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A Giant New Trimerellide Brachiopod from the Wenlock (Early Silurian) of New South Wales, Australia

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ABSTRACT. *Keteiodoros bellense* n.gen. and n.sp. is a remarkably large trimerellide brachiopod from the Wenlock Driestone Formation, southeast of Wellington, central New South Wales. The probable articulatory mechanism is unusual for trimerellides. It apparently involved both flattened sections of the lateral commissures which acted as pivots for opening and closing the shell, and a large and strongly modified articulating plate (which partly envelopes a robust dorsal umbo) articulating with the pseudointerarea at the posterior end of the ventral platform. The heavy dorsal umbo probably acted as a counterbalance to the anterior part of the valve; the diductor muscles were apparently attached to the umbo at the sides of the articulating plate, and to the anterior end of the ventral platform.

The trimerellides occur in presumed life position in nearly monospecific beds which are interpreted as having formed in a quiet inshore shallow subtidal area on a sloping shelf, protected by coral biostromes but periodically disrupted by storm action. They are considered to represent a low-diversity quiet-water Benthic Assemblage 2 community.

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At a length of nearly 200 mm, the huge Silurian trimerellide brachiopod described herein as the new taxon *Keteiodoros bellense*, and a possibly ancestral genus in older (Ordovician) rocks about 70 km south of Mumbil, are amongst the largest known brachiopods. Trimerellides are

a distinctive group formerly classified within the "Inarticulata", indicative of the fact that they supposedly lacked articulatory structures. Following recent re-evaluation of higher level brachiopod systematics, the trimerellides have now been moved to a position closer to

the old division "Articulata", based on their primitive, transitional hinging apparatus. The value of *Keteiodoros* is enhanced by its Wenlock age, since trimerellide brachiopods of that age are rare. Finally, it—and its probable Ordovician ancestor—provides useful insight into the functional morphology and phylogeny of the group, and the concomitant evolution of Palaeozoic shallow-water brachiopod communities

The brachiopod specimens were found in the core of the Oakdale Anticline northwest of Mumbil, in the Wellington district of central New South Wales (Fig. 1). The Mumbil area was first mapped in any detail by Strusz (1960); the anticline received closer attention from Vandyke (1970, unpublished), whose geological results were published by Vandyke & Byrnes (1976). Vandyke & Byrnes noted the presence of trimerellide banks at several localities in their Catombal Park Formation (now Bell River Member, Dripstone Formation, of probable late Wenlock age); the species was briefly described by Vandyke (now Byrnes) in her unpublished thesis.

Stratigraphy

The Bell River Member is the upper member in the Dripstone Formation (see Colquhoun *et al.*, 1997), and is overlain by the Narragal Limestone (Fig. 1). It reaches a maximum thickness of about 120 m, and comprises mostly acid volcanics, with subordinate shale and silty limestone (best developed at the base). A discontinuous dirty limestone at this level is partly biostromal, with an abundant fauna of rugose and tabulate corals and stromatoporoids, some in life position, and rare other taxa, including the trilobite *Pacificurus* (formerly a subgenus of *Encrinurus*, and placed in synonymy with *Batocara* by Holloway, 1994, a move with which Strusz disagrees). The coral fauna was described by Strusz (1961), with revisions of the rugosans by McLean (1975), and some of the tabulates by Webby & Semeniuk (1969). The dominant rugosan is *Palaeophyllum oakdalensis*, associated with which are *Aphyllum lonsdalei*, *Holmophyllum struzi* and *Holmophyllia maculosa*; the tabulates include *Propora conferta*, *Multisolenia tortuosa*, *Favosites gothlandicus*, *Acanthohalysites australis*, *Falsicatenipora bellensis* and *F. chillagoensis*. The taxonomic positions of the various taxa (whose authorship can be found in the above-mentioned papers) have been updated in Strusz (1996). Vandyke & Byrnes (1976) listed some of the coral localities in Strusz (1961) which they considered to lie within the "Catombal Park Formation". From data held by Strusz, those should include S71, S122, S208, and S285 (see Fig. 1); the collection from S65, at the base of a steep ridge, may be a mixed fauna, including specimens derived from the younger Narragal Limestone higher on that ridge.

Age

Largely on the regional relationships of the faunal association characterised by that of the Dripstone Formation, Vandyke & Byrnes (1976) argued for a late

Wenlock or, less probably, early Ludlow age. Although no new information has been obtained on the age of the Bell River Member, diagnostic conodonts have recently been recovered from the base of the overlying shallow-water Narragal Limestone, as well as from outcrops of probable Wylinga Member (basal Dripstone Formation) within an unfaulted sliver to the west of the Oakdale Anticline.

New South Wales Geological Survey conodont sample C1430, from the basal Narragal Formation, contains *Coryssognathus dubius* (Rhodes, 1953). In the British succession (Miller & Aldridge 1993) this species extends through strata of latest Gorstian and Ludfordian age (i.e. upper Ludlow). In northeastern Victoria Simpson & Talent (1995) found it in strata ranging from possibly latest Wenlock (but no older) to Ludlow. At Yass, N.S.W. (Link & Druce 1972; stratigraphic terminology following Owen & Wyborn, 1979), *Coryssognathus dubius* is sparingly represented in the Cliftonwood Limestone Member (Yass Formation), Euralie Limestone Member (Laidlaw Formation), and Hume Limestone Member (uppermost Silverdale Formation). According to Simpson (1995), the range at Yass may start in the Wenlock and extends into the *siluricus* Zone (early Ludfordian) of the late Ludlow. Therefore, while the base of the Narragal Limestone may be as old as Wenlock, the majority of this formation is of Ludlow age. The overlying Barnby Hills Shale (see Fig. 1) contains an horizon with abundant *Bohemograptus*, suggesting for it a Gorstian-Ludfordian age; Rickards & Wright (1997) suggested correlation with the *B. kozlowskii* Biozone (Ludfordian) for this graptolite fauna. The Barnby Hills Shale is overlain by the Cuga Burga Volcanics which, nearer Wellington, also overlies the Camelford Limestone. The latter unit straddles the Silurian/Devonian boundary (Chatterton *et al.*, 1979).

The probable Wylinga Member conodont sample (C1453) contains *Ozarkodina excavata eosilurica*, which ranges through the *celloni* and *amorphognathoides* Zones, of Telychian (late Llandovery) to early Wenlock age.

Thus the Bell River Member, which succeeds the Wylinga Member and overlying Warderie Volcanics, and is itself overlain disconformably by the Narragal Limestone, is almost certainly Wenlock, and most probably Homeric in age.

Occurrence and environment

Keteiodoros bellense is known from three localities, S122, S285 and S208 (Fig. 1), in a silty limestone within the shaly basal part of the Bell River Member. The best exposures are at and near S285, where several *in situ* shell banks are developed, interspersed with biostromes of *Palaeophyllum oakdalensis*. The majority of the shells are oriented umbo-down, with the valves conjoined, resting in life position (Fig. 2). The sediment below the lowest bank is brown siltstone, apparently devoid of fauna. Thin sections of the silty carbonate rock surrounding the beak of one *in situ* specimen (Fig. 3) show it to be an orange-brown skeletal wackestone, with shelly debris distributed in terrigenous mud; algae are present. Field observation shows that the enclosing sediment contains a few

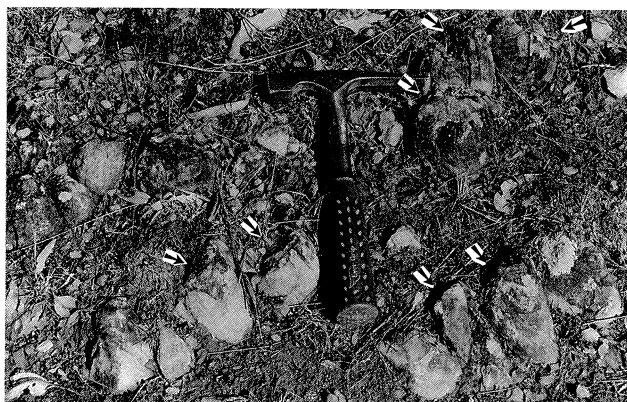


Figure 2. Outcrop photo of several successive shell layers below the main *Palaeophyllum* biostrome; arrowed are shells clearly in life position (umbo down), with truncated upper ends.

providing a temporary stable surface on a mud substrate, permitting settling of larval trimerellides. While the algae observed in the Bell River Member are not mat-like, but rather are vertically-radiating in growth form, they could still have acted as initial attachment points above the substrate.

