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Early Myriapodous Arthropods from Australia:
Maldybulakia from the Devonian of New South Wales

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ABSTRACT. The myriapodous arthropod *Maldybulakia* Tesakov & Alekseev, 1998, was first described from the Lower Devonian (Pragian-Emsian) in central Kazakhstan. The geographic and stratigraphic distributions of *Maldybulakia* are broadened by the discovery of Devonian species in Australia. The Lochkovian or Pragian *Maldybulakia angusi* n.sp. occurs in abundance in the Sugarloaf Creek Formation near Taemas, NSW. *Maldybulakia malcolmi* n.sp. occurs in late Givetian or early Frasnian strata of the Boyd Volcanic Complex near Eden, south coastal NSW. Two trunk tagmata are present in *Maldybulakia*. The strong tergal exoskeleton of posteriorly overlapping diplopleurotergites suggests closest affinities with Dignatha and, particularly, Kampecarida. Along with arthropleurids and kampecarids, *Maldybulakia* represents another major myriapod bodyplan in the mid-Palaeozoic. Although occurring in lacustrine and fluvial sediments, the associated flora, likely myriapod affinities, and presence of spiracles in *Maldybulakia* suggest terrestrial habits.

Myriapods have a sparse fossil record prior to the Carboniferous Period (see Almond [1985] and Shear [1990] for reviews of Silurian-Devonian body fossils). Among extant myriapod groups, millipedes and centipedes are known to have evolved by the Přídolí (Upper Silurian) (Almond, 1985; Shear *et al.*, 1998). Myriapodous fossils range back to the Lower Silurian (Mikulic *et al.*, 1985a,b), but the systematic position of these forms is uncertain. The extinct Class Arthropleuridea, best represented in the Upper Carboniferous (Briggs & Almond, 1994), extends back to the Přídolí, with new Devonian occurrences recently coming to light (Shear & Selden, 1995; Shear *et al.*, 1996). In spite of the patchy fossil record, several factors indicate that the major events in myriapod evolution

had occurred by the Devonian. Among these is the cladistically derived position of Middle Devonian centipedes, which nest within some extant groups (Shear & Bonamo, 1988). Further, the Upper Silurian occurrence of Diplopoda predicts that the other extant lineages in the Progoneata and Dignatha, the Symphyla and Pauropoda, had diverged by that time (Kraus & Kraus, 1994).

Except for trace fossil indications (Trewin & McNamara, 1995), all that is known about Silurian-Devonian myriapods has come from the northern hemisphere, and in particular the Old Red Continent. The only citation of mid-Palaeozoic myriapods from Gondwana has been fraught with controversy. Bergström (1979: 9–10) mentioned "undescribed myriapod material from the

Silurian of Australia", but Almond (1985) cited the view of H.B. Whittington that this material was actually Devonian and its myriapod affinities were highly question-able. The present work documents this controversial material and provides a formal taxonomy based on extensive new collections.

H.B. Whittington (pers. comm., 1994, 1995) informed me that the enigmatic fossils in question were shown to him by K.S.W. Campbell. Campbell revealed that these arthropods were collected from an Early Devonian site in the Taemas-Wee Jasper district, New South Wales, and led a trip to the locality in 1995. Disarticulated sclerites of a large, apparently myriapodous, arthropod were found in the Sugarloaf Creek Formation in an abundance rivaled by few fossil myriapod sites. The species is described here as *Maldybulakia angusi* n.sp. Also in 1995, Alex Ritchie informed me of a Devonian site from which he had collected parts of a myriapodous arthropod near Eden on the south coast of New South Wales. Collecting at this locality revealed a second species of *Maldybulakia* Tesakov & Alekseev, 1998, and showed the genus to range into the Middle or Upper Devonian. This second species is named *Maldybulakia malcolmi* n.sp.

The Australian species are considered congeneric with the enigmatic myriapodous taxon *Maldybulakia mirabilis* (Tesakov & Alekseev, 1992), from the Lower Devonian of central Kazakhstan. The new material adds considerable clarity to the nature of tagmosis in this arthropod, and sheds more light on the affinities of *Maldybulakia*. While Tesakov & Alekseev (1992) employed descriptive terminology used for millipedes, they made no more precise systematic placement for the genus than to regard it as myriapod-like. Material at both Australian localities consists of trunk tergites and pleurotergites alone (the sternum and limbs were clearly less mineralised, and unpreserved). The heads of all three species are unknown. Tesakov & Alekseev (1992) interpreted the trunk tergites of *Maldybulakia* as diplosegments, divided into prozonites and metazonites. I have accepted this interpretation in describing the Australian species, for reasons elaborated below.

Specimens illustrated in this work are housed in the Palaeontology type collections of the Australian Museum (prefixed AM F.).
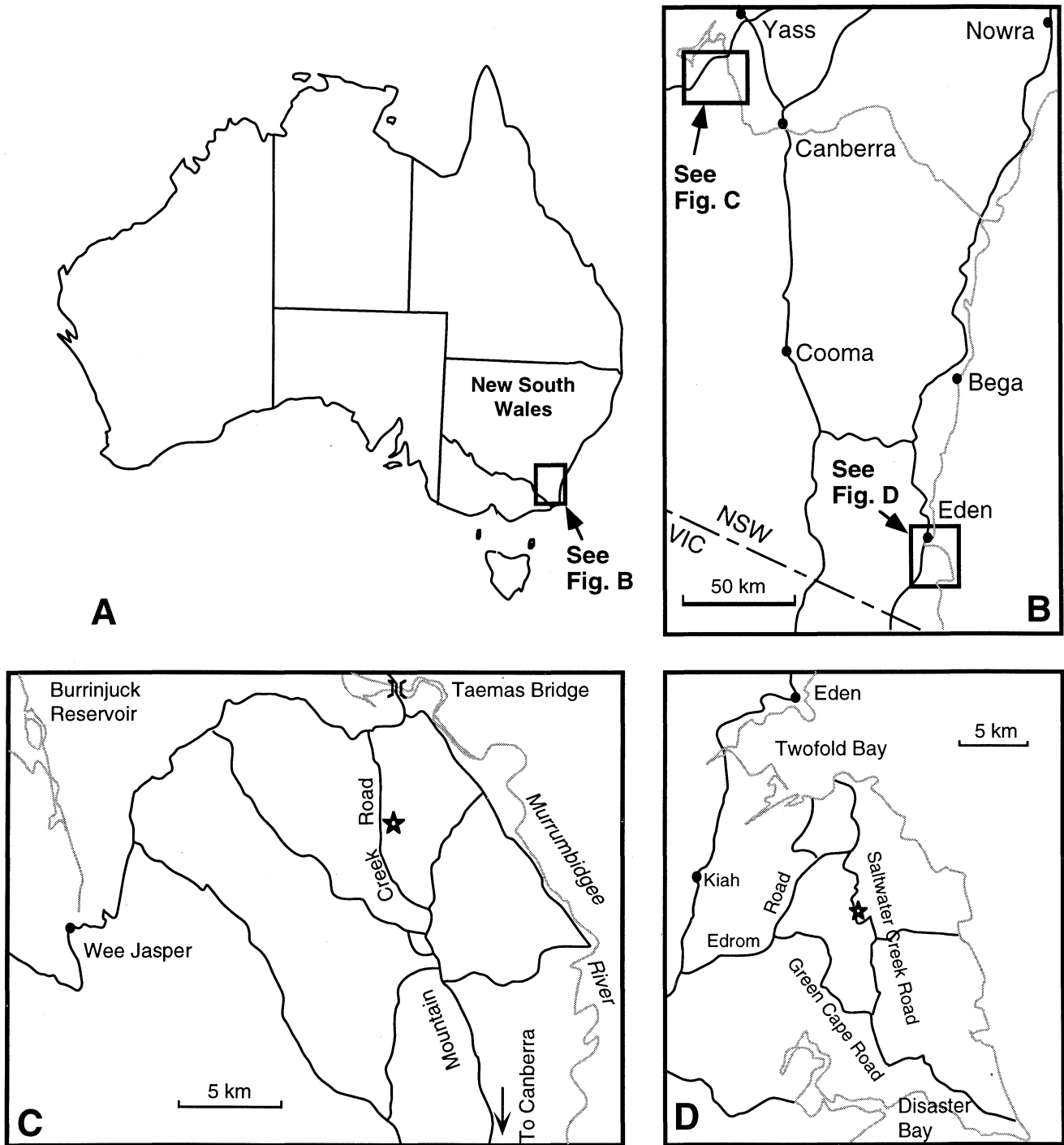
Occurrences

Localities, environments, and ages. *Maldybulakia* is at present known from two localities in the Devonian of New South Wales (Fig. 1).

Maldybulakia angusi occurs in the Sugarloaf Creek Formation, near the eastern outcrop limit of the formation. The site (35°04'S 148°51'E) is located about 400 m east of Mountain Creek Road, and is accessed 400 m south of Three Oaks homestead (Fig. 1C). The Sugarloaf Creek Formation consists of massive, lenticular arenites deposited in alluvial fans in the western part of the outcrop belt (towards Wee Jasper), but is composed of thinner, parallel-bedded arenites, siltstone and shale in the eastern extent where *Maldybulakia angusi* was collected (Owen &

Wyborn, 1979). The fossils occur as totally disarticulated moulds in fine-grained sandstones rich in volcanic rock grains derived from the underlying Mountain Creek Volcanics. No other animal fossils have been found associated with *M. angusi* (only very rare plant fragments), yet this single species is sufficiently abundant as to locally litter bedding surfaces. The depositional environment of the arenites in the eastern extent of the Sugarloaf Creek Formation has been interpreted as fluvial (Owen & Wyborn, 1979). Although fossils were not previously recognised from the Sugarloaf Creek Formation, a latest Lochkovian to earliest Pragian age assignment was made by Owen & Wyborn (1979) based on an early Pragian dating for the conformably overlying Cavan Limestone. The age of the Cavan Formation has, however, been reassessed based on conodonts (Mawson *et al.*, 1992), its lower part representing the late Pragian *pireneae* Zone. The Sugarloaf Creek Formation is thus less constrained within the Lochkovian-Pragian interval.

Maldybulakia malcolmi is common through an approximately 30 cm interval in mudstone and siltstone at an outcrop along Saltwater Creek Forest Road, near Edrom, 12 km SSE of Eden. The site (37°09'S 149°57'E) is located 3.6 km from the intersection of Saltwater Creek Road and Edrom Road in East Boyd State Forest (Fig. 1D). Fergusson *et al.* (1979: fig. 5) documented this section as examplar of lacustrine mudstones in their Facies 3 of the Boyd Volcanic Complex. They noted the occurrence of *Maldybulakia* [as "Arthropods (unidentified genus)"] with lycopods, which are abundantly represented at these levels. Some of these can be identified as *Lepidosigillaria yalwalense*, usually regarded as Middle Devonian in age (M.E. White, pers. comm., 1995). However, bothriolepid and phyllolepid placoderms indicative of a Givetian-Frasnian age are known from Facies 3 of the Boyd Volcanic Complex at other localities (Fergusson *et al.*, 1979; G.C. Young, pers. comm., 1996). The same flora occurs with late Givetian or early Frasnian fish in Facies 2 of the Boyd Volcanic Complex (Bunga Beds). On this evidence, *Maldybulakia malcolmi* can be assigned an age in the late Givetian to early Frasnian interval. The site was extensively excavated in April 1997 by the author and 11 other collectors.

Both Australian species of *Maldybulakia* are thus known from sediments deposited in fresh water, and disarticulated tergites and pleurotergites occur as rich accumulations. The geological and inferred ecological context of *M. mirabilis* in Kazakhstan is similar. The latter species occurs as abundant, mostly disarticulated, moulds in beds of tuffaceous siltstone. Tesakov & Alekseev (1992) regarded the depositional setting of these sediments as lacustrine, similar to the interpretation of mudstones bearing *M. malcolmi* (Fergusson *et al.*, 1979; P.C. Lewis *et al.*, 1994). *Maldybulakia* is, however, likely to have been terrestrial rather than aquatic, based on the inferred presence of a tracheal respiratory system (see interpretation of spiracles in *M. malcolmi* below). This in itself is not a definite indicator (aquatic insects providing an obvious exception). Comparisons with the habits of related extant arthropods are weakened by the imprecision with

Figure 1. Occurrences of *Maldybulakia* in Australia. A, Australia, showing location of map B. B, southeastern New South Wales, with locations of maps C and D indicated by insets. C, Taemas-Wee Jasper region, with type locality of *M. angusi* indicated by star. D, Eden region, with type locality of *M. malcolmi* indicated by star.

which the affinities of *Maldybulakia* are known. In spite of this limitation, it must be observed that the myriapod affinity suggested by the apparently diplosegmental trunk (see "Phylogenetic affinities" below) leans towards a terrestrial mode of life. The only associated fossils, the abundant lycopod flora with *M. malcolmi*, are terrestrial, so the abundance of specimens in aquatic

facies cannot rule out a terrestrial habitus in life. The robust construction of the exoskeleton with its strong intertergal articulations would certainly allow transport (Allison, 1986). Indeed, the concentrations of specimens and a bias towards small specimens remaining articulated, discussed below for *M. malcolmi*, are suggestive of some transport.

Systematic palaeontology

A traditional ranked classification would recognise *Maldybulakia* as distinct from other myriapodous arthropod taxa at a high level (class or subclass). As did Tesakov & Alekseev (1992), I have abstained from assigning *Maldybulakia* at most supergeneric ranks; a series of redundant, monotypic taxa does not provide insight into its systematic position. Justification for likely membership in Dignatha is presented under "Phylogenetic affinities". The taxon Myriapoda is of uncertain status (see "Phylogenetic affinities") and is not employed in this classification.

