

NEW SPIRIFERID BRACHIOPODS FROM THE LOWER DEVONIAN OF NEW SOUTH WALES

by N. M. SAVAGE

ABSTRACT. Five species and subspecies of spiriferid brachiopods are described from the early Siegenian Mandagery Park Formation, New South Wales: *Cyrtina praecedens* Kozłowski, *Proreticularia beddii* sp. nov., and the new subspecies *Quadrithyris robusta molongensis*, *Ambocoelia praecox dorsiplicata*, and *Howellella nucula australis*. There is a close resemblance to species from eastern Europe and a general affinity to species from central Asia.

RECENT investigations in the vicinity of Manildra, New South Wales, have led to the discovery of several interesting Lower Devonian brachiopod assemblages. Of these the most important consists of delicately preserved silicified material of probable early Siegenian age. Two new genera from this fauna have been described (Savage 1968 *a, b*) and several complementary papers are in preparation. This paper is concerned with the spiriferids.

The Lower Palaeozoic deposits of the Manildra district form part of the Cowra Trough sediments of the Lachlan geosyncline (Packham 1960). Within this depositional trough a thickness of at least 10 000 ft. of sediments accumulated during Silurian and Early Devonian times. No detailed palaeontological work took place until Hill and Jones (1940) and Hill (1942) established the Lower to Middle Devonian age of corals from the Garra Limestones immediately to the east. More recently Strusz (1965 *a, b*, 1966, 1967) has investigated the Garra Formation further and described many more of the corals.

The stratigraphy of the Manildra district has been described in detail elsewhere (Savage 1969) together with faunal lists and a discussion of possible correlations. It is suggested that a new group, the Gregra Group, should consist of the Maradana Shale, the Mandagery Park Formation, and the Garra Formation. The first two are new formations, of late Gedinnian and Siegenian age, respectively. The third is a relatively well-known sequence of limestones and shales of probable late Siegenian to early Eifelian age. All three formations are calcareous, shallow-water deposits with rich shelly faunas.

The Lower Devonian spiriferids from the Mandagery Park Formation show a close resemblance to forms from Bohemia and Podolia, and it is with these forms that the present taxonomic discussion is largely concerned. There is also a general affinity with other spiriferids from the whole Eurasian faunal province, which in Early Devonian times extended from eastern Europe, across Asia, and into western North America. These affinities are also evident in other groups of Manildra brachiopods.

In the systematic treatment below, specimen numbers used are those of the Palaeontology Collection, Department of Geology and Geophysics, University of Sydney.

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SYSTEMATIC PALAEOLOGY

Phylum BRACHIOPODA
Suborder SPIRIFEROIDEA
Superfamily RETICULARIACEA Waagen 1883
Family RETICULARIIDAE Waagen 1883
Genus QUADRITHYRIS Havlíček 1957

Type species. *Spirifer robustus* Barrande 1848, by original designation.

Quadrithyris robusta molongensis subsp. nov.

Plate 89

Diagnosis. A form close to *Q. robusta* (Barrande) but with a more prominent fold and sulcus. The lateral slopes bear no trace of plications.

Material. The total of 61 silicified specimens consists of 16 complete or nearly complete conjoined shells, 15 dorsal valves, and 30 ventral valves. Specimen SU 19590 is designated the holotype.

Description. Exterior. The shell is transversely elliptical in outline with the maximum width between mid-length and the posterior margin. The cardinal margins are evenly rounded and the anterior margin is straight or emarginate. In lateral profile the shell is strongly biconvex with the thickness almost equal to the length and greatest near the umbones.

The strongly convex ventral valve has a prominent umbo and an erect to slightly incurved beak. An apsacline interarea is concave with an apical angle of 110–20°. The delthyrium includes an angle of about 45°. Narrow, ribbon-like, deltidial plates project normal to the interarea along the delthyrial margins (Pl. 89, fig. 26).

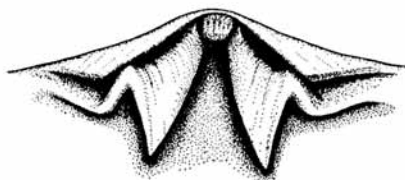
The dorsal valve is less strongly convex than the ventral valve. It has a broad umbo and a prominent, incurved beak. The interarea is low and orthocline to apsacline with an open notothyrium which includes an angle of 125–35°.

The ventral valve bears a broad, rounded sulcus and the dorsal valve a corresponding fold. Both commence at the umbones and extend to the strongly uniplicate anterior commissure. The surface ornament consists of fine growth lamellae spaced at 5 or 6 per mm.

Ventral interior. A deep delthyrial cavity is bounded by strongly receding, subvertical dental lamellae which converge posteriorly before meeting the valve floor (Pl. 89, fig. 33). The teeth are small and stubby with a subtriangular cross-section. A prominent median septum, extending half the valve length, is high in the middle with a concave edge anteriorly and dorsally (Pl. 89, fig. 30). The ventral muscle field is not sufficiently impressed to be discernible in the material available.

Dorsal interior. Long, widely divergent sockets are supported on strong hinge plates (Pl. 89, figs. 28, 29). On their inner edges the sockets are bounded by strong inner socket ridges, triangular in section and becoming higher and stronger anteriorly (text-fig. 1). Narrow crural lamellae slope sharply down from the socket ridges but do not reach the valve floor. Slender crural bases are attached along the inner edges of these crural lamellae (Pl. 89, fig. 28). A large, well-rounded, cardinal process is occasionally

preserved in this silicified material. In some specimens traces of several lobes are present (text-fig. 1). A partly complete laterally directed spire with 4 volutions is present in one specimen and it appears that a complete spire would have 5 or 6 volutions. The muscle field is long and narrow and extends within the dorsal fold about one-third of the distance to the anterior commissure (Pl. 89, figs. 28, 31, 32).



TEXT-FIG. 1. *Quadrithyris robusta molongensis* subsp. nov.
Reconstruction of the dorsal cardinalia based on several
incomplete specimens. Approx. $\times 10$.