It seems likely that the environment was lagoonal, subject to occasional storm disturbance. For the thickest shell bed this is strongly indicated by the orientation of the shells in life position, and the destruction of their anterior (i.e. upper) ends at distinct levels within the bed. Many of the damaged shells have large shell fragments (including parts of juvenile shells) within their mud-filled body cavities, indicating severe turbulence. At least one level of disturbed and randomly oriented adult shells is present near locality S285, immediately overlain by a monospecific *Palaeophyllum* biostrome. Between this biostrome and another approximately 8–10 cm above it lies an horizon of *in situ* juvenile shells. This we interpret as an attempt to recolonise the substrate by the *Keteiodoros* community, which was then catastrophically destroyed by another storm, probably smothering the juveniles with sediment before they grew to maturity. There thus appears to have been a consistent vertical (and possibly lateral) depth relationship in the Bell River Member between *Keteiodoros* and *Palaeophyllum*, with biostromes of the latter overlying banks of the former. The biostromes show every evidence of an energetic environment, in contrast to the shell banks which represent a quieter one disrupted periodically by storms. This suggests to us that the shell banks were in shallow water, possibly lagoonal, normally protected by the corals (perhaps forming a wave barrier offshore from a volcanic island), and not in an open shelf environment. The regional geology precludes the possibility of gently sloping open shelf areas with significant basinward extent.

These large shells must have been relatively heavy, since the walls are posteriorly very thick and the umbonal regions solid. It is likely that the posterior third of a large shell would have been buried in the generally fine

sediment, thus imparting considerable stability. Their size and robustness makes it tempting to compare these trimerellides with the massive bivalve *Eurydesma cordatum*, the ecology of which was described by Runnegar (1979). Runnegar deduced that when disinterred from its normal semi-infaunal position the equivalved *Eurydesma* was able to maintain its upright orientation in an active water environment in the manner of a roly-poly toy. *Keteiodoros*, however, has strongly asymmetrical valves and a protruding ventral beak, so that, unlike *Eurydesma*, reorientation would not have been possible. Thus while both shells lived partly buried in the substrate to a similar relative depth, and similarly developed a low centre of gravity enhanced by grossly thickened umbonal regions for stabilisation, *Eurydesma* was adapted to turbulent water and a resulting coarse-grained substrate, whereas *Keteiodoros* could only colonise quiet environments with a muddy substrate. The trimerellide presumably used its weight, and a degree of mutual crowding, to remain stable while keeping the anterior part of the shell above the sediment surface, so avoiding sediment-fouling of the body cavity (compare *Eodinobolus* as discussed in Webby & Percival, 1983). The biotic diversity of the *Eurydesma* community appears to be much higher than the nearly

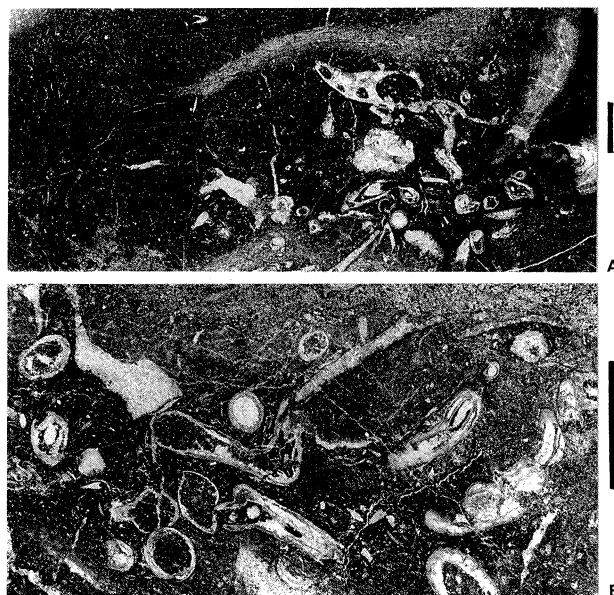


Figure 3. A–B—thin sections of the rock surrounding the beak of in-situ paratype MMF 33364; **A**—slide MMF 33364b; **B**—slide MMF 33364a, both scale bars 5 mm. The rock is an orange-brown skeletal wackestone, the matrix being terrigenous mud incorporating shelly debris, including ostracods (**B**). There are also pockets of coarser debris, usually 1–10 mm across but up to 25 mm; components include disarticulated juvenile *Keteiodoros* (**A**, top centre), the tabulate coral *Syringopora*, the stromatoporoid *Ecclimadictyon*, a fine stenoporoid bryozoan, three different algae (including a solenoporacean and *Ortonella*?), and rare gastropod and echinoderm fragments. The fragments show little sign of erosion, suggesting they have not been moved far.

monospecific *Keteiodoros* beds. A final difference is that *Eurydesma* was a high-latitude cold-water species, while in the Silurian the Lachlan Fold Belt was in subtropical to tropical latitudes (Walley *et al.*, 1990).

Benthic Assemblage position

In terms of the level-bottom Benthic Assemblages of Boucot (1975), the Trimerelloid Community Group of Wang *et al.* (1987) is usually considered to be a low-diversity high-energy B.A. 3 group of communities, and this was followed by Strusz & Garratt in Boucot & Lawson (in press) for the Catombal Park occurrences. The more detailed evidence cited above, and also that from Late Ordovician trimerellide shell banks documented from central N.S.W. by Webby & Percival (1983), suggests that more inshore (and hence, shallower water) habitats flanking volcanic islands were also preferentially colonised by these brachiopods. Indeed, Percival & Webby (1996) interpreted the *Eodinobolus* biofacies of the Molong High to have occupied a restricted marine (most likely lagoonal or protected embayment) setting equivalent to a B.A. 1 or upper B.A. 2 position, i.e. intertidal to very shallow subtidal. The environment inhabited by the nearly contemporaneous rotund trimerellide *Belubula* was also interpreted as lagoonal (Percival, 1995). Normal open-shelf shallow-water B.A. 1 & 2 environments are above wave base, while B.A. 3 is within the photic zone but subtidal, below normal wave base. However, in protected shallow water habitats such as lagoons, normal wave activity is of less consequence to the marine benthos than are tidal currents and, in particular, storms, and the normal depth connotations are difficult to apply. The difficulties in relating low-diversity low-energy B.A. 2 communities to normal B.A. 2 and B.A. 3 communities have already been discussed by Boucot (1975: 34–36). As noted above, *Keteiodoros* lived in such a quiet environment, but subject to storm damage (apparent even in thick gerontic shells of *Keteiodoros*, the anterior ends of which are typically eroded, or, in some complete specimens, stove in—see Fig. 2). In conclusion, we assign the *Keteiodoros* shell beds to a quiet-water B.A. 2 position, inshore of a protective *Palaeophyllum* wave barrier—thus different from the low-diversity high-energy B.A. 3 Trimerelloid Community as defined by Boucot (1975—who did note on p. 236 that more ecologically-oriented study may reveal greater complexity). It may be significant that in two of the three Molong High occurrences noted here (of *Belubula* and *Keteiodoros*), the trimerellides are larger and far more rotund than those found in the B.A. 3 Community, while the third comprises a moderately rotund but very large *Eodinobolus*. *Adensu* may occur in a quiet-water B.A. 2 setting, but the information provided by Popov & Rukavishnikova (1986), while recalling the *Keteiodoros* situation in some respects, is not detailed enough for a positive conclusion.

Preparation techniques

The information on which the description and analysis of *Keteiodoros bellense* are based has been obtained in several ways, because none of the specimens is sufficiently well preserved to provide all the data. The interiors of two apparently suitable specimens were mechanically prepared, but when that task (made very difficult because the matrix is no softer than the shell) was well advanced it became clear that there were problems in the umbonal area, and so a specimen was serially sectioned, and acetate peels made. Recrystallisation made these acetate peels difficult to interpret (compare Fig. 8), even when the surfaces were stained with Alizarin Red. In the end, the polished and etched surfaces were covered with abutting wide strips of “Magic tape”, and the structures traced on this in pencil under the microscope. This done, even wider strips of clear polyester tape were laid across the “Magic tape”, and the tracings lifted and transferred to clean paper. Xerographic copies of each traced surface were checked against the original surfaces under the microscope to make sure no preservational artefacts had been wrongly interpreted as structures, and corrected drawings were then prepared on a light table. A reconstruction of the interior was prepared from these. To check the interpretation of several problematic structures, other specimens were cut as close to the median plane of symmetry as possible, or at right angles to it, and polished. Finally, one of us (IGP) found a few silicified specimens on a subsequent visit to the locality, and careful etching (and reinforcing of the very fragile fragments) revealed hitherto undetected structures and internal relationships. No one method had provided sufficient information; put together, they have, we believe, given us a clear picture of this unusual brachiopod.

Systematic description

We adopt the supra-familial classification proposed by Popov *et al.* (1993) as modified by Williams *et al.* (1996). Terminology and generic authorship follow the Treatise on Invertebrate Paleontology, Part H (Williams & Rowell in Williams *et al.*, 1965) unless otherwise noted. Type material is lodged with the Australian Museum (registration acronym AM F) in Sydney, the Commonwealth Palaeontological Collection (CPC) maintained by the Australian Geological Survey Organisation in Canberra, and the New South Wales Department of Mineral Resources Palaeontological Collection (MMF), Mineral Resources Development Laboratory, Lidcombe, Sydney. Additional material is held by those organisations and the School of Geosciences, University of Wollongong.