Arthropoda Siebold & Stannius, 1845

Atelocerata Heymons, 1901

?Dignatha Tiegs, 1947

Maldybulakia Tesakov & Alekseev, 1998

1992   *Lophodesmus* Tesakov & Alekseev, 1992 (non *Lophodesmus* Pocock, 1894).

Type species. *Lophodesmus mirabilis* Tesakov & Alekseev, 1992.

Diagnosis. Large myriapodous arthropod with strongly mineralised pleurotergum, unmineralised sternum; cuticular surface with dense, polygonal sculpture; cuticle densely penetrated by large pore canals; trunk composed of two tagmata of presumed diplotergites; anterior tagma of one or possibly two subtrapezoidal tergite(s) having rounded corners; posterior tagma composed of at least four pleurotergites with pair of triangular lateral lobes on metazonites and short to long paratergal spines; pleurites coalesced with metazonites only; posterior-most (fifth) bilobate tergite with median spine-like process; spiracle in pleural furrow on third pleurotergite of posterior tagma; presumed telson composed of two small sclerites.

Discussion. *Maldybulakia* Tesakov & Alekseev, 1998, was recently proposed as a replacement name for *Lophodesmus* Tesakov & Alekseev, 1992, a name occupied by the extant polydesmid millipede *Lophodesmus* Pocock, 1894. The generic diagnosis employed by Tesakov & Alekseev (1992) is modified to account for newly discovered diversity in the Devonian of Australia.

A major morphological contribution of new Australian species of *Maldybulakia* is to elucidate the nature of trunk tagmosis in this arthropod. Tesakov & Alekseev (1992) identified two tergite types in beds containing *Maldybulakia mirabilis*. The type material consists of tergites regarded by them as diplosegments, with the lateral part of the "metazonite" swollen into a rounded lobe, and a spinose projection from the lateral edge of the paratergum. This tergite type will hereafter be referred to

as a bilobate pleurotergite or B-pleurotergite (specimens of *M. malcolmi* n.sp. are interpreted as having pleurites fused to the tergum, thus the use of "pleurotergites").

Associated with the B-pleurotergites is a second, less common tergite type of "simple structure and rounded-rectangular outline" (Tesakov & Alekseev, 1992: 19). Noting that the rectangular (or, more accurately, trapezoidal) tergites bore a similar sculpture to the bilobate diplotergites/B-pleurotergites, Tesakov & Alekseev (1992) acknowledged the likelihood that they could belong to the same animal. However, they interpreted the trapezoidal tergites as neck segments, but (assuming one neck segment per animal, as for the dignathan collum) found them to be anomalously common relative to the typical B-pleurotergites.

Conclusive evidence that the trapezoidal tergites (here abbreviated T-tergites) are actually part of *Maldybulakia* is provided by the Australian species, in particular by several articulated specimens of *M. malcolmi*. Four articulated specimens of *M. malcolmi* have a single T-tergite attached or slightly displaced from the front of a series of B-pleurotergites. In the holotype, a T-tergite of nearly the same size as the articulated one (width 14.4 versus 14.8 mm, respectively) is displaced 14 mm from the front of the specimen. Considering the scarcity of specimens this small it is not unlikely that the displaced tergite belongs to the same individual, which would thus possess two T-tergites. The failure to find T-tergites in articulation with each other in any specimens may derive from a mainly membranous attachment and simple overlap (in contrast to the strong articulations developed between B-pleurotergites). *Maldybulakia angusi* reveals a range of morphology within this tergite type, suggestive of two or more T-tergites represented within a tagma of generally similar tergite form. The T-tergites vary in the presence or absence of a posteromedian spine, the prominence of tubercles, the degree of sinuosity of the transverse furrow, and the presence or absence of lateral swellings. *Maldybulakia malcolmi* and *M. mirabilis* display less morphological differentiation between the tergites of this tagma than is the case for *M. angusi*. This is consistent with evidence from the tagma composed of B-pleurotergites, wherein *M. angusi* shows a much greater degree of variation than seen in the other two species.

The frequency of occurrence of the trapezoidal tergites—27 percent of the sample (N=44)—was cited by Tesakov & Alekseev (1992) as a difficulty for their interpretation of the T-tergites as neck segments. Variable frequencies of occurrence of the T- and B-tergites are observed for the two Australian species of *Maldybulakia* (Fig. 2). The relative extent of the two tagmata might be estimated by the relative abundance of T- and B-tergites, although it appears that taphonomic factors have biased the samples. Three articulated specimens of *M. malcolmi* (AM F.102533, 102535, 102357) have a single T-tergite followed by four B-pleurotergites, then a caudal tergite as figured for *M. mirabilis* by Tesakov & Alekseev (1992). The caudal tergite is quite clearly a modified B-pleurotergite, showing the rounded lateral lobes and depressed, anterior overlapped surface (prozonite) typical

of those pleurotergites. This serial homology is also obvious in *M. malcolmi*, in which the caudal tergite possesses small posterolateral projections as in the B-pleurotergites.

For *Maldybulakia angusi*, a survey of 301 sclerites that could be confidently identified.as either a T-tergite, ring tergite, B-pleurotergite or caudal tergite shows that T-tergites comprise 32 percent of the sample and B-pleurotergites 66 percent (Fig. 2c). It might thus be inferred that the anterior tagmata composed of T-tergites is half the length of the tagmata comprising B-pleurotergites, which would accord well with the two T-tergites and four B-pleurotergites seen in the holotype of *M. malcolmi*. A ring-like tergite that overlies the prozonite of the anteriormost B-pleurotergite (and has processes permitting articulation of the T-tergite) in *M. malcolmi* is represented by only 4 of 301 specimens of *M. angusi* and is unreported in the sample of *M. mirabilis* (Fig. 2d). Given that each individual possesses one of this sclerite type it is underrepresented in the sample. Caudal tergites are significantly underrepresented, known from only two specimens.

The relative abundance of disarticulated tergites in *M. malcolmi* differs from the 2:1 ratio of B:T tergites in the sample of *M. angusi* as well as the 4:1 or 4:2 ratio predicted by articulated specimens (Fig. 2a,b). Of disarticulated tergites of *M. malcolmi*, 185 are B-pleurotergites (83 percent) and 28 are T-tergites (12.6 percent). The apparent over-abundance of B-tergites is at the expense of ring tergites (3.1 percent) and caudal tergites (1.3 percent). These differences between the three species, if not entirely due to differential transport of the various sclerite types, might result from a greater number of T-tergites in *M. angusi* compared to *M. malcolmi*. There is a significant taphonomic bias observed in the case of articulation. Articulated specimens of *M. malcolmi* are smaller than most of the disarticulated material, presumably because larger specimens did not survive transport intact.

Although the trunk of *Maldybulakia angusi* displays much more serial variation than that of *M. malcolmi*, it has proven possible to identify most tergites of the former according to their position in the latter, and it cannot be ruled out that *M. angusi* may possess the same number of tergites in the trunk as known for *M. malcolmi* (one or possibly two T-tergites, a ring tergite, four B-pleurotergites and a caudal tergite). The minimal number of tergites in *M. angusi* is discussed more fully after description of that species.

Tesakov & Alekseev's (1992) evidence for regarding the B-pleurotergites of *Maldybulakia mirabilis* as diplosegmental (diplotergites) was their "distinct two-part structure". This refers to the separation of the anterior, articulating surface of the tergite from the posterior lobate part by a strong transverse groove or stricture. The T-tergites are of comparable proportions (length versus width) to the B-pleurotergites, and are also divided lengthwise by a transverse furrow in Australian species of *Maldybulakia*. This would suggest that they, too, would be diplotergites if the posterior trunk tergites were confirmed as being diplosegmental. All of the Palaeozoic

myriapodous arthropods that might be compared with *Maldybulakia* on the basis of tergite form have proven to be diplosegmental when the appendages became known. Examples are kampecarids (Almond, 1986), euphoberiid millipedes (Burke, 1979), and arthropleurids (Briggs & Almond, 1994). It is thus likely that the trunk tagmata of *Maldybulakia* are composed of diplosegments. The strong intertergal articulations and overlap of the prozonite of the B-pleurotergites by the preceding metazonite suggest that *Maldybulakia* had the capacity to enroll.

A pair of articulated sclerites are preserved just behind the caudal pleurotergite of the holotype of *Maldybulakia malcolmi* (Fig. 3a,g). They are also known from disarticulated specimens (Fig. 4g). Their positioning on the articulated specimen is a strong indication that they represent the posterior sclerites, although the nature of their (presumed) articulation to the caudal pleurotergite is not understood. Their small size, inferred posterior position, and overall structure invite a comparison with the telson of myriapods, which may also incorporate multiple sclerites (e.g., preanal sclerite or preanal ring, anal valves, and subanal plate in diplopods; Enghoff, 1990: 14–15). In the descriptions below, these two sclerites are called telson sclerites.

Information on pleural morphology is supplied by *Maldybulakia malcolmi*. The lateral exoskeletal component of *Maldybulakia* is regarded as a mineralised part of the pleuron (i.e., pleurites), rather than the tergum (para-tergites) because of its marked topographic separation from the tergum. Alternative interpretations of pleural structures are addressed under discussion of *M. malcolmi*.

The lack of sampling of a head in the Australian occurrences is curious, given the abundance of trunk tergites known for both species. Almond (1986) observed that articulated heads were rare in the possibly allied kampecarids, even when the trunk was fully articulated, and attributed this to a delicate attachment by arthrodial membrane, as is the case in millipedes. The head tergite of *Kampecaris* is a rather featureless plate (or pair of plates, the second possibly a collum according to Almond, 1986). The narrow sclerite alleged to be the head of *Arthropleura* (Briggs & Almond, 1994: figs. 1, 2; Brauckmann *et al.*, 1997) requires confirmation, as it may instead represent a collum-like tergite (W.A. Shear & H. Winkelmann, pers. comm., 1997). Even if the head of *Maldybulakia* likewise involved a simple plate it is unlikely that it has been overlooked because sclerites of this sort were deliberately sought, yet no candidates have appeared. Heads likely underwent a different transport history than the trunk, perhaps because of a membranous attachment. The possibility that specimens such as the holotype of *M. malcolmi* are complete, with the T-tergite being cephalic, is not favoured. This sclerite deviates from an expected morphology of an arthropod cephalon (e.g., lacking eyes or structures to accommodate them; lacking antennal sockets or notches), its transverse stricture and shape of the doublure conforming to a trunk diplotergite. The abrupt anterior termination of the doublure (Fig. 6b) indicates a more anterior sclerite. The possibility that a species may possess two of these tergites further weakens the case for
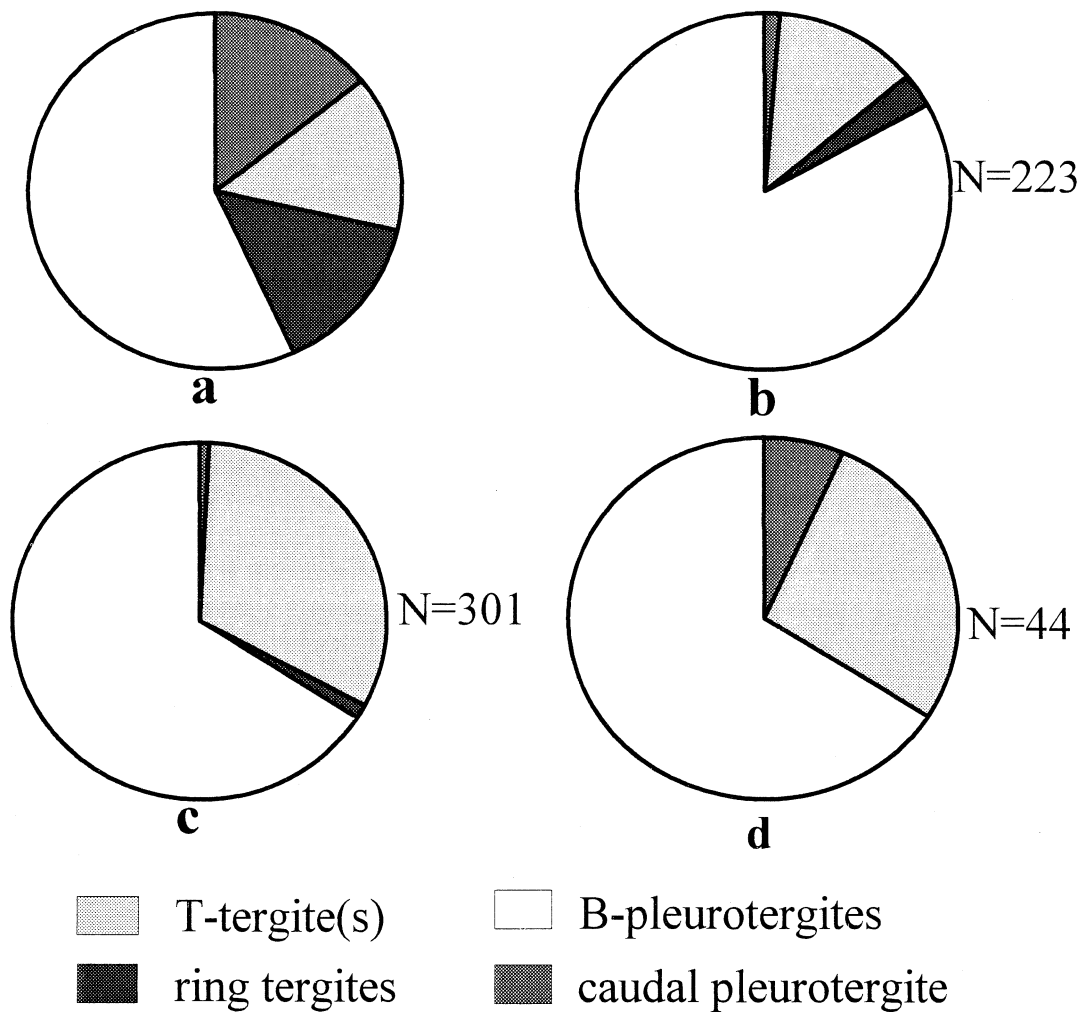
Figure 2. Relative abundances of different sclerite types at localities yielding *Maldybulakia*. (*a*) expected frequency of occurrence for *M. malcolmi* n.sp. based on one T-tergite, one ring tergite, four B-pleurotergites, and one caudal pleurotergite in articulated specimens. (*b*) sampled frequency of occurrence based on 223 disarticulated sclerites of *M. malcolmi*. (*c*) sampled frequency of occurrence based on 301 disarticulated sclerites of *M. angusi* n.sp. (*d*) sampled frequency of occurrence based on 44 disarticulated sclerites of *M. mirabilis* (Tesakov & Alekseev, 1992).

a cephalic identity. All of these factors outweigh the crude similarities in outline between a T-tergite and some arthropod head shields (e.g., the prosoma of bunodid xiphosurids, which has typical cephalic structures such as a cardiac lobe and ophthalmic ridges that are lacking in *Maldybulakia*).

