmann which ranges into Kazanian times (Waterhouse 1976, p. 13). Off shoots from the long lived *Tornquistia* stock were: *Anopliopsis* Girty in the Early Carboniferous, by modification of the dorsal internal structures, *Demonedys* Grant in the Early Permian, by development of a prominent ventral fold and *Glabrichonetina* Waterhouse in the Late Permian, possibly developing from *Domonedys*. Less clear is the development of *Chonetina* Krotov in the Stephanian (Böger & Fiebig 1963, p. 147-148). *Chonetina*, as discussed below, is herein interpreted as being a smooth genus.

SYSTEMATIC PALAEONTOLOGY

SUBORDER CHONETIDINA Muir-Wood, 1955

SUPERFAMILY CHONETACEA Bronn, 1862

FAMILY ANOPLIIDAE Muir-Wood, 1962

(nom. transl. Boucot and Harper 1968, p. 167 ex Anopliinae and Muir-Wood 1962, p. 32, 53).

DIAGNOSIS: Small, strongly concavo-convex chonetaceans, smooth or costate, with the presence, absence or differing combination of three internal structures of the dorsal valve, namely the lateral septa, accessory septa and the median septum. Median septum usually less well developed than accessory septa. Origin of the median septum is anterior to the origin of the lateral septa. Pseudodeltidium and chilidium may be present.

DISCUSSION: Since raised to family status by Boucot Harper (1968), an event foreshadowed by the numerical study of chonetids by Rowell (1967), the content of the family has increased by nine genera. Winkler-Prins (in Martinez Chacon & Winkler — Prins 1977, p. 11) noted the desirability of subdividing the family. The present study has indicated that the fundamental feature of external ornament, presumably reflecting a function of the mantle edge during growth of the shell, is a reasonable criterion for distinguishing two major groups or stocks within the family. It can be noted that internal structures, especially those of the dorsal valve are very variable from genus to genus and do not permit, at this stage, any readily apparent subgroupings to be differentiated. The content of the two subfamilies of the Anopliidae — Anopliinae Muir-Wood, 1962 and Caenanopliinae subfam. nov. — are discussed below. There are, however, three other genera of chonetid brachiopods that deserve some comment as they possess features reminiscent of the Anopliidae. The genus *Trichonetes* Roberts (1976, p. 22, pl. 3, figs. 10-21) was placed by him, with a query in the subfamily Strophochonetinae. Roberts considered that despite the presence of twin septa in the dorsal valve the genus could not be placed in the Anopliidae because of its 'large size, transverse outline and low concavo-convex profile'. While the genus is not included in the Anopliidae in this study it is noted that the inclusion of the Early Permian genus *Permochonetes* already extends the traditional view of the family particularly with respect to size and profile. Another problem genus is *Airtonia* Cope, 1934. This genus, placed by Muir-Wood in a subfamily by itself is convergent in its dorsal interior structures with the anopliids (Rowell 1967). As yet, however the genus has not been shown to possess the row of ventral spines — characteristic of all members of the Anopliidae — and therefore the author agrees with Muir-Wood (1962, p. 96) and retains the genus in the family Daviesiellidae Sokolskaya, 1960.

Racheboeuf (1976, p. 68) described the genus *Davoustia* in the family Anopliidae. However the row of pits along the internal edge of the ventral interarea and the barely visible corresponding denticules of the dorsal valve make the inclusion of *Davoustia* in the Anopliidae difficult unless, as suggested by Racheboeuf (p. 69), the genus belongs to a distinct new subfamily.

SUBFAMILY ANOPLIINAE Muir-Wood 1962

DIAGNOSIS: Small, strongly concavo-convex anopliids possessing a smooth external shell.

GENERA INCLUDED: *Anoplia* Hall and Clarke, 1892, p. 309; type species *Leptaena? nucleata* Hall, 1857, p. 47-48. *Anoplia* encompasses smooth anopliids with lateral septa and prominent accessory septa in the dorsal valve. The genus has been well reviewed by Boucot and Harper (1968, p. 168).

Shagamella Boucot and Harper, 1968 type species *Shagamella ludloviensis* Boucot and Harper, 1968, p. 168, pl. 29, figs. 4-12. *Shagamella* includes smooth anopliids possessing lateral septa with, at times, a median septum and faint or absent accessory septa in the dorsal valve.