Subphylum **Craniiformea**
Popov, Bassett, Holmer & Laurie, 1993

Class **Craniata**
Williams, Carlson, Brunton, Holmer & Popov, 1996

Order **Trimerellida**
Goryansky & Popov, 1985

Superfamily **Trimerelloidea**
Davidson & King, 1872

Family **Trimerellidae**
Davidson & King, 1872

***Keteiodoros* n.gen.**

Type species. *Keteiodoros bellense* n.sp. Wenlock, New South Wales. No other species are presently known.

Derivation of name. Greek κητειος = sea-monstrous + δορος = leather bag; neuter gender. The name is an allusion to original environment, size, and resemblance to an ovoid football.

Diagnosis. Very large and strongly equibiconvex trimerellide brachiopod, each valve with deeply excavated steep-sided platform supported by long median septum; deep umbonal cavities in ventral valve; ventral umbo long, incurved; dorsal umbo strongly incurved, bulbous, fitting against posterior end of ventral platform; long thick longitudinally and transversely curved articulating plate more or less concentric with umbo, extending from dorsal beak almost to surface of ventral platform; valve margins slightly overlapping dorsoventrally in front of flattened zones which served as articulation pivots.

Discussion. Because of the unusual morphology of this form, discussion of its relationships follows the specific description.

***Keteiodoros bellense* n.sp.**

Figs. 4–13, Table 1

Type material. HOLOTYPE: AM F101116, a partly prepared incomplete shell (Fig. 7A). PARATYPES: AM F101117–101128, 101133–101135, CPC 34408–34416, MMF 30558, 33364–33367.

Other material. AM F101129–101132, 101136–101147, CPC 34417–34419, MMF 30557, 30559, 33368–33370.

Type locality. Between localities S208 and S285 of Strusz (1961), above the head of a small gully within the Oakdale Anticline about 750 m north-northwest of “Catombal Park” (formerly “Barnby Hills”) homestead, Parish of Mumbil southeast of Wellington, New South Wales (extended grid

reference 686970E, 6381300N, Wellington 1:50,000 sheet 8632 I+IV). See Fig. 1.

Type horizon, age. Low in the Bell River Member, Dripstone Formation, Mumbil Group. Homerian?, late Wenlock, Early Silurian.

Diagnosis. As for genus.

Description. *External morphology:* The shell is large, globose, thick-walled, approximately equibiconvex; smooth apart from growth lines (Fig. 5A). The only well-preserved complete shell of the very few known (paratype AM F101117, Fig. 4) has its greatest depth at mid-length, greatest width at about $\frac{3}{4}$ length (see Table 1 for dimensions). Other relatively little-damaged shells suggest the greatest depth is often further forward. In cross section the shell is ovoid, generally deeper than wide. The commissure is sinuous laterally, and anteriorly shows a broad shallow dorsally-directed tongue. The ventral valve is medially flattened for most of its length, the flattened zone changing to a broad sulcus near the anterior margin. The dorsal valve is also boat-shaped in cross-section: gently curved laterally and medially, strongly curved in between. The ventral umbo is long, rather flattened, pointed, anacline, and suberect to strongly incurved (Figs. 4, 5). No specimen is well enough preserved to show the inner surface of the beak, while transverse sections (Fig. 6) and one silicified fragment (MMF 33367) are equivocal, so the presence of a pseudointerarea cannot be firmly established, but we interpret the area on the ventral valve posterior to the dorsal umbo and more or less continuous with the ventral platform as a poorly defined pseudointerarea. There is no sign of a homeodeltidium. The dorsal umbo is deeply incurved, strongly swollen, and generally concealed beneath the ventral beak; its ventral surface matches the transverse profile of the pseudointerarea where the two are in contact (see Figs. 6, 7). Dark lines in longitudinal sections, probably indicating the buried surface of the dorsal platform, show a spiral trace through as much as 300°. One of the silicified paratypes (MMF 33365, Fig. 9) reveals a sharply pointed beak with an apical angle of 110°; the beak is also markedly asymmetric, being directed right-ventrolaterally at about 60° to the commissure. Similar but much weaker asymmetry is also apparent in another silicified paratype (MMF 33366, Fig. 10).

Posterior to about 20% of total length (about 55 mm in the sectioned shell, Fig. 6), the margins of the dorsal valve are broadly rounded, and lie within the ventral valve, merging posteriorly with the swollen dorsal umbo. Somewhat forward of that level (at about 60 mm in Fig. 6) they become thinner, and rest against the outer edge of the ventral valve margin. Where the dorsal valve margins change from being inside to outside the ventral valve margins, there are short transitional zones where both margins have thick flattened tops which we interpret as pivot surfaces for valve movement (55–58 mm in the sectioned shell, and apparent in paratypes CPC 34410, Fig. 7B, and MMF 33364, Fig. 8). Forward from there (60–75

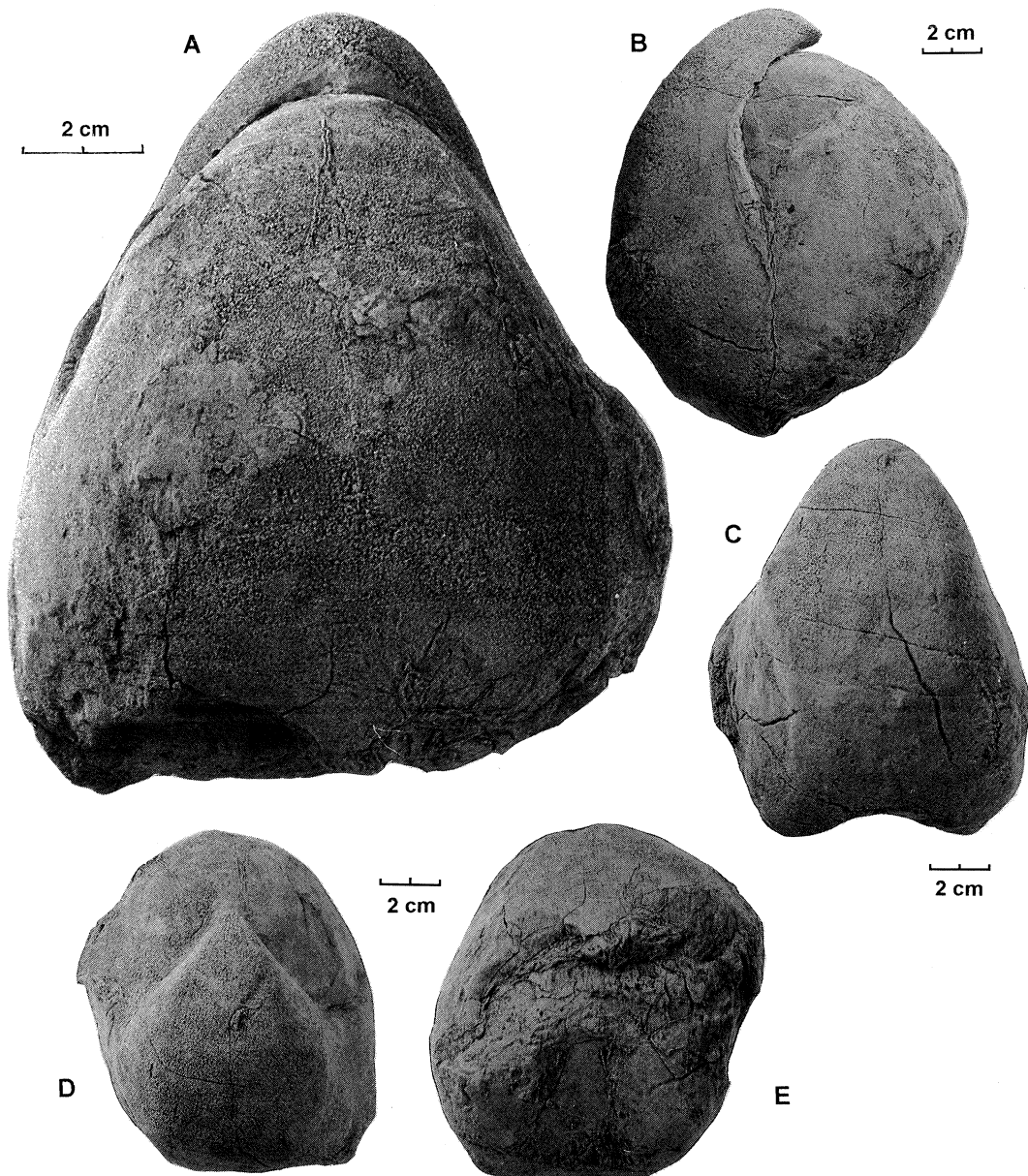


Figure 4. A–E—the only well preserved nearly complete (although somewhat worn) shell, paratype AM F101117. A—dorsal view; B–E—lateral, ventral, anterior and posterior views (dorsal valve uppermost in D and E); 2 cm scale bars. The anterior edges of the valves are slightly damaged (E); the rapid development of the ventral sulcus near the anterior margin is clearly visible in C and E, while B shows the relationship of the valve margins behind and in front of the pivot zone.

mm), a low flange develops on the inner edge of each ventral valve margin which fits into a groove near the inner edge of each dorsal valve margin. The inner edges of the grooves disappear forwards, leaving the tapered outer edges of the dorsal valve margins resting against the outer surfaces of the ventral flanges. The flanges in turn become lower, the ventral valve margins narrow, and from about the shell mid-length the commissure assumes a more conventional appearance, without any overlap of dorsal valve over ventral valve.

