EARLY CAMBRIAN LOBOPODIAN SCLERITES AND ASSOCIATED FOSSILS FROM KAZAKHSTAN

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ABSTRACT. A low diversity fossil assemblage dominated by *Mongolitubulus* spines, from the Early Cambrian Geres Member of the Shabakhty Formation at Koksu, Malyi Karatau, Kazakhstan, enables identification of its sclerite variability within the scleritome. No other sclerotised structures could be matched with the spines, indicating that these were the only sclerotised part of the body and were periodically shed. The prominent spines of *Mongolitubulus* have a scale-like external ornamentation and fibrous internal structure. Possibly they armed the body of a lobopodian similar to *Xenusion*. The *Mongolitubulus* spines belong to a series of Cambrian phosphatic fossils, the other end members of which are sclerites of *Microdictyon*, the second most abundant component of the Koksu assemblage. The latter superficially resemble schizochroal trilobite eyes, but in life covered the dorso-lateral sides of the body segments, as is evident from complete specimens from the Chinese Chengjiang locality. A pair of sclerites of *Microdictyon*, representing uncompleted exuviation, from Koksu show that each hole originally contained a non-phosphatised lenticular body. This makes a compound eye nature of the *Microdictyon* sclerites likely, and even their homology with arthropod eyes cannot be excluded.

KEY WORDS: lobopodians, sclerites, Early Cambrian, Kazakstan.

AFTER more than 30 years of extensive research on Cambrian phosphatic and secondarily phosphatised skeletal microfossils, initiated by the classic works of Rozanov and Missarzhevsky (1966) and Rozanov *et al.* (1969), a lot of assembled information on isolated sclerites awaits anatomical interpretation. How risky it is to use such data to restore soft anatomy is strikingly exemplified by discoveries of complete fossil organisms (or recognition of earlier finds) which were the bearers of sclerites of the *Hadimopanella-Milaculum* type (Kraft and Mergl 1989; Hinz *et al.* 1990; Conway Morris 1997), *Microdictyon* (Chen *et al.* 1989, 1995) or *Halkieria* (Conway Morris and Peel 1990, 1995). In all of these cases earlier attempts to guess the relationships of the fossils failed. The real anatomy has appeared too bizarre to be inferred from the limited morphological evidence provided by sclerites alone. Even now, for only a fraction of the Cambrian sclerites can zoological affiliations be offered. To wait, however, for the discovery of complete soft body fossils for many other kinds of sclerites would not be practical. Working hypotheses on affinities and function of isolated sclerites are of use simply to guide the search for more complete fossils. In fact, sclerites are usually poorly preserved in otherwise exquisitely preserved soft bodied fossils. One approach to interpretation, which has a long tradition, is to arrange the data into a morphology transition series with forms of known relationships included as end-members. Its reliability depends on the specificity of the morphology, how much of the series of morphologic transformations is complete, and how much time and space separate particular links of the chain.

A necessary prerequisite for any such inference is knowledge of reasonably complete sets of sclerites belonging to the same fossil animals (scleritome of Bengtson 1985). An unusually rich collection of spines from the Lower Cambrian of Kazakhstan, once coating the body of one such inadequately known organism, viz. *Mongolitubulus*, are used here to comment on the range of their variability within the scleritome. In Kazakhstan, *Mongolitubulus* co-occurs with one of the few Cambrian sclerites with already clearly established affinities, specifically *Microdictyon*. This co-occurrence makes their preservation comparable. The affinities of *Microdictyon* are known owing to the recovery of numerous complete soft-bodied fossils from the Lower Cambrian of Chengjiang (Chen *et al.* 1989, 1995). I attempt to show, also using data from other Cambrian localities, that there is a series of morphologic transitions connecting these

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otherwise disparate fossils. *Mongolitubulus* and *Microdictyon* may, therefore, belong to the same high rank taxonomic group. Furthermore, some new data on the sclerite structure of *Microdictyon* provide new hints as to its function.

The Kazakhstan material, which is extremely rich in specimens but of a very low taxonomic diversity, may be helpful in specifying the habitat of the bearer of *Mongolitubulus* spines and the undoubted lobopodian, *Microdictyon*. Rare fossils associated with *Mongolitubulus* spines in the same fossil assemblage are briefly reviewed in the hope that they will allow the ecological conditions in which these animals lived to be determined.

MATERIAL

The specimens come from a sandy dolomitic limestone, collected from the base of bed 11, at the locality of Koksu (fossil site 1239 of Ergaliev and Pokrovskaya 1977). This bed (numbered 12 in Missarzhevsky and Mambetov 1981) is about 3 m thick (Text-fig. 1). According to Missarzhevsky and Mambetov (1981) it represents the Geres Member of the Shabakhty Formation. The Geres Member is underlain by about 6 m of the thickly-bedded unfossiliferous dolomites of the Taldybulakh Member. These overly the phosphorites of the Chulaktau Formation, and the deposition of dolomites started with a conglomerate bed. At Koksu the thickness of the phosphorite-bearing strata is the greatest in the whole area but that of the overlying dolomitic unit is extremely reduced. The sandy limestone of bed 11 is restricted to the vicinity of this locality (Ergaliev and Pokrovskaya 1977). Although only phosphatic microfossils have been identified here, elsewhere in the Koksu Valley the sandy limestone bed of the Geres Member also contains an assemblage of trilobites, including *Kootenia* and *Redlichia*, which indicate a Botomian age (Ergaliev and Pokrovskaya 1977). Using phosphatic microfossils, Missarzhevsky and Mambetov (1981) argued, however, that these strata are of latest Atdabanian age.