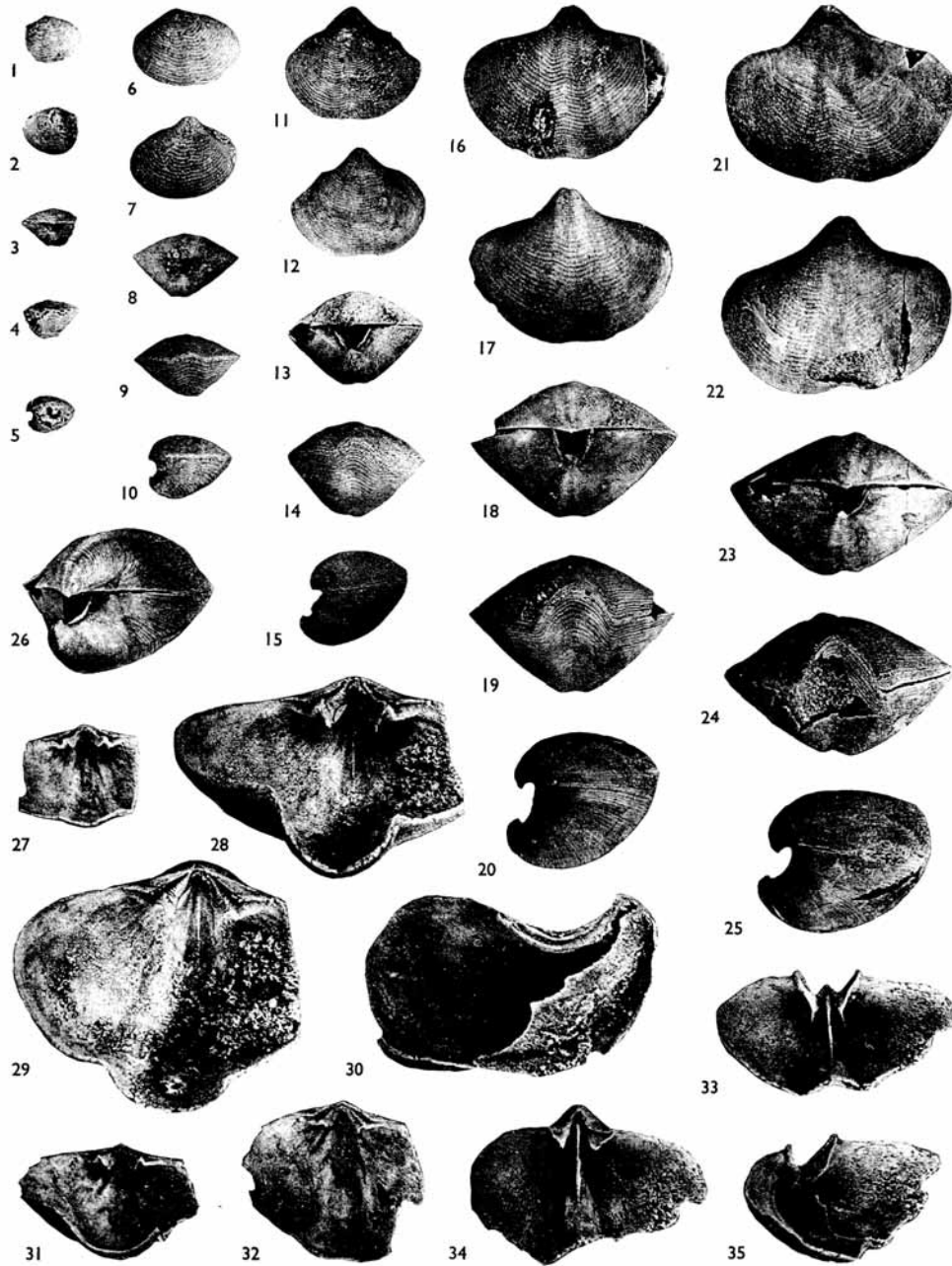
Measurements. The dimensions of 4 specimens are given below in mm.

		<i>Length</i>	<i>Width</i>	<i>Thickness</i>
SU 19588	Complete shell	5.8	7.0	4.7
SU 19589	Complete shell	8.0	10.1	6.9
SU 19590	Complete shell	8.9	11.5	7.2
SU 19597	Dorsal valve	9.6	13.6	—

Ontogeny. From the relatively small and broken collection, sufficient specimens of different ontogenetic stages are present to allow an examination of the morphological development during most of the growing period. The youngest form available has only a very gentle fold and sulcus and a ventral umbo which does not project posteriorly

EXPLANATION OF PLATE 89

Figs. 1–35. *Quadrithyris robusta molongensis* subsp. nov. Mandagery Park Formation, Manildra. 1–25, Dorsal, ventral, posterior, anterior, and lateral views of five specimens of progressively increasing size. 1–5, SU 19586, a very young stage with a low fold and sulcus (fig. 4) and a ventral umbo which does not project posterior of the hinge-line (fig. 1). 6–10, SU 19587, a young stage also with a low fold and small ventral umbo. 11–15, SU 19588, a larger form with a prominent ventral umbo (fig. 15), a distinct ventral interarea and ribbon-like deltidial plates projecting normal to the interarea (fig. 13). 16–20, SU 19589, a mature form with a pronounced fold and sulcus (fig. 19), and incurved umbones (fig. 20). 21–5, SU 19590 (holotype), a relatively large form with a ventral umbo projecting well past the hinge-line and a strongly uniplicate anterior commissure (fig. 24). 26, Postero-lateral view of SU 19590 showing the ventral interarea and the thin ribbon-like deltidial plates projecting normal to it. 27, Antero-ventral view of dorsal valve SU 19595. 28, 29, Antero-ventral and ventral views of dorsal valve SU 19597 showing the inner socket ridges becoming higher and stronger anteriorly and the narrow inner hinge plates suspended from these ridges and not meeting the valve floor (fig. 28). 30, Lateral view of large broken ventral valve SU 19598 showing the long median septum with its concave anterior edge. 31, 32, Antero-ventral and ventral views of dorsal valve SU 19591 showing the widely divergent sockets, the strong inner socket ridges, and the adductor muscle scars. 33–5, Dorso-anterior, dorso-lateral, and dorsal views of ventral valve SU 19592 showing the strongly receding dental lamellae (fig. 35), and the long tooth ridges. (Figs. 1–26 $\times 3$, figs. 27–35 $\times 4$.)



SAVAGE, *Quadrithyris*

past the hinge line (Pl. 89, figs. 1–5). As growth proceeds the fold and sulcus become more pronounced and the ventral umbo extends well past the hinge line (Pl. 89, figs. 21–5). Both the dorsal and ventral beaks change from an erect position in the younger stages, to an incurved position in the mature shell (Pl. 89, figs. 10, 15, 25).

Internally the ventral median septum becomes relatively longer and the dental lamellae relatively shorter, whilst in the dorsal valve the hinge plates thicken and a low median myophragm becomes visible in the muscle field.

Discussion. The relatively smooth lateral slopes and growth lamellae, in combination with the high ventral median septum and prominent dental lamellae, place this form in the genus *Quadrithyris* Havlíček. The closely related genus *Quadrithyrina* Havlíček lacks dental lamellae.

Q. robusta molongensis is distinguished by receding dental lamellae, lateral slopes with no trace of plications, and a high median septum extending half the valve length. It closely resembles specimens of *Q. robusta* (Barrande) although the Bohemian type species has a less-pronounced fold and sulcus. Other Bohemian species are *Q. kotýsensis* Havlíček and *Q. falco* (Barrande). Both have a sulcus bounded on each side by a low plication and a fold bounded by weak furrows. *Q. trisectus* (Kayser), from the Rhenish Schiefergebirge, differs from the Manildra form, and also from the type species, in possessing a very long median septum flanked by almost equally long dental lamellae.

Q. robusta molongensis is one of the earliest species of *Quadrithyris* known. Siegenian species have been recorded from Nevada by Johnson (1965) and from the Altai Mountains by Kulkov (1963) but all other recorded species are from deposits of Emsian or Eifelian age.

Genus *PRORETICULARIA* Havlíček 1957

Type species. *Spirifer carens* Barrande 1879, by original designation.

Proreticularia beddiei sp. nov.

Plate 90, figs. 22–38

Diagnosis. A wide *Proreticularia* with evenly rounded lateral margins and a strongly incurved ventral umbo.

Material. A total of 120 silicified specimens consists of 29 complete or nearly complete conjoined shells, 45 dorsal valves, and 46 ventral valves. Externally very fine growth lines and radial striations are preserved but no spines have been observed. Specimen SU 16620 is designated the holotype.