Ventral interior: The ventral platform is strongly developed, about 40% as high as the valve and occupying about a third of the total width anteriorly. It extends well beyond mid-length, and covers a large cavity which is divided into two long vaults by an even longer median septum which may reach the start of the anteroventral sulcus. In cross-section the sides are steep to slightly overhanging, and gently convex, while the upper surface is a broad shallow trough which longitudinal sections and the excavated shell show is not a continuous smooth curve

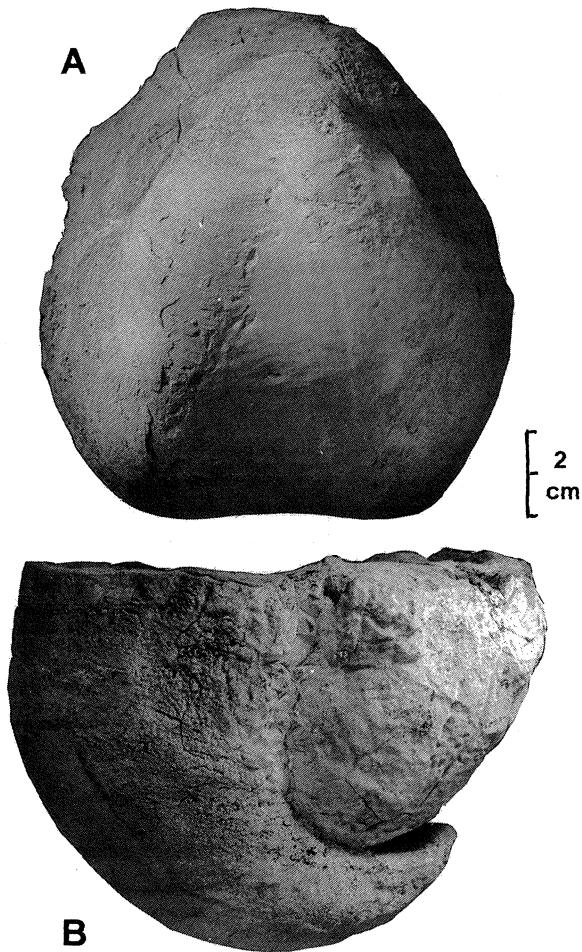


Figure 5. Incomplete large shell, paratype CPC 34408; 2 cm scale bar. The exterior of the ventral valve displays growth lines where adhering sediment has been mechanically removed, and anteriorly a broad very shallow sulcus. The side view shows the shell in inferred life position; the preserved part of the shell was probably below the sediment-water interface, and so protected from storm damage by the surrounding sediment. The restricted space between ventral and dorsal umbos is evidence for the severe limit imposed on the angle of gape.

in front of the contact zone with the dorsal umbo, but terraced, the faces of the terraces facing forward. The one silicified ventral valve fragment (MMF 33367) shows a strong but fairly smooth bulge in a position just forward of where the remnant of the dorsal umbo rests against the pseudointerarea. Posteriorly, the upper edges of the platform rise steeply and flare outwards then forwards to merge with the valve margins in continuity with (and so buttressing) the marginal flanges which interlock with the dorsal valve. They thus enclose deep umbonal cavities whose apices are about level with or slightly behind the flattened pivot surfaces on the valve margins (Fig. 6). The platform vaults are increasingly constricted posteriorly by thickening of the top and sides of the platform; from the sections, the

vaults start in front of the umbonal cavities. There is also a narrow and relatively short conical cavity at the junction of the platform and median septum. No muscle impressions have been seen on the available specimens.

Dorsal interior: The dorsal platform is similar in extent and form to that in the ventral valve, including a strong median septum and long vaults, but its edges merge posteriorly with the swollen beak rather than with the valve margins. The platform surface appears to be smooth, without any indication of muscle insertion. Umbonal cavities are apparently absent but, as with the ventral platform, there is a narrow cavity at the front of the platform, at its junction with the median septum. There is a close fit between the dorsal umbo and the posteriorly raised margins of the pseudointerarea (Figs. 5, 6). Partly enveloping the dorsal beak is a thick curved plate (see Fig. 8), which arises from a large mass of dense tissue resting on the posterior end of the dorsal platform. This plate is concentric with, but raised above, the dorsal umbo, and extends longitudinally through an arc of about 120 to 150°, such that it approaches the surface of the ventral platform. In paratype MMF 33366 its base is supported by a distinct ridge extending straight up from the surface of the platform; this, presumably the cardinal buttress, is not evident in the transverse sections. Silicified paratypes MMF 33365 and 33366 (Figs. 9, 10) show that the laterally placed recesses between plate and umbo are striated; they are presumed to have been sites of diductor muscle attachment (see discussion below). Longitudinal sections (Fig. 11) show that the distal end of the articulating plate faces a terrace on the ventral platform. Beneath that terrace distinct closely

Table 1. Dimensions in millimetres of selected shells; dimensions are approximate, with those in brackets estimated on the basis of predicted complete outline.

		length	width	depth
Holotype	AM F101116	(180)	>110	130
Paratype	AM F101117	145	115	125
Paratype	AM F101128	(135)	101	112
Paratype	AM F101133	(139)	108	116
	AM F101142	144	>85	>105
Paratype	CPC 34408	(180)	>120	130
Paratype	CPC 34409	(135)	95	85
Paratype	CPC 34411	(170)	120	135
Paratype	CPC 34412	(160)	>145	120
Paratype	MMF 30558	>130	105	120
Paratype	MMF 33364	126	127	
	MMF 30557	>102	123	122
	MMF 30559	>140	118	(125)
	MMF 33368	>160		
	MMF 33369	>135		>84
	MMF 33370	>98	>82	(75)