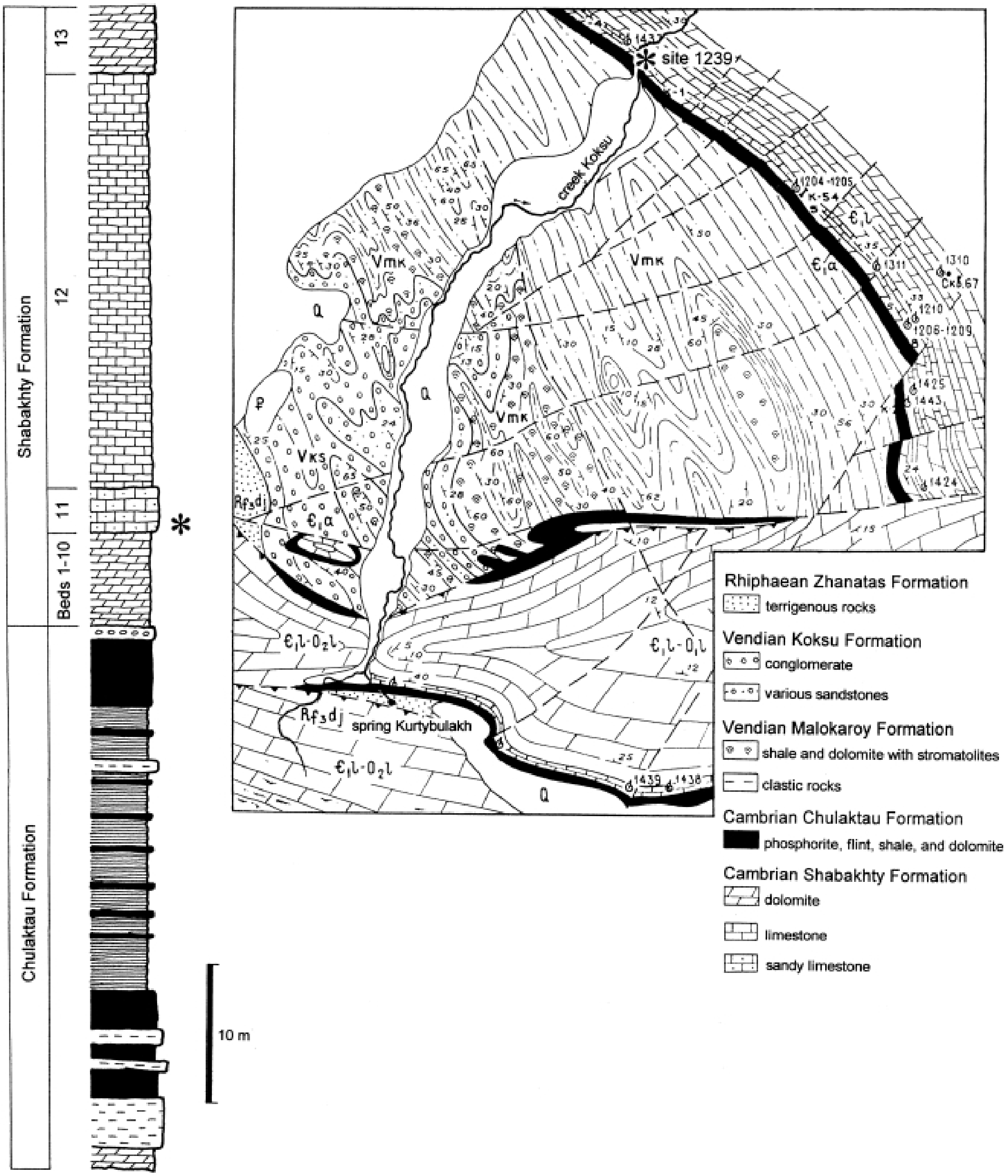
As reviewed below in more detail, the sample yielded numerous *Mongolitubulus* spines, several sclerites of *Microdictyon*, rare *Protohertzina* sclerites of unknown affinities (‘protoconodonts’), a few phosphatised ostracodes, and rare fragmentary acrotretid brachiopods. All of the fossils were either originally phosphatic or show early diagenetic phosphatisation but they now indicate at least some degree of secondary silicification. Silica infiltrated the boundaries between calcitic sparite crystals resulting in an irregular polygonal network on the sclerite surface.

MONGOLITUBULUS BODY ARMING SPINES

In common with numerous Early Cambrian phosphatic fossils *Mongolitubulus* shows an almost world-wide distribution, despite the rather low number of specimens recovered. They are known from Mongolia (Missarzhevsky 1977*a*, *b*; Esakova and Zhegallo 1996), Kazakhstan (Missarzhevsky and Mambetov 1981), China (*Tumuliolynthus macrospinosus* of Luo *et al.* 1982), Greenland (Peel and Blaker 1988), and Antarctica (Wrona 1989).

