An Unusual Micromorphic Brachiopod from the Middle Cambrian of North-Eastern New South Wales, Australia

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ABSTRACT. *Anomalocalyx cawoodi* new genus and new species, from Middle Cambrian (Floran-Undillan) allochthonous limestone clasts of the Murrawong Creek Formation, north eastern New South Wales, is characterised by a deep, tapering, conical ventral valve with a pair of simple teeth, an arched pseudodeltidium, well defined radial costae, crossed at more or less regular intervals by continuous concentric growth lamellae, and a presumed calcium carbonate shell composition, all suggesting an affinity with the Brachiopoda. *Anomalocalyx cawoodi* also possesses a number of unusual morphological features including an elongate, tapering interior tube extending along the inner posterior margin of the ventral valve, under the pseudodeltidium, that may be interpreted as a spondylium. Though possible cnidarian and molluscan affinities are fully explored, the weight of available evidence suggests the affinities of *A. cawoodi* are with the Brachiopoda.

Williams *et al*. (1996) erected five new classes of brachiopods united by a number of shared synapomorphies within the subphylum Rhynchonelliformea including, (*a*) the presence of a pair of calcareous shells held together by an articulatory device at the posterior hinge line between the two shells, (*b*) an acoelomic pedicle core, and (*c*) the presence of a diductor system to control the opening of the shells. Williams *et al*. (1996) placed another calcareous class, the Craniata, characterised by a lack of articulation and functional pedicle, in a separate "inarticulate" subphylum. All five rhynchonelliform classes are represented in the Cambrian radiation and display a wide range of unusual morphological adaptations, particularly with regard to valve articulation, musculature and pedicle opening (Popov, 1992; Popov *et al*., 1996; Williams *et al*., 1996). Typical morphological variations manifest in these early groups include the development of simple, presumably primitive, articulation mechanisms as exemplified by early obolellids (such as *Bicia* Walcott), kutorginids and nisusiids (Roberts & Jell, 1990; Popov, 1992; Popov *et al*., 1996), and the evolution of unique features in a number of short-lived taxa. Examples of such features include the unusual spoon-shaped apical plate and supporting pedestal in the ventral valve of the naukatid genera *Bynguanoia* Roberts

(in Roberts & Jell, 1990) and *Oina* Popov & Tikhonov, 1990, the arcuate plate along the hingeline in the ventral valve of the monospecific taxon *Bajarinovia* Aksarina & Pelman, 1978, and the posterior plate or colleplax in chileids (Popov *et al.*, 1996).

In addition to taxa that can, more or less, be comfortably placed within the concept of the phylum Brachiopoda (or Phylum Brachiozoa, subphylum Brachiopoda *sensu* Cavalier-Smith, 1998), there are a number of aberrant Cambrian organisms that secreted bivalved calcareous shells that cannot be placed in the Brachiopoda with any confidence. As an example, the Early Cambrian taxa *Apistoconcha* and *Aroonia* from the Flinders Ranges, South Australia (Conway Morris & Bengtson, in Bengtson *et al.*, 1990), and *Tianzhushanella* from China (Lui, 1979), are brachiopod-like in possessing a pair of calcareous shells with a posterior hinge axis of articulation, and a plane of bilateral symmetry bisecting the midline of both valves. However, the overall form of the valves, and the unique nature of the articulatory mechanism in these taxa, led Conway Morris & Bengtson (in Bengtson *et al.*, 1990: 184) to conclude that they were not true brachiopods, but possibly represented a sister lophophorate lineage. Parkhaev (1998) recently placed *Apistoconcha* and *Tianzhushanella* in a new Class, the Siphonoconcha, and suggested an affinity with the Mollusca or Stenothecoida, rather than with the Brachiopoda.