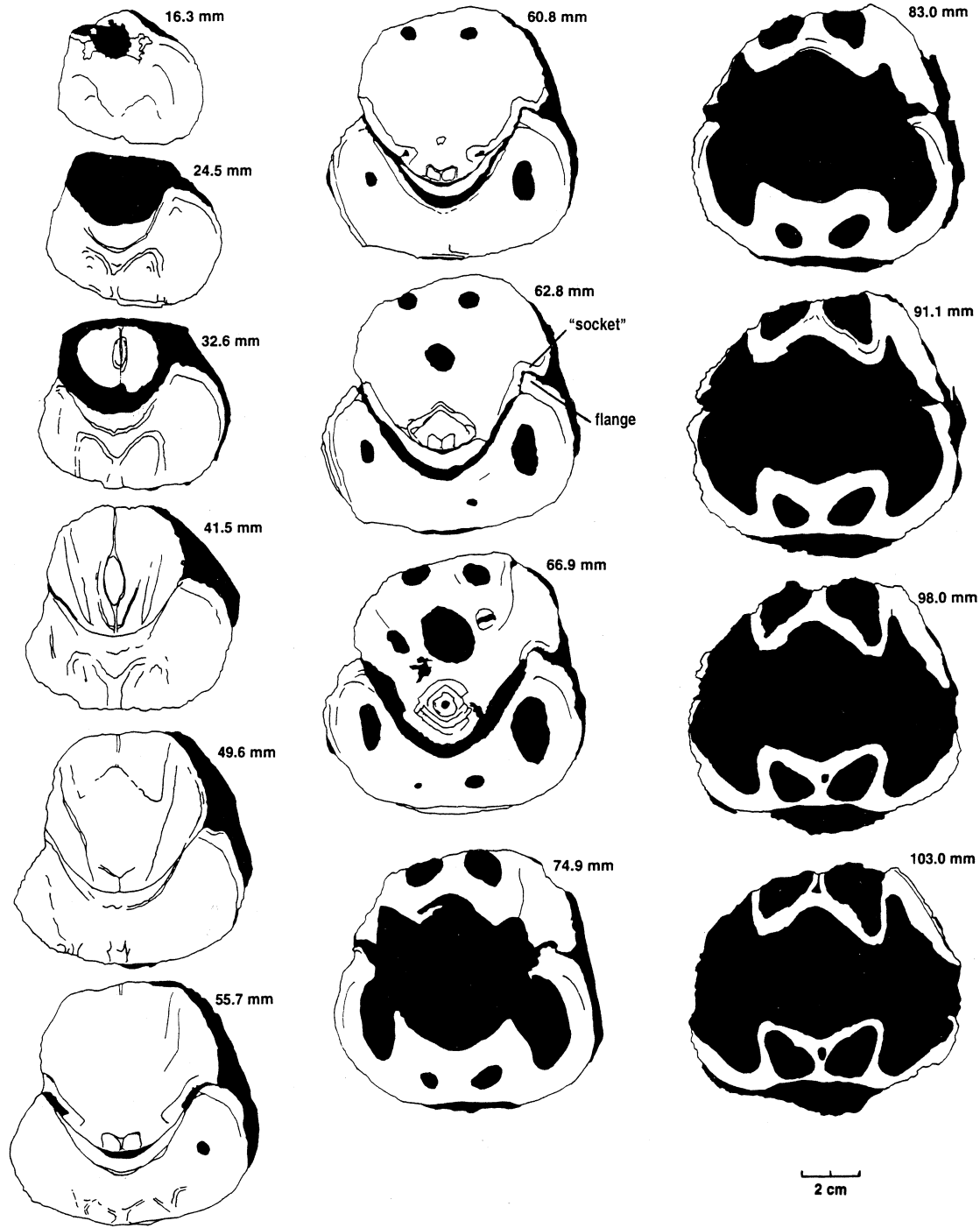


Figure 6. Selected serial sections of a nearly complete shell, paratype CPC 34409; distances are from the ventral umbo, parallel to the plane of commissure, and black areas are adhering or infilling sediment; 2 cm scale bar at lower right. The last section with traces of shell was at 157 mm, and the reconstructed longitudinal profile (see Fig. 13) suggests this was close to the relatively abrupt anterior closure of the shell. The interlocking flange-“socket” arrangement in front of the pivot zones on the valve margins is labelled on the 62.8 mm section.

spaced growth traces can be seen, and the tissue here is clearly a pad resting on the surface of the ventral platform, rather than being part of the platform structure itself; it probably corresponds to the swelling seen in MMF 33367.

Dimensions (Table 1). There are only one or two more or less complete shells, all others being damaged. In most cases only the posterior half (more or less) of the shell is preserved, and examination of the outcrop reveals that this is a function of the living position. The shells occur in

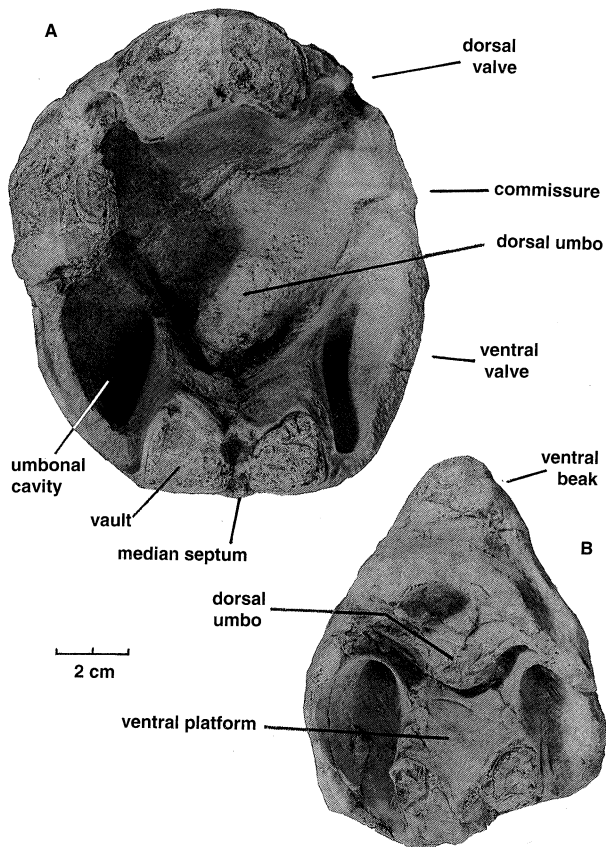


Figure 7. A–B—two prepared incomplete shells; 2 cm scale bar at lower left. **A**—holotype AM F101116 in anterior view; the vaults on both valves have not been cleaned out, and there is still some sediment at top left adhering to one side of the dorsal valve; the dorsal umbo has been partly removed during preparation, as it was difficult to distinguish recrystallised matrix from recrystallised shell, and such a large umbo was not expected in that position. **B**—paratype CPC 34410 in anterodorsal aspect, a partly prepared incomplete ventral valve with part of the dorsal umbo still resting on the ventral platform.

relatively crowded layers, mostly beak downwards, and each layer has been truncated by storm action, removing or damaging the anterior ends of the larger shells. In many shells the valves are gaped and slightly dislocated. The originally probably aragonitic shells are recrystallised (at times very coarsely—see Figs. 8, 11) to calcite, and weathered-free shells have generally lost part or more often all of the outer surface. Consequently in most cases the dimensions for width and depth shown in Table 1 are approximate, and for length or depth an estimate using the one complete shell provides a guide to probable outline.

Discussion. Few described trimerellides approach *Keteiodoros bellense* n.sp. in size or convexity. Closest are the gigantic *Belubula* Percival, 1995, from the Upper Ordovician Belubula Limestone southwest of Orange, NSW, and the somewhat smaller *Adensu* Popov & Rukavishnikova, 1986, from rocks of similar age in

southern Kazakhstan. *Belubula*, estimated to have reached a length of 20 cm, is also comparable with *Keteiodoros* in its deep ventral umbonal cavities, but the ventral platform is low, not vaulted or excavated, and there is a stout cardinal buttress; the dorsal platform, too, is relatively low. At a length of about 90 mm and a depth of 50 to 70 mm, *Adensu* is only half the maximum size of the Australian shells. The genus was made the type of a new trimerellide family based partly on large size and great convexity, but mainly in having raised dorsal muscle fields separated by deep grooves, and lacking the typical trimerellide platforms in both valves. Percival (1995) did not think the available material justified a separate family, and pointed out similarities with gerontic *Eodinobolus stevensi* Percival, 1995, from the Fossil Hill Limestone.

While *Trimerella* and *Dinobolus* have vaulted platforms in both valves, their shells are much less convex, the ventral beaks are high and not strongly incurved, with well differentiated pseudointerareas, and the dorsal umbos are small. In all these features they are unlike *Keteiodoros*. Articulation in *Trimerella* is obscure but, in *Dinobolus*, *Eodinobolus* and *Gasconsia*, and possibly *Monomerella* and *Adensu*, it appears to comprise a transverse cardinal socket overhanging the platform in the ventral valve, in which rests the posterior edge of an articulating plate which is effectively the thickened and protruding posterior margin of the dorsal valve (Norford, 1960; Norford & Steele, 1969; Hanken & Harper, 1985; Popov & Rukavishnikova, 1986; precise details of the articulation have been questioned by Mergl, 1989). The simpler term “hinge plate” is already used for part of the cardinalia in rhynchonellate brachiopods. The arrangement in *Keteiodoros* is seemingly more complex: it uses areas on the valve margins as pivoting surfaces, while medially there is articulation between the ventral surface of the dorsal umbo on the one hand, and the surface of the pseudointerarea on the other, a little like a unidirectional “ball and socket” joint; the articulating plate appears to have served mainly as a “stop” to unwanted longitudinal movement, and as a protective cover for the diductor muscle attachment.

Possibly related is *Monomerella ovata* Whiteaves, 1884, from the Ludlow-age Guelph Dolomite of Ontario (Holmer, pers. comm., 1997). Dorsal internal structures, critical to generic assignment, have not been described, but the ventral interior illustrated by Hall & Clarke (1892, pl. IVD, fig. 15) differs in its long well-differentiated pseudointerarea and much shorter platform. In Australia, Talent (pers. comm., 1995) has collected rather smaller but externally very similar specimens from the Wenlock-Ludlow Yarrangobilly Limestone in New South Wales, and the Silurian at Chillagoe in northern Queensland; these remain undescribed.