Description. Exterior. In outline the shell is transversely oval with the greatest width at about mid-length. The cardinal and lateral margins are evenly rounded and the anterior margin is gently rounded to emarginate. The lateral profile is unequally biconvex with the ventral valve the deeper. Maximum thickness is just posterior of mid-length.

The ventral valve is strongly convex with the greatest curvature in the high umbonal region. An apsacline, strongly concave interarea has a curvature which increases apically and a width slightly more than half the maximum shell width. The beak ridges are very weak. An open delthyrium includes an angle of 40–50° and is bordered by prominent deltidial plates which project normal to the interarea (Pl. 90, fig. 24).

The dorsal valve is convex in lateral profile with a broad umbo terminating in a small incurved beak. A concave interarea is apsacline and very short with an apical angle of about 150° . The notothyrium is open and includes an angle of $125\text{--}35^\circ$.

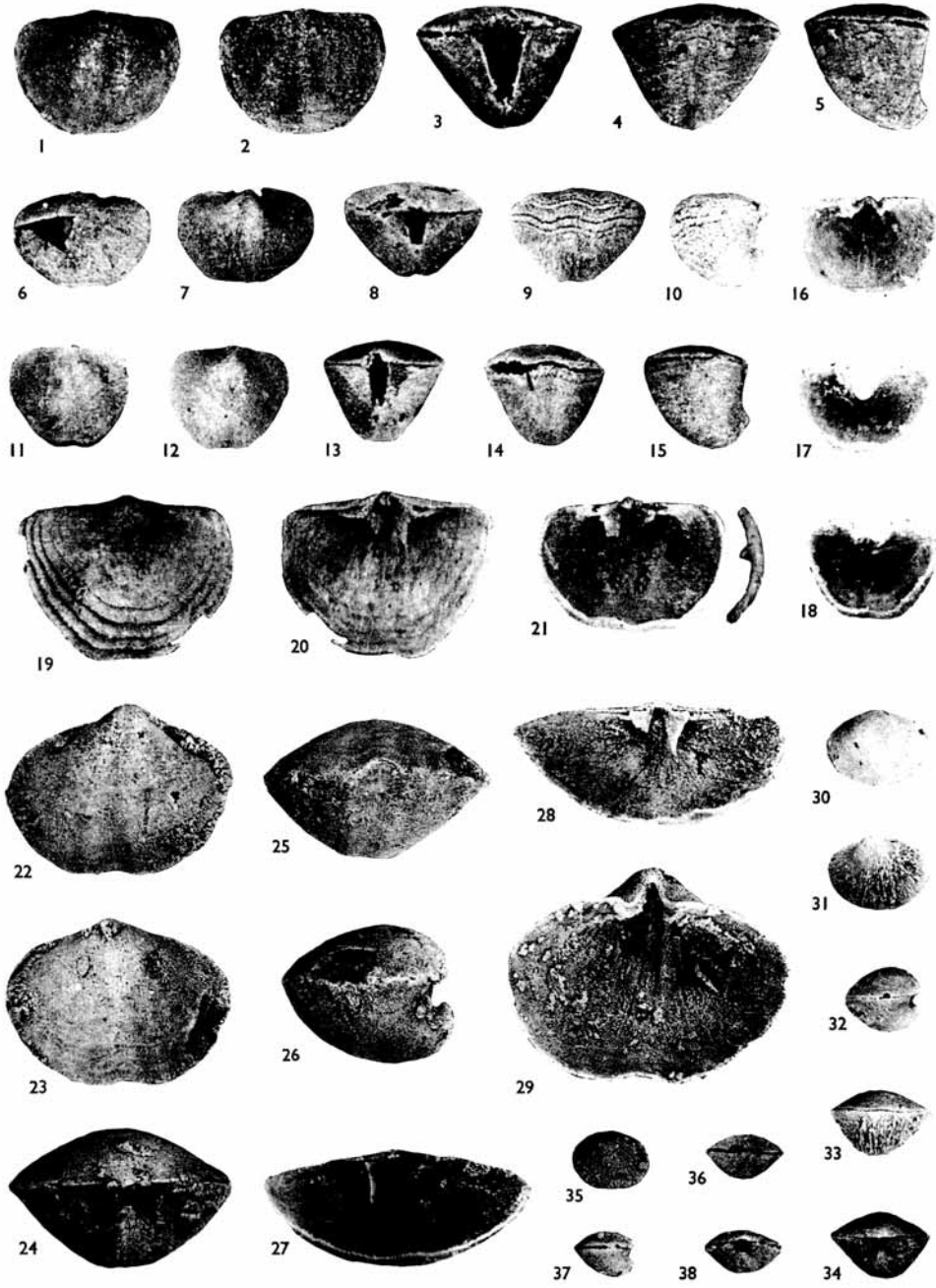
The ventral valve has a faint sulcus and the dorsal valve a barely discernible fold. Where they meet anteriorly the commissure is rectimarginate or weakly uniplicate (Pl. 90, fig. 25). A surface ornament of fine concentric growth-lines also shows traces of very fine radial lines (Pl. 90, fig. 22). No spines are visible, probably because of the nature of the preservation.

Ventral interior. The ventral interior is without dental lamellae. Narrow tooth ridges border the delthyrium and thicken markedly on the inner surfaces prior to projecting as short strong teeth. In a single specimen the ventral muscle field is visible as a number of linear radiating impressions (Pl. 90, fig. 29).

Dorsal interior. Small hinge plates extend for about one-third of the maximum shell width (Pl. 90, fig. 28). The cardinal process, placed at the very apex of the notothyrium, is poorly preserved in most of the material but in some specimens occurs as a wide structure with several ill-defined lobes (text-fig. 2). Deep, narrow sockets are widely divergent at about 140° and are supported on narrow hinge plates. The inner socket ridges are low proximally but become wider and higher distally to terminate in projections which articulate with crural fossettes (Pl. 90, figs. 27, 28). Thin, triangular crural lamellae slope downwards from the inner edges of the socket ridges but do not meet the valve floor. They extend between one-fifth and one-quarter the distance to the anterior margin and are strongly convergent downwards and moderately divergent