The focus of this paper is to describe the unique features of another aberrant calciate brachiopod taxon, from the Middle Cambrian Murrawong Creek Formation, northeastern New South Wales, Australia, and to probe the functional morphology and possible zoological affinities of this problematic organism.
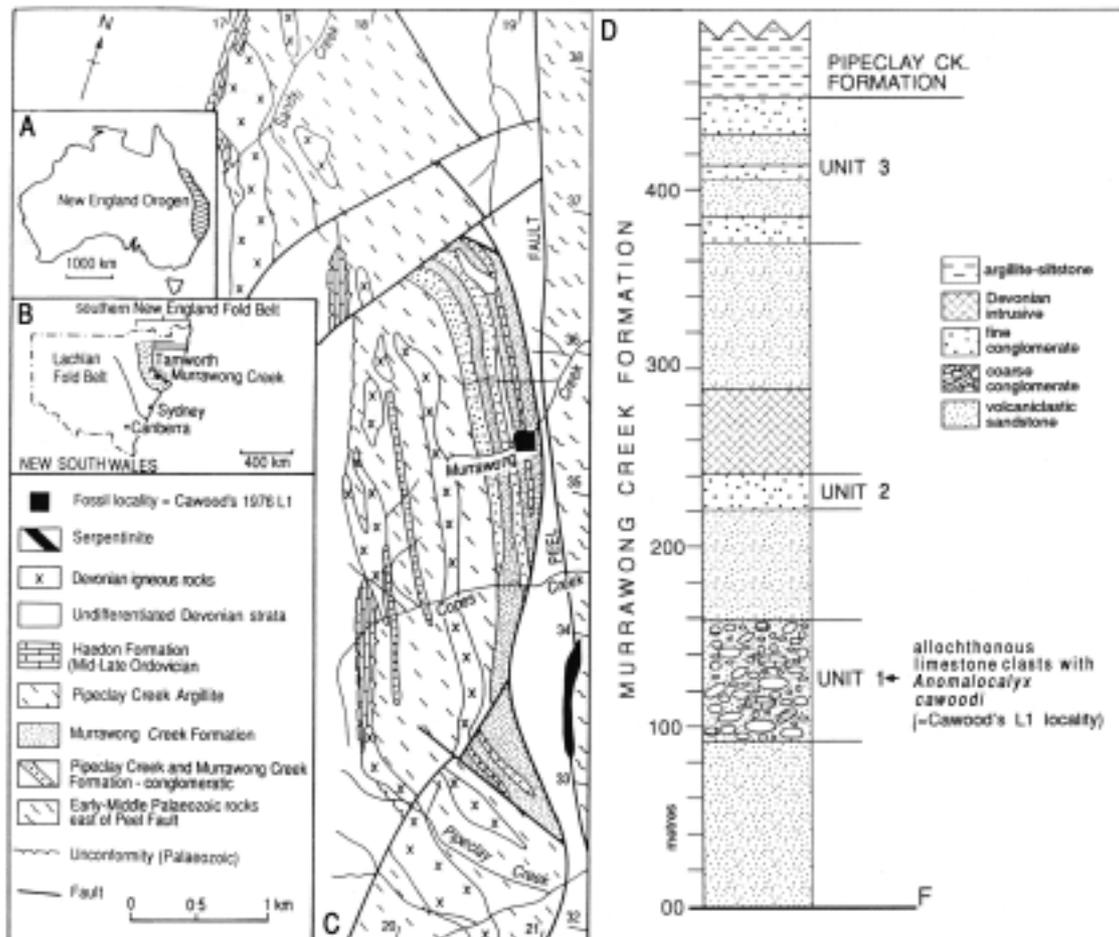

Figure 1. A, generalised map of Australia showing extent of rocks associated with the New England Fold Belt. B, generalised map showing exposures of the southern New England Fold Belt and the locality of the Murrawong Creek area. C, geological map of the Murrawong Creek–Copes Creek area (modified after Leitch & Cawood [1987]). Black box depicts area where 21 allochthonous limestone clasts were re-collected in 1992 from Cawood's (1976) original L1 locality, Unit 1 in Murrawong Creek (grid reference: 198₇ 352₄, Woolomin 1:25,000 topographic sheet 9135-111-N, 31°18'08"S 151°96'08"E). D, type section of the Murrawong Creek Formation, along Murrawong Creek, showing sampled conglomerate horizon, Unit 1 of Leitch & Cawood, 1987 (= Cawood's [1976] L1 locality). Modified after Leitch & Cawood, 1987, fig. 2.

Geological setting and age

The geology, stratigraphy and depositional environment of the Murrawong Creek Formation have been outlined in some detail by Brock (1998a,b), so only a summary is presented here. The Murrawong Creek Formation (Cawood, 1980) is the oldest of three lithostratigraphic units in the Copes Creek-Murrawong Creek region of the southern New England Fold Belt, with sporadic outcrops in a 4.5 km north–south trending tract of interbedded siltstone, sandstone and conglomerate, some 25 km south-southeast of Tamworth, 31°18'08"S 151°06'28"E (Fig. 1A–C; Cawood, 1976, 1980; Leitch *et al.*, 1988; Leitch & Cawood, 1996). The type section, along Murrawong Creek, consists of 450 metres of poorly outcropping, interbedded coarse to fine debris flow conglomerates, turbiditic sandstone, siltstone, siliceous mudstone and ash-fall tuffs (Fig. 1D). The base of the section is faulted against undifferentiated ?Devonian metasediments. Leitch & Cawood (1987, fig. 2) recognised three conglomerate horizons in the Murrawong Creek Formation, informally designated Units 1–3. Unit 1, the coarsest of the three units (Fig. 1D), includes 85 m of poorly outcropping, polymictic paraconglomerate with angular to subrounded, mostly volcanic, clasts (0.01–1.5 m in diameter) set in a poorly sorted sand to granule grade volcaniclastic matrix. The largest clasts are represented by fossiliferous limestones (Fig. 2).