Anopliopsis Girty, 1938, p. 281; type species *Chonetina subcarinata* Girty, 1926, p. 27, pl. 5, figs. 10-16. *Anopliopsis* encompasses smooth anopliids, with the development of a very narrow shallow ventral sulcus. Internally the dorsal valve possesses very small lateral septa (Girty 1938, p. 280, fig. 13), long accessory septa with many additional septa inserted between the lateral septa and the accessory septa. Median septum weakly developed anteriorly or absent. This genus has recently been reviewed by Martinez Chacon and Winkler-Prins (1977, p. 11). *Anopliopsis* occurs in Texas, Tennessee and Oklahoma (U.S.A.) and Mere, Spain. The occurrence of *Anopliopsis* in Asia (Transbaykal) recorded by Kotlyar Popeko (1967, p. 91, pl. 15, fig. 13-15) has not been reliably established according to Afanas'yeva (1975, p. 4).

Chonetina Krotov, 1888, p. 500; type species *Chonetella artiensis* Krotov, 1885, p. 255, pl. 4, figs. 16-18. *Chonetina* includes smooth anopliids, which possess a narrow strongly developed ventral sulcus and strongly developed accessory and additional septa in the dorsal valve. This genus is restricted to smooth forms in the present study in contrast to Grant (1976) and others. Grant noted the disagreement between Krotov's (1885) figures, which indicate costae, and his descriptions, which specifically state that the shell is smooth, as had Muir-Wood (1962, p. 57) and Ramsbottom (1953, pp. 13-14). Ramsbottom examined topotypic ventral valves in the British Museum and found them to be smooth. Muir-Wood (1962) defined the genus as being smooth but included costate forms within the genus. Boucot & Harper (1968, p. 167) also defined the genus as being smooth. Specimens of *Chonetina* figured by Mironova (1960, pl. 1, figs. 1-3; 1964, pl. 1, figs. 1-3) and Ifanova (1972, pl. 2, figs. 10-22) from the Petchora Basin in northern Russia are all smooth as are specimens from northeastern Russia figured by Afanas'yeva (1977b, pl. 1, figs. 1-2). Fredericks (1925, pl. 1, figs. 54-57) figured several internal moulds of ventral valves from the Soviet Far East. The ventral valve figured by Sokolskaya (1960, pl. 33, fig. 6) as *Chonetina artiensis* is smooth except for two or three radial crenulations near the anterior margin of the left flank, but these do not appear to be true costae; they do not extend to the posterior of the valve. Afanas'yeva (1978a, p. 105) from a study of topotypic material confirms the smooth nature of the genotype of *Chonetina*. Several recent monographs (e.g. Dunbar 1955, Gobbett 1964) have incorrectly attributed species to *Chonetina*.

Chonetina noenygaardi Dunbar, 1955 (p. 67) is striate and the interior structures are unknown — this species is probably a *Chonetinella*. *Chonetina superba* Gobbett, 1964 (p. 118) is costate and flattish in profile. No internal views were figured. The costate specimens illustrated by Grant (1976, pl. 12, figs. 1-19) as *Chonetina* sp. indet., are regarded as being representatives of a 'New Genus' belonging to the Caenanopliinae subfam. nov.

Glabrichonetina Waterhouse, 1978a, p. 130; type species *Glabrichonetina kuwaensis* Waterhouse, 1978a, p. 131, pl. 25, figs. 5, 6, 8, 10-15. This genus includes smooth anopliids with a slightly swollen ventral valve and almost flat dorsal valve. The dorsal interior is characterised by several rows of pustulose septa. The ventral valve exhibits a long median septum.

?Tornquistia sp. nov. of Campbell and McKelvey (1972, p. 31, pl. 2, figs. 13-17), may represent a new anopliinid genus although, as those authors state, their specimens are not adequate to stand as type material. Their specimens indicate a large, smooth anopliinid with a distinct, though shallow, ventral sulcus. Providing both valves lack radial ornament, the species may be mid-way between *Tornquistia* and *Chonetina*.

Genus **Tornquistia** Paeckelmann, 1930
(= *Paeckelmannia* Licharew, 1934, p. 509)

TYPE SPECIES: *Leptaena* (*Chonetes*) *polita* McCoy, 1852(= *Leptaena (Chonetes) polita* McCoy 1854, 1855).

DIAGNOSIS: Anopliinids with short lateral septa and prominent accessory septa in dorsal interior. Ventral interior with short thin median septum. Ventral valve swollen, strongly convex.