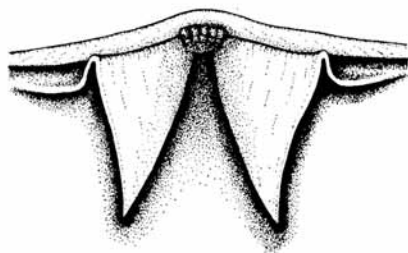
EXPLANATION OF PLATE 90

- Figs. 1–21. *Ambocoelia praecox dorsiplicata* subsp. nov. Mandagery Park Formation, Manildra. 1–5, Dorsal, ventral, posterior, anterior, and lateral views of SU 16614 showing the large ventral interarea (fig. 3), and the small dorsal plication in the anterior commissure (fig. 4). 6–10, Dorsal, ventral, posterior, anterior, and lateral views of SU 16609 showing the more inflated ventral umbo (fig. 10), and the gently plicate anterior commissure (fig. 9). 11–15, Dorsal, ventral, posterior, anterior, and lateral views of SU 16610 showing the slightly emarginate anterior margin (fig. 11) and the high, gently concave interarea (fig. 15). 16–18, Three dorsal views of ventral valve SU 16612 showing the narrow tooth-ridges along the delthyrial margins and the absence of dental lamellae and a median septum. 19, 20, Dorsal and ventral views of dorsal valve SU 16615 showing the bifid cardinal process, the long widely divergent sockets, and the broad crural lamellae meeting the valve floor posteriorly. 21, Ventral view of dorsal valve SU 22668 together with a crus broken from it. (All figures $\times 9$.)
- Figs. 22–38. *Proreticularia beddiei* sp. nov. Mandagery Park Formation, Manildra. 22–6, Dorsal, ventral, posterior, anterior, and lateral views of SU 16620 (holotype) showing the distinct fold and sulcus (fig. 25), the emarginate anterior margin (fig. 23), the narrow strip-like deltidial plates projecting normal to the interarea (fig. 24), and the large incurved ventral umbo (fig. 25). 27, Antero-ventral view of dorsal valve SU 16622 showing the broad cardinal process and the large sub-triangular crural lamellae. 28, Antero-ventral view of dorsal valve SU 16623 showing the hinge plates supporting the large crural lamellae. 29, Dorsal view of large ventral valve SU 16621 showing the narrow tooth ridges, the absence of a median septum, and the large deeply striated muscle field. 30–4, Dorsal, ventral lateral, anterior, and posterior views of SU 16617, a young form with an almost perfectly elliptical outline and a rectimarginate anterior commissure (fig. 34). 35–8, Dorsal, anterior, lateral, and posterior views of SU 16616, a very young form. (All figures $\times 6$.)



SAVAGE, *Ambocoelia* and *Proreticularia*

anteriorly (Pl. 90, figs. 27, 28). From the lower edges of the crural lamellae slender crura curve upwards. Spires have not been observed. The dorsal muscle field extends between one-third and one-half the distance to the anterior margin. It is divided into a narrow, elongate pair of medial adductors confined to the faint internal impression of the fold, and a pair of shorter, more rounded lateral adductors.



TEXT-FIG. 2. *Proreticularia beddiei* sp. nov. Reconstruction of the dorsal cardinalia based on several incomplete specimens. Approx. $\times 20$.

Measurements. The dimensions of 5 specimens are given below in mm.

		<i>Length</i>	<i>Width</i>	<i>Thickness</i>
SU 16616	Complete shell	1.5	2.0	1.3
SU 16617	Complete shell	1.9	2.6	1.7
SU 16620	Complete shell	4.5	6.0	3.6
SU 16621	Ventral valve	4.8	6.9	—
SU 16622	Dorsal valve	4.2	6.8	—

Ontogeny. This species is not well represented in the collection and most of the specimens are damaged to some degree. As with the other spiriferid genera described herein, the most obvious ontogenetic changes are the accentuation of the fold and sulcus, the increasing prominence of the ventral umbo posteriorly, and the incurving of the beaks (Pl. 90, figs. 22–6). In this species the dorsal fold is very gentle in even the mature forms, and in the youngest stages it is scarcely visible at all (Pl. 90, fig. 36). As growth proceeds the ventral sulcus becomes more marked than the dorsal fold with the result that the anterior margin is emarginate in the mature specimens.

Discussion. This Manildra form resembles the type species from the Ludlovian Kopanina Limestone, Bohemia. However, specimens of *Proreticularia carens*, sent to the author by Dr. Havlíček, are less wide and have a less incurved ventral umbo than *P. beddiei* and this difference is also clear from the published illustrations (Havlíček 1959, pl. 25, figs. 1, 2). *P. candida* Havlíček, 1959, from the Koněprusy Limestone, is also narrower than the Manildra species and it differs further in having shallow furrows bounding the low dorsal fold. *Proreticularia* has not been recorded previously outside Bohemia and Asiatic Russia.

Superfamily CYRTIACEA Frederiks 1919 (1924)

Family AMBOCOELIIDAE George 1931

Genus AMBOCOELIA Hall 1860

Type species. Orthis umbonata Conrad 1842, by original designation.

Members of the Ambocoeliidae show considerable variation, even from the same locality, and precise distinctions between species, and even genera, are often difficult for this reason. Vandercammen (1956) attempted to group the genera primarily on the basis of dental lamellae, separating those with dental lamellae from those without, whereas Havlíček (1959) laid particular emphasis on the presence or absence of a fold or sulcus in the dorsal valve. Neither of the resulting groupings has proved satisfactory and in the Brachiopod treatise (1965) Pitrat has not attempted to subdivide the Ambocoeliidae into subfamilies.

The *Manildra* species described below shows considerable variation in the degree of plication (see Pl. 90) and it is unlikely that minor departures of the anterior commissure from the rectimarginate condition are of generic significance. In the form of the interarea, and the internal features of both the ventral and dorsal valves, the *Manildra* form closely resembles the type species of *Ambocoelia* and it is to this genus that it is referred herein.

Ambocoelia praecox dorsiplicata subsp. nov.

Plate 90, figs. 1-21

Diagnosis. A form of the species *Ambocoelia praecox* Kozłowski with a weak dorsal fold and a uniplicate anterior commissure.

Material. Of a total of 55 silicified specimens, 30 are complete or nearly complete shells with conjoined valves, 10 are dorsal valves, and 15 are ventral valves. The internal features, including spiralia and crura, are often visible in this material but the finer external detail is not preserved. Specimen SU 16609 is designated the holotype.

Description. Exterior. The shell is small, subquadrate to semicircular in outline, and widest near the hinge line. The cardinal margins are sharply rounded and the anterior margin is often emarginate. In lateral profile the shell is very unequally biconvex.

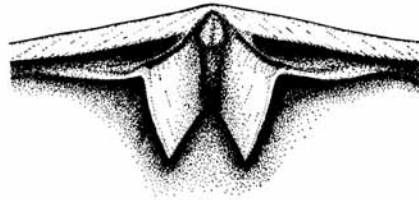
The ventral valve is deep with a swollen, strongly arched umbo and a suberect beak (Pl. 90, figs. 5, 15). The lateral slopes are gently concave postero-laterally, and gently convex antero-laterally. A high interarea is apsacline and concave, with the curvature increasing apically; it has a width about two-thirds that of the shell and an apical angle of about 90°. The large open delthyrium is triangular and includes an angle of 25-35°.

The dorsal valve is evenly convex with a broad umbo. A low, concave interarea is anacline to orthocline and the notothyrium is open, often with the cardinal process visible apically.

A low sulcus on the ventral valve extends from the umbo. The dorsal valve has a low fold, bounded either side by a broad furrow. Anteriorly the fold and sulcus form a gently uniplicate commissure (Pl. 90, figs. 4, 9, 14). The shell surface is smooth, or ornamented with fine concentric growth lines. Fine radial striations are present, and often a further set of stronger growth lines is irregularly superimposed (Pl. 90, fig. 19). No spines have been observed.

Ventral interior. The ventral interior is without dental lamellae. Narrow tooth ridges, which border the delthyrium, are continuous with the teeth. No median septum is present. The muscle field has not been observed in the material available.