Provenance investigations of the cobble and pebble sized igneous clasts from the Murrawong Creek Formation revealed that the clasts are from a low-K orogenic suite, and the absence of detritus characteristic of continental crust is consistent with an interpretation favouring derivation from an intra-oceanic island arc rather than a continental margin arc (Leitch & Cawood, 1987, 1996). The presence of small quantities of volcanic beta quartz fragments in the allochthonous limestone clasts also implies proximity to an island arc (Engelbretsen, 1996). The allochthonous volcaniclastic debris of the Murrawong Creek Formation and the conformably overlying Pipeclay Creek Formation were probably deposited as gravity flows in an inner submarine environment into relatively deep water conditions (Leitch & Cawood, 1987: 635) from an eroded western source (Leitch & Cawood, 1987; Leitch *et al.*, 1988). The faunal content of the limestone clasts includes diverse trilobite assemblages (Sloan, 1991), lingulate brachiopods (Engelbretsen, 1996), calciate brachiopods (Brock, 1998a), molluscs (Brock, 1998b) and an array of undescribed small shelly fossils that indicate the original setting for the fossiliferous carbonates was a relatively shallow-water carbonate platform, possibly fringing a volcanic island or islands.

The trilobite assemblage from the allochthonous limestone clasts (see Brock [1998a,b] for details of taxa) containing the new brachiopod *Anomalocalyx cawoodi*
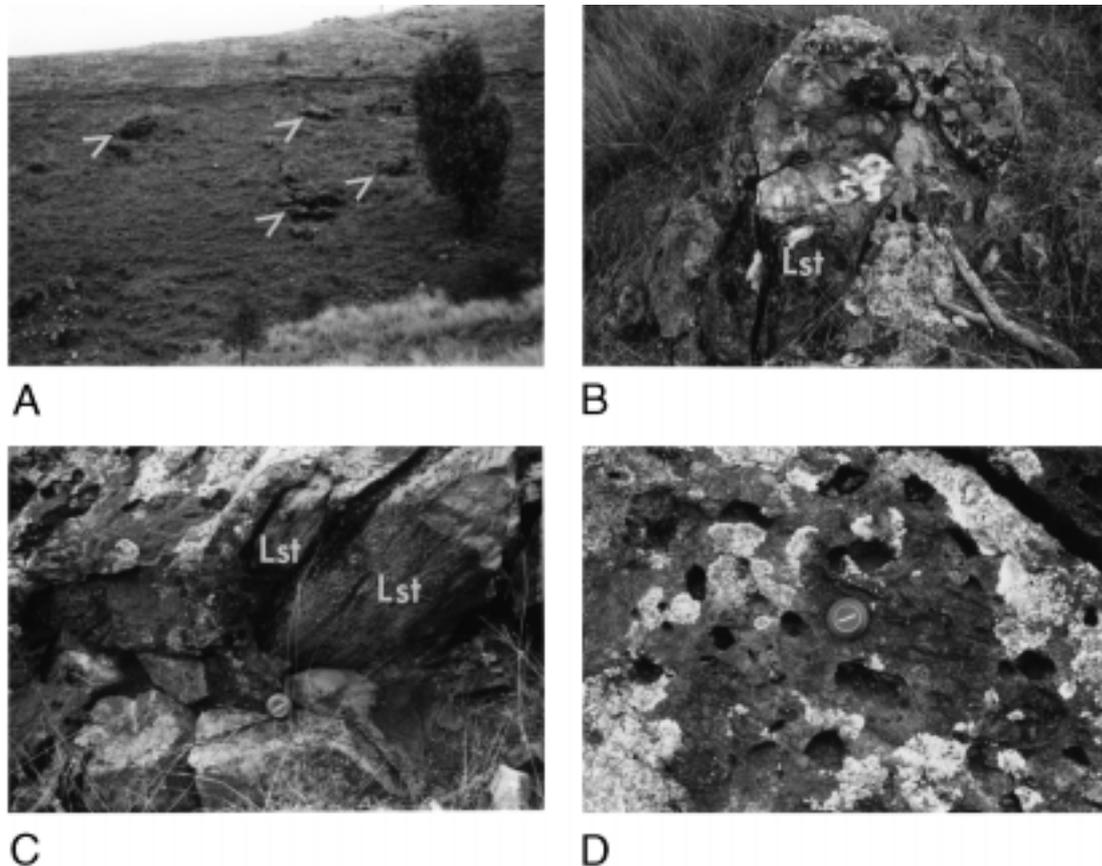

Figure 2. Field photographs of the Murrawong Creek Formation. A, wide angle shot, looking south, at some of the conglomeratic exposures of Unit 1 (arrowed); Murrawong Creek in foreground. B, lenticular, subrounded fossiliferous limestone clast (Lst), set in coarse volcaniclastic matrix of Unit 1. C, close-up of lenticular limestone clasts (Lst) in volcaniclastic matrix of Unit 1. D, weathered clast cavities in Unit 1 matrix. Lens cap 55 mm across in photographs B–D.

support an age spanning the *atavus–punctuosus* zones (Floran-Undillan Stages) using the Australian Middle Cambrian time-scale (Shergold, 1995).