DISCUSSION: Since the discussion of Muir-Wood (1962, pp. 58-62) and the refiguring of the lectotype (Brand, 1970, pl. 8, fig. 3) this genus has been well understood. The genus appears to have a substantial geological range — Famennian to Kungurian. Many species of chonetid brachipods with smooth ventral valves from Permian deposits have been referred to *Tornquistia* or *Paeckelmannia*). Gobbett (1964, p. 120, pl. 15, figs. 7-18) referred three species, including *Chonetes capitolinus* Toula, 1875b to *Paeckelmannia*. *C. capitolinus* is now the type species of *Svalbardia* Barkhatova (1970, p. 78). Gobbett's illustrations, including his figure of the dorsal internal structures (1964, pl. 15, fig. 13), indicate none of his material is of anopliid affinity. Dunbar (1955, p. 68-69) also discussed *Paeckelmannia*; however his specimens, while being smooth, possess a dorsal interior comparable with *Svalbardia capitolinus* (Toula). Other species externally homeomorphic with *Tornquistia* include *Chonetes novozemlianus*.

Licharew (in Miloradovich 1936, p. 42 and Licharew and Einor 1939, p. 25), now placed in the genus *Eolissochonetes* Hoare, 1960 by Sokolskaya, 1970, p. 76, and *Chonetes rotundatus* Toula, 1875a, referred to *Lissochonetes* by Ifanova 1972. From the available information it thus appears that the distribution of the genus *Tornquistia* in the Permian is somewhat restricted, being found in Western Australia, Thailand (Grant 1976), possibly the Salt Range, Pakistan (in the form of *Chonetes ambiensis* Waagen, 1883), Eastern Siberia (Zavodowsky 1960, 1971 and Afanas'yeva 1977b) and the Yukon region of Arctic Canada (Bamber & Waterhouse

1971). At least three Permian species are present in Western Australia.

Tornquistia occidentalis sp. nov.
(Pl. 25, Figs. 1-4; Figs. 2-3)

MATERIAL: 14 conjoined shells, 3 isolated ventral valves, 2 internal moulds of ventral valves. One specimen was sectioned to reveal the internal structures.

LOCALITIES: a. CPC 19127. Bureau of Mineral Resources Field Number GW78. Basal bed of Callytharra Formation, Callytharra Springs. Lat. 25°52′; Long. 115°30′. b. GSWAF 10995-11005. GSWA Sample No. 44559. Glenburgh Map Sheet. Yard Grid ref. 356 793. Callytharra Formation. c. MUGD 5191-5192. Locality P.498, Callytharra Formation, Callytharra Springs (G. A. Thomas measured section) about 38 metres from base of section. d. MUGD 5193-5194 — Locality P.501, Callytharra Formation, Callytharra Springs (G. A. Thomas measured section) about 42 metres from base of section. e. MUGD 5195. Locality 5664, Callytharra Formation, Bidgemia Station. (G. A. Thomas measured section) about 8.4 metres from base of section.

MEASUREMENTS: (in mm), Holotype CPC 19127 (a complete shell).

Specimen Number	*Length*	*Hinge Width*	*Mid-Width*	*Thickness*
CPC 19127	7.1	8.8	8.2	2.9
GSWA F 10995	6.6	8.2	8.5	3.4
GSWA F 10996	6.9	—	7.4	3.5
GSWA F 10997	5.8	8.8	8.1	2.1
GSWA F 10998	6.3	9.8	9.0	3.2
GSWA F 10999	7.2	11.2	9.7	3.4
GSWA F 11000	7.1	10.2	9.1	3.6
GSWA F 11001	7.2	—	9.7	3.1
GSWA F 11002	—	10.1	8.8	—
GSWA F 11003	6.1	8.8	8.4	3.2
GSWA F 11004	6.9	12.0	11.2	—
MUGD 5191	7.5	11.2	10.0	3.5
MUGD 5192	—	10.5	9.4	—
MUGD 5193	8.0	11.2	9.7	—
MUGD 5194	6.8	10.4	9.7	—
MUGD 5195	7.6	11.0	10.2	—

AGE: Early Permian, Sakmarian Stage, Sterlitamakian Substage.

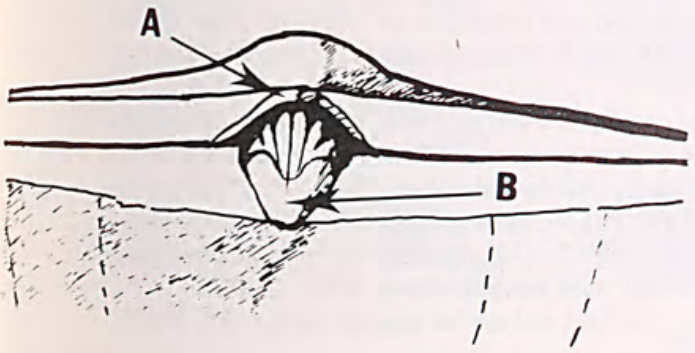

FIG. 2 — Ventral and dorsal interareas and cardinal process of *Tornquistia occidentalis* Drawn from Holotype × 18. A Pseudodeltidium, B = Chilidium.