Finally, it is interesting to compare the quite specialised *Keteiodoros*, with its complex morphology and gigantic size, with *Ussunia* Nikitin & Popov, 1984, from the late Llandeilo to early Caradoc of Kazakhstan. An early trimerellide-like genus displaying features transitional from craniopods, *Ussunia* is biconvex but not at all globose, with an undifferentiated pseudointerarea extended anteriorly as a flattened limbus. Muscles were inserted

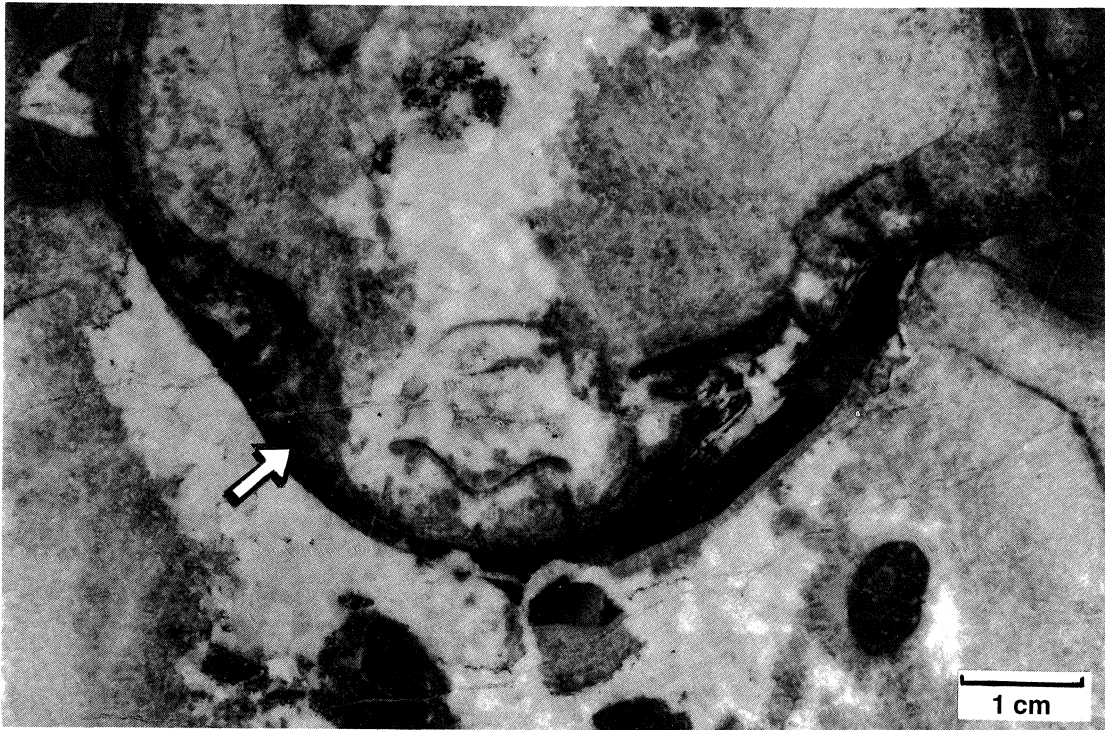


Figure 8. A peel taken from a transverse serial section of paratype MMF 33364, at 60.3 mm from the posterior end; 1 cm scale bar. The swollen articulating plate (arrowed), and the slots it conceals (which we interpret as locations of diductor attachment), are clearly visible in the centre of the photograph, as is the trace of the dorsal platform. At right can be seen the relationship between the valve margins at the pivot zone. Note the heavy but irregular recrystallisation.

directly on to the valve floor—platforms were not developed. The shell was thick and solid, without umbonal excavation to lighten the valves. *Ussunia* has no form of mechanical articulation, and the dorsal beak showed no sign of enrolling. *Keteiodoros* averages 4 to 5 times the length and width of *Ussunia*, and is about 7 times as globose. The two genera are separated in time by about 35 million years; *Ussunia* represents the small unspecialised ancestral stock, while *Keteiodoros* is the highly specialised, complex and gigantic descendant on a line soon to pass into oblivion. Cope's Rule was rarely more clearly expressed.

Functional morphology. The most distinctive feature of this new trimerellide, apart from its size and strong biconvexity, is the inferred method of articulating the valves. This involves the valve margins, the dorsal umbo, and the pseudointerarea.

Polished and serial sections (e.g., Figs. 6, 11), and prepared shells (Fig. 7), show that the dense posterior part of the dorsal valve, greatly enlarged and extremely strongly incurved, fitted laterally within the limits of the posteriorly equally dense ventral platform and pseudointerarea. In front of this region where the dorsal umbo sat within the pseudointerarea over its full width, the lateral margins of the dorsal valve expanded rapidly, such that a solid shelf formed on each side which rested on the flattened top of the ventral valve margin (Fig. 6, from 55.7 mm; Fig. 8).

This zone of flattened valve margins was short, and was where the margins crossed over one another as seen dorsoventrally. These flattened zones are inferred to have acted as pivots (not teeth and sockets) for the opening and closing of the shell. This is a form of articulation which, while rudimentary, is nevertheless somewhat reminiscent of that in some non-strophic rhynchonellate shells such as pentamerides. In front of the pivot zone each dorsal valve margin developed a broad somewhat oblique groove, into which fitted a similarly oblique flange arising from the inner edge of the ventral valve margin (Figs. 6, 7, 12). Functionally, the result was an interlocking system which, when the shell was closed, prevented relative movement of the two valves in the plane of commissure. When the shell was open, the close fit of the dorsal umbo in the pseudointerarea probably also constrained by the position of the adjacent muscles, would have provided significant restraint on relative lateral and skewing movements between the valves.

None of the available material is well enough preserved to show muscle scars but, if one considers the musculature involved in shell articulation, it can be assumed that the adductors would have extended from one platform to the other, as inferred for other trimerellides (Norford & Steele, 1969, text-fig. 2; Mergl, 1989). Given the size and probable weight of the valves, the considerable strength of such short thick muscles would probably have been very necessary to close the shell, and even more so to keep it

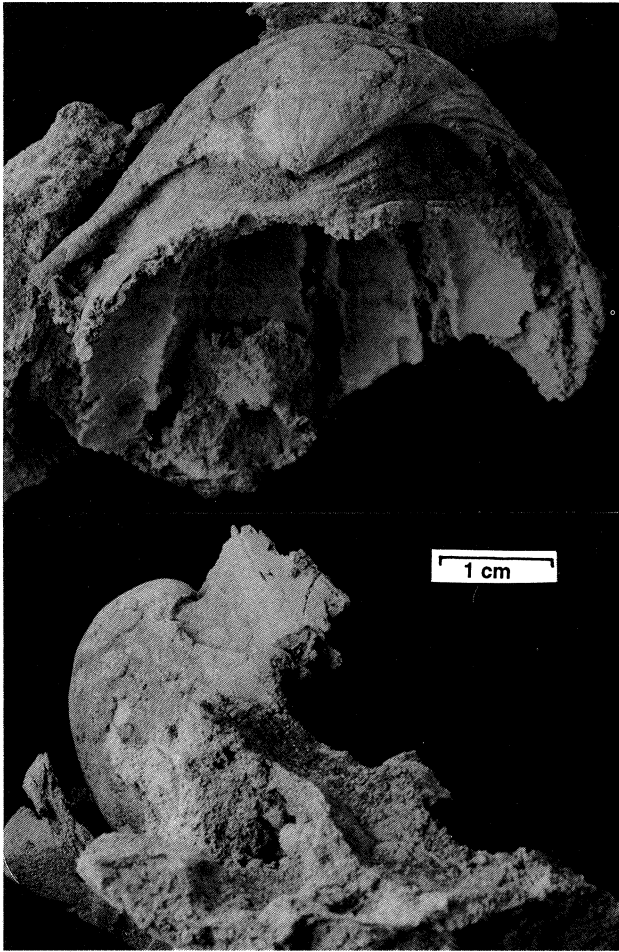


Figure 9. Paratype MMF 33365, a silicified fragment of a dorsal umbo, in approximately ventral (top) and lateral (bottom) aspects; 1 cm scale bar. Note the distinct asymmetry of the sharp incurved beak (apical angle 110° , directed right-ventrally at about 60° to the commissure), and the tracks of the bottom edges of the dorsal platform. Only the proximal part of the articulating plate is preserved, but its relationship to the beak is clear. The flat-bottomed ridged channel between beak and plate (compare Figs. 8, 10) we interpret as the site of diductor attachment.

closed against adverse conditions. However, the method of opening the shell poses problems, especially in view of the close fit between pseudointerarea and dorsal umbo.

Muscles extending forward from the anterior surface of the dorsal umbo to the ventral platform upon contraction would have served not to open the shell, but simply to pull the dorsal valve forward (which the interlocking of the valve margins and the bulge on the ventral platform in front of the dorsal umbo would have prevented anyway). To achieve proper leverage, muscles operating as diductors (we have no way of establishing precise homologies, so in this paper use the term “diductors” in a purely functional sense, as the muscles responsible for opening the shell) must have extended forward from somewhere on the dorsal umbo behind or ventral to the above-described marginal pivot zones. Muscles attached to the distal face of the

curved articulating plate and extending to an attachment area well forward on the ventral platform would have met this criterion, but there are two difficulties: when the shell was closed, there would have been little if any room between plate and platform for passage of the muscles, and contraction of the muscles would have put significant strain on the base of the plate, possibly enough to break it. Examination of serial and longitudinal sections, and of the silicified specimens, suggests an alternative (Fig. 13): that the dorsal ends of the diductors were attached to the umbonal surface in the lateral slots at the sides of the articulating plate, and emerged to either side of the plate. There are appropriate gaps at the sides of the dorsal umbo between sections at 55.7 and 60.8 mm in Fig. 6, approximately aligned with, but ventral to, the marginal pivot zones, and also in the peels from MMF 33364, Fig. 8. As already noted, MMF 33365 and 33366 reveal appropriately situated striated areas suitable for such attachment. With the diductors attached to the outer parts of the ventral platform in front of its mid-length, there would have been adequate space for the viscera and adductors medially. Mechanically this would have formed an effective lever system, opening the shell about the proposed pivot points to at least a 10° gape and possibly as much as 20° . However, one effect of such a system is that the dorsal umbo would have slid on the pseudointerarea unless restrained by soft tissue and periostracum. The geometry visible in longitudinal sections would have allowed for this movement, and the posterior geometry of the shell appears to be such that neither the exterior space between the two umbos (which is in any case not very large) nor the visceral space posterior to the dorsal umbo changed significantly during such a movement. The laminated pad on the floor of the pseudointerarea occupying the zone where such sliding would have occurred, may have formed a bearing surface for such movement, perhaps also serving by a close fit of the two surfaces to exclude sediment. Moreover, the articulating plate would have protected the dorsal ends of the laterally placed muscles from damage during such movement. A thickened zone of periostracum may have been present, but this is uncertain because of the state of preservation of the shells.