Stewart (1995) reported the discovery of an assemblage of paraconodonts including *Muellerodus, Herzina, Prooneotodus* and *Furnishina*, and a number of minute forms similar to *Clavohamulus* and *Westergaardodina* from a dark, thinly bedded, spiculitic chert of the Pipeclay Creek Formation (Fig. 1D) in Copes Creek. The abundance of paraconodonts and the lack of euconodonts is consistent with a Middle Cambrian to early Late Cambrian age for this formation. It is thus clear that the Middle Cambrian allochthonous limestone clasts of the conformably underlying Murrawong Creek Formation are set in a matrix of similar age, as originally interpreted by Cawood (1976, 1980).

Preservation

All known specimens of *Anomalocalyx cawoodi* are preserved as epitaxial coatings of epidote. This type of preservation has previously been reported from the Murrawong Creek Formation in the coralomorph taxon *Tretocylichne perplexa* by Engelbretsen (1993: 55). A similar type of preservation, consisting of phosphatic epitaxial coatings, has also been described in the bivalve *Pojetaia runnegari* (Runnegar & Bentley, 1983) and the brachiopod-like taxon *Apistoconcha* (Bengtson *et al.*, 1990: 171, fig. 113).

The epidote coating covers all inner and outer surfaces of *Anomalocalyx*, faithfully replicating elements of the external and internal morphology, including fine surface detail. The internal space between the inner and outer layers of the coating attests to an original calcareous shell composition subsequently dissolved during acetic acid processing. The presence of a calcareous shell in *Anomalocalyx* is supported by the fact that only taxa known to possess a calcareous shell (e.g., articulate brachiopods, *Nisusia* and *Arctohedra*, molluscs, chancelloriids, and hyolithids) are preserved in a similar manner.

The preservation of *Anomalocalyx* ranges from fine to very coarse, resulting in a wide variation of gross morphology, especially in shell outline, the shape of the coniform ventral valve, and the preservation of fine features of the external ornament.

Systematic palaeontology

All type specimens are held in the Australian Museum (AM); registration numbers are given below.

Phylum **Brachiopoda** Dumeril

Subphylum **?Rhynchonelliformea** Williams, Carlson, Brunton, Holmer & Popov, 1996

Class, Order, Superfamily, Family **Uncertain**

Anomalocalyx n.gen.

Type species. *Anomalocalyx cawoodi* n.sp.

Diagnosis. Minute, deeply coniform, tapering ventral valve with very high, variably convex to flattened, catacline to weakly procline, interarea; delthyrium narrow, covered for entire length by a well-developed, evenly convex pseudodeltidium. Radial costae low, wide, anteriorly bifurcating, becoming fluted at commissural margin. Costae crossed at more or less regular intervals (70–100 µm) by low, undulose concentric growth lamellae. Valve outline variably subquadrate to subhexagonal. Teeth simple, rounded, dorsally directed, nub-like projections situated on the posterior valve wall either side of the delthyrium; an elongate, tapering, tube-like structure extends ventrally along the entire length of the delthyrial cavity directly under the convex pseudodeltidium. Dorsal valve with well-developed incurved umbo, broad median sulcus and anterior tongue. Interior with small, simple, divergent and shallow socket-like plates excavated into the posterior valve wall. Notothyrium wide, but poorly defined; other cardinal features absent. Musculature and vascular markings in both valves unknown.

Discussion. *Anomalocalyx* displays a number of features indicative of a brachiopod assignment. These include, (*a*) a bivalved shell with the plane of bilateral symmetry bisecting the midline of both valves, (*b*) a pair of simple dorsally directed, nub-like teeth projecting from the posterior shell wall of the ventral valve, (*c*) a high, flattened ventral interarea bisected medially by an elongate delthyrium covered by a prominent, arched pseudodeltidium, (*d*) well defined radial costae, crossed at more or less regular intervals by continuous concentric growth lamellae, (*e*) a convex dorsal valve with simple socket plates, and (*f*) an inferred calcium carbonate shell composition. The presence of a calcareous shell composition, simple teeth in the ventral valve with an arched pseudodeltidium covering the delthyrium and dorsal sockets either side of a wide notothyrial gap conforms, at least partly, with the concept of the subphylum Rhynchonelliformea as outlined by Williams *et al.* (1996: 1192). *Anomalocalyx* is therefore referred, with some hesitation, to the Rhynchonelliformea.