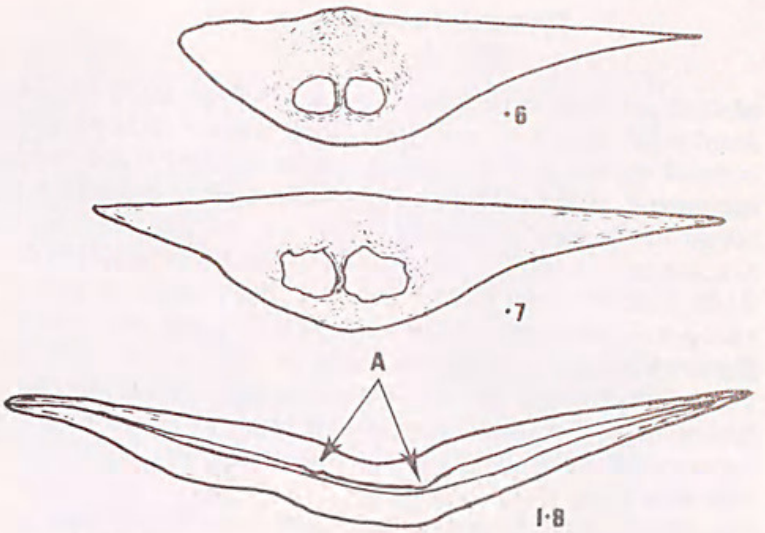

FIG. 3— *Tornquistia occidentalis* sp. nov. Transverse sections of specimen GSWAF 19005, × 18. The numbers refer to the position of the section in mm, from the posterior extremity of the shell. A = Accessory septa. Orientation of calcite fibres shown semi-diagrammatically. Pseudopunctae (taleolae) not shown.

DIAGNOSIS: Average sized species for the genus. Convexity of ventral valve, moderate in juvenile individuals, becoming increasingly developed with strongly inflated mesial portion of valve in adult individuals. Dorsal valve deeply concave. Greatest width of shell at hinge. Exterior surface of shell smooth with distinct growth lines. Pronounced ventral interarea twice the height of the dorsal interarea. Cardinal spines short, widely spaced (2.5 mm interval). Ventral umbo sharp and finely pointed.

Ventral interior with large thick teeth. Delthyrium distinct with marked thickening of the shell beneath it. Small pseudodeltidium present in the apex and extending along the sides of the delthyrium. High narrow median septum bisects delthyrium and extends anteriorly as a low delicate structure for half of the valve length. Valve floor–except for weakly impressed muscle area–marked by regularly spaced pustules.

Dorsal interior (deduced from acetate peels) with long accessory septa, no median septum, distinct large alveolus and randomly placed pustules. Small chilidium fused on to external face of cardinal process.

DISCUSSION: This species is closest to *T. magna* sp. nov. from which it is distinguished by its smaller size and the remarkable convexity of the latter species. *Tornquistia tropicalis* Grant, 1976, p. 68, is far less convex than the present species. *Tornquistia gibbera* Afanas'yeva, 1977b, p. 12, pl. 1, figs. 12-14, from the Late Carboniferous Paren Horizon of the Kolyma-Omolon region, USSR, is closer in size and convexity although internal structures appear more weakly developed in that species. Also close, although differing in outline, is *T. convexa* Zavodowsky, 1960, p. 63, pl. 1, figs. 2-4; 1971, p. 78, pl. 61, fig. 18, from the Late Permian Omolon Horizon, Kolyma-Omolon Region, USSR. Species recorded from Alaska (Brabb & Grant 1971) and the Yukon (Bamber & Waterhouse 1971) have not been described adequately to warrant close comparison.

Tornquistia magna sp. nov.
(Pl. 25, figs. 5-13)

MATERIAL: Two large isolated ventral valves and 2 internal moulds of ventral valves. One block with several hundred isolated valves and conjoined shells has provided many specimens, some of which have been treated with HCl to reveal the internal structures.