A few disarticulated sclerites do not conform to those in articulated specimens of *Maldybulakia malcolmi*, and their position in the exoskeleton is unknown. A unique specimen of *M. malcolmi* (Fig. 5g,h) has a prominent, square embayment in could be presumed to be the posterior margin (this assuming that the strongly convex, ridge-like edge of the specimen is overlapped in

articulation, as is the case for the prozonites). The conical median swelling warrants comparison with the caudal pleurotergite, although this swelling is strongly dorsally directed. The size and shape of the embayment invite speculation that the telson sclerites (Fig. 4g) might attach here. However, it does not seem possible that such a large, robust sclerite could be positioned posteriorly in the trunk yet be missing from the holotype and other articulated specimens. As such, it is more likely situated anterior to the T-tergites, but attempts to interpret it as a head are unconvincing, lacking any landmarks indicative of an arthropod cephalic shield or head capsule.

Maldybulakia malcolmi n.sp.

Figs. 3–8

Maldybulakia new species 1 Edgecombe, 1998: fig. 1.

Etymology. For Malcolm Young.

Diagnosis. *Maldybulakia* with relatively minor serial variation in B-pleurotergites; lacking long paratergal spines, posteromedian spines, and tuberculation; caudal pleurotergite with lateral lobes set off by shallow furrows; median projection on caudal pleurotergite blunt, conical, rather than spinose.

Types. HOLOTYPE articulated trunk AM F.102533 (Fig. 3a–d,f,g), composed of one T-tergite, four B-pleurotergites, a caudal tergite, disarticulated telson sclerites; and possibly associated T-tergite; length from anterior end of T-tergite to posterior end of caudal pleurotergite 31.8 mm. Boyd Volcanic Complex (late Givetian or early Frasnian), Saltwater Creek Road, East Boyd State Forest, NSW (37°09'S 149°57'E). Collected by Z. Johanson. PARATYPES AM F.102534–102556, 102581, from type locality.

Description. Trunk up to 115 mm long, as inferred from size of largest known B-pleurotergite scaled to articulated specimen.

T-tergite(s) of length up to 16.4 mm in known specimens, but inferred to be larger based on relative size of B-pleurotergites; smallest disarticulated specimen 5.1 mm long medially. Length 38–44 percent of width; of even, moderate convexity (tr.). Anterior part of prozonite a forward-sloping scarp that evenly lengthens medially to about 45 percent the length of the prozonite. Stricture moderately deep and approximately transverse medially, then weakly curving backwards laterally, abruptly shallowing and recurving forward, then inward, such that lateral part of stricture is C-shaped. Metazonite 64–75 percent length (sag.) of prozonite; gently convex (sag.). Lobate posterior projections lie against anterodistal socket-like processes on underlying ring tergite, serving as point of articulation. Posterior margin gently convex forwards between posterior projections. Doublure wide beneath lateral and posterolateral edges of T-tergite, shortening and scalloped on each side of a flange-like median section that has a transverse course; doublure abruptly truncated anteriorly, with straight anteromedial margin.

Ring tergite (Fig. 5b,d–f) divided by sharp transverse furrow into short, crest-like anterior band of even length and long, elevated posterior band; furrow strongly shallow or effaced near distal margin. Anterior band extended laterally well outside posterior band as slender, pointed process; anterodistal edge folded as a small socket-like process. Posterior band lenticular in outline, convex (sag.), moderately arched transversely. Ring tergite overlapping prozonite of first B-pleurotergite, with distal edge of posterior band extending to inner edge of anterior process

on prozonite of B-pleurotergite.

Posterior tagma composed of four B-pleurotergites and caudal pleurotergite, widest across first pleurotergite then gently, evening narrowing posteriorly; largest known disarticulated specimen (second B-pleurotergite) of length 25.8 mm, width 45 mm; smallest disarticulated specimen (fourth B-pleurotergite) 7.5 mm long, but as short as 6 mm in articulated specimens. Relative length and width of pleurotergites variable (compare Figs. 3a and 5i for relatively narrow and wide examples, respectively); each pleurotergite longer relative to its width than the preceding one. Furrows separating prozonite and metazonite on all four pleurotergites of similar, moderate depth, long medially, narrower but with comparable depth against lateral lobes. In sagittal profile, prozonites gently convex, metazonites flat or weakly convex along most of length; median lobe raised well above lateral lobes. Lateral lobes of all four pleurotergites triangular, with short, blunt posterolateral projections, in some specimens developed as weak spines. Metazonites progressively more strongly arched (tr.) posteriorly in trunk. Diagonal furrows separating lateral and median lobes of equal impression on each B-pleurotergite, gently convex backward.

First B-pleurotergite (Figs. 3e, 6c–e) with outer margin of lateral lobe oriented posterolaterally in dorsal view, gently convex outward, this margin posteriorly directed on the succeeding three pleurotergites with a corresponding posterior redirection of the posterolateral projections. Prozonite lenticular, with a strong process at anterodistal edge that is lacking on succeeding pleurotergites. Lateral edge of tergum sharply folded down as vertical scarp; lenticular pleurite separated by sharp, curved pleural furrow; pleural furrow effaced posteriorly; separation of pleuron and tergum not marked by suture on posterior part of pleurotergite; posteroventral edge of pleurotergite turned out as a rounded shelf.

Second B-pleurotergite (Fig. 6g–j) having anteroventral edge of prozonite forming a narrow, steep rim; anterolateral corner of tergite with ledge-like protrusion markedly distal to pleuron; small ventrally directed pleural process at anterior corner of metazonite, ventral margin of pleuron abruptly flexed ventrally immediately behind this process; pleuron bisected by anterodorsally oriented groove; posterior part of pleuron lensoid in outline, gently sloping outward; pleural furrow indistinct on posterior part of pleurotergite.

Third B-pleurotergite (Fig. 3b,c,f) with pleural furrow expanded anteriorly to form a shallow, elongate basin within which a deep, elliptical canal (spiracle) projects inwards; pleurite narrow beneath spiracular region, then abruptly widening; rounded ventral projection on anterior part of pleurite as on preceding diplopleurotergite; sharp, shallow suture between pleurite and pleural furrow anteriorly.