The lack of information regarding muscle scars, mantle canal pattern and nature of the ventral umbo in *Anomalocalyx* precludes confident assignment to higher taxonomic levels within the Brachiopoda at the present time. The presence of a well-developed, convex pseudodeltidium flanked by flattened propareas in the ventral valve and a wide, triangular, open notothyrium (lacking a cardinal process) bordered by socket plates in the dorsal valve indicates *Anomalocalyx* may have some relationship to the order Kutorginida (Popov *et al.*, 1997). However, kutorginids are characterised by a large posterior median opening that is interpreted to have been the opening of a posteromedianly directed anus. The highly incurved dorsal valve and the nature of the articulation of the valves indicates no such opening existed in *Anomalocalyx* (Fig. 3C). Though some kutorginids, such as *Nisusia alaica* (Popov &

Tikhonov, 1990, pl. 3, fig. 23), possess moderately coniform ventral valves, none have the exaggerated form of *Anomalocalyx*, nor has any been described with an interior tube.

The elongate, irregular, tapering conical shape of the ventral valve of *Anomalocalyx* (Figs. 3C, 4A–L), though unusual amongst Cambrian calciate brachiopod orders, can be found in a few highly specialised, aberrant post-Cambrian taxa, such as the Silurian triplesiid *Onychotreta* Ulrich & Cooper (see Amsden, 1968), the highly specialised cemented ventral valves of the Permian richthofenioid brachiopods *Cyclacantharia* and *Sacchinella* (see Cooper & Grant, 1975), and the Permian nasute (coralliform) gemmellaroid genera *Cyndalia* and *Gemmellaroia* (Grant, 1993). *Cyndalia*, in particular, displays a remarkable number of features similar to *Anomalocalyx*. Both taxa are micromorphic with calcium carbonate shells, and possess an elongate, tapering ventral valve (extravagant in *Cyndalia*) with well-developed pseudodeltidium. Though a short pedicle tube is present in species of the obolellid genus *Trematobolus* (Geyer & Mergl, 1995), the elongate tube-like structure situated directly under the arched pseudodeltidium and extending along the entire ventral wall of the ventral valve in *Anomalocalyx* has not previously been described in a Cambrian articulate brachiopod. Geyer & Mergl (1995) suggested the tube in *Trematobolus* probably housed a specialised pedicle similar to that found in *Discinisca*. The function of this tube in *Anomalocalyx* remains enigmatic, but it shows a remarkable similarity to the elongate, tapering tube-shaped structure in *Cyndalia* (see Grant, 1993, fig. 6) described as a tube-like spondylium produced by the coalescence of dental plates and a median septum, suggesting they formed a moving muscle attachment area (Grant, 1993: 55). The lateral margins of the tube-like structure in *Anomalocalyx* appear as though they are attached either side of the delthyrium, directly under the dorsally directed nub-like teeth (Figs. 3B, 4A,J–K,M), as would be expected if the structure were a spondylium for muscle attachment (Fig. 3C). If a spondylium interpretation is accepted, the function of the u-shaped groove on the outer surface of the spondylial tube (Figs. 3B, 4J) remains enigmatic. The fact that all ventral valves of *Anomalocalyx* have a broken apex makes it difficult to determine the presence or absence of an apical pedicle foramen. It seems unlikely that the tube actually housed a pedicle given the extraordinary length of the tube inside the ventral valve.