Dorsal interior. The hinge plates extend from one-half to two-thirds of the valve width. A shallow notothyrial cavity is partly filled by a bifid cardinal process which has a long, inclined shaft (Pl. 90, fig. 20). The sockets are long and widely divergent (text-fig. 3). They are bounded posteriorly by the valve margin and anteriorly by narrow inner socket



TEXT-FIG. 3. *Ambocoelia praecox dorsiplicata* subsp. nov.
Reconstruction of the dorsal cardinalia based on several
incomplete specimens. Approx. $\times 30$.

ridges which are low proximally, but become higher distally. Broad crural lamellae rest on the valve floor with their inner edges almost parallel (Pl. 90, fig. 20), but occasionally they only join the valve floor posteriorly and are suspended from the socket plates for most of their length. The lamellae are strongly convergent downwards and moderately divergent anteriorly. The crura are long and subparallel with short, hook-like, ventrally curved processes projecting from them at about one-third the valve length (Pl. 90, fig. 21). The spines are directed laterally, each with 4 or 5 volutions. A long, narrow, muscle field extends three-quarters of the valve length but the individual impressions are indistinct.

Measurements. The dimensions of 5 specimens are given below in mm.

		<i>Length</i>	<i>Width</i>	<i>Thickness</i>
SU 16609	Complete shell	1.6	2.3	1.5
SU 16610	Complete shell	1.7	2.0	1.6
SU 16612	Ventral valve	1.7	2.2	—
SU 16614	Complete shell	1.9	2.6	1.9
SU 16615	Dorsal valve	2.6	3.5	—

Discussion. Considerable variation of form is present in this material and it is difficult to find two specimens really alike. Examples of this variability are seen in Plate 90. *Ambocoelia praecox* Kozłowski, from the Borszczow beds of Podolia, is very close to the Manildra material. The only real difference is the rectimarginate anterior commissure of the Podolia species compared with the dorsal fold in the form from New South Wales.

Of the Bohemian species, *A. operculifera* Havlíček, from the early Emsian Řeporyje Limestones, differs from the Manildra form in being distinctly sulcate, though it is

worthy of note that one of the figured specimens (Havlíček, 1956, fig. 17) shows very weak plications laterally. The younger species, *A. mesodevonica* Havlíček, from the Middle Devonian Acanthopyge Limestones, also shows weak plications anteriorly. Both *A. praecox* from Podolia, and *A. praecox dorsiplicata* from Manildra, differ from the North American type species in having a higher ventral interarea and a non-sulcate dorsal valve.

Superfamily DELTHYRIDACEA Phillips 1841
 Family DELTHYRIDIDAE Phillips 1841
 Subfamily ACROSPIRIFERINAE Termier and Termier 1949
 Genus HOWELLELLA Kozłowski 1946

Type species. Terebratula crispus Hisinger 1826, by original designation.

Howellella nucula australis subsp. nov.

Plate 91

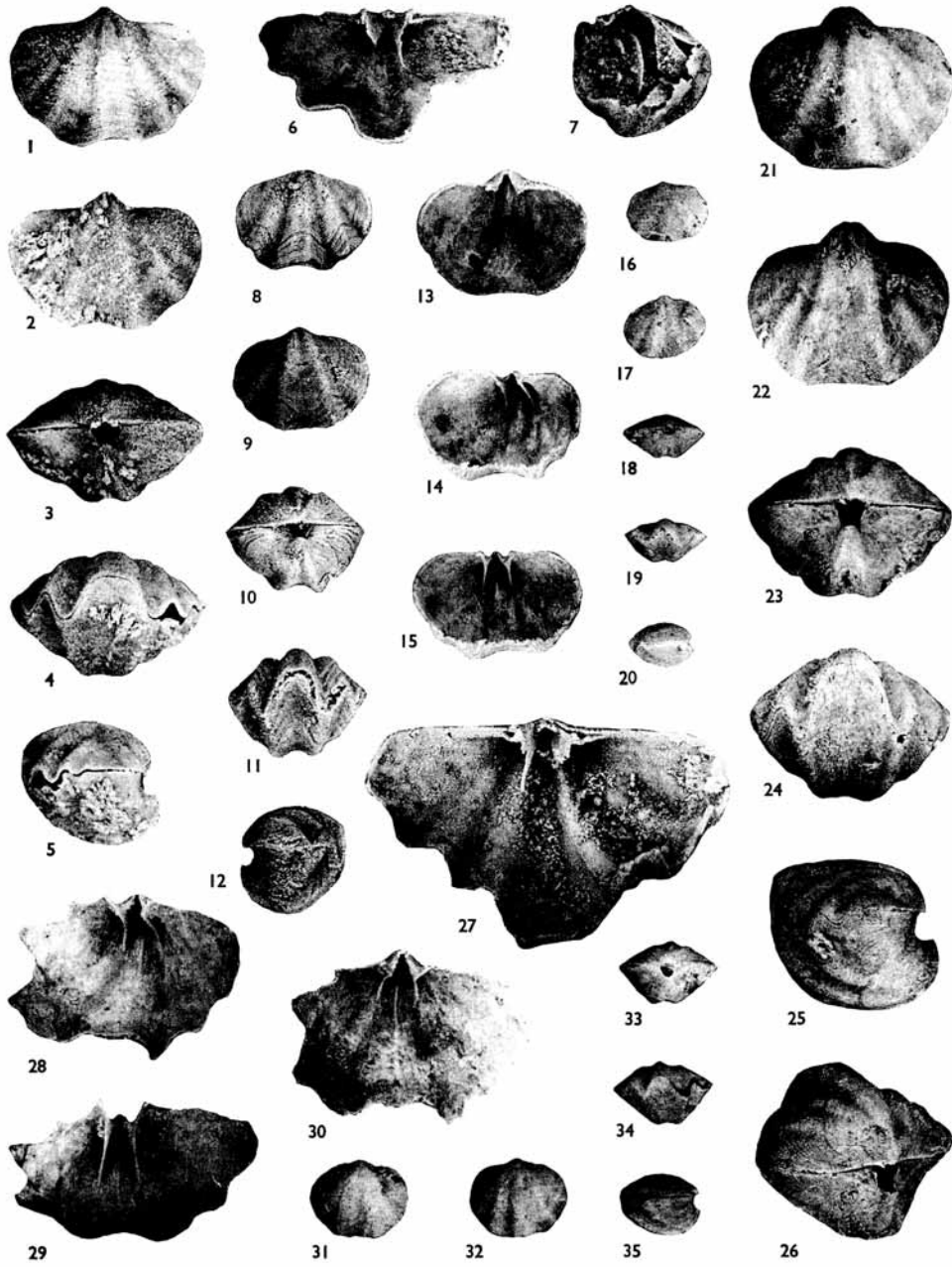
Diagnosis. A form of *Howellella* close to *H. nucula* (Barrande) but with a very small median septum in the extreme apex of the umbonal cavity.

Material. A total of 716 silicified specimens consists of 426 complete or nearly complete shells with conjoined valves, 157 dorsal valves, and 133 ventral valves. The internal features, including the spiralia in some cases, are well preserved but the finer external ornament is not present. Specimen SU 16603 is designated the holotype.

Description. Exterior. The shell is small and transversely oval in outline with the maximum width just posterior of mid-length. It has broadly rounded cardinal margins and more gently rounded anterior and lateral margins. In lateral profile the shell is strongly biconvex with the ventral valve deeper than the dorsal valve. The thickness is often equal to the length with the maximum thickness at about mid-length and the anterior slopes almost vertical.