Fourth B-pleurotergite with lateral lobes of metazonite terminating as posteriorly-directed angulations. Weak nodose swelling usually distinguishable on posteromedian part of median lobe of metazonite (Figs. 3a, 5k), occasionally discernible on other B-pleurotergites. Pleural furrow deep, incised as a V-shaped groove along most of
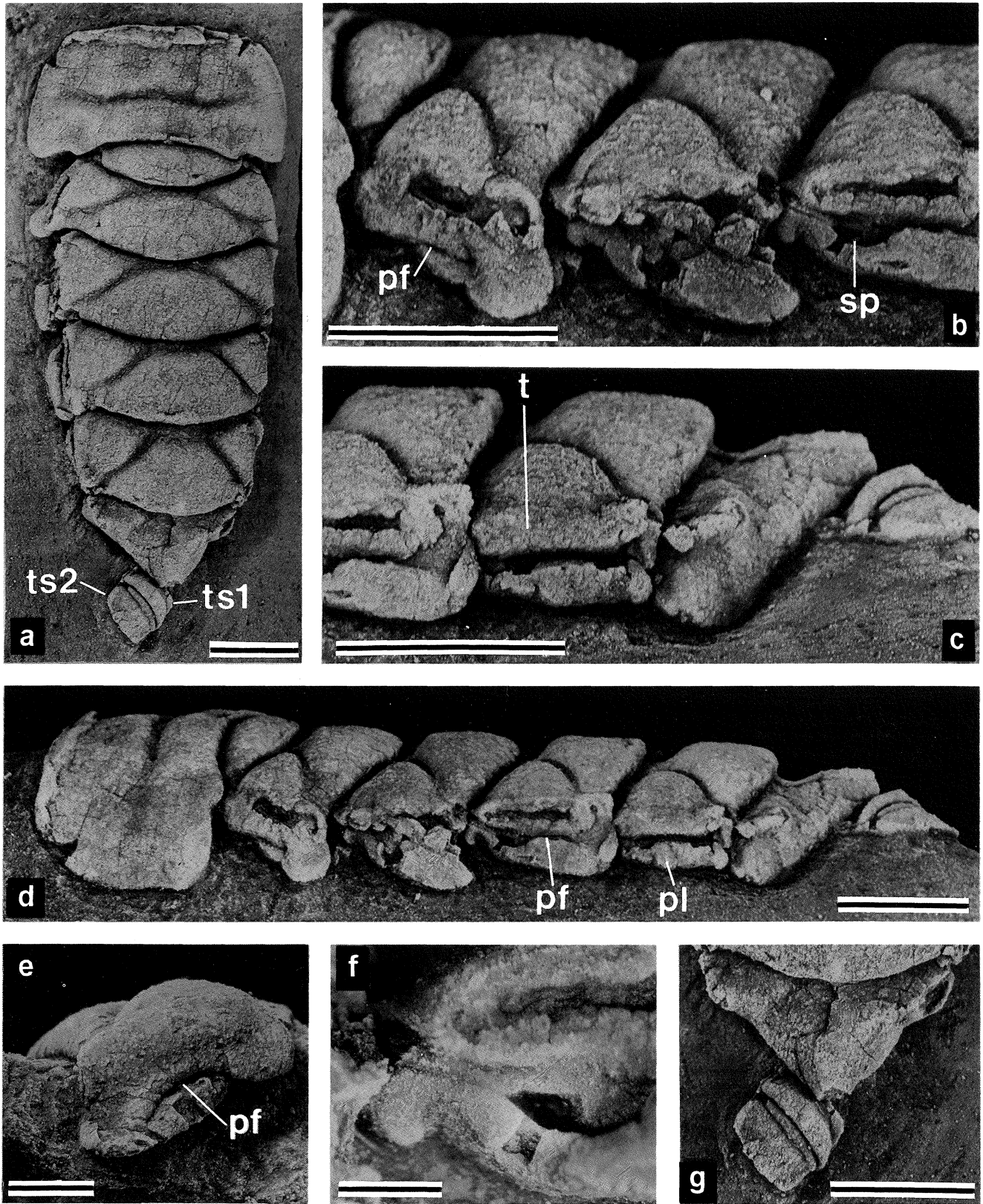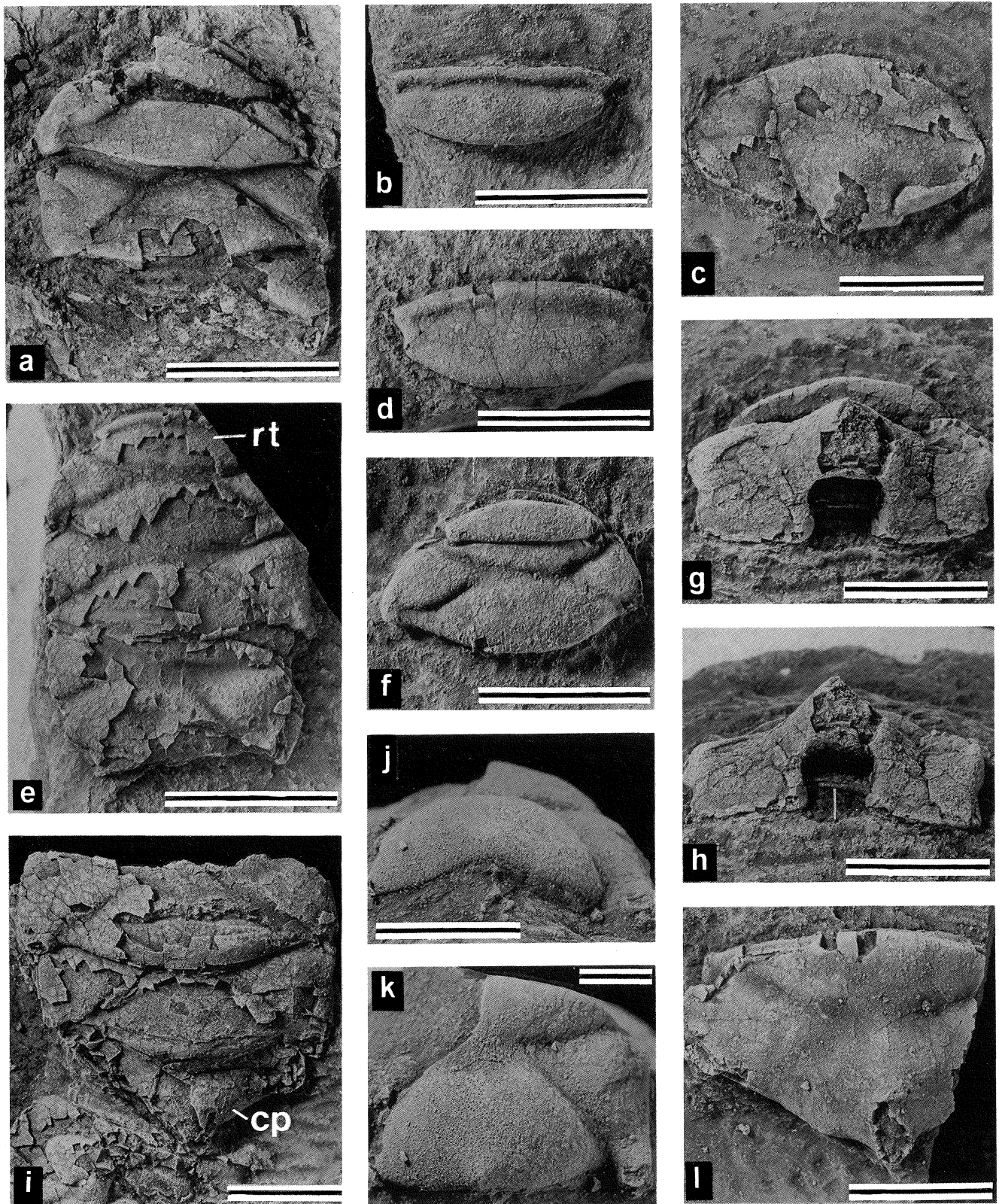
Figure 3. *Maldybulakia malcolmi* n.sp. Scale bars 5 mm except *f*, 1 mm. Abbreviations: pf, pleural furrow; pl, pleurite; sp, spiracle; t, lateral edge of tergum; ts1, anterior telson sclerite; ts2, posterior telson sclerite. (*a–d,f,g*) holotype articulated trunk AM F.102533. (*a*) dorsal view of complete specimen. (*b,c*) lateral views of anterior and posterior B-pleurotergites, respectively. (*d*) lateral view of complete specimen. (*f*) lateral view of third B-pleurotergite with spiracle. (*g*) dorsal view of caudal pleurotergite and telson sclerites. (*e*) posterolateral view of first B-pleurotergite AM F.102552 (see Fig. 6d for dorsal view), showing pleural furrow (pf).
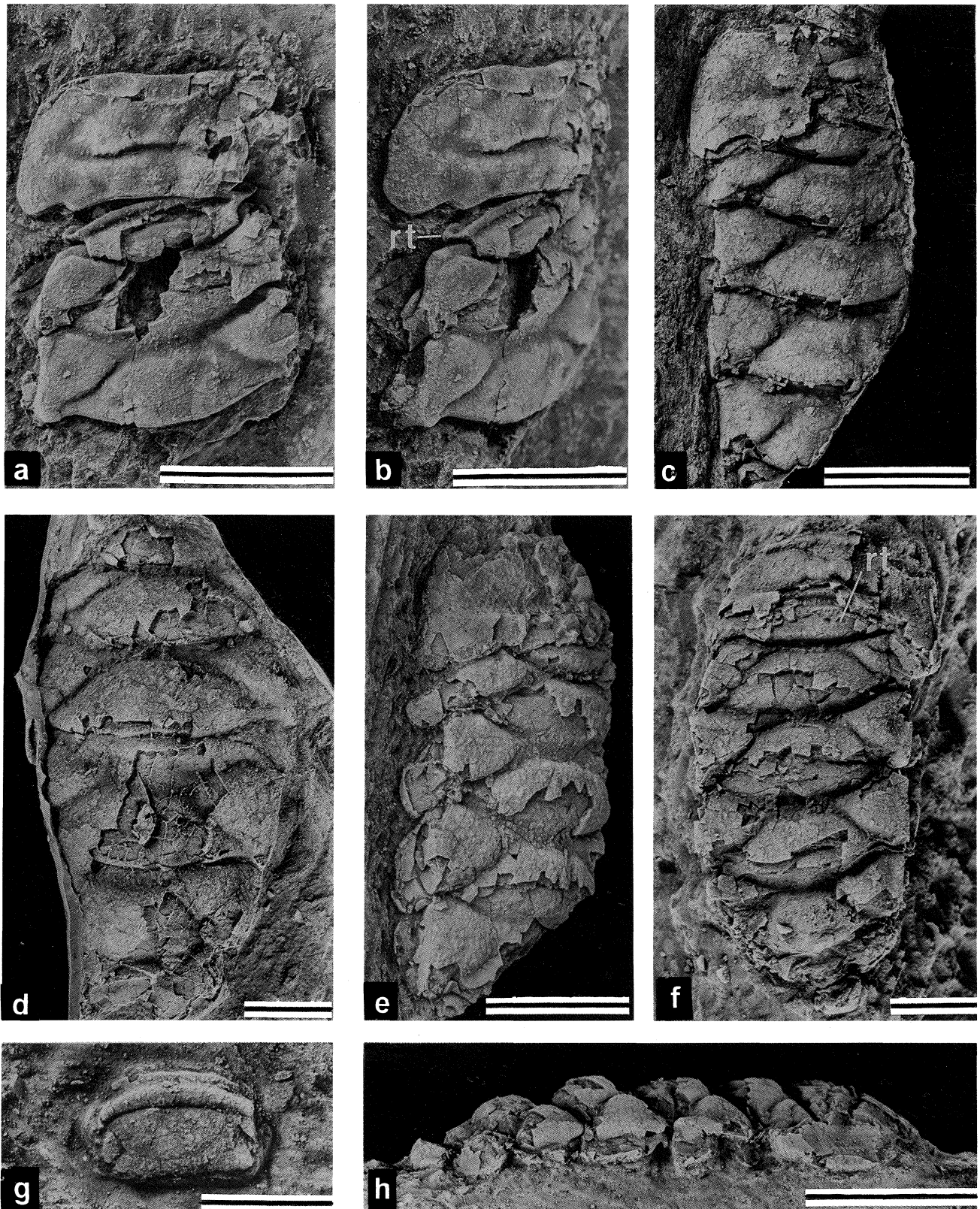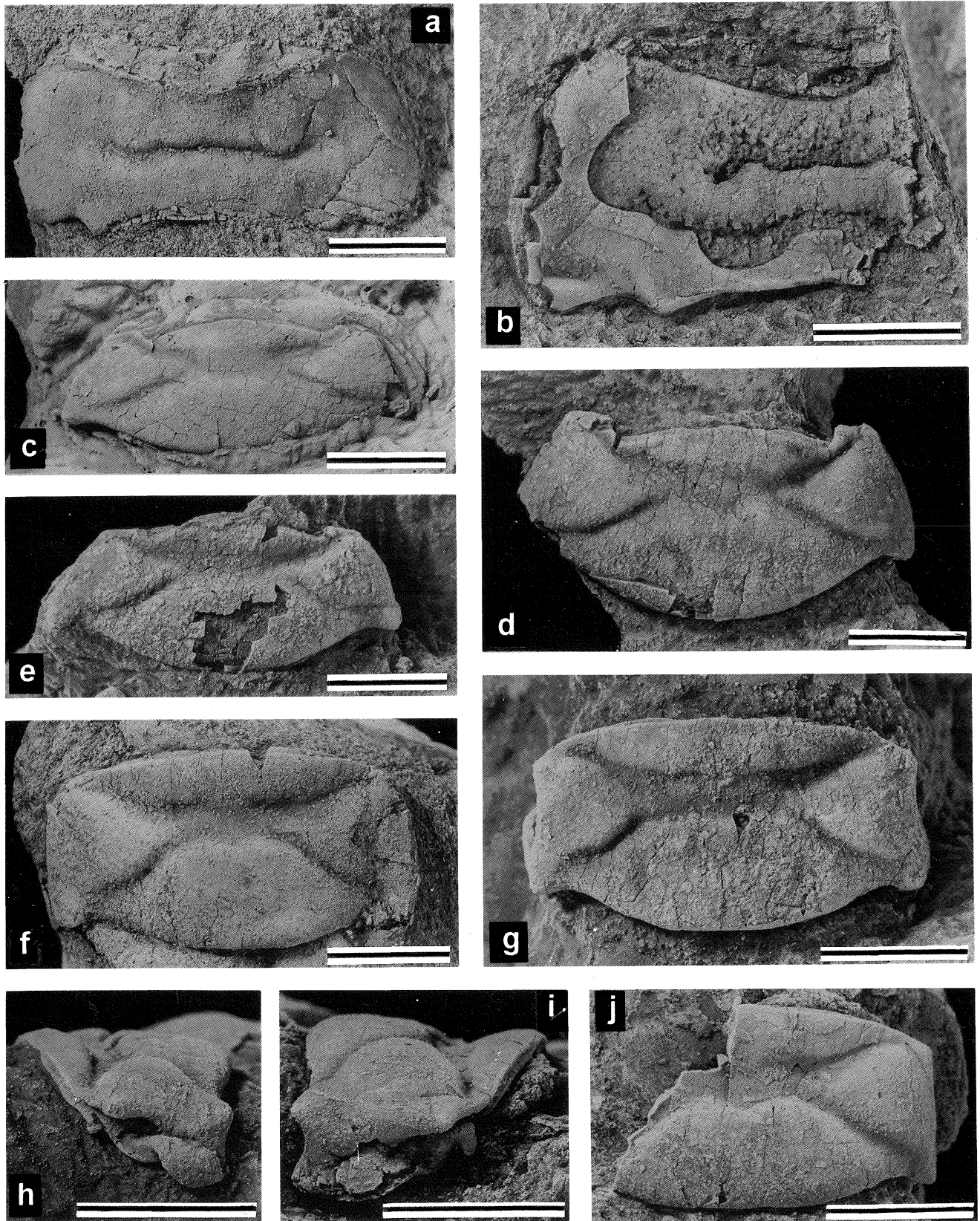
Figure 4. *Maldybulakia malcolmi* n.sp. Scale bars 10 mm except *d,f,g*, 5 mm. (*a,b*) dorsal and left dorsolateral views of T-tergite, ring tergite, and first two B-pleurotergites, AM F.102534. (*c*) dorsal view of latex cast of articulated trunk AM F.102535a, showing T-tergite, ring tergite, four B-pleurotergites and part of caudal pleurotergite. (*d*), dorsal view of latex cast of ring tergite and four B-pleurotergites, AM F.102536. (*e*) left dorsolateral view of trunk AM F.102535b (see Fig. 4c for counterpart). (*f,h*) dorsal and right lateral views of articulated trunk AM F.102537, showing posterior part of T-tergite, ring tergite (rt), four T-pleurotergites, and part of caudal pleurotergite. (*g*) dorsal view of telson sclerites AM F.102538.
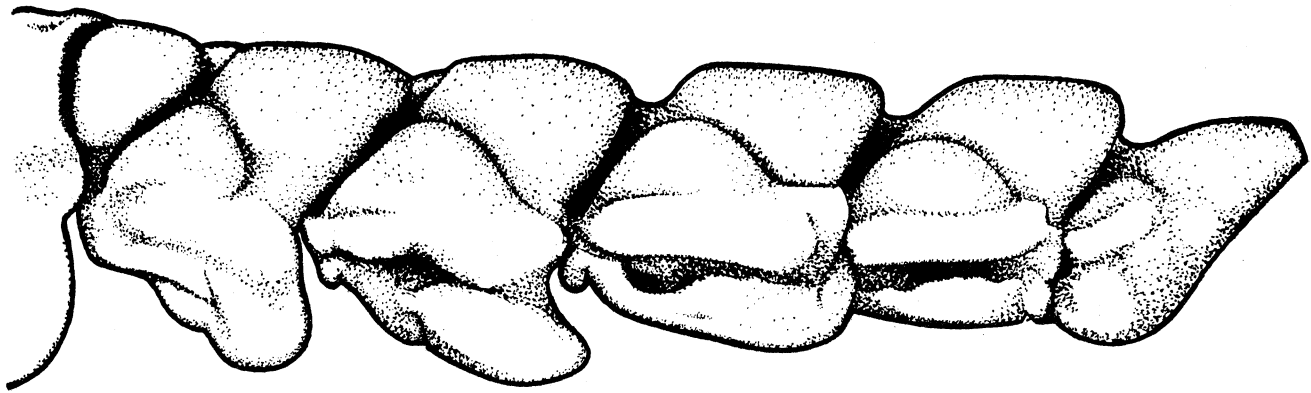
Figure 5. *Maldybulakia malcolmi* n.sp. Scale bars 10 mm except *k*, 5 mm. (*a*) dorsal view of ring tergite and three B-pleurotergites, AM F.102539. (*b*) dorsal view of ring tergite AM F.102540. (*c*) dorsal view of caudal pleurotergite, AM F.102541. The median swelling in this specimen is more dorsally directed than in other specimens. (*d*) dorsal view of ring tergite AM F.102542. (*e*) dorsal view of ring tergite (rt) and three B-pleurotergites, AM F.102543. (*f*) dorsal view of ring tergite and first B-pleurotergite, AM F.102544. (*g,h*) dorsal and anterior or posterior view of unique sclerite of unknown position, AM F.102545. White line in *h* indicates limit of exoskeleton in the embayment. (*i*) dorsal view of posterior two B-pleurotergites and caudal pleurotergite (cp), AM F.102546. (*j,k*) posterior and dorsal views of fourth B-pleurotergite, AM F.102547. (*l*) dorsal view of caudal pleurotergite AM F.102548.