Close affinity between *Anomalocalyx* and *Cyndalia* is unlikely given their disjunct stratigraphic positions. The degree of morphological similarity between these two taxa may well be the result of convergent evolution, reflecting an analogous evolutionary response to specialised environmental circumstances. The ecology of both taxa is imperfectly known, but Grant (1993: 59) envisaged *Cyndalia* inhabiting a turbid, muddy, shallow water, lagoonal setting. Given the allochthonous setting of the *Anomalocalyx*-bearing clasts, the original environmental setting is even more difficult to reconstruct, but contemporaneous faunal assemblages suggest *Anomalocalyx*
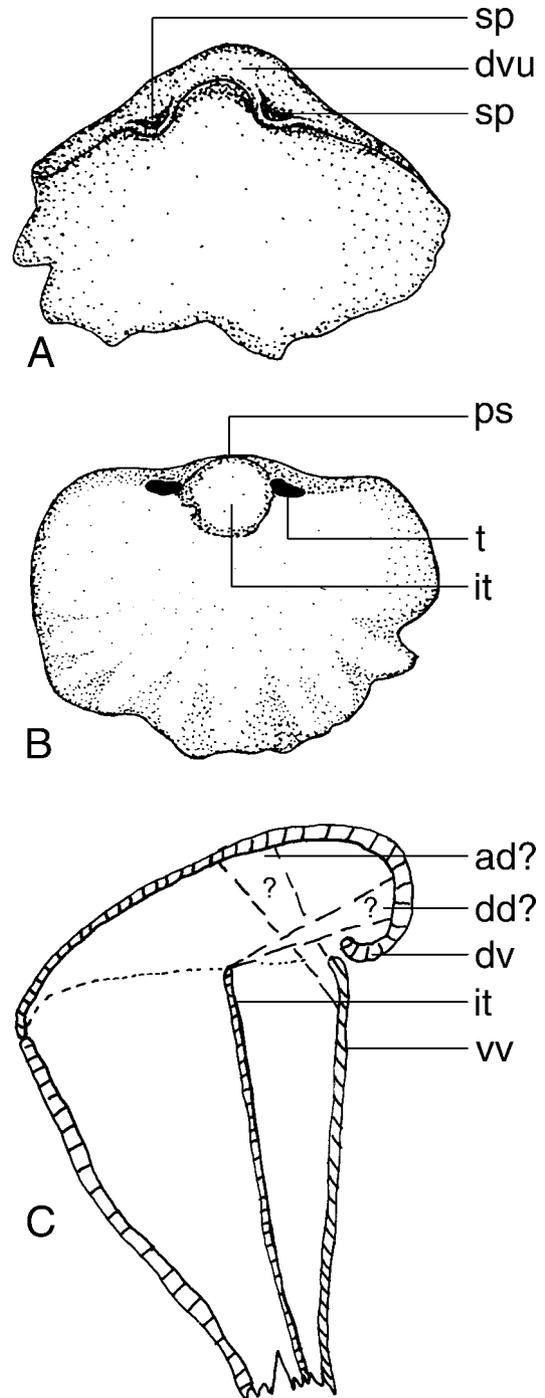

Figure 3. A, dorsal valve interior of *Anomalocalyx cawoodi* n.gen. et n.sp., based on AM F107869; valve width 1 mm. B, ventral valve interior of *Anomalocalyx cawoodi* n.gen. et n.sp., based on numerous specimens; valve width approximately 1.5 mm. C, tentative reconstruction along axial longitudinal plane of conjoined specimen of *Anomalocalyx cawoodi* n.gen. et n.sp. showing speculative position of adductor and diductor muscles. The interior tube in the ventral valve is reconstructed as a spondylial platform. Abbreviations: ad?, speculative adductor muscle; dd?, speculative diductor muscle; dv and dvu, dorsal valve and dorsal valve umbo; it, interior (spondylial) tube; ps, pseudodeltidium; sp, socket plates; t, tooth; vv, ventral valve.

was probably associated with a shallow water carbonate platform fringing a volcanic island arc (Brock, 1998a,b). The elongate ventral valves of both taxa are similar to those found in some rudist bivalves, and are best explained as an adaptation for keeping the aperture elevated above the muddy substrate (Grant, 1993: 59). However, because of the millimetric dimensions of the shell, an infaunal, epifaunally attached, or cryptic life habit cannot be completely ruled out.

The possibility that *Anomalocalyx* may represent a new type of coral-like organism similar to *Tretocylichne* Engelbretsen, 1993 or the operculate *Cothonion* Jell & Jell, 1976 cannot be completely ruled out. However, close comparison of these two unusual forms reveals that *Anomalocalyx* lacks the octagonal outline, longitudinal septa on the inner surface of the calyx, perforate expanded base, and thecal budding characteristic of *Tretocylichne* Engelbretsen, 1993. The slightly older operculate genus, *Cothonion* described by Jell & Jell (1976) from the early Middle Cambrian Coonigan Formation, western New South Wales has a similar shape to the putative ventral valve of *Anomalocalyx*, but *Cothonion* can be discriminated by the presence of strong internal septa, and the operculum is generally flattened or upturned (concave) at the midpoint, and internally, is characterised by the development of strong radial septa. No coralomorph taxon yet described has been discovered with the brachiopod-like teeth or the interior tube characteristic of *Anomalocalyx*.

Etymology. The Greek word *anomalos* for unusual, abnormal, deviating from the general rule is combined with *kalyx* (Greek) for cup.

Anomalocalyx cawoodi n.sp.