EXPLANATION OF PLATE 91

Figs. 1–35. *Howellella nucula australis* subsp. nov. Mandagery Park Formation, Manildra. 1–5, Dorsal, ventral, posterior, anterior, and lateral views of SU 16602. 6, Antero-ventral view of dorsal valve SU 16608 showing the conspicuous cardinal process and the large triangular crural lamellae. 7, Antero-lateral view of broken specimen SU 16605 showing part of the exposed spire. 8–12, Dorsal, ventral, posterior, anterior, and lateral views of SU 16601. 13–15, Dorsal, dorso-lateral, and antero-dorsal views of ventral valve SU 16606 showing the dental lamellae and low myophragm. 16–20, Dorsal, ventral, posterior, anterior, and lateral views of SU 19599, a young stage showing a relatively gentle fold and sulcus (fig. 19), and dorsally directed beaks (fig. 20). 21–6, Dorsal, ventral, posterior, anterior, lateral, and postero-lateral views of mature specimen SU 16603 (holotype) showing the prominent ventral umbo (fig. 25) and pronounced fold and sulcus (fig. 24) which are typical of the larger specimens. 27, Ventral view of dorsal valve SU 16604 showing the divided hinge-plate, the broad cardinal process, the widely divergent sockets, and the large crural lamellae suspended from the socket ridges. 28–30, Dorso-lateral, antero-dorsal, and dorsal views of ventral valve SU 16607 showing the gently advancing dental lamellae (fig. 28), the small median septum at the extreme apex of the umbo (fig. 29), and the distinct myophragm (fig. 30). 31–5, Dorsal, ventral, posterior, anterior, and lateral views of SU 16600, a relatively young form. (All figures $\times 5.5$.)

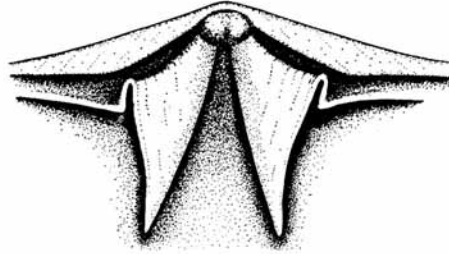


SAVAGE, *Howellella*

The ventral valve has a concave, apsacline interarea with a width half the maximum shell width and an apical angle of about 110° . This is bordered by low, poorly defined beak ridges. An open, triangular delthyrium includes an angle of $30\text{--}40^\circ$ and is bordered by narrow deltidial plates which project normal to the interarea surface (Pl. 91, fig. 10). The ventral umbo is prominent and the beak incurved.

The dorsal valve has a small suberect beak and a low anacline interarea. An open notothyrium includes an angle of about 140° .

The ventral sulcus and dorsal fold are both rounded in section and strongly defined. They commence at the beaks and expand rapidly to occupy two-thirds of the shell width at the anterior commissure. The lateral plications are broadly angular with straight slopes and sharply rounded crests and troughs (Pl. 91, fig. 11). Generally there are 3 plications each side of the sulcus and 2 each side of the fold. The finer ornament is poorly preserved but numerous regularly spaced concentric growth-lines are visible.



TEXT-FIG. 4. *Howellella nucula australis* subsp. nov. Reconstruction of the dorsal cardinalia based on several incomplete specimens. Approx. $\times 20$.

Ventral interior. Well-developed slender dental lamellae extend one-quarter to one-third of the valve length along the line of the plications bordering the median sulcus (Pl. 91, fig. 28). The lamellae diverge anteriorly and downwards, and have concave anterior edges which drop sharply from the overhanging delthyrial margins to advance along the valve floor (Pl. 91, fig. 29). Small slender teeth have shallow crural fossettes directed antero-medially (Pl. 91, fig. 15). A very short median septum is present in the posterior extremity of the umbonal cavity. The ventral muscle field, which is weakly impressed in the material available, extends up to half the valve length and is divided medially by a low myophragm (Pl. 91, fig. 29).

Dorsal interior. Short hinge-plates extend laterally for two-fifths of the maximum shell width and separated by a wide notothyrial cavity. (text-fig. 4). The cardinal process is broad and strongly recurved posteriorly to protrude through the notothyrium (Pl. 91, fig. 6). Finer details of the cardinal process are seldom preserved but two specimens have a bilobed process (text-fig. 4) and one has a trilobed process. Narrow sockets are widely divergent at about 125° . They are variable in length and supported by the strongly curved hinge-plates which arise from beneath the interarea. The inner socket ridges are narrow with prominent projections distally which articulate with the crural fossettes of the ventral valve (Pl. 91, fig. 27). Large blade-like crural lamellae extend downwards from the inner socket ridges but do not reach the valve floor. They meet the valve wall posteriorly directly below the cardinal process (text-fig. 4). The lamellae are strongly

convergent downwards and divergent anteriorly, with concave anterior edges extending one-third of the distance to the anterior margin (Pl. 91, fig. 6). From the lower edges of the crural lamellae arise crural bases from which long crura project anteriorly and then curve sharply upwards to point postero-ventrally. Distally the crura are attached to the laterally directed spires, each of which has 4 or 5 volutions. The faintly impressed dorsal muscle-field is confined to the trace of the fold. It extends about one-third of the valve length.

Measurements. The dimensions of 5 specimens are given below in mm.

		<i>Length</i>	<i>Width</i>	<i>Thickness</i>
SU 16601	Complete shell	2.5	3.3	2.7
SU 16602	Complete shell	3.4	4.6	3.0
SU 16603	Complete shell	3.7	4.7	3.5
SU 16604	Dorsal valve	5.7	9.3	—
SU 16606	Ventral valve	3.2	4.3	—

Ontogeny. From the numerous specimens in the collection a good ontogenetic series is available. The main changes which occur with growth are the accentuation of the fold and sulcus, the projection posteriorly of the ventral umbo, and the gradual incurving of the ventral beak (Pl. 91). As maturity approaches the thickness of the shell is increased by the deposition of shell material along the lateral and posterior margins, and this is responsible for the incurving of the beaks and the increasing prominence of the ventral umbo. In the young internals examined the features differed little from the mature forms.

Discussion. *Howellella nucula* (Barrande 1879), from the Ludlovian Kopanina Limestones of Bohemia, is very close to the Manildra material. Externally the forms are identical, with a similar fold and sulcus bordered by two or three gentle plications. Internally the arrangement of the crural lamellae and dental lamellae is the same, and there is a low median myophragm in both ventral valves (compare Pl. 91, herein, with Havlíček 1959, figs. 41, 42). However, there is a median septum at the very apex of the umbonal cavity in the Manildra form which is not present in the Bohemian species (Havlíček 1959, fig. 41). Though distinct, this median septum is very short and different from that in *Delthyris*.

Other related Bohemian species include *H. koněprusensis* Havlíček, from the Koneprusy Limestones, which differs from the Manildra form in having an angular fold and sulcus and more lateral plications. *H. spuria* (Barrande), from the Kopanina Beds, has a broader fold and sulcus flanked by incipient lateral plications, and *H. inchoans* (Barrande), from the Lochkov Limestones, has numerous weak lateral plications.