Figure 6. *Maldybulakia malcolmi* n.sp. Scale bars 10 mm. (*a*) dorsal view of T-tergite AM F.102549. (*b*) ventral view of T-tergite AM F.102550, showing doublure. (*c*) dorsal view of first B-pleurotergite AM F.102551. (*d*) dorsal view of first B-pleurotergite AM F.102552. (*e*) dorsal view of first B-pleurotergite AM F.102553. (*f*) dorsal view of B-pleurotergite AM F.102554. (*g,h*) dorsal and left lateral views of second B-pleurotergite AM F.102555. (*i,j*) right lateral and dorsal views of second B-pleurotergite AM F.102556.

Figure 7. *Maldybulakia malcolmi* n.sp. Reconstruction of trunk in lateral view, showing serial variation in structures of the pleurotergum. Based mostly on AM F.102533 (Fig. 3*b–d*).

juncture between tergum and pleuron, abruptly shallowing near posterior margin. Pleurite clavate, narrowest anteriorly, projecting only slightly outside lateral edge of tergum.

Caudal tergite (Figs. 3c,g, 5i,l) with prozonite longer than on preceding B-pleurotergites, weakly convex (sag.); furrow between prozonite and metazonite shallow medially, distinctly deeper against lateral lobes; lateral lobes flat, set off by weak furrow; lateral edge of tergum forming a slender ridge that gently bulges beyond otherwise triangular outline of metazonite in dorsal view; pleural furrow not impressed; posteromedian process large, conical, triangular or elliptical in section posteriorly, gently turned up; posterolateral margin vertically inclined, gently convex.

Two small telson sclerites (Figs. 3g, 4g). Anterior telson sclerite divided into a depressed anterior band that resembles an articulating edge and a longer, convex, strongly arched (tr.), posterior band; about 40 percent width of caudal pleurotergite. Posterior telson sclerite divided by a sharp transverse furrow into short anterior band and flattened, broadly quadrate posterior plate; anterior band overlapped by anterior telson sclerite.

Dorsal surface of cuticle densely covered with honeycomb-like, shallow, polygonal pits; density of polygons the same on prozonite, stricture, and metazonite. Cuticle replaced with chalcedony, divided into a thin outer layer (0.04 mm) and thicker main layer (0.45 mm), measured in thin section; internal fabric of main layer obliterated by chalcedony aggregates. Large, densely arranged canals run through cuticle perpendicular to its surface (Fig. 8a), opening to variable-sized, rounded pits on ventral surface (Fig. 8b).

Discussion. The description of this species regards the trunk as being composed of pleurotergites, the pleurites being fused to the tergal metazonites (Fig. 7). The two components are set off by a deep groove, described as a pleural furrow. That the pleuron is actually fused to the tergum is most evident in the posterior part of the first (Fig. 3b,e) and second (Fig. 6i) pleurotergites, where they

are in direct continuity, the first pleurotergite without even a trace of a suture behind the abruptly-effaced pleural furrow. The morphology of the pleuron is frequently complicated by crushing, on occasion giving the appearance of several pleurites. In the holotype in particular, this appearance is compounded by fracture along the lateral edge of the tergum on the first three pleurotergites (Fig. 3b–d). Comparison with other specimens (Figs. 3e, 6h,i) which have an intact down-folded edge of the tergum clarifies the structures (Fig. 7). Every B-pleurotergite (even disarticulated ones) preserves the pleuron in association with the tergites, and they have characteristic morphologies on each of the four B-pleurotergites. Were the pleurites separate, unfused elements (e.g., as in centipedes) this invariant association with the tergum would not be maintained. Whether the pleural component of the pleurotergum may consist of multiple, fused pleurites is not certain. In at least some pleurotergites (Fig. 3c, particularly the fourth B-pleurotergite) the pleuron consists of a simple, elongate band without sutures, and seems likely to be composed of a single pleurite.

Serial variation in the B-pleurotergite series includes a progressive decrease in the height of the lateral edge of the tergum, and an increase in the length of the pleural furrow (short on the first B-pleurotergite versus the entire length of the fourth B-pleurotergite). The pit interpreted as a spiracle is present on a single pleurotergite, and is only distinguishable on the holotype (Fig. 3b,f). This opening is not a preservational artifact because it is entirely lined with cuticle, forming a distinct, ovate canal. The position of such a canal at the juncture between the tergum and pleuron resembles that of some tracheates (e.g., pleurostigmophoran chilopods, hexapods). The existence of only one such opening, rather than a series along the trunk, does not negate identity as a spiracle, although it is peculiar given the substantial size of *Maldybulakia*; presence of only one or two spiracles in extant myriapods (e.g., Symphyla and some lithobiomorphs) is reasonably regarded as linked to minute body size. To consider alternative interpretations, the tube in *Maldybulakia* is situated in the appropriate position for an ozopore, the
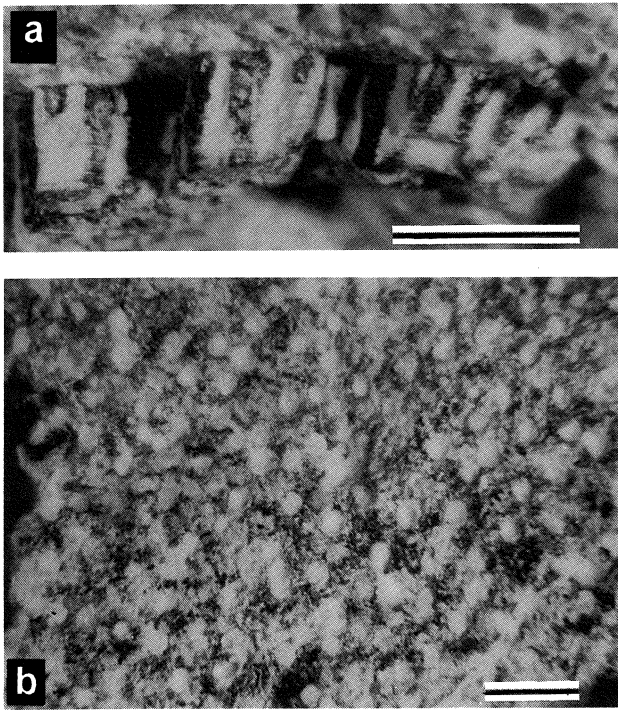
Figure 8. *Maldybulakia malcolmi* n.sp. Scale bars 1 mm. (*a,b*) T-tergite AM F.102581. (*a*) dorsoventral section through exoskeleton on lateral part of metazonite, ventral surface down, anterior to left, showing large canals filled with clay and silt matrix (light colour, versus darker exoskeleton). (*b*) ventral surface of exoskeleton on lateral part of metazonite, showing openings of canals as large, round pores filled with light-coloured matrix.

opening for the repugnatorial glands in helminthomorph diplopods (see Shear, 1993: fig. 2 for a fossil example). Such an identity is considered less likely than a spiracle because an ozopore would be expected to be smaller, whereas myriapod spiracles can be very large (e.g., in scolopendrid chilopods; see J.G.E. Lewis *et al.*, 1996).

A lesser degree of serial variation within the two trunk tagmata is a character uniting *Maldybulakia malcolmi* and *M. mirabilis* to the exclusion of *M. angusi*. Suppressed variation is, however, presumed to be a primitive condition (with outgroup comparison to other myriapods), and not indicative of a sister species relationship between *M. malcolmi* and *M. mirabilis*. Given that *M. malcolmi* has only four B-pleurotergites (not counting the caudal pleurotergite), it is likely that the four articulated B-pleurotergites in the holotype of the very similar *M. mirabilis* (Tesakov & Alekseev, 1992: fig. 1a,b) represent the entire B-pleurotergite series. *Maldybulakia malcolmi* is distinguished from *M. mirabilis* by its pronounced transverse furrow on the T-tergite (as opposed to a pair of chevron-shaped, longitudinally aligned furrows in *M. mirabilis*), much finer granulation on the tergites, shallow (versus deep) furrows setting off the lateral lobes on the caudal pleurotergite, and a less spinose median projection on that sclerite.

Maldybulakia angusi n.sp.

Figs. 9–12

Maldybulakia new species 2 Edgecombe, 1998: fig. 2.

Etymology. For Angus Young.

Diagnosis. *Maldybulakia* with considerable serial variation in B-pleurotergites; posteromedian spine present on some tergites of anterior and posterior trunk tagmata; very long, posterolaterally-directed paratergal spines on most bilobate trunk pleurotergites; caudal tergite bearing long median spine; many tergites bearing robust tuberculation.

Types. HOLOTYPE trunk pleurotergite (B-pleurotergite) AM F.102565 (Fig. 10a); length 24.6 mm. Sugarloaf Creek Formation (Lochkovian or Pragian), near Three Oaks, Taemas district, New South Wales (35°04'S 148°51'E). PARATYPES AM F.102557–102564, 102566–102580, from type locality.

Description. T-tergites (Fig. 9a–h) with length 32–39 percent of width. Anterior part of prozonite a flattened, boomerang-shaped surface that slopes forwards and lengthens medially to about 50 percent the length of the prozonite; rear edge of this surface forms a crest-like rise above posterior part of prozonite; well preserved specimens show dense, scaly sculpture (Fig. 9c). Posterior part of prozonite with pair of moderately wide longitudinal furrows varying from faint to distinctly incised. Stricture moderately deep, gently convex forward medially, recurved distally around elliptical or teardrop shaped lateral lobes. Metazonite 70–86 percent length of prozonite. Postero-median spine absent or short. Posterior margin approximately transverse between lobate processes which vary from broad and rounded to angular to short, slender spines. Tuberculation usually strong, rarely faint, sometimes more prominent on prozonite than on metazonite. Doublure (Fig. 9a) as described for *M. malcolmi*.

Ring tergite (Fig. 9i) as for *M. malcolmi*.