In the sample from Koksu, the *Mongolitubulus* sclerites are the most numerous of the fossils found, 3815 specimens having been extracted from about 1 kg of the rock. Missarzhevsky and Mambetov (1981) had previously collected ten specimens of *Mongolitubulus* from a sandy dolomite in the Geres Member (unit 5; interval 6) at the locality of Ushbas, and at the same level (differently numbered as unit 2; interval 5) at the locality of Babaata. Their samples also yielded *Microdictyon* and were apparently taken from the same bed (Ergaliev and Pokrovskaya 1977). At Koksu, however, they reported *Mongolitubulus* only from the overlying strata with trilobites. Missarzhevsky and Mambetov (1981) noticed some morphological differences between the original material from Mongolia, but attributed both samples to the same species. According to them, the Koksu specimens show relatively smaller surface scales in respect to the diameter of the tube, which is also more rounded in cross-section in the sample from Malyi Karatau.

The published evidence on morphology and structure of the *Mongolitubulus* sclerites is very limited. Missarzhevsky and Mambetov (1981) suspected that the spiny tubes were open at both ends, but as shown by the Mongolian (Esakova and Zhegallo 1996) and Koksu specimens with preserved apices this is not the case. Previous authors did not speculate on their relationships to other fossil or Recent organisms, other



TEXT-FIG. 1. Stratigraphic column and location of the sampled site 1239 (asterisk) at the Koksu locality in the Malyi Karatau range, Kazakhstan (based on Ergaliev and Pokrovskaya 1977, figs 4–5). Beds 1–10 correspond to the Taldybulakh Member and beds 11–13 to the Geres Member of the Shabakhty Formation of Missarzhevsky and Mambetov (1981). For explanation of details, see Ergaliev and Pokrovskaya (1977; scale for the map not given in the original).

than pointing out their similarities to 'protoconodonts' (Esakova and Zhegallo 1996). These are basically different in structure from true conodonts (Bengtson 1976) and possibly related to the chaetognaths (Szaniawski 1982). The new material described below offers some evidence on the internal structure of *Mongolitubulus* sclerites, shows that their surface ornamentation is specifically distributed along the spine, and that there are separate morphological classes within their variability. These data will be used to discuss the possible systematic position of the organism armed with them.

Preservation and structure

The walls of *Mongolitubulus* are built of phosphatic laminae. In thin section the layers immediately below the sclerite surface are almost translucent whereas the interior of the wall tends to be darker (apparently rich in an organic matter). In specimens crushed before diagenesis the laminae tend to split at the point of breakage. The inner cavity of the sclerite is frequently filled with diagenetic phosphate. Many specimens are represented by only a thin phosphatic coat which remained after the weakly phosphatised original sclerite dissolved during preparation. Usually the sclerite apex is not preserved and most specimens represent the tubular middle part of sclerites. When preserved, the apex may be strongly mineralised (Text-figs 2B–C, E–H, 3A–B), with a transparent amber-coloured tip. This is shown also in the sclerites from the lower Middle Cambrian of the Mount Cap Formation at Little Bear, north-western Canada, referred by Butterfield and Nicholas (1996) to *Rushtonites*-like spines.

The external sclerite surface is covered with scale-like protuberances. Both the surface of the scales and the area in between are smooth (Text-fig. 3D). This is not the case with the interior of the basal cavity, which is always of a more or less irregular appearance. A longitudinal striation is visible in places (Text-fig. 3C). This is suggestive of the sclerite wall being built of parallel, longitudinal fibres (noticed also in Antarctic specimens by Wrona 1989). The original composition of these fibres is not known.