Figs. 3A–C, 4A–P

Type material. HOLOTYPE: ventral valve from clast W10, AM F97383, Fig. 4A–E. PARATYPES 11 ventral valves (VV hereafter) and 22 dorsal valves (DV hereafter) as follows: 3 VV, AM F97384 (Fig. 4F–I), AM F107867 (Fig. 4J–L) and AM F97385 (Fig. 4M); 3 DV, AM F107868 (Fig. 4N), AM F107869 (Fig. 4O) and AM F107870 (Fig. 4P); 6 DV, AM F112571–76, and 2 VV, AM F112577–78, from clast W1; 3 DV, AM F112579–81, from clast W3; 2 DV, AM F112582–83, and 2 VV, AM F112584–85, from clast W10; 2 DV, AM F112586–87, and 1 VV, AM F112588, from clast W38; 6 DV, AM F112589–94, and 3 VV, AM F112595–97, from clast W/L1/S4.

Type locality. Allochthonous limestone clasts, Unit 1, Murrawong Creek Formation. Equivalent to Cawood's (1976) original L1 locality (Fig. 1C). Grid Reference: 198_7 352_4, Woolomin 1:25,000 topographic sheet 9135-111-N, 31°18'08"S 151°06'28"E.

Diagnosis. As for genus.

Description. Shell minute (maximum width 2 mm, maximum length 1.8 mm), with variable shell outline ranging from semicircular to subquadrate to sub-hexagonal. Maximum shell width approximately mid-valve. External ornament consists of between 10–14 low, wide (0.2–0.3 mm), rounded costae increasing anteriorly by bifurcation, becoming fluted at the commissure. Intercostal furrows wide and shallow. Costellation and intercostal regions crossed by a series of continuous, low and undulose concentric growth lamellae spaced at intervals of approximately 0.1 mm.

Ventral valve deep, curved, irregularly conical, tapering apically, with high (max. 3.0 mm), variably developed, cataclined to weakly procline interarea. Interareas flattened to weakly convex; barely perceptible in some specimens as they merge and arch medially forming a single convex pseudodeltidium. Concentric lamellae cross interareas and pseudodeltidium. All known ventral valves broken, so apical morphology (including presence or absence of a foramen) unknown. Interior of ventral valve with an elongate, tapering tube-like structure (maximum width 0.6 mm) extending ventrally along the entire delthyrial cavity directly under the pseudodeltidium. A u-shaped groove (0.15 mm wide), narrowing gradually with the ventral direction of valve taper, present on anterolateral surface of tube. Short, stubby, dorsoventrally flattened, convergent teeth arise as simple, dorsoanteriorly directed projections from posterior shell wall in most specimens. Muscle scars not preserved.

Putative dorsal valve strongly convex, with short, curved hingeline and broad, shallow, anteriorly widening, median sulcus. Umbo enlarged and recurved, almost forming a hood over the notothyrium. External ornament similar to ventral valve, though radial costae tend to arise via implantation rather than bifurcation. Small, simple, divergent and shallow socket-like plates excavated into the posterior valve wall. Notothyrium wide, but poorly defined; other cardinal features absent. Musculature and vascular markings in both valves unknown.