B-pleurotergites up to 24.6 mm in length. Anteriormost B-pleurotergite (Fig. 10b,f,h,i) distinguished by relatively short, wide proportions and short, knob-like projections at anterolateral edge of prozonite as seen in this pleurotergite only in *M. malcolmi*. Prozonite about 25 percent length of tergite, with cuticular sculpture of dense polygonal depressions amidst a network of low ridges (Fig. 10i). Lateral lobes of metazonite teardrop shaped, outer margin rounded, strongly inflated, with steep lateral and anterior edges encircled by well-impressed furrow. Posteromedian spine on median lobe of metazonite short, conical, and posterodorsally directed or absent. Paratergal spines long, strongly divergent (directed back 40–50 degrees from transverse line), largest known specimen 88 mm wide across spines (extrapolated from one half); inferred width across spines up to approximately 115 mm (based on size relative to largest known B-pleurotergites); dorsal and
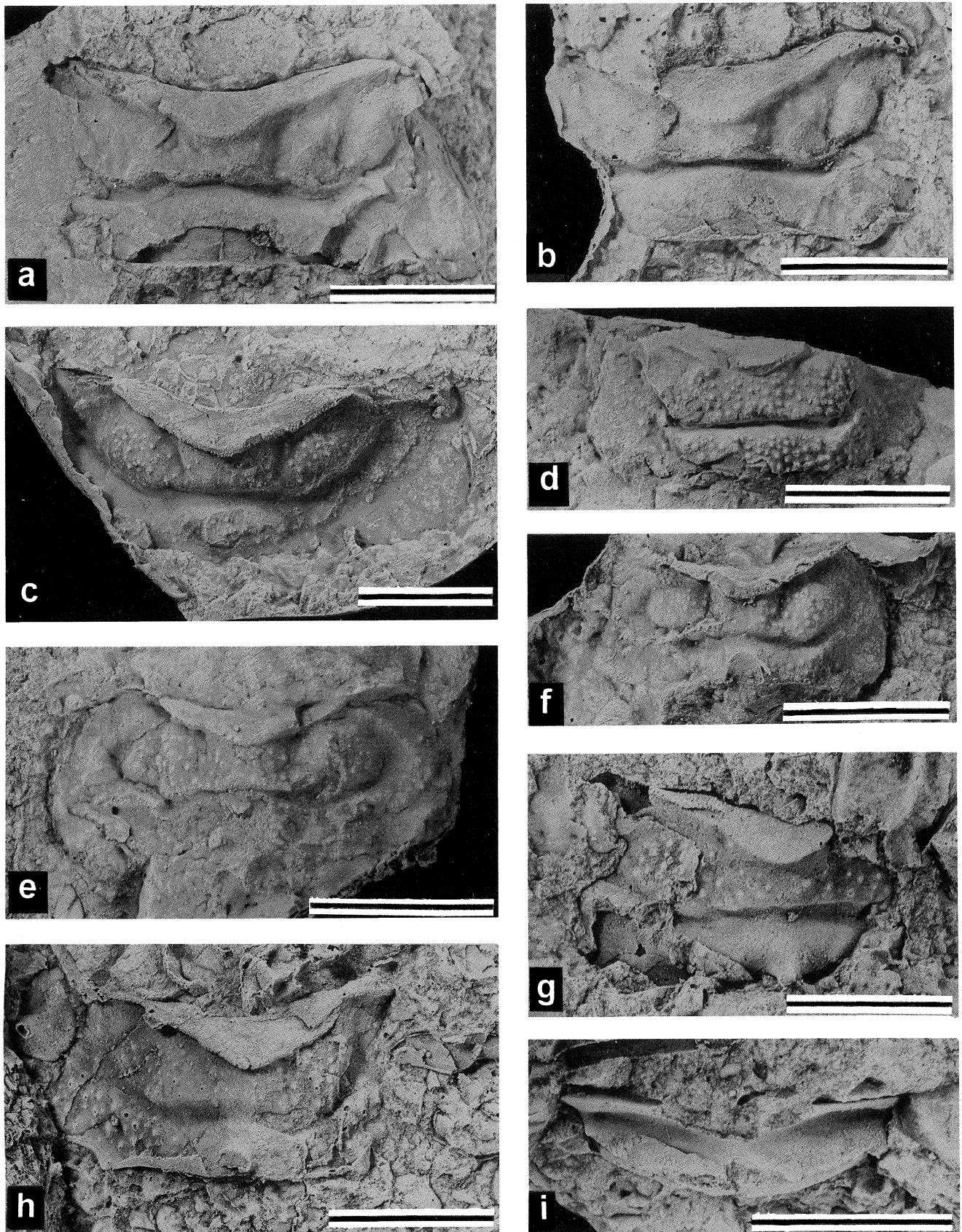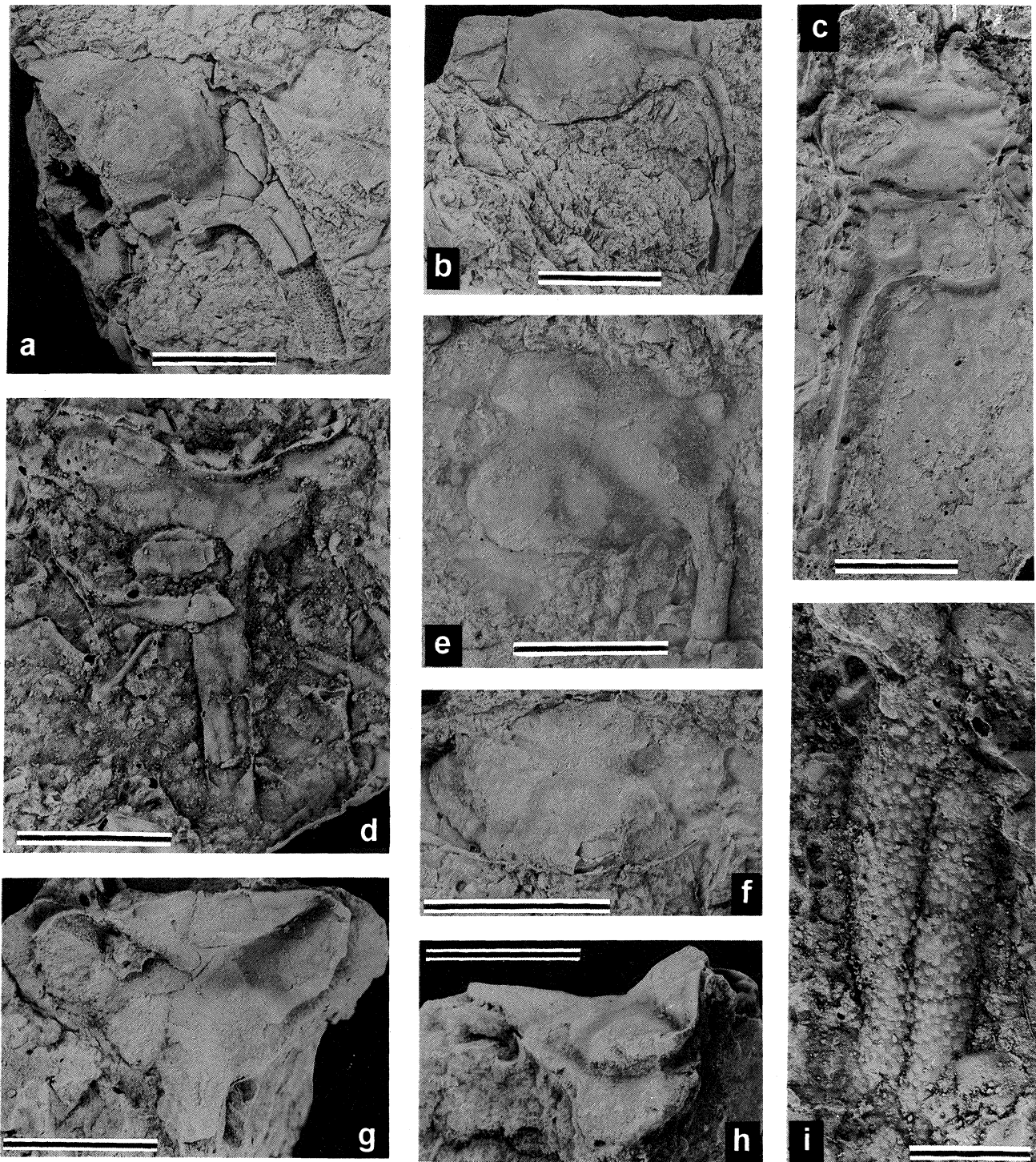
Figure 9. *Maldybulakia angusi* n.sp. Scale bars 10 mm. Latex casts from external moulds except *a, d, e, i*, internal moulds. (*a,b*) dorsal views of T-tergite AM F.102557b and AM F.102557a. Note doublure in *a*, with median flange and expanded posterolateral portion. (*c*) dorsal view of T-tergite AM F.102558. (*d*) dorsal view of T-tergite AM F.102559. (*e*) dorsal view of T-tergite AM F.102560. (*f*) dorsal view of T-tergite AM F.102561. (*g*) dorsal view of T-tergite AM F.102562. (*h*) dorsal view of T-tergite AM F.102563. (*i*) anterodorsal view of ring tergite AM F.102564.
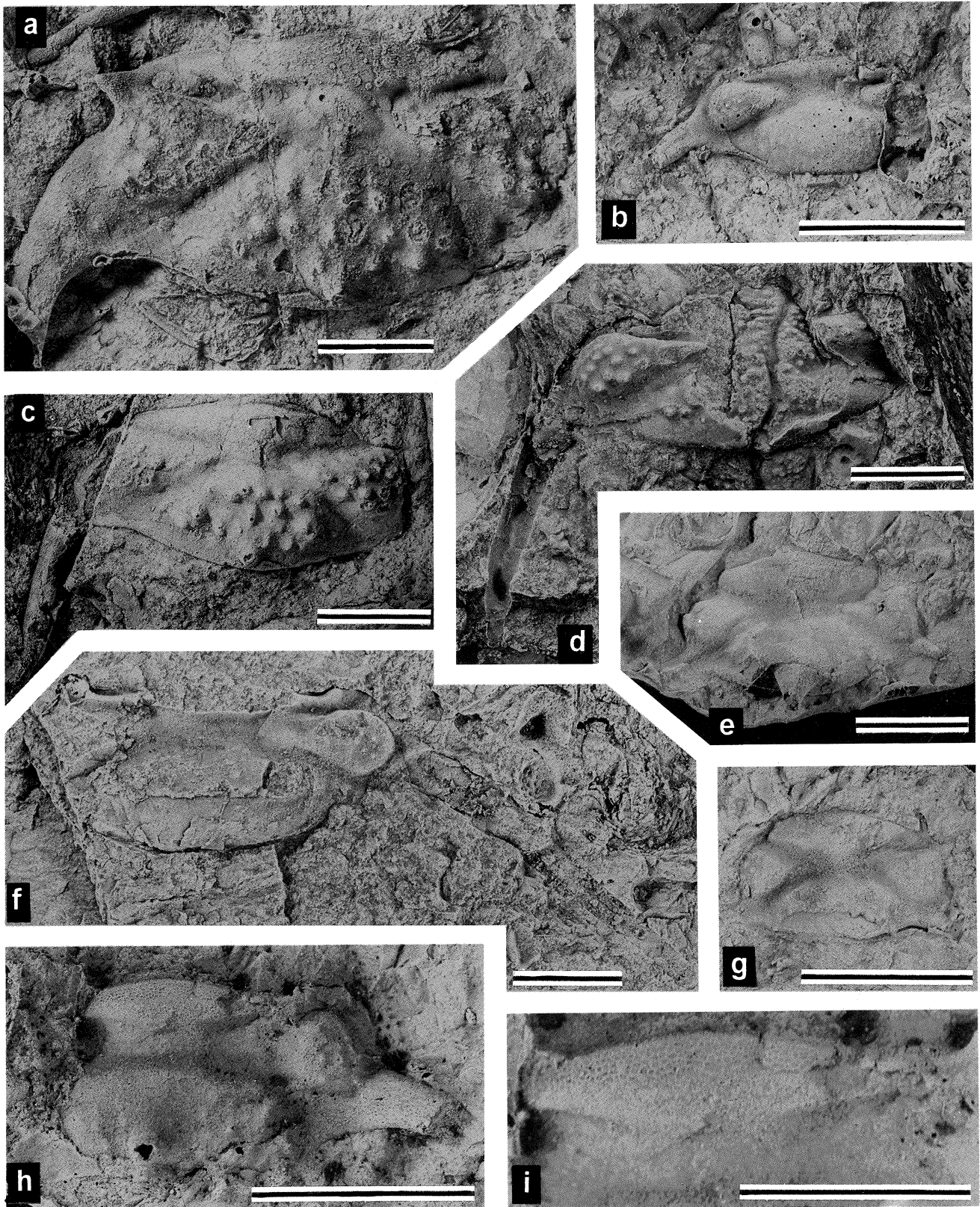
Figure 10. *Maldybulakia angusi* n.sp. Scale bars 10 mm, except *b*, 5 mm. Latex casts from external moulds except *d, f, g*, internal moulds. (*a*) dorsal view of holotype B-pleurotergite AM F.102565. (*b*) dorsal view of first B-pleurotergite AM F.102566. (*c*) dorsal view of B-pleurotergite AM F.102567. (*d*) dorsal view of B-pleurotergite AM F.102568. (*e*) dorsal view of B-pleurotergite AM F.102569. (*f*) dorsal view of first B-pleurotergite AM F.102570. (*g*) dorsal view of B-pleurotergite AM F.102571. (*h,i*) dorsal views of first B-pleurotergite AM F.102572. (*i*) detail showing polygonal sculpture on prozonite.

Figure 11. *Maldybulakia angusi* n.sp. Scale bars 10 mm except *i*, 5 mm. Latex casts from external moulds except *a, b, g, h*, internal moulds. (*a*) dorsal view of posteriormost B-pleurotergite AM F.102573. (*b*) dorsal view of posteriormost B-pleurotergite AM F.102574. (*c*) dorsal view of B-pleurotergite AM F.102575, with ventral view of another B-pleurotergite. (*d*) dorsal view of caudal pleurotergite AM F.102576. (*e*) dorsal view of posteriormost B-pleurotergite AM F.102577. (*f*) dorsal view of B-pleurotergite AM F.102578. (*g,h*) dorsal and right lateral views of caudal pleurotergite AM F.102579. (*i*) dorsal view of spine AM F.102580, probably paratergal spine of posteriormost B-pleurotergite.

ventral surfaces of spine bisected by shallow furrow along all but proximalmost part. Small and moderate sized tubercles abundant on lateral and median lobes of metazonite, somewhat stronger on lateral lobes.

B-pleurotergite of uncertain position (Fig. 10e,g) with short, posterolaterally directed paratergal spines. Prozonite relatively elongate, about 35 percent length of tergite. Short anterolaterally-directed, conical process at anterolateral corner of metazonite. Posteromedian spine on median lobe of metazonite varying from absent (Fig. 10g) to strong (Fig. 10e), variably more posteriorly- or dorsally-directed. Tubercles on lateral lobes of metazonite faint to moderately strong; tubercles weaker on median lobe, sometimes obscure.

B-pleurotergites (probably second or third) from middle of tagma (Fig. 10a,c,d) with prozonite about 25 percent length of tergite. Anterolateral corner of pleurotergite extended as a short angulation that gently rises distally. Robust tubercles usually present, abundant on lateral and median lobes of metazonite. Polygonal sculpture grading into transversely elongate, scaly sculpture along anterior margin of prozonite and posterior margin of metazonite and fine tubercles on paratergal spines. Lateral lobes relatively longer than on first B-pleurotergite, less inflated. Paratergal spine long, more posteriorly directed than that on first B-pleurotergite, nearly straight or gently curved for much of length, with slightly stronger posterior curvature distally; spine flattened proximally, more rounded near tip; rounded, ventrally directed process on posterior margin at base of paratergal spine.

Posteriormost B-pleurotergite (Fig. 11a,b,e) with prozonite up to 35 percent length of tergite. Anterolateral corner of metazonite forming a blunt, gently swollen angulation, separated from lateral lobe by shallow furrow. Median lobe relatively narrow, raised central part set off by pair of shallow longitudinal furrows. Tuberculation of median and lateral lobes subdued in most specimens. Paratergal spine long, approximately straight, weakly directed inwards, markedly flattened in section along entire length; longitudinal furrow on dorsal and ventral surfaces of spine deeper than on other pleurotergites, narrow but well-incised; spines with sculpture of small, crowded tubercles.

Caudal pleurotergite (Fig. 11d,?f,g,h) with teardrop shaped or subtriangular lateral lobes; lobes substantially inflated, tuberculate, set off from median lobe by furrows of similar depth to or shallower than those on other B-pleurotergites; outer edge of lateral lobes steep, set off from more gently sloping outer border by shallow furrow. Lateral margin strongly convex outward. Median spine gently upturned, of about even width along entire known length, bisected by shallow longitudinal furrow.

Telson sclerites unknown.