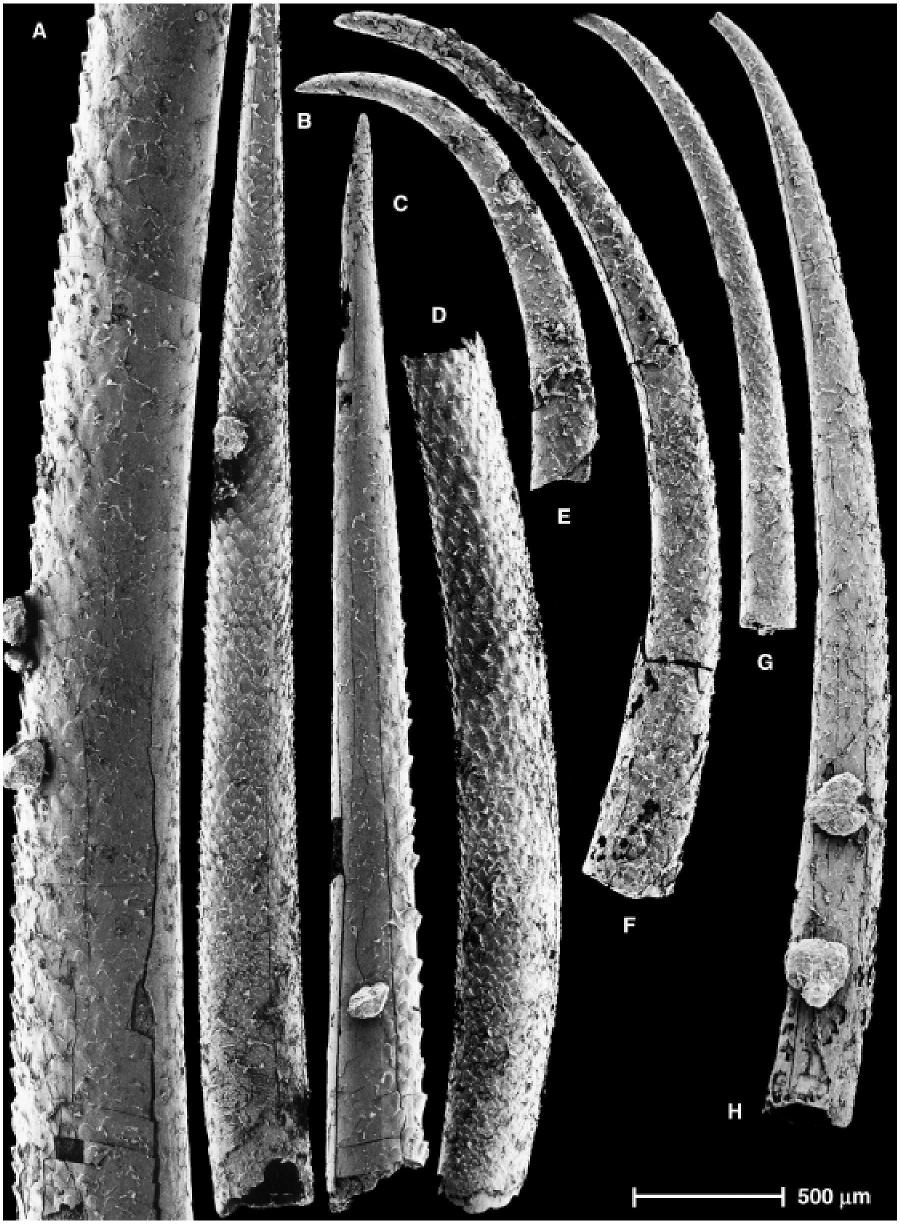
Scleritome composition and species identity

In the sample studied, the *Mongolitubulus* sclerites show considerable variability. This is expressed mostly in their cross-section, curvature, and surface ornamentation, and there seems to be a complete gradation between particular morphologies. Few specimens, however, show a round cross-section at the base. The section is more or less oval. The axis of the oval is either in the plane of curvature (sclerites called here compressed) or transverse to it (depressed) (Text-fig. 4B–C). Amongst a sample ($n = 408$) of relatively well-preserved sclerites, 205 were compressed and 203 depressed. Among compressed sclerites, those with preserved apices show them to be either straight ($n = 48$) or curved to a varying degrees ($n = 47$).

The depressed sclerites show relatively low variability in their curvature (Text-figs 2B, 4B). Their apices are invariably straight, and only the region close to the base is more or less curved with their outer side a little more flattened. They vary somewhat in the degree of curvature, which does not seem to be related to size. Evidently sclerites were of different shape irrespective of their growth stage or size. The surface ornamentation is variable but generally rather fine, when compared with that of compressed sclerites.

Compressed sclerites are generally larger (Text-fig. 4B–C), the degree of compression being correlated with their size. Most of them had almost straight sharp apices, but among specimens with a preserved apex those with more or less curved apices are equally common. Unlike the apices, the main part of the compressed sclerites is rather uniformly and gently curved. This makes attribution to either class of specimens with broken apices difficult. It seems that large specimens mostly had straight apices. Conversely, the more curved the apex, the smaller the sclerite. Some straight sclerites show a robust sculpture on one side only, the other being smooth. In specimens with well-preserved proximal parts, the scales become increasingly smaller proximally and disappear at the base (Text-figs 2D, 3E).