H. laeviplicata Kozłowski, from the Borszczow beds of Podolia, is also close to the Manildra species. Only a single ventral section is figured by Kozłowski (1929, fig. 60A), and this does not show a myophragm. However, Kozłowski states in his description that the internal features are essentially the same as in *H. angustiplicata* which he illustrates with several serial sections (op. cit., fig. 64). These show the crural lamellae suspended from the hinge-plates for most of their length, as in the Manildra specimens. Material with affinities both to the eastern European forms and those from New South Wales, is found further east, in central Asia. The Siberian species *H. khalfini* Kulkov, 1963, from

the Lower Devonian Solovikha Limestone in the Altai Mountains, is less inflated than the Australian form and does not possess advancing dental lamellae.

Of the species described from south-east Australia, *H. scabra* Philip, from the Cooper's Creek Formation at Tyers, Victoria, is less gibbous than the Manildra form. Both have 2 or 3 lateral plications each side of a strong median fold and sulcus, but whereas the Victorian species has 2 very short dental lamellae, the lamellae of *H. nucula australis* extend up to one-third of the valve length. Philip (1962, p. 222) states that the Tyers material has extremely short crural bases but makes no mention of the crural lamellae, possibly because the form of these structures is not apparent from slots visible in mould material when species with 'suspended' crural lamellae are examined. *H. textilis* Talent, from the Tabberabbera Formation, Victoria, is known only from deformed material which is not easily compared with the silicified material from Manildra. Another Victorian species, *H. lirata* Talent, differs from *H. nucula australis* in being wider and having a lower fold and sulcus flanked by more numerous lateral plications.

Superfamily SUESSIACEA Waagen 1883

Family CYRTINIDAE Frederiks 1912

Genus CYRTINA Davidson 1858

Type species. *Calceola heteroclita* DeFrance, 1828, by the subsequent designation of Hall and Clarke, 1894.

Cyrtina praecedens Kozłowski 1929

Plate 92

1929 *Cyrtina praecedens* Kozłowski; p. 207.

1954 *Cyrtina praecedens* Kozłowski; Nikiforova, p. 150.

Material. The collection consists of 472 silicified specimens of which 329 are complete, or almost complete, with the valves united. Of the remainder 55 are dorsal valves and 88 are ventral valves. The preservation is sufficiently delicate to show the external punctation.

Description. Exterior. The shell is small and hemipyramidal. In outline it is semicircular with right-angular cardinal extremities and evenly rounded lateral and anterior margins. The lateral profile is subtriangular with the maximum thickness at the posterior margin.

The ventral valve is hemipyramidal with a high umbonal region. The steep slopes are slightly convex laterally and more strongly convex anteriorly. A prominent, suberect beak projects just past the hinge line and the very high interarea is apsacline to catacline with an apical angle of 85–95°. The interarea bears growth striations parallel to the hinge line. A long, narrow delthyrium includes an angle of about 20° and is closed for most of its height by a deltidium which is gently convex near the hinge-line but strongly arched and hood-like about a round or oval apical foramen (Pl. 92, fig. 28).

The dorsal valve is convex with a broad umbo and a suberect or nearly straight beak. It has a very low, anacline interarea.

A dorsal fold and ventral sulcus are prominent. Both extend from the posterior margin to the strongly parasulcate anterior commissure. The fold is elevated above the remainder of the valve anteriorly and at the commissure it accommodates a semicircular tongue from the ventral sulcus. Both valves have 3–5 pairs of strong, rounded plications which arise along the cardinal margins (Pl. 92, figs. 1, 2). The furrows bordering the fold, and

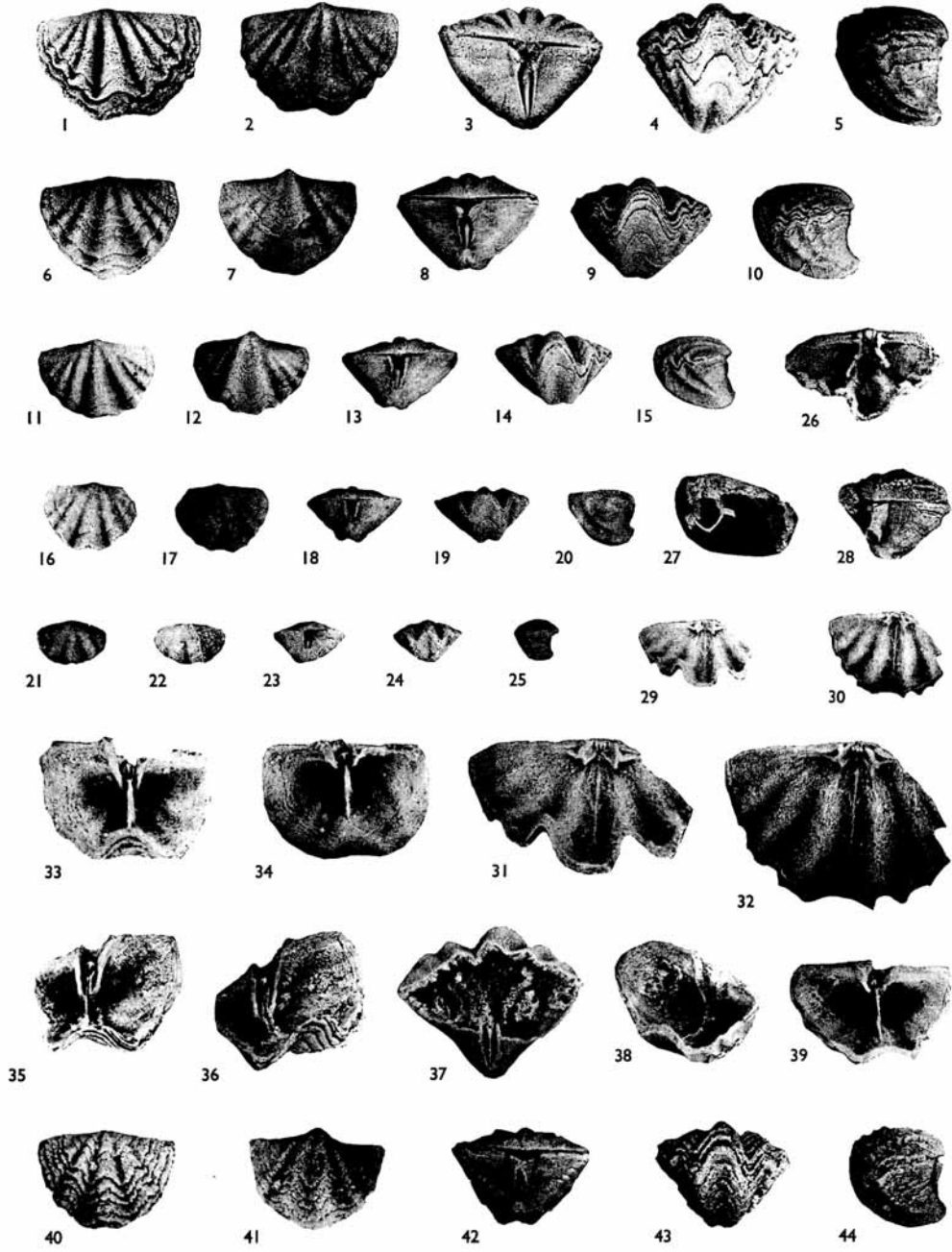
the plications bordering the sulcus, are particularly pronounced. Several strongly lamellose growth-lines are usually present in mature specimens. The shell material is finely punctate.