Discussion. Although *Maldybulakia angusi* is distinguished from its congenerics by numerous autapomorphies, a separate genus cannot be upheld unless reasonable synapomorphies are identified for *M. malcolmi* and *M. mirabilis*. As noted above, most of the similarities between the latter pair of species are probably symplesiomorphies
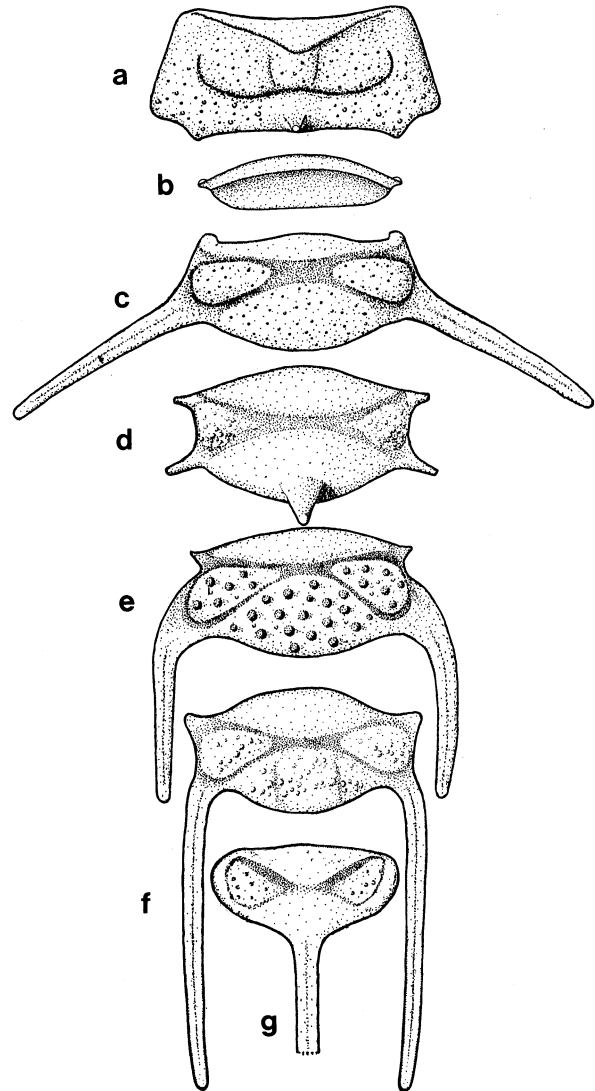
Figure 12. *Maldybulakia angusi* n.sp. Reconstructions of discrete morphological classes of trunk sclerites, indicating minimal number of tergites. (*a*) T-tergite. (*b*) ring tergite. (*c*) inferred anteriormost B-pleurotergite. Median spine on metazonite sometimes present. (*d*) B-pleurotergite of uncertain position. Presence of posteromedian spine is variable. (*e*) B-pleurotergite from middle part of tagma. (*f*) inferred posteriormost B-pleurotergite. (*g*) caudal pleurotergite.

and, if so, restricting *Maldybulakia* to these two species would recognise a paraphyletic group. In fact, certain characters might instead serve to unite the two Australian species to the exclusion of *M. mirabilis*. The flattened, sloping anterior scarp on the prozonite of the T-tergite is a distinctive modification shared by these two species but appears less developed in *M. mirabilis* (Tesakov & Alekseev, 1992: fig. 1g).

Considerable variability is observed in the strength of tuberculation on T-tergites as well as B-pleurotergites in *M. angusi*. Some specimens have only weak expression of tubercles (Figs. 9b, 10e, 11e), whereas most show them to

be more distinct or pronounced. Because of continuous gradation in tuberculation in otherwise similar tergites this is not regarded as an important criterion for distinguishing different pleurotergites. Presence or absence of a median spine on the metazonite is a feature that varies between tergites that are otherwise similar. This is observed on the T-tergites (compare Fig. 9b and 9g) as well as on various B-tergites that appear to represent the same position (e.g., Fig. 10b versus 10h; Fig. 10e versus 10g). Presence or absence of a median spine is considered to vary between individuals.

The antero-posterior position of B-pleurotergites can be largely determined based on the progressively more posterior direction of the paratergal spines on posterior segments (as observed analogously in other spiny myriapods, such as euphoberiid diplopods). Consistent with this line of evidence are other correspondences with known positions in *M. malcolmi*: the anterior pleurotergites are shorter relative to their width, and the anteriormost B-pleurotergite is distinguished by its anterolateral processes on the prozonite (Figs. 10f, 12c; compare with Fig. 6d). The posteriormost B-pleurotergite (immediately anterior to the caudal pleurotergite) is identified by its posteriorly-directed paratergal spines and relatively long median lobe on the metazonite (Figs. 11a,b,e, 12f).

Given the above considerations, the minimal number of sclerites in the trunk of *Maldybulakia angusi* is depicted in Fig. 12. The B-pleurotergites can be sorted into four morphological groups (Fig. 12c–f), excluding the caudal pleurotergite (Fig. 12g), thus allowing that the number of pleurotergites may be identical to that in *M. malcolmi* and, apparently, *M. mirabilis*. The position of the B-pleurotergite reconstructed in Fig. 12d is uncertain, constrained only by the likelihood that those shown in Figs. 12c and 12f are the first and last in the series based on their morphological correspondences to *M. malcolmi*. The specimen in Fig. 11f conforms to a caudal pleurotergite except for the absence of a median spine, although this is possibly due to breakage. Its lensoid outline (i.e., absence of paratergal spines) with tightly curved lateral margins is similar to caudal pleurotergites that have a median spine (Fig. 11g). In *M. malcolmi*, this specimen is most comparable to a lensoid specimen regarded as a caudal pleurotergite (Fig. 5c).

The best preserved external moulds display a cuticular sculpture of dense polygonal depressions amidst a maze of low ridges (Fig. 10i), as is also seen in *M. malcolmi* (Fig. 5j,k) and *M. mirabilis* (Tesakov & Alekseev, 1992: fig. 1i). This character is, accordingly, general for *Maldybulakia*.

Phylogenetic affinities

In the absence of information on cephalic structure, appendages, position of the gonopore, and genital morphology, the position of *Maldybulakia* within the Arthropoda is contentious. The discussion below outlines evidence in favour of myriapod affinities, and is followed by evidence that weakens the most likely alternative, a relationship to Crustacea.

Myriapoda. Tesakov & Alekseev (1992) recognised *Maldybulakia* as myriapod-like based upon the relative serial homonymy of the trunk tergites of *M. mirabilis* and the interpretation that the B-pleurotergites correspond to diplosomites. As noted above, I have accepted that the T-tergite and B-pleurotergites of *Maldybulakia* are similar in their construction to diplo(pleuro)tergites.

Evidence from serial variation in the trunk must now consider the fact that *Maldybulakia* possesses two well-differentiated trunk tagmata, as well as the fact that some species (such as *M. angusi*) display considerable serial variation within the two tagmata (this, however, very likely being specialised relative to the more homonymous condition of *M. malcolmi*). The extent of tagmosis in *Maldybulakia* exceeds that known for any myriapod, living or fossil. However, being a primitive attribute of atelocerates (or, for that matter, arthropods), a homonymous trunk is not a shared derived character of myriapods and does not provide positive evidence for group membership. The tagmosis of *Maldybulakia* could only be used to negate myriapod affinities if it can be shown to be shared with some other group of arthropods. There is little compelling evidence for drawing parallels between the two trunk tagmata of *Maldybulakia* and, for example, the thorax and abdomen of Hexapoda or pereion and pleon of Crustacea.

Myriapoda has been repeatedly dismissed as a paraphyletic grade group (Dohle, 1980, 1997; Kraus, 1997; Kraus & Kraus, 1994, 1996), although this interpretation conflicts with molecular studies that support myriapod monophyly (Regier & Shultz, 1997; Wheeler, 1998). Only two characters are repeatedly cited by Kraus (e.g., 1997) to unite the Progoneata with Hexapoda to the exclusion of Chilopoda and both of these are contentious. One, a maxillary plate with the ventral side of the mouth bordered by the second maxillae, is disputed by embryological, innervation, and muscular evidence that pauropods and diplopods lack second maxillae (Dohle, 1997, contra the claims of Kraus & Kraus, 1994, 1996 based on external morphology). The second, coxal vesicles and styli, exhibits considerable homoplasy (e.g., absences of both in many diplopods; absence of styli in pauropods and Ellipura) and homologies are dubious. Notably, eversible vesicles in some groups (e.g., the pair of sacs at the end of the *Ventraltubus* in Ellipura) are of appendicular nature, whereas those of others are extra-appendicular (Matsuda, 1976). The latter include the vesicles of Symphyla, which arise on the so-called "ventral organs" associated with gangliar formation (Tiegs, 1940), these being segmental thickenings of the embryonic ventral ectoderm. The paraphyly hypothesis denies that any synapomorphies can be identified to defend membership in "Myriapoda"—the defining characters of the group are more general, basal for Atelocerata. Incomplete preservation does not permit most of the putative atelocerate apomorphies to be checked in *Maldybulakia*: such features include uniramous limbs, Malpighian tubules, suppression of the second cephalic somite, a cephalic fat body, loss of the mandibular palp, molar hooks on the mandible, Tömösváry organs, a single pretarsal (depressor) muscle, and anterior tentorial arms. Characters that have alternatively been used to define a

monophyletic Myriapoda, such as the "swinging" tentorium (Manton, 1964), a mandibular gnathal lobe, and loss of the median eyes, will rarely be known from fossils, and likewise cannot be checked in *Maldybulakia*.

In spite of the preponderance of missing data, the presence of tracheae is inferred based on the interpretation of openings in the pleural furrow in *M. malcolmi* as spiracles. Tracheae have traditionally been regarded as a synapomorphy for atelocerates, although some workers have cautioned that the variable position of spiracles may imply multiple origins of a tracheal system (Kraus & Kraus, 1996; Kristensen, 1991). The hypothesis of multiple origins of tracheae has been taken to an extreme by Dohle (1997) and Kraus (1997), both of whom regard a tracheal system evolving independently at least four to six times in Atelocerata. The interpretation of the lateral exoskeletal component as pleural also implies atelocerate affinities for *Maldybulakia*. Manton (1979) recognised that myriapods and hexapods shared pleural structures not shared with other arthropods, including the development of pleurites.

At a less general level, a trunk composed of diplotergites suggests affinities to various subgroups of myriapods, notably Diplopoda, Arthropleuridea, and Kampecarida. Although representing three classes (Shear, 1997), available evidence suggests these taxa are closely related, the latter two extinct classes apparently allied to the Dignatha. Comparison with *Kampecaris* Page, 1856 (Přídolí-early Pragian, Great Britain) reveals some similarities that may suggest a relationship. A detailed exposition on the morphology, affinities, and habits of *Kampecaris* was undertaken in an unpublished thesis by Almond (1986), partly summarised by Shear (1997). *Maldybulakia* and Kampecarida share a few distinctive characters that are also shared by millipedes. These include a heavily-calcified tergal exoskeleton and a posterior trunk with posteriorly-overlapping diplotergites (diplosegment-ation in *Kampecaris* is confirmed, the legs being known). The sternum of *Kampecaris* was described by Almond as poorly known, in contrast to a strongly calcified tergum with ball-and-socket intertergal articulations, which is similar to the case in *Maldybulakia* (for which the lack of sternites—compared to hundreds of tergites—is strong evidence for their lack of mineralisation). *Kampecaris* shares a few other characters with millipedes that cannot at present be checked in *Maldybulakia* (e.g., limbs articulating wholly with the sternites; a long femur and simple, pointed tarsus). Almond (1986) excluded *Kampecaris* from the Diplopoda, suggesting a high-level taxonomic separation. His basis for this was several novel features of *Kampecaris* that are not shared by any diplopod. These include a subdivision of the head by a transverse suture or articulation into two subunits, an inflated caudal tagma, and the tergal cuticle perforated by sizable, closely spaced canals. *Maldybulakia malcolmi* likewise displays large, densely arranged pores on the cuticular surface (Fig. 8b) that run through the cuticle as vertical canals (Fig. 8a), while Tesakov & Alekseev (1992: 22) described similar pores in *M. mirabilis*. It is possible that the pore/canal structure of the cuticle in *Maldybulakia* and Kampecarida

is a shared, derived character of these two groups of mid-Palaeozoic taxa. It is doubtful that these large canals are the homologues of the gland ducts in extant myriapod cuticles (Blower, 1951), which are much finer structures.

Maldybulakia is readily distinguished from *Kampecaris* by its uniquely derived characters (notably differentiation of trapezoidal and bilobate pleurotergites) and the lack of certain autapomorphies of *Kampecaris* (e.g., the inflated caudal tagma). These do, not, however, negate the possibility of a close relationship between them. Almond (1985) interpreted the tail plate of *Kampecaris* as a modified diplotergite, an interpretation that also applies to the caudal pleurotergite of *Maldybulakia*.

There is little evidence at hand to ally *Maldybulakia* closer to diplopods than to *Kampecaris*. The association of pleural elements with the metazonites in varying degrees of coalescence to form pleurotergites was noted by Hoffman (1969: 586) as characteristic of nearly all helminthomorph diplopods, and regarded by Enghoff (1984) as a synapomorphy of eugnathan diplopods that evolved independently in platydesmids. Homology of the metazonal pleurotergites in millipedes and *Maldybulakia* must be regarded with suspicion given the relatively derived position of the Eugnatha within the Diplopoda. The condition of pleurites in Kampecarida is uncertain. Almond (1986) noted the absence of free pleurites but allowed that they could be fused to the tergum to form pleurotergites. Similarities to large, spiny millipedes, notably Carboniferous euphoberiids, are very likely superficial. Euphoberiids such as *Myriacantherpestes* Burke, 1979, do not have trunk tagmosis (versus the marked separation of the trapezoidal and bilobate tergites in *Maldybulakia*). The long-spined bilobate pleurotergites of *Maldybulakia angusi* display a superficial resemblance to *Myriacantherpestes* that is less strong in the other species of *Maldybulakia*. Details of tergite construction, however, fail to support an especially close relationship. Likewise, it is not possible to identify any features shared by *Maldybulakia* and Arthropleuridea that are not also shared with Kampecarida and Diplopoda. The simple overlap of the tergites in arthropleurids differs strikingly from overlap on the prozonite of *Maldybulakia* and, as noted above for diplopods, arthropleurids do not display trunk tagmosis.