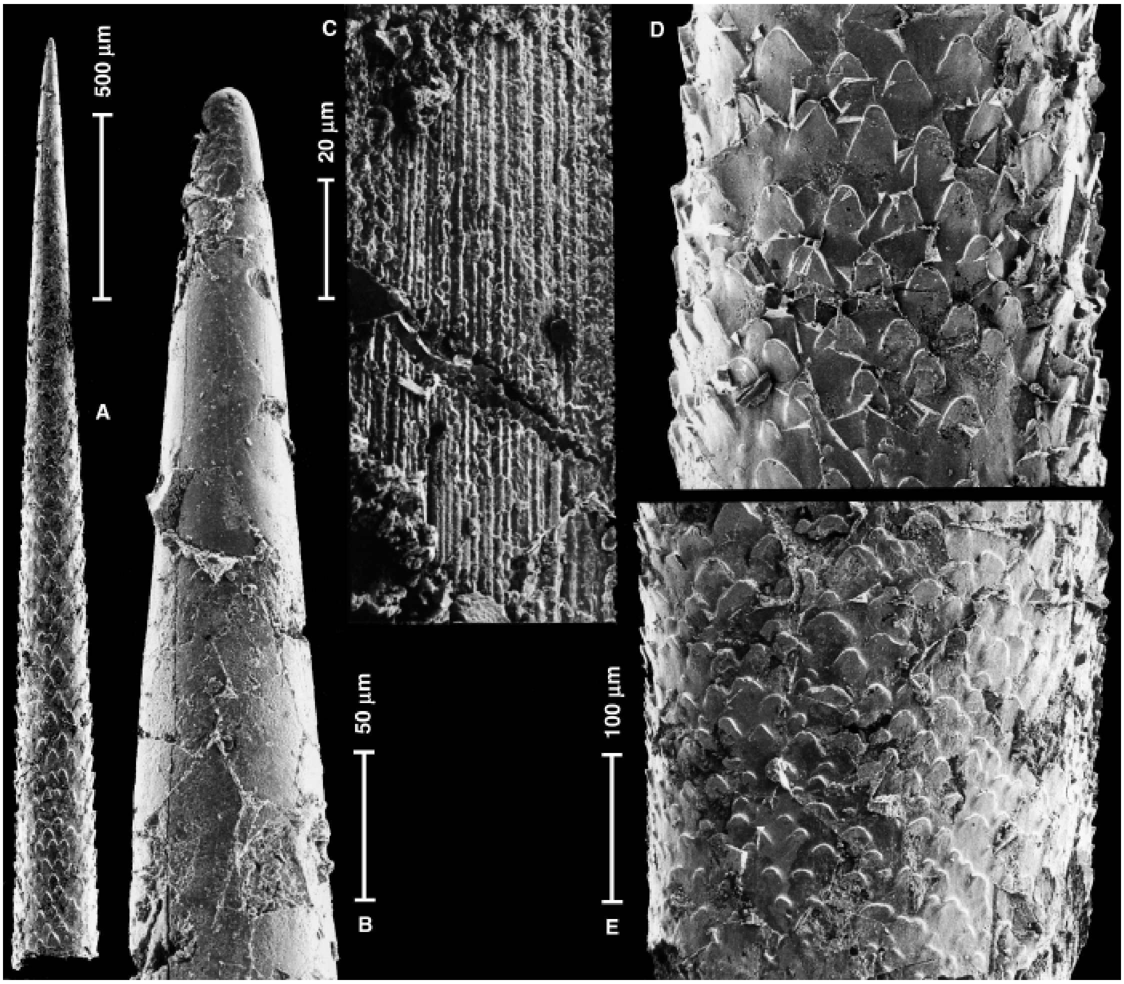
The bimodal sclerite variability, i.e. one compressed, the other depressed, may represent two species being represented in the sample or, alternatively, two different kinds of sclerites in the body of the same organisms. This can only be determined if several samples yielding a statistically significant number of specimens are available: if one of the types is missing in at least one of them, or ratios vary significantly, then the hypothesis of two species is more likely. Unfortunately, the published occurrences of



TEXT-FIG. 2. Sclerites of *Mongolitubulus squamifer* Missarzhevsky, 1977 from the base of bed 11 of the Geres Member of the Shabakhty Formation at the Koksu locality, fossil site 1239, Malyi Karatau, Kazakhstan; Late Atdabanian, Early Cambrian. A, C, E–H, compressed spines ZPAL K/7, 10, 2, 9, 1 and 5 respectively. B, D, depressed spines ZPAL K/8 and 3.

Mongolitubulus refer to very small samples. Because of the observed transition between both sclerite classes, it is provisionally assumed that all the Kazakh sclerites were derived from the same organism.

For the same reason it is not easy to name the Kazakh species. The holotype of the type and only species of *Mongolitubulus*, *M. squamifer* Missarzhevsky, 1977 (GIN 429772) comes from sample 180, taken from the Khairkhan Formation at the Salaany-Gol section in north-western Mongolia (Missarzevsky 1977). It is



TEXT-FIG. 3. Sclerites of *Mongolitubulus squamifer* Missarzhevsky, 1977 from the base of bed 11 of the Geres Member of the Shabakhty Formation at the Koksu locality, fossil site 1239, Malyi Karatau, Kazakhstan; Late Atdabanian, Early Cambrian. A–B, compressed spine ZPAL K/11 with well-preserved apex. C, inner surface of spine ZPAL K/4 showing fibrillar microstructure. D, regular distribution of scales on depressed spine ZPAL K/8 (also Text-fig. 2B). E, basal part of depressed spine ZPAL K/3 showing emergence of scales.

not known whether it is a typical specimen of its population. It seems, however, to have more densely packed ‘scales’ than even the most prominently ornamented Kazakh specimens. Esakova and Zhegallo (1996) resampled the type section. Numerous phosphatic microfossils were recovered from limestone pebbles occurring within the clastic Khairkhan Formation, which overlies an archaeocyathid-algal mud-mound limestone of the Salaany-Gol Formation, but *Mongolitubulus* was not found. In the same area, however, they collected nine more specimens in four other sections. These occurrences have been used to establish the *Mongolitubulus squamifer* Assemblage Zone.

According to Esakova and Zhegallo (1996) the Khairkhan Formation is Botomian. They claimed that their new collection contained specimens of *Mongolitubulus* with densely distributed rhombic scales, closely similar to the holotype. All the illustrated specimens (n = 5) from the Ikh-Bajan-Ajgar-Ula section (associated with a gracile spine of *Rhombocorniculum cancellatum* and poorly preserved, fragmentary *Microdictyon*) show, however, an arrangement and shapes of scales that are more irregular than is typical for the Malyi Karatau sample. In the Kazakh specimens such surface ornamentation can be found only in basal parts, not in the middle section of the spine. In contrast, two of the numerous *Mongolitubulus* specimens from the Henson Gletscher Formation of Greenland (also in beds with *Kootenia*) illustrated by Peel and Blaker (1988) show a more prominent and regular distribution of scales than is typical for Malyi Karatau. Additional sampling from the type locality seems necessary to clarify the relationships between the Mongolian and Kazakh populations. Missarzhevsky and Mambetov (1981) considered them to be conspecific.