The manner of posterior closure, and the way in which the valves moved during opening, is important, because the shells sat freely umbo-down in sediment, and the space between dorsal and ventral umbos could only have been occupied by either tissue or silt. There appears to be no room for passage of a pedicle (in common with other trimercellides), and so it is unlikely there was organic tissue filling the space, but unless the silt were either extremely soft and fluid (thixotropic?) or shaped by the animal into a firm stable cavity, it would have been an impediment to valve opening. The proposed opening mechanism would not have been strong enough to work against loose but resistant material, and the diductors would probably have served (in conjunction with relaxation of the adductors) simply to initiate opening. This is supported by the observation that the weight distribution of the dorsal valve about the pivots appears to have been evenly balanced when the shell was closed. The large solid beak on the ventral side of the pivot-line was balanced by the larger volume of thinner-walled platform

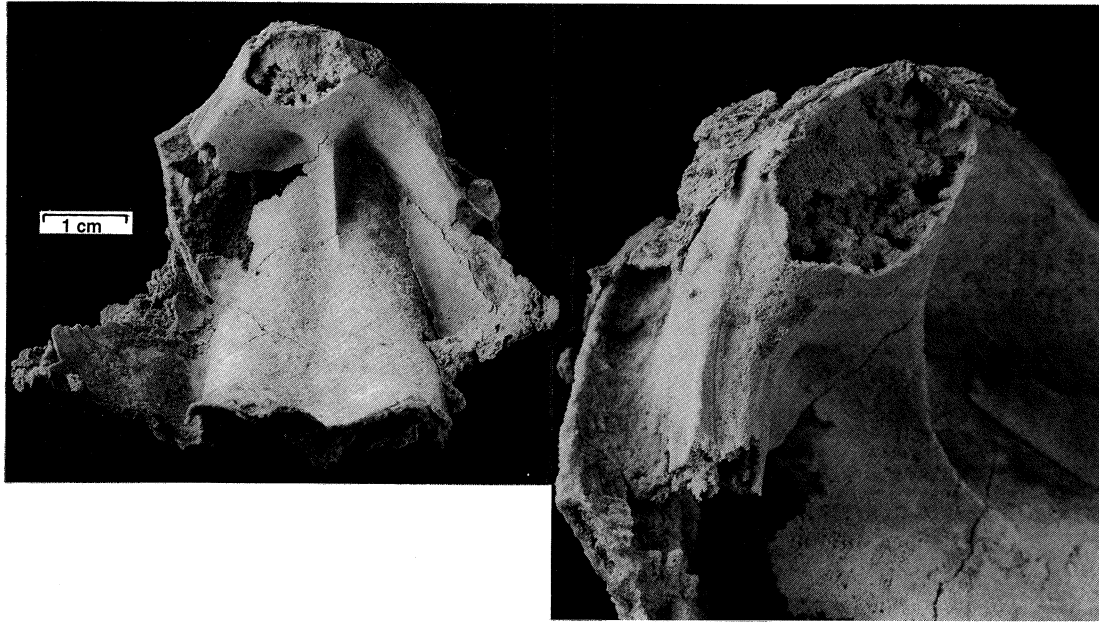


Figure 10. Paratype MMF 33366, a well-preserved silicified fragment of a dorsal valve interior, in anteroventral aspect at left (1 cm scale bar), and with the umbonal region enlarged in oblique lateral view at right. The dorsal beak is not preserved. The posterior part of the dorsal platform is gently concave longitudinally and strongly vaulted anteriorly, producing a shallow median longitudinal depression which gradually widens anteriorly. Supporting the platform above the now-missing valve floor is a Y-shaped septum. At the broken anterior end of the platform, a small triangular cavity is formed between the divergent arms of the Y and the overlying platform floor. Anteriorly the platform is approximately 30 mm wide, and is estimated to have stood above the valve floor by at least 23 mm. At the posterior end of the platform, a thin median septum (?= cardinal buttress) about 10 mm long extends nearly vertically from the platform floor, expanding posterodorsally to merge with a bulbous medial expansion at the base of the articulating plate. The greater part of the articulating plate is broken away, revealing a horizontally ovoid cross-section. As in MMF 33365 there is asymmetry present: in the aspect figured at left, the septum and articulating plate bulge display a slight but obvious anticlockwise rotation. The articulating plate is much more robust than that in MMF 33365, which was possibly from a juvenile individual. The lateral edges of the articulating plate are flattened and slightly extended, giving the base of the plate a broadly lanceolate cross-section. There are growth lamellae on the posterior surface of the plate, which is separated from the remnant of the valve margin by a deep channel (compare Fig. 9).

and shell wall making up the anterior part of the valve. Stability in that position was increased by the solid shell mass making up that part of the dorsal valve posterior to (hence below) the pivot-line. However, once opening movement was initiated, the weight of the anterior part of the dorsal valve, moving through a perceptible arc, would have overcome the weight of the dorsal umbo which barely changed its orientation relative to the pivot zone.

The considerable weight of the dorsal valve would have required the constraint of strong adductor muscles to stop it from sliding downwards out of the bearing surface formed by the pseudointerarea. The size and elevation of the platforms suggests that the adductors were indeed strong, but this function may also have been aided by the close conjunction of the distal end of the articulating plate with the terraced face of the tissue pad which formed the bearing surface on the top of the pseudointerarea. Moreover, at least in gerontic shells the strongly incurved ventral beak formed a cup effectively restraining the dorsal valve from below. A further implication of the weight of the valve is that closing the shell would at least initially have required the strong adductors suggested above.

Phylogenetic relationships

The new genus is characterised by gigantic size and a unique articulatory mechanism comprising dorsal articulating plate, robust zones on the edges of the ventral valve pivoting against equally robust zones on the dorsal margins, and, in front of those zones on the valve margins, oblique ventral flanges restraining twisting movement by articulating with marginal dorsal “sockets” (Fig. 12). These and other associated morphological features adapted *Keteiodoros* well to its preferred environment.

Taken by themselves, tendencies towards gigantism or oblate/spheroidal shape have relatively little phylogenetic significance. For example, *Adensu* Popov & Rukavishnikova, 1986, is a monotypic Late Ordovician trimerellide, endemic to Kazakhstan, which has a similar shape to, and dimensions approaching those of *Keteiodoros*. However, *Adensu* lacks both raised muscle platforms and umbonal cavities, and its articulating plate lies parallel to the commissure. Accordingly it is not thought to be closely related to *Keteiodoros*.

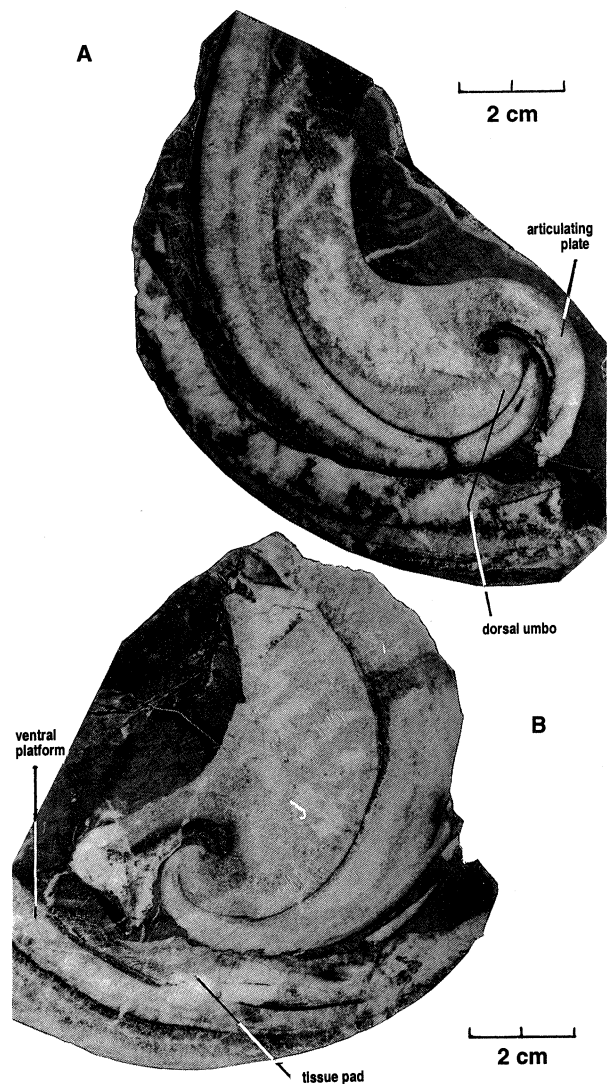


Figure 11. A–B—axial longitudinal sections of two incomplete shells. A—AM F101121; B—AM F101120 (2 cm scale bars) showing the present relationship between the dorsal umbo and ventral platform, the curved articulating plate which is inferred to cover the dorsal ends of the diductor muscles, and the layered pad of tissue on the pseudointerarea against which the dorsal umbo may have moved during opening and closing (compare Figs. 7, 12). Note also the strong spiral trace of the surface of the dorsal platform, and the extensive recrystallisation.