Crustacea. The plasticity of exoskeletal morphology observed within the malacostracan crustaceans, notably in such groups as Isopoda, suggests the possibility that *Maldybulakia* could be accommodated within the Malacostraca. It is considered unlikely that *Maldybulakia* could belong to any malacostracan (or indeed crustacean) group with a carapace, as all sites preserving *Maldybulakia* lack any carapace remains (the same argument would apply to chelicerate assignments, based on the absence of a prosoma). Given the apparently different taphonomic histories at each of the three sites it seems exceedingly improbable that all three would preserve abdominal (or opisthosomal) tergites in abundance without a single carapace (or prosoma). Evidence has already been given for why the T-tergite is regarded as a trunk tergite rather than as a cephalic shield.

The small number of tergites in *Maldybulakia* conflicts with the post-cephalic segmentation of malacostracans, which have eight thoracic somites (pereonites) and seven abdominal somites (pleonites). Specimens such as the holotype of *M. malcolmi* are regarded as posteriorly complete (the caudal pleurotergite and telson sclerites comprising a typical arthropod body termination). As such, a malacostracan model that accounts for the observed shortfall of segments by positing unpreserved pleonites is unacceptable. In order to accommodate the post-cephalic segmentation of malacostracans in *Maldybulakia* it is necessary to make such conjectures as the caudal pleurotergite incorporating the entire pleon (which is possible, by comparison to the pleotelsons of some isopods, although atypical), in which case the putative pereon is still too short, even if the ring-like tergite is considered a separate pereonite.

A malacostracan crustacean hypothesis might interpret the lateral opening in the third B-pleurotergite as a gonopore. Although accounting for the singularity of this structure, it is weakened by the fact that malacostracan gonopores are typically associated with the coxae or the sternite medial to the coxae, rather than the pleuron. It also requires that this segment be the sixth (female) or eighth (male) pereonite, which puts severe constraints on the more posterior tergites (demanding that they incorporate the entire pleon if not also part of the pereon). In summary, a myriapod interpretation incorporates more positive character evidence and conflicts with less evidence than a crustacean interpretation.

Euthycarcinoidea. A reviewer of this paper encouraged a comparison between *Maldybulakia* and the Euthycarcinoidea. Euthycarcinoids, known from ten aquatic species of Silurian to Triassic age, have been assigned to nearly every major group within the Arthropoda (see Schram & Rolfe [1982] for an overview of euthycarcinoid morphology). The most recent assessment of myriapod fossils (Shear, 1997) concluded that atelocerate affinities for euthycarcinoids can neither be ruled out nor strongly supported. A close relationship between euthycarcinoids and *Maldybulakia* is dubious given that trunk tagmosis in the former group involves a wide preabdomen and a narrow postabdomen. *Maldybulakia* clearly lacks this style of tagmosis. Furthermore, most euthycarcinoids have serially variable lengths of the preabdominal tergites, these corresponding to varying numbers of sternites and appendages, and homologues of the pleurites of *Maldybulakia* are absent. A comparison could, however, be made between the specialisations of the anterior tergites of the trunk in the two groups. Euthycarcinoids have an enlarged first preabdominal tergite followed by a reduced haplotergite, with the apparently corresponding positions in *Maldybulakia* being the T-tergite and ring tergite. At present, no other potentially synapomorphic characters are identified to support a particularly close relationship between *Maldybulakia* and Euthycarcinoidea.

References

Allison, P.A., 1986. Soft bodied animals in the fossil record: the role of decay in fragmentation during transport. *Geology* 14: 979–981.

Almond, J.E., 1985. The Silurian-Devonian fossil record of the Myriapoda. *Philosophical Transactions of the Royal Society of London, B. Biological Sciences* 309: 227–237.

Almond, J.E., 1986. *Studies on Palaeozoic Arthropoda.* Unpublished Ph.D. thesis, University of Cambridge.

Bergström, J., 1979. Morphology of fossil arthropods as a guide to phylogenetic relationships. In *Arthropod Phylogeny*, ed. A.P. Gupta, pp. 3–56. New York: Van Nostrand Reinhold.

Blower, G., 1951. A comparative study of the chilopod and diplopod cuticle. *Quarterly Journal of Microscopical Science* 92: 141–161.

Brauckmann, C., E. Gröning & M. Thiele-Bourcier, 1997. Kopf- und Schwanz-Region von *Arthropleura armata* Jordan, 1854 (Arthropoda; Ober-Karbon). *Geologica et Palaeontologica* 31: 179–192.

Briggs, D.E.G., & J.E. Almond, 1994. The arthropleurids from the Stephanian (Late Carboniferous) of Montceau-les-Mines (Massif Central—France). In *Quand le Massif Central Était sous l'équateur: Un Écosystème Carbonifère á Montceau-les-Mines*, eds. C. Poplin & D. Helyer, pp. 127–135. Paris: Mémoires de la Section des Sciences 12, Éditions du Comité des Travaux Historiques et Scientifiques.

Burke, J.J., 1979. A new millipede genus, *Myriacantherpestes* (Diplopoda, Archipolypoda) and a new species, *Myriacantherpestes bradebirksi*, from the English Coal Measures. *Kirtlandia* 30: 1–24.

Dohle, W., 1980. Sind die Myriapoden eine monophyletische Gruppe? Eine Diskussion der Verwandtschaftsbeziehungen der Antennaten. *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg* 23: 45–104.

Dohle, W., 1997. Myriapod-insect relationships as opposed to an insect-crustacean sister group relationship. In *Arthropod Relationships*, eds. R.A. Fortey & R.H. Thomas, pp. 305–315. London: Chapman & Hall.

Edgecombe, G.D., 1998. Devonian terrestrial arthropods from Gondwana. *Nature* 394: 172–175.

Enghoff, H., 1984. Phylogeny of millipedes—a cladistic analysis. *Zeitschrift für zoologische Systematik und Evolutionsforschung* 22: 8–26.

Enghoff, H., 1990. The ground-plan of chilognathan millipedes (external morphology). In *Proceedings of the 7th International Congress of Myriapodology*, ed. A. Minelli, pp. 1–21. Leiden: E.J. Brill.

Fergusson, C.L., R.A.F. Cas, W.J. Collins, G.Y. Craig, K.A.W. Crook, C.McA. Powell, P.A. Scott & G.C. Young, 1979. The Upper Devonian Boyd Volcanic Complex, Eden, New South Wales. *Journal of the Geological Society of Australia* 26: 87–105.

Heymons, R., 1901. Die Entwicklungsgeschichte der Scolopender. *Zoologica, Stuttgart* 13: 1–244.

Hoffman, R.L., 1969. Myriapoda, exclusive of Insecta. In *Treatise on Invertebrate Paleontology, Part R, Arthropoda 4*, ed. R.C. Moore, pp. 572–606. Boulder: Geological Society of America and University of Kansas Press.

Kraus, O., 1997. Phylogenetic relationships between higher taxa of tracheate arthropods. In *Arthropod Relationships*, eds. R.A. Fortey & R.H. Thomas, pp. 295–303. London: Chapman & Hall.

Kraus, O., & M. Kraus, 1994. Phylogenetic system of the Tracheata (Mandibulata): on "Myriapoda"—Insecta interrelationships, phylogenetic age and primary ecological niches. *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg* 34: 5–31.

Kraus, O., & M. Kraus, 1996. On myriapod / insect inter-relationships. In *Acta Myriapodologica*, eds. J.-J. Geoffroy, J.-P. Mauriès & M. Nguyen Duy-Jacquemin, pp. 283–290. Paris: Mémoires du Museum National d'Histoire Naturelle, Tome 169.

Kristensen, N.P., 1991. Phylogeny of extant hexapods. In *The Insects of Australia*, ed. CSIRO, pp. 125–140. Melbourne: University of Melbourne Press.

Lewis, J.G.E., T.J. Hill & G.E. Wakley, 1996. The structure and possible function of the spiracles of some Scolopendridae (Chilopoda, Scolopendromorpha). In *Acta Myriapodologica*, eds. J.-J. Geoffroy, J.-P. Mauriès & M. Nguyen Duy-Jacquemin, pp. 441–449. Paris: Mémoires du Muséum National d'Histoire Naturelle, Tome 169.

Lewis, P.C., R.A. Glen, G.W. Pratt & I. Clarke, 1994. Explanatory notes, Bega-Mallacoota 1:250 000 geological sheet. Geological Survey of New South Wales.

Manton, S.M., 1964. Mandibular mechanisms and the evolution of arthropods. *Philosophical Transactions of the Royal Society of London, B. Biological Sciences* 247: 1–183.

Manton, S.M., 1979. Uniramian evolution with particular reference to the pleuron. In *Myriapod Biology*, ed. M. Camatini, pp. 317–343. London: Academic Press.

Matsuda, R., 1976. *Morphology and Evolution of the Insect Abdomen*. Oxford: Pergamon Press.

Mawson, R., J.A. Talent, G.A. Brock & M.J. Engelbretsen, 1992. Condont data in relation to sequences about the Pragian-Emsian boundary (Early Devonian) in southeastern Australia. *Proceedings of the Royal Society of Victoria* 104: 23–56.

Mikulic, D.G., D.E.G. Briggs & J. Klussendorf, 1985a. A Silurian soft-bodied biota. *Science* 228: 715–717.

Mikulic, D.G., D.E.G. Briggs & J. Klussendorf, 1985b. A new exceptionally preserved biota from the Lower Silurian of Wisconsin, U.S.A. *Philosophical Transactions of the Royal Society of London, B. Biological Sciences* 311: 75–85.

Owen, M., & D. Wyborn, 1979. Geology and geochemistry of the Tantangara and Brindabella area. *Bureau of Mineral Resources, Geology and Geophysics, Bulletin* 204: 1–52.

Page, D., 1856. *Advanced Textbook of Geology*, first edition. Edinburgh: Blackwood & Sons.

Pocock, R.I., 1894. Chilopoda, Symphyla, and Diplopoda from the Malay Archipelago. In *Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien* volume 3, ed. M. Weber, pp. 307–404.

Regier, J.C., & J.W. Shultz, 1997. Molecular phylogeny of the major arthropod groups indicates polyphyly of crustaceans and a new hypothesis for the origin of hexapods. *Molecular Biology and Evolution* 14: 902–913.

Schram, F.R., & W.D.I. Rolfe, 1982. New euthycarcinoid arthropods from the Upper Pennsylvanian of France and Illinois. *Journal of Paleontology* 56: 1434–1450.

Shear, W.A., 1990. Silurian-Devonian terrestrial arthropods. In *Arthropod Paleobiology. Short Courses in Paleontology, 3*, ed. D.G. Mikulic, pp. 197–213. Knoxville: Paleontological Society.

Shear, W.A., 1993. Myriapodous arthropods from the Viséan of East Kirkton, West Lothian, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 84: 309–316.

Shear, W.A., 1997. The fossil record of the Myriapoda. In *Arthropod Relationships*, eds. R.A. Fortey & R.H. Thomas, pp. 211–219. London: Chapman & Hall.

Shear, W.A., & P.M. Bonamo, 1988. Devonobiomorpha, a new order of centipeds (Chilopoda) from the Middle Devonian of Gilboa, New York State, USA, and the phylogeny of centiped orders. *American Museum Novitates* 2967: 1–30.

Shear, W.A., P.G. Gensel & A.J. Jeram, 1996. Fossils of large terrestrial arthropods from the Lower Devonian of Canada. *Nature* 384: 555–557.

Shear, W.A., A.J. Jeram & P.A. Selden, 1998. Centiped legs (Arthropoda, Chilopoda, Scutigeromorpha) from the Silurian and Devonian of Britain and the Devonian of North America. *American Museum Novitates* 3231: 1–16.

Shear, W.A., & P.A. Selden, 1995. *Eoarthropleura* (Arthropoda, Arthropleurida) from the Silurian of Britain and the Devonian of North America. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 196: 347–375.

Siebold, C.T.E., & H. Stannius, 1845. Lehrbuch der vergleichenden Anatomie der wirbellosen Tiere. Berlin: Veit.

Tesakov, A.S., & A.S. Alekseev, 1992. Myriapod-like arthropods from the Lower Devonian of central Kazakhstan. *Paleontological Journal* 26: 18–23.

Tesakov, A.S., & A.S. Alekseev, 1998. *Maldybulakia*—new name for *Lophodesmus* Tesakov and Alekseev, 1992 (Arthropoda). *Palaeontological Journal* 32: 49.

Tiegs, O.W., 1940. The embryology and affinities of the Symphyla, based on a study of *Hanseniella agilis*. *Quarterly Journal of Microscopical Science* 82: 1–225.

Tiegs, O.W., 1947. The development and affinities of the Pauropoda, based on a study of *Pauropus silvaticus*. *Quarterly Journal of Microscopical Science* 88: 165–257, 275–336.

Trewin, N.H., & K.J. McNamara, 1995. Arthropods invade the land: trace fossils and palaeoenvironments of the Tumblagooda Sandstone (?late Silurian) of Kalbarri, Western Australia. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 85: 177–210.

Wheeler, W.C., 1998. Molecular systematics and arthropods. In *Arthropod Fossils and Phylogeny*, ed. G.D. Edgecombe, pp. 9–32. New York: Columbia University Press.