The nature of the sclerites

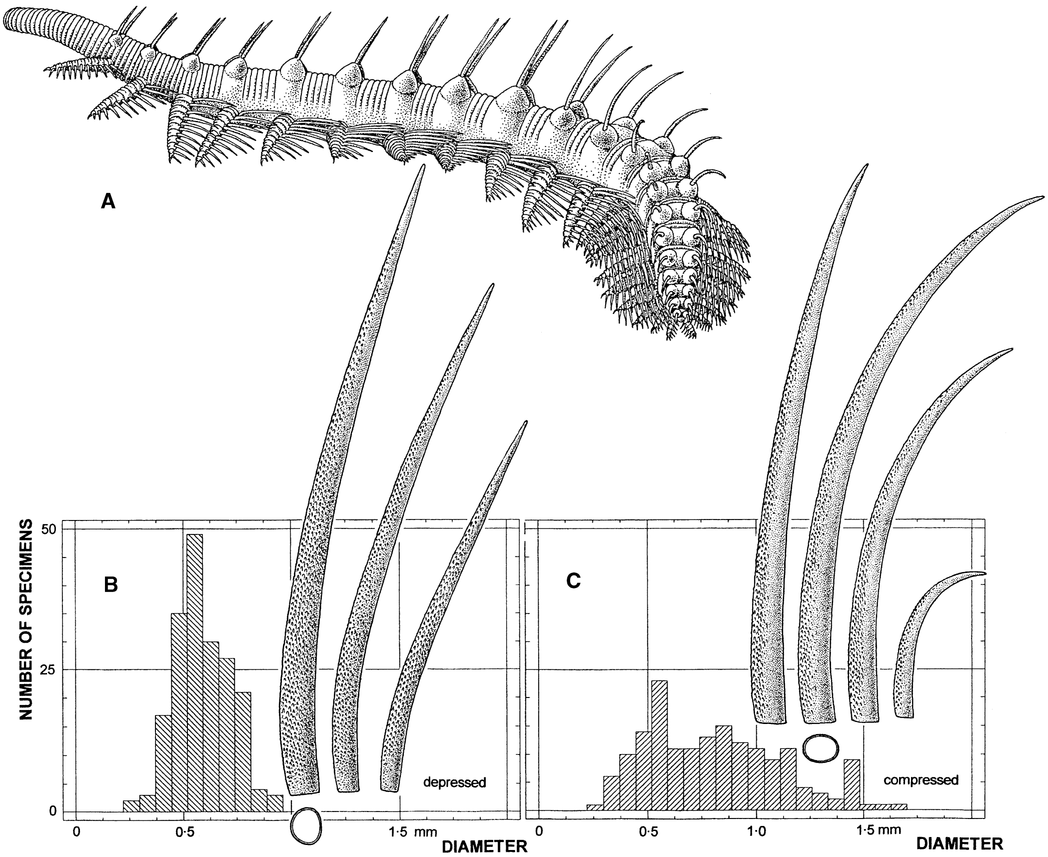
The *Mongolitubulus* sclerites, with their sharp and strongly sclerotised apices and fibrous walls, are interpreted as spines that armed the body of an animal. They are virtually bilaterally symmetrical but some signs of asymmetry can be seen in the uneven distribution of scale-free surfaces on what is probably the posterior side. It is, thus, likely, although not certain, that they arose as paired organs (additional arguments for this, given below, refer to a proposed homology with the clearly asymmetric sclerites of *Rhombocorniculum*). The scales resemble structures commonly occurring on the surface of arthropod cuticle. Despite the considerable variation in size of the *Mongolitubulus* sclerites, there are no signs of incremental growth. This suggests that they may have been exuviated. In principle, this restricts possible affinities of *Mongolitubulus* to the ecdysozoan phyla.

In fact, Melnikova (2000) proposed that *Mongolitubulus* sclerites were carapace spines of the bradoriid crustaceans. Her evidence is based on the association, on the bedding surfaces, of spiny objects, which remotely resemble *Mongolitubulus* (NB: they show spinose ornamentation even on internal moulds; Melnikova 2000, pl. 7, fig. 7B) with bradoriid carapaces, as well as the occurrence of *Rushtonites* sclerites in other beds at the same locality. Rare, but well preserved, bradoriids (reviewed below) also occur in the Shabakhty Formation sample. They do not show, however, any resemblance to associated *Mongolitubulus* sclerites in either colouration or wall structure. This makes structural continuity between *Mongolitubulus* spines and bradoriid carapaces unlikely. No other sclerotised structures co-occur with *Mongolitubulus*, which might belong to the same scleritome. Instead, the basally thinning wall and diminishing sculpture (Text-fig. 3E) are suggestive of the spines originally being attached to an unornamented and weakly sclerotised body surface. Rather, the *Mongolitubulus* animal affinity has to be looked for among ecdysozoans with rather soft body covers, instead of typical arthropods with sclerotised body covers.