LOCALITIES: a. CPC 19134-19137, 19139-19141, 19143. BMR Field Number G.279-280. 7½ miles south of west of Moogooree Homestead Lat. 24° 05½'S Long. 115° 06'E. Basal 25 metres of Bulgadoo Shale. b. CPC 19142, 19138. BMR Field number ML 87. Bulgadoo (now Madeline Fm.) lowest fossiliferous horizon. North bank of Lyndon River between Burdghin Murrow and salt pools, 8½ miles from Mia Mia Homestead bearing 82°.

MEASUREMENTS: (in mm), Holotype CPC 19137 (internal mould of complete shell)

Specimen Number	*Length*	*Hinge Width*	*Mid-Width*	*Thick-ness*
CPC 19142	10.8	13.0	12.4	5.4
CPC 19138	10.3	12.6	—	6.1
CPC 19136	4.5	6.0	—	—
CPC 19135	5.8	9.2	—	—
CPC 19143	7.3	11.4	10.0	—
CPC 19141	6.6	10.4	8.9	—
CPC 19134	7.4	10.0	9.8	—
CPC 19139	7.4	14.0e	11.0	—
CPC 19137	6.2	11.0	9.8	—

AGE: Early Permian, Artinskian Stage, Early Baigendzinian Substage.

DIAGNOSIS: Shell very large for the genus, semi-circular in outline. Convexity of ventral valves distinct in juveniles and very pronounced in adults. Dorsal valve deeply concave. Greatest width at hinge line. Surface smooth except for very weak growth lines. Interareas low, dorsal interarea very low. Cardinal spines short and blunt. Ventral teeth large and blunt. Delthyrium small. Ventral median septum high posteriorly, low anteriorly, extends as low ridge for posterior half of valve length. Pustules restricted to periphery of valve — Muscle area large but very weakly impressed.

Cardinal process poorly known. Socket plates short but distinct. Lateral septa small. Accessory septa long, extend anteriorly for two thirds of valve length. Several additional, variably developed pairs of septa occur between the accessory septa and the lateral septa. Median septum absent or poorly developed as short ridge between accessory septa. Pustules present around periphery of valve but not abundant.

DISCUSSION: The very large size, the very great convexity of the ventral valve, and the strongly inflated mesial portion of the ventral valve distinguish this species. Even relatively juvenile specimens possess the inflated mesial portion of the ventral valve. *Chonetes* sp. of Reed (1930, p. 42-45, pl. 4, fig. 5) from Rio Tayó, Brazil has a ventral valve comparable to the present species in size and convexity. However, no mention is made of internal structures and the dorsal valve is unknown.

Tornquistia sp. aff. **T. tropicalis** Grant, 1976
(Pl. 25, figs. 14-16)

MATERIAL AND OCCURRENCE: Three isolated ventral valves, CPC 19128 to 19130, from Minilya River, approximately 14.6 km southeast of Middalya Homestead, 0.2 km northwest of well. The locality carries BMR field number MG 108 and is shown on the Minilya 4 mile geological series map sheet as occurring in the Cundlego Formation.

MEASUREMENTS: (in mm)

Specimen Number	*Length*	*Hinge Width*	*Mid-Width*	*Thick-ness*
CPC 19128	7.9	—	11.3+	3.1
CPC 19129	6.3	9.2	8.6	1.6
CPC 19130	5.4	—	7.2	1.4

AGE: Early Permian, Late Baigendzinian Substage of the Artinskian Stage.

DIAGNOSIS: Small to medium sized valves, convexity rather low, mesial portion of valve slightly inflated, greatest width at hinge line. Surface covered in very weak growth lines. Ventral interarea very low. Ventral internal unknown. Dorsal valve unknown.

DISCUSSION The little material that is available is clearly distinct from both *T. occidentalis* and *T. magna* both of

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PLATE 25

All figured specimens other than holotypes are paratypes. Magnifications × 3.5 throughout.

Figs. 1-4 —*Tornquistia occidentalis* sp. nov. (1a-d) Shell in ventral, posterior, anterior, and dorsal views, CPC 19127, Holotype. (2a-b) Ventral valve in dorsal and ventral views, MUGD 5191. (3a-b) Ventral valve in ventral and dorsal views, GSWAF 10997. (4a-b) Ventral valve in ventral and anterior views, GSWAF 10996.

Figs. 5-13 —*Tornquistia magna* sp. nov. (5) Internal mould of shell in dorsal view, CPC 19134. (6) Internal mould of shell in dorsal view, CPC 19135. (7) Internal mould of shell in dorsal view, CPC 19136. (8a-c) Internal mould of shell in posterior, ventral, and dorsal valve, CPC 19137, Holotype. (9a-b) Ventral valve in ventral and posterior views, CPC 19138. (10) Ventral valve in ventral view, CPC 19139. (11) External mould of dorsal valve, CPC 19140. (12) Ventral valve in ventral view, CPC 19141. (13a-c) Ventral valve in posterior, anterior, and ventral views, CPC 19142.