Ventral interior. Convergent dental lamellae project anteriorly from the delthyrial margins but do not reach the valve floor. These lamellae meet to form a vertical spondylium which extends anteriorly for about one-sixth of the valve length (Pl. 92, figs. 35, 39). Above the spondylium the dental lamellae become progressively reduced to form stout, vertical pillars which border the delthyrial cavity and project as short rounded teeth. Supporting the spondylium is a high median septum with a concave forward edge. The septum protrudes into the spondylial cavity as a subvertical tichorhinum with a hollow interior partly divided by a thin vertical plate, complete at the apex, but for the most part consisting of two separate septa (Pl. 92, figs. 35, 39). The closed apical part of the tichorhinum is visible through the foramen (Pl. 92, fig. 37). No ventral muscle-scars have been observed in this material.

Dorsal interior. The dorsal interior has a broad cardinal process consisting of three primary lobes and numerous secondary lobes (Pl. 92, fig. 31). The sockets, which are deep and triangular, are supported on strong, thickly developed hinge-plates (text-fig. 5). Crural lamellae extend downwards from short, widely divergent inner socket ridges but do not meet the valve floor; the lower parts form crural bases which diverge anteriorly at 65–75°. Subparallel crura extend about one-quarter of the valve length and are joined by a slender, V-shaped jugum with its pointed end directed anteriorly (Pl. 92, fig. 27). The spiralia are large and occupy most of the shell interior. Each is elongate and laterally

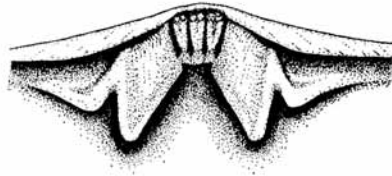
EXPLANATION OF PLATE 92

Figs. 1–44. *Cyrtina praecedens* Kozłowski. Mandagery Park Formation, Manildra. 1–25, Dorsal, ventral, posterior, anterior, and lateral views of five specimens of progressively decreasing size. 1–5, Specimen SU 16628, a large mature form with successive growth thickenings at the valve margins (fig. 5). The closed apical part of the tichorhinum and the horizontal striations on the ventral interarea are also visible (fig. 3). 6–10, Specimen SU 16627, a mature form with the dorsal fold distinctly elevated above the lateral plications (fig. 10). 11–15, Specimen SU 16626, a younger stage with less pronounced plications. 16–20, Specimen SU 16625, a young form with only two plications each side of the fold (fig. 16). 21–5, Specimen SU 16624, a very young form with gentle plications and relatively rounded contours. 26, Antero-ventral view of dorsal valve SU 22669 showing the attachment of the crura to the crural lamellae. 27, Anterior view of broken specimen SU 16634 showing the slender V-shaped jugum joining the subparallel crura. 28, Postero-lateral view of specimen SU 16633 showing the strongly arched deltidium with a hood-like foramen. 29, 30, Ventral and antero-ventral views of dorsal valve SU 16636. 31, 32, Enlargements of figs. 29, 30 showing the trilobed cardinal process with its numerous secondary subdivisions (fig. 31), the deep sockets partly overhung by the inner socket ridges (fig. 30), the widely divergent crural lamellae, and the long narrow muscle-field divided by a low myophragm (fig. 30). 33, 34, Two dorsal views of ventral valve SU 16629 showing the dental lamellae converging to form a spondylium into which the high median septum protrudes as a hollow subvertical tichorhinum. The latter is partly divided by a thin vertical plate which can be seen on both the posterior and anterior sides. 35–6, Dorsal and dorso-lateral views of ventral valve SU 16631. (The hollow nature of the median septum within the spondylium is probably the result of incomplete silicification.) 37, Postero-dorsal view of SU 16632 showing the partly exposed spires. 38, 39, Dorso-lateral and dorsal views of ventral valve SU 16630. 40–44, Dorsal, ventral, posterior, anterior, and lateral views of SU 16635 showing unusually prominent growth lamellae. (Figs. 31, 32 $\times 8$, remaining figures all $\times 4$.)



SAVAGE, *Cyrtina*

directed with 5-6 volutions (Pl. 92, fig. 37). The adductor muscle-field is long and narrow, extending two-thirds of the distance to the anterior margin, and consisting of small posterior adductors and larger, more elongate, anterior adductors. A low myophragm divides the muscle field medially (Pl. 92, fig. 32).



TEXT-FIG. 5. *Cyrtina praecedens* Kozłowski. Reconstruction of the dorsal cardinalia of the *Manildra* specimens based on several incomplete specimens. Approx. $\times 35$.

Measurements. The dimensions of 4 specimens are listed below in mm.

		<i>Length</i>	<i>Width</i>	<i>Thickness</i>
SU 16625	Complete shell	2.7	3.8	2.2
SU 16626	Complete shell	3.2	4.5	2.8
SU 16627	Complete shell	4.0	5.7	4.0
SU 16628	Complete shell	4.5	6.5	5.2

Variation. There is some variation in the strength of the growth-lines and in a few specimens these are particularly pronounced and produce a very uneven, lamellose surface (Pl. 92, figs. 40-4). In other specimens the growth-lines are more gentle, though equally numerous (Pl. 92, figs. 6-10). Differences in the form of the deltidium are commonly the result of breakage, but there is evidently some variation for a few specimens have a strongly convex plate with a hooded foramen (Pl. 92, figs. 28), while the majority have a far less convex plate with a longer, non-hooded foramen (Pl. 92, fig. 42).

Ontogeny. A good ontogenetic series is present for this species. There are few external differences between stages apart from the increase in the number and height of the lateral plications (Pl. 92, fig. 1-25). In the gerontic stage successive growth lamellae are closely spaced at the lateral and anterior margins and become more conspicuous (Pl. 92, fig. 4), than in younger specimens. Internally there is a thickening of the hinge-plates in older specimens and a broadening of the cardinal process as the three primary lobes divide and multiply.

Discussion. Although the *Manildra* specimens are smaller and have fewer plications than those from Podolia described by Kozłowski, an attempt has been made to allow for environmental stunting and to avoid the introduction of a new species name when only size and related characteristics are distinctive.

The type species from Western Europe, *Cyrtina heteroclita*, is not well known and its relationship to the *Manildra* material is difficult to assess. The form from Santa Lucia identified as *C. heteroclita* by Oehlert (1901) is seen in his illustrations to have an unbroken septum dividing the tichorhinum. If this is a constant characteristic it may

have taxonomic significance, for in specimens of *C. praecedens* from Podolia and from Manildra the septum is not continuous across the tichorhinum. Another reported feature of *C. heteroclita* which needs substantiation is the absence of an apical foramen (Kozłowski 1929, p. 210).

Of the other European species, *C. teta* Havlíček, from the late Emsian or early Eifelian of Bohemia, resembles *C. heteroclita* externally although the interarea is considerably longer. It is more angular than the Manildra form and has more prominent horizontal striations across the interarea.

C. heteroclita gregale Talent, from Sandy's Creek, Victoria, resembles the Manildra form in shape and the number of plications but the growth lamellae are very weak or absent in the material described. Another eastern Australian form, described by Dun (1907) as the new species *C. wellingtonensis*, is also close to *C. praecedens*. It is larger than the material from Manildra but possibly lived in a more favourable environment.

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