Among ‘soft-bodied’ ecdysozoans are the nemathelminthan worms (priapulids and palaeoscolecids), but nothing in the known anatomy of their Cambrian representatives is suggestive of such spines being part of their body plan. ‘Soft-bodied’ arthropods cannot be excluded, but I am not aware of any Cambrian species bearing structures similar to the *Mongolitubulus* sclerites. The choice of other ecdysozoans, specifically the xenusians, is intriguing because of the prominent spines arming the body of the Early Cambrian *Xenusion* (Text-fig. 4A). The specimens of *Xenusion*, preserved in a coarse sandstone, do not provide any details of the morphology of the spines, but in one specimen the basal part of a dorsal spine is well preserved, while imprints of spines on the appendages are well represented in the other (Dzik and Krumbiegel 1989). Their inferred size and general shape roughly fits that of *Mongolitubulus* sclerites. The body of *Xenusion* was more than 200 mm long, with dorsal spines presumably of centimetre length, those arming appendages being smaller. The large compressed spines of *Mongolitubulus* could thus match the dorsal spines of *Xenusion*, while the generally smaller depressed ones are comparable to those arming appendages. The estimated length of the largest spines of Kazakh *Mongolitubulus* is 18–20 mm.

COMPOUND EYES ON EACH BODY SEGMENT IN *MICRODICTYON*?

Microdictyon plates, known from lower and middle Cambrian strata (Bengtson *et al.* 1986), are gently convex and composed of a network of externally smooth walls delimiting more or less circular holes in a comb-like hexagonal pattern. At the point of coalescence of the walls, conical tubercles (nodes) are normally developed, of oval outline and with sharp margins. The walls were probably originally



TEXT-FIG. 4. Restoration of *Xenusion* showing arrangement of spines (relative size and curvature in A is completely conjectural; Dzik and Krumbiegel 1989; Dzik 1991) possibly homologous to those of *Mongolitubulus*, and size frequency distribution of *Mongolitubulus squamifer* Missarzhevsky, 1977, better preserved depressed (B) and compressed (C) spines from the base of bed 11 of the Geres Member of the Shabakhty Formation, Koksu fossil site 1239, Malyi Karatau, Kazakhstan; Late Atdabanian, Early Cambrian. Restored appearance of characteristic shapes given based on composite drawings of several specimens; this spectrum does not cover complete variation in shape (see Text-fig. 2).

phosphatic. The sclerite organisation is so complex that from the beginning of research on them a special function had been assumed. It was, therefore, a great surprise to find in the excellent Chengjiang specimens, with completely preserved soft parts (Chen *et al.* 1995; Hou and Bergström 1995), that these were plates attached to a lobopodian body.

Apart from the rare ostracods and brachiopod shell fragments, these are the only fossils in the sample studied from Kazakhstan with well-established zoological affinities. They almost certainly represent the type species of the genus, *Microdictyon effusum* Bengtson *et al.* (*in* Missarzhevsky and Mambetov 1981), the holotype of which probably comes from the same stratum. The morphology of *M. effusum* has been described in detail by Bengtson *et al.* (1986) and there is no need to repeat this. Important new evidence has emerged, however, concerning the histology and function of the sclerites.

Lenticular structures

Among several *M. effusum* sclerites from Koksu one is unusual in having another sclerite attached basally (Text-fig. 5C). This second sclerite is not complete; the parts underlying the tuberculation and external framework are missing, but specific holes of both sclerites match. In the old sclerite the basal layer covers the whole surface of the holes. In this respect it is not different from the type specimens of the species (Bengtson *et al.* 1986). In specimens of *M. rhomboidale* Bengtson *et al.*, 1986 from Kyzyl-Kum in Uzbekistan (Bengtson *et al.* 1986, fig. 6) and of Australian *M. depressum* Bengtson, 1990 from the Ajax Limestone (Bengtson *et al.* 1990, p. 333) that are incompletely mineralised basally, only a thin wall delimits this surface and the hole is usually open basally. This probably changed with maturation of the structure, as in completely developed *Microdictyon* sclerites. Alternatively, in their marginal parts their wall constricts below each of the holes to form a convex, hemispherical basal layer (see Bengtson *et al.* 1986; Hinz 1987, pl. 1, fig. 1).

Owing to incomplete mineralization of the Koksu specimen, the external network can be seen from the basal side (Text-fig. 5C–D). A thin lining covers apertures of some of the external hole openings. This thin external wall is in continuity with the inner margin of the rim surrounding the hole. The wall is regular in form and hemispherically concave when seen from the sclerite base. The convexity of the external lining of the holes in the basally attached sclerite from Koksu is similar to that of the basal layer but oriented in the opposite direction. Between the external rim and the basal wall of the hole there is a lateral depression surrounding the hole interior. The wall of the hole, together with its external membrane and basal wall, therefore delimits a non-phosphatic body of lenticular shape (Text-fig. 6A). Its external convexity is reproduced by the membrane, which apparently originated as a phosphatic lining of the lenticular surface.