Figs. 14-16 —*Tornquistia* sp. aff. *tropicalis* Grant. Ventral valves in ventral view, CPC 19128, 19129, 19130 respectively.

Figs. 17-19 —*Demonedys granti* sp. nov. (17a-b) Ventral valve in ventral and posterior views, CPC 19131, Holotype. (18a-b) Ventral valve in ventral, and posterior views, CPC 19132. (19a-c) Shell in ventral, anterior, and posterior views, CPC 19133.


1a
1b
1c
1d
2a
2b
3a
3b
4a
4b
5
6
7
8a
8b
8c
9a
9b
10
11
12
13a
13b
13c
14
15
16
17a
17b
18a
18b
19a
19b
19c

PLATE 25

which exhibit much greater convexity of the ventral valve. These specimens are tentatively ascribed to *T. tropicalis* Grant (1976, pl. 14, figs. 1-11) from Thailand from which they differ only in being uniformly larger.

Genus **Demonedys** Grant, 1976

TYPE SPECIES: *Demonedys fastigata* Grant, 1976.
DIAGNOSIS: Smooth anopliids with short lateral septa and well developed accessory septa in dorsal interior. Ventral interior with very short median septum. Ventral valve with well developed fold. Dorsal valve strongly concave.
RANGE AND DISTRIBUTION: Since being recognized from the Late Artinskian of Thailand by Grant (1976, p. 66) this genus has been recorded only from the Late Permian of Nepal (Waterhouse 1978, p. 23, 114). It is now described from the Late Artinskian of Western Australia with *D. granti* sp. nov. close to the type species.

Demonedys granti sp. nov.
(Pl. 1, figs. 17-19; Fig. 4)

ETYMOLOGY: Named in honour of Dr. R. E. Grant, the first to recognise this striking genus of the Anopliidae.
MATERIAL: Three conjoined shells. One specimen sectioned to reveal internal structures.
LOCALITIES: a. CPC 19131-19133. BMR Field Number MG 108. Minilya River, approximately 14.6 km southeast of Middalya Homestead; .2 km northwest of well. Shown on Minilya 4 mile geological series Map sheet as Cundlego Formation. b. Poorly preserved specimens referred to *Demonedys granti* sp. nov. are also known from BMR Field Number ML 83, Minilya syncline, north bank of river, 217 feet above base of Wandagee Formation, and also a generalized MUGD Wandagee Formation collection labelled '*Calceolispongia* Bed, East Limb of Syncline at Minilya River (material collected by C. Teichert).'

MEASUREMENTS: (in mm) Holotype CPC 19131

Specimen Number	*Length*	*Hinge Width*	*Mid-Width*	*Thickness*
CPC 19131	6.0	7.7	7.4	2.8
CPC 19132	4.9	6.5	6.1	2.0
CPC 19132	4.4	6.2	5.8	2.0

AGE: Early Permian, Artinskian Stage, Late Baigendzinian substage.
DIAGNOSIS: Small shells. Outline triangular, in juvenile shells, to semicircular, in adult shells. Shells widest at hinge. Ventral umbo, small, sharply curved. Ventral interarea low. Commissure sulcate. Fold arises at ventral umbo, height increases rapidly towards anterior commissure, with strongly curved profile. Growth lines weakly developed posteriorly, more frequently developed anteriorly. Spines along ventral hinge point laterally, spaced every 1.8 to 2 mm. Dorsal valve concave with well developed sulcus. Body cavity narrow with most volume along midline. Cardinal process fills ventral delthyrium.

Ventral interior with short high median septum posteriorly; septum occupies slot between halves of bilobed