Remarks. Though no articulated specimens of *A. cawoodi* have been recovered, a number of convex valves of appropriate size, with similar outline and ornament to the ventral valve have been identified as matching dorsal valves (Figs. 3A, 4N–P). Internally, the cardinal area of the putative dorsal valve is very simple, with a wide notothyrium bordered by simple socket-like plates excavated into the posterior shell wall (Figs. 3A, 4N–O). Multiple epitaxial coatings of these valves is sometimes so thick that the socket plates become extravagantly enlarged, making the edges of the socket-plates project forward like teeth, mimicking the morphology of a simple ventral valve. Inspection of paratypic dorsal valves without multiple coatings of epidote display an unmistakable, but simple, dorsal valve morphology (Figs. 3A, 4N–O). The articulatory mechanism in *A. cawoodi* was clearly very rudimentary. The simple, rounded, nub-like teeth must have slotted into the matching sockets excavated in the posterior shell wall of the dorsal valve. There is no evidence of a cardinal process. The dorsal valve has an unusually enlarged, incurved umbo, almost forming a notothyrial hood, and this may have been the site for direct muscle attachment (Fig. 3C). A consequence of the enlarged dorsal umbo is that, when articulated, a restricted valve gape must have resulted, and there would
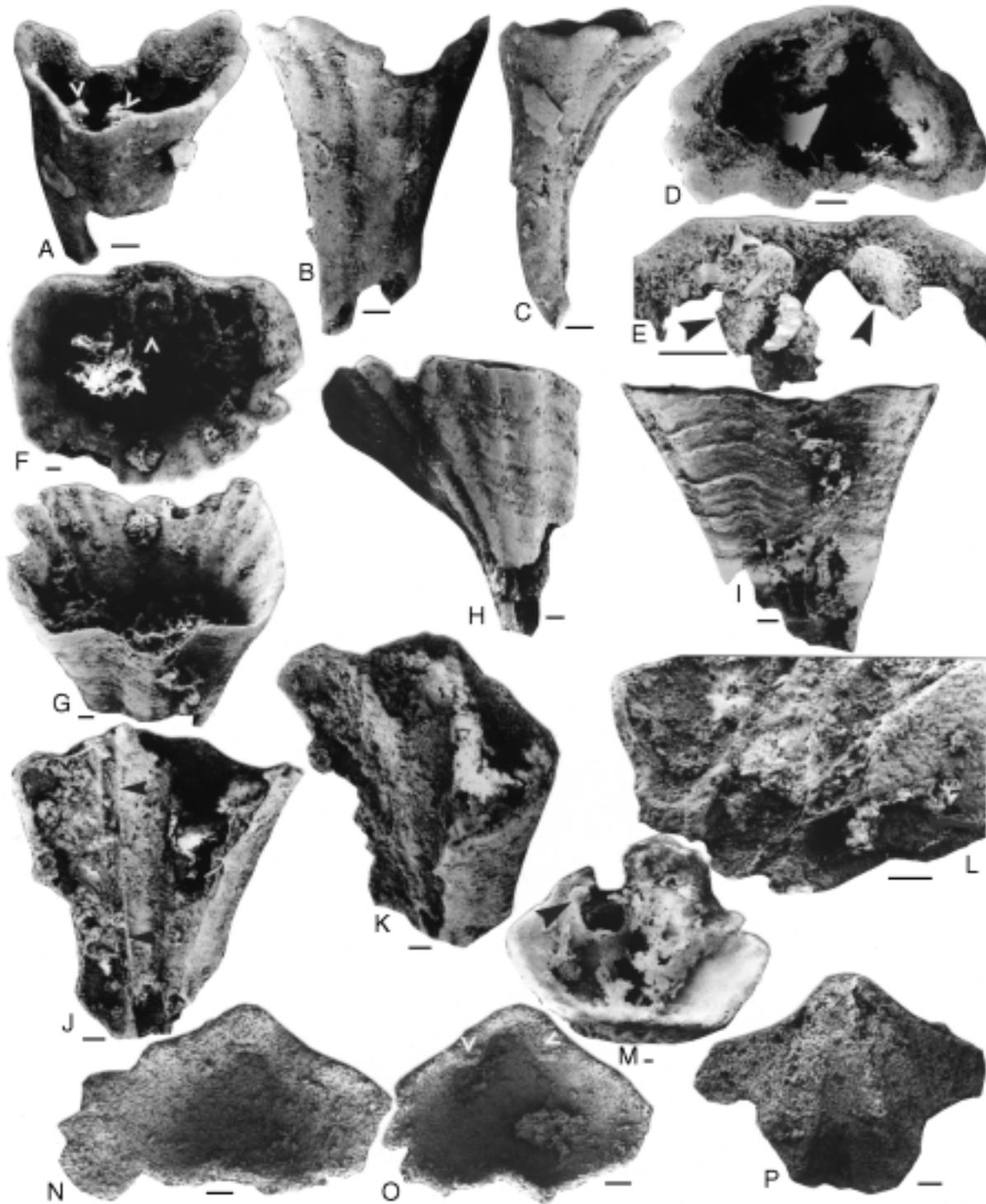
Figure 4. A–P, *Anomalocalyx cawoodi* n.gen. et n.sp. A–E, AM F97383, holotype from clast W10: A, oblique posterior view of holotype ventral valve showing teeth (arrowed); B, anterior view showing sulcate commissure; C, lateral view showing elongate, curved and tapering ventral valve; D, interior view; E, close-up of teeth (arrowed) in holotype. F–I, AM F97384, paratype ventral valve from clast W10: F, oblique interior showing interior tube (arrowed) with teeth broken away in specimen; G, oblique posterior view showing well-developed interarea and arched pseudodeltidium; H, lateral view; I posterior view showing undulose concentric growth lines. J–L, AM F107867, broken paratype ventral valve from clast W1: J, broken interior of ventral valve showing tapering interior (spondylial) tube with u-shaped external groove (arrowed); K, oblique view showing interior tube; L, close up of posterior portion of interior tube (infilled with sediment). M, AM F97385, paratype ventral valve from clast W10, showing dorsal portion of interior tube and a nub-like tooth (arrowed). N, AM F107868, interior of abraded paratype dorsal valve from clast W1 showing wide notothyrial gap. O, AM F107869, interior of abraded paratype dorsal valve from clast W1 showing simple socket plates (arrowed). P, AM F107870, exterior of abraded paratype dorsal valve from clast W1 showing anterior tongue. All scale bars 100 μm.

have been no posterior gap between the posterior edge of the pseudodeltidium and the dorsal umbo for a pedicle opening.

Etymology. In honour of Dr Peter Cawood, who discriminated and named the Murrawong Creek Formation and was the first to discover Cambrian fossils in this formation.

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