Substantial umbonal shell thickening is a typical means in many unrelated brachiopods (e.g., pentamerides) of preventing dislodgement by waves or currents of shells lacking pedicle or cementation attachment. Long umbonal cavities are likewise common to most known Silurian trimerellide genera, as are prominent ventral platform vaults. The only known trimerellides with strongly vaulted dorsal platforms are *Paradinobolus* Li & Han, 1980 and *Prosoptionella* Li, 1984 (both from the early Ashgill of South China), and the widely distributed and long-ranging *Trimerella* (late Ordovician to middle Silurian). A single silicified incomplete dorsal valve with such a platform,

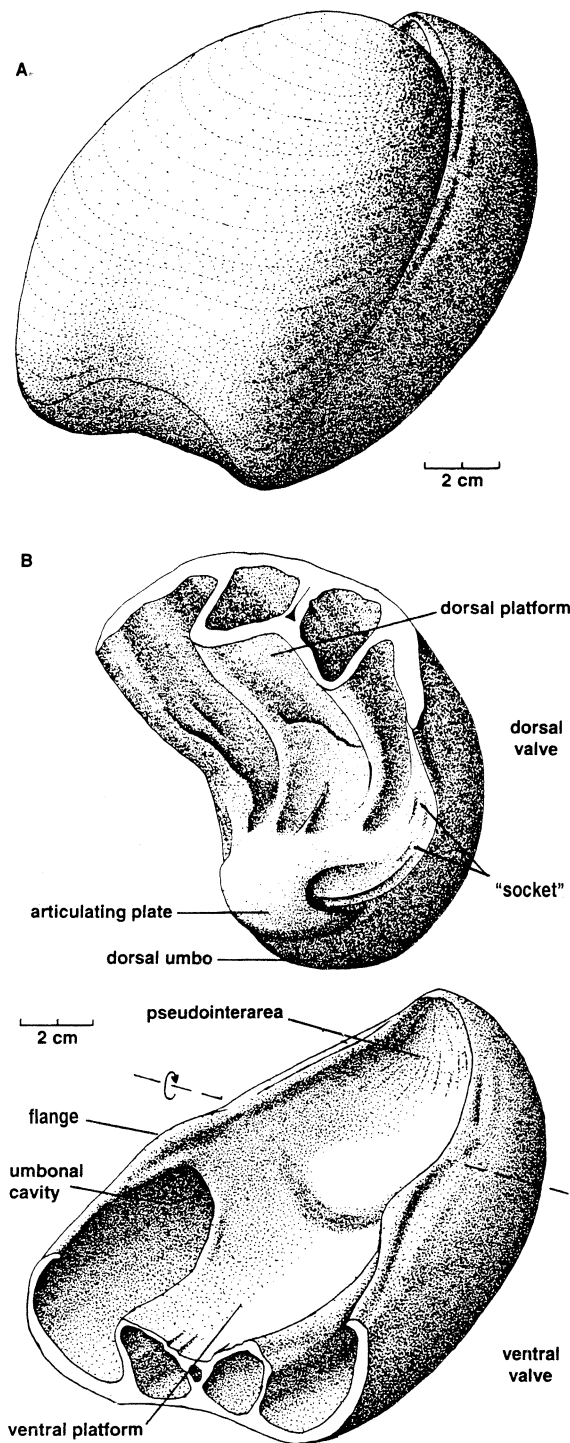


Figure 12. A–B, oblique views of the shell exterior (A) and interior (B) of *Keteiodoros bellense* n.sp., reconstructed from the complete paratype AM F101117 (Fig. 4) and serially sectioned paratype CPC 34409 (Fig. 6), and modified after the holotype (Fig. 7) and the silicified dorsal valve, paratype MMF 33366 (Fig. 10); 2 cm scale bars. In B, the open valves have been truncated anteriorly to show their cross-sections, while the dorsal valve has been strongly rotated, and lifted vertically above the ventral valve, to show its interior; the inferred position of the “hinge” line is shown as a dashed line.

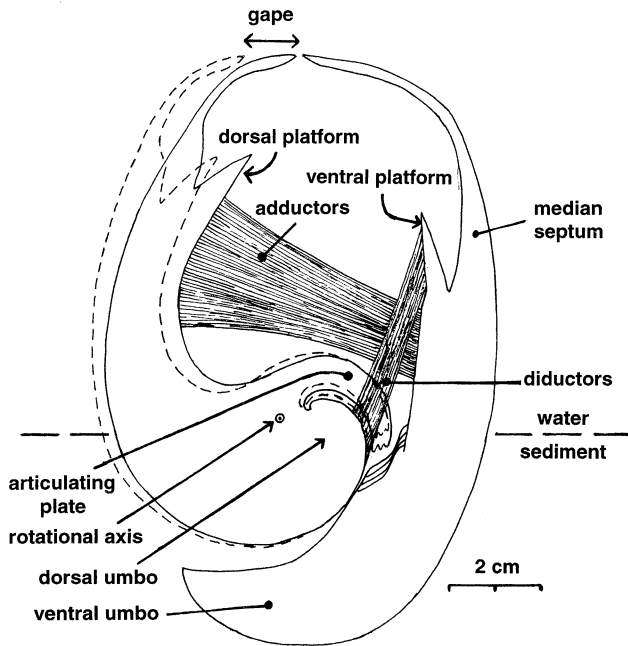


Figure 13. Reconstructed axial longitudinal section of a shell, with the inferred positions of the adductor and diductor muscles projected onto that plane. A dashed line gives the dorsal valve in open position, showing the minimum amount of gape possible under this scheme. Based on the serially sectioned shell, which has been used to project the axis of rotation of the dorsal valve from its inferred position at the valve margins, and on the longitudinal section of AM F101121 (Fig. 11A).

referred doubtfully to *Paradinobolus*, is also known from the Late Ordovician Malongulli Formation in central New South Wales. Superficial similarities aside, none of these trimerellides share sufficient characters in common with *Keteiodoros* to be considered directly related.

The specialised articulatory mechanism of *Keteiodoros* is likely to provide the best clue to its evolutionary relationships. One trimerellide, *Belubula spectacula* Percival, 1995, from the Late Ordovician (early Eastonian, equivalent to late Caradoc) Belubula Limestone of central New South Wales, is a potential ancestor to *Keteiodoros*. Although separated in time by approximately 25 million years, and without intervening evolutionary stages being known at present, the two genera share significant morphological similarities, habitat preferences, and geographic proximity. *Belubula* is of gigantic size for Late Ordovician trimerellides, reaching an estimated 200 mm in length and 100 mm in width; the largest individuals are thus comparable in length with *Keteiodoros*, though the latter is relatively much wider and deeper. In profile, both are similarly strongly equibiconvex. Note also that both genera display asymmetry (compare Percival, 1995: Fig. 4J with MMF 33365, Fig. 9), although the direction of asymmetry of only the ventral valve of *Belubula* is apparent from the figure. Grossly thickened posterior regions of the ventral valves in both *Keteiodoros* and *Belubula* contain large conical umbonal cavities. Of particular significance

is one gerontic individual of *Belubula* (Percival, 1995: Fig. 4C) which exhibits an incipient modification of the dorsal homeochilidial (or articulating?) plate which could well have led to the specialised articulation of *Keteiodoros*. Percival (p. 50) noted in reference to this particular silicified dorsal valve that in gerontic specimens this plate “can enlarge to form a prominent curved bulbous plate, bearing growth striations, & extending ventrally above level of commissure with a knife-edge anteroventrally”. It is reasonable to suggest that over the ensuing 25 million years of evolution this plate developed into the robust incurved articulating plate of *Keteiodoros*, bearing a median bulge and buttressed anteriorly by a median ridge, and forming part of a large ball-like dorsal umbo bearing against the concave pseudointerarea. Whereas a massive muscle (attached to the ventral cardinal socket and inserted in the dorsal subcardinal depression) was essential in *Belubula* to prevent a shearing motion of the valves during articulation, paired diductors attached at the sides of the articulating plate, lateral to the ball joint, could have served the same purpose in *Keteiodoros*.

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