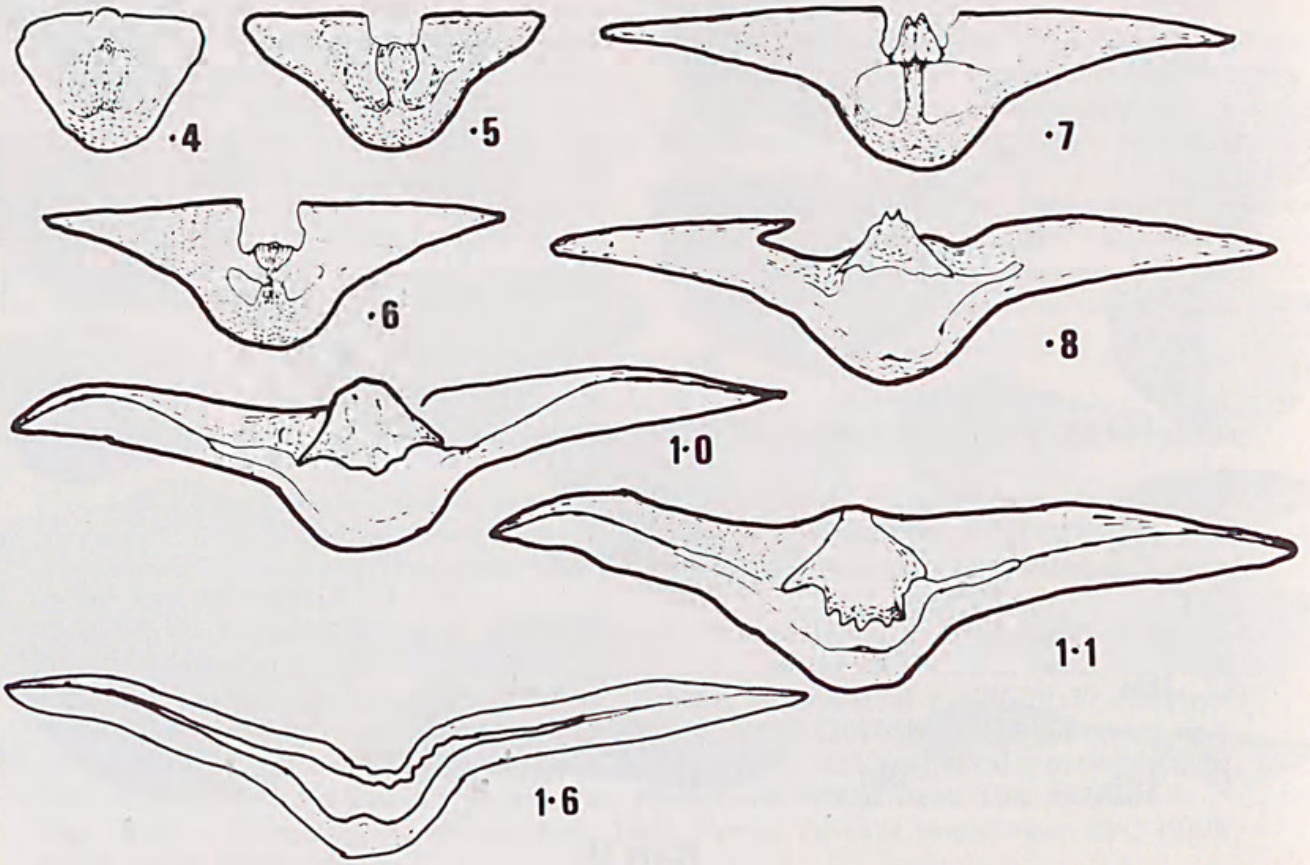

FIG. 4 —*Demonedys granti* sp. nov. Transverse sections of specimen CPC 19133, × 18. The numbers refer to the position of the section, in mm, from the posterior extremity of the shell. Orientation of calcite fibres shown semi-diagrammatically. Pseudo-punctae (taleolae) not shown.

cardinal process. Interior postules randomly developed on lateral flanks of valves.

Dorsal interior with well developed large cardinal process, bilobed and grooved. Socket ridges poorly developed. Lateral septa low and poorly developed. Accessory septa well developed on interior of dorsal sulcus, apparently two pairs, extending anteriorly for considerable distance. Internal pustules (taleolae) randomly developed.

DISCUSSION: This species is quite close to *Demonedys fastigiata* Grant, the type species. However that species differs by its more triangular outline, lower ventral fold and apparently flatter dorsal valve. Specimens figured by Waterhouse (1978, pl. 1, figs. 10-12, pl. 22, figs. 8-9) are too poorly preserved to warrant close comparison.

The small smooth *Chonetella? dunbari* of Newell (1934, p. 427, pl. 55, figs. 5a-c) should also be mentioned here. This has a well developed ventral fold and is comparable in size (from the figured specimen) with the largest specimen of *Demonedys granti*. If it was found in a Permian assemblage, rather than mid-Pennsylvanian, in either Western Australia or Thailand, rather than North America, there is little doubt it would be classified as a representative of *Demonedys*. Its internal structures are, unfortunately, unknown.

SUBFAMILY CAENANOPLIINAE subfam. nov.

DIAGNOSIS: Small to medium sized, concavo-convex anopliids with a costate exterior.

GENERA INCLUDED: *Eoplicanoplia* Boucot and Harper, 1968, p. 168; type species *Chonetes colliculus* Foerste, 1909, p. 24-5, pl. 1, figs. 10a-c. This genus includes caenanoplinids with lateral septa and a faint median septum in the dorsal valve. The genus was well described and figured by Boucot and Harper (1968, pp. 168-169).

Plicanoplia Boucot and Harper, 1968, p. 169; type species *Chonetes fornacula* Dunbar, 1923, p. 130, pl. 2, fig. 25. This genus encompasses costate anopliids with strongly developed lateral septa and accessory septa in the dorsal valve.

Cyrtoniscus Boucot and Harper, 1968, p. 172; type species *Chonetes nectus* Clarke, 1907, pp. 263-4, figs. on p. 264. *Cyrtoniscus* includes costate anopliids which have marked discontinuity in the surface of the ventral cale. Lateral and accessory septa are present on the dorsal valve.

Austronoplia Isaacson, 1977, p. 178; type species *Chonetes stubeli* Gurich, 1893, p. 80, pl. 5, figs. 3, 4. This genus includes caenanoplinids with angular costae as well as lateral septa and a medium septum in the dorsal valve. The interior of the dorsal valve with many prominent rows of papillae resembles the much younger *Permochonetes*.

Corbicularia Lyashenko, 1973, p. 29; type species *Chonetes menneri* Lyashenko, 1958, p. 119, pl. 1, figs. 4-11. *Corbicularia* is characterised by small fine costae. The median septum, lateral septa and brachial ridges are all absent.

Globosochonetes Brunton, 1968, p. 48; type species *Globosochonetes parseptus* Brunton, 1968, p. 48, pl. 7, figs. 8-27. *Globosochonetes* includes strongly concavo-convex caenanoplinids. Strong accessory septa and weak lateral septa are present on the dorsal interior where a short dorsal median septum may also be present.

Subglobosochonetes Afanas'yeva, 1976, p. 307; type species *Chonetes* (*Rugosochonetes*) *malevkensis* Sokolskaya, 1950, p. 23, pl. 1, figs. 1-16. The genus is restricted to caenanopliinids with no median septum or accessory septa in the dorsal valve. Lateral septa are short.

Caenanoplia Carter, 1968, p. 1143; type species *Caenanoplia burlingtonensis* Carter, 1968, p. 1143, pl. 145, figs. 1-26. *Caenanoplia* includes strongly concavo-convex caenanopliinids with lateral septa but no median septum or accessory septa in the dorsal valve. It is a genus close to *Subglobosochonetes* but is distinguished from that genus by its more trigonal outline and the greater convexity of the ventral valve. This is a more weakly costate genus than others of the subfamily but it is noted that internal moulds of the genus (Carter 1968, pl. 145, figs. 21-22) exhibit radial rows of papillae. The close correspondence between these rows and the external ribbing was noted by Brunton (1968, p. 48).

Costachonetes Waterhouse, 1975, p. 2; type species *Chonetes uralica* Möller var. *pygmaea* Loczy, 1897, pp. 64-5, text figs. 13 and 14. This genus includes caenanopliinids with a swollen ventral valve which carries a narrow ventral sulcus — at least posteriorly. The dorsal interior carries a thin median septum and small lateral septa (Chao 1928, p. 20, pl. 1, fig. 13).

Permochonetes Afanas'yeva, 1977a, p. 138; type species *Permochonetes pamiricus* Afanas'yeva, 1977, p. 138, text figs. 1, 2. This genus includes finely costate shells which are large for the family. Lateral septa, accessory septa and a median septum are absent from the dorsal valve. Rows of radial papillae are present.

'New Genus' was illustrated by Grant (1976, pl. 12, figs. 1-19) as *Chonetina* sp. indet. It appears to be a caenanopliinid with lateral septa, accessory septa and a short posteriorly developed median septum in the dorsal valve. Confirmation of the novelty of this material is left to those with access to the Thai material and hence the nomenclature is left open. The concept of *Chonetina* used herein has already been discussed above.

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ADDENDA

The genus *Yagonia* Roberts (in Roberts et. al. 1976) from the Visean of New South Wales was inadvertently excluded from the above discussion of the family Anopliidae. It is an extraordinarily large, smooth form and presumably belongs to the subfamily Anopliinae as defined herein. Its phylogenetic relationships to other members of the subfamily are not clear.

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