Possible eye function

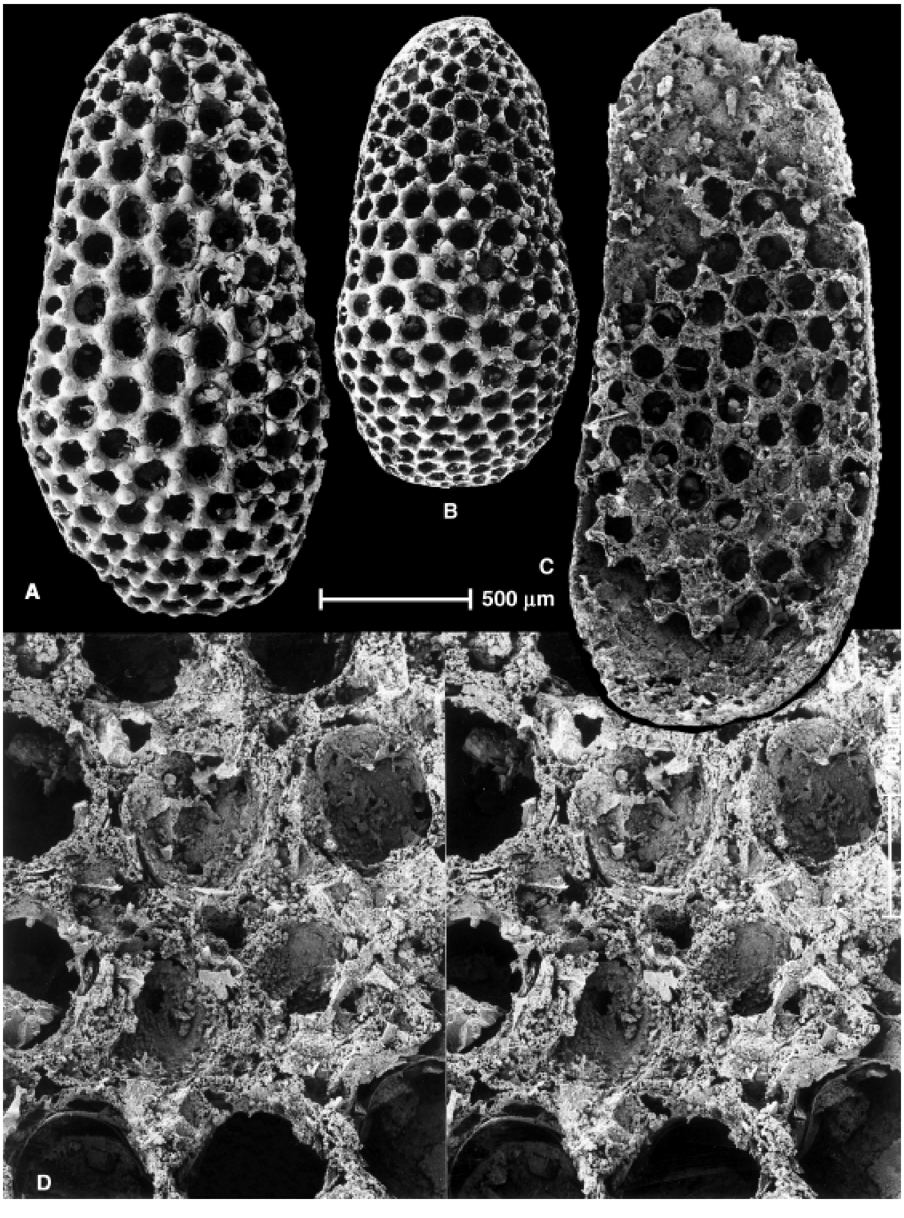
Although the shapes of plates in different species of *Microdictyon* vary, they remain rather compact and vaguely resemble the schizochroal eyes of trilobite. A similarity to the pagetinid trilobites (abathochroal) eye structure has been indicated by Brasier (1989, p. 134). The authors of the original description discussed this possibility but rejected it (Bengtson *et al.* 1986). Their crucial argument was that the basally continuous layer of the plate makes impossible a continuity between the content of the holes and hypothetical compound eye cones, which had to be located below.

However, the presence of a non-phosphatised lens-shaped body in each hole of the *Microdictyon* sclerite (though their original mineralisation with, say, calcite cannot be excluded) reinforces their vague similarity to the cuticular part of a trilobite eye. The stacked *Microdictyon effusum* plates preserved at the stage of moulting suggest that the continuous basal layer may be a feature of maturity immediately preceding exuviation, not necessarily being so thick while they were functional. Moreover, there is no need to assume that this layer was opaque during life.

Anatomical location of sclerites

The Cambrian lobopodians had a body shape and size similar to that of Recent onychophorans (Dzik and Krumbiegel 1989; Ramsköld and Hou 1991). They differed, however, from them in having (1) the mouth in terminal position, typically unassociated with any specialised sense or feeding appendages, and (2) a relatively thick cuticle, which suggests lack of a hydraulic body skeleton (which seems to be a derived feature of the onychophorans). There is evidence that the external body cover was well sclerotised in the Cambrian lobopodians and shed periodically (Robison 1985; Dzik and Krumbiegel 1989), which indicates these were Ecdysozoa (see Aguinaldo *et al.* 1997; Aguinaldo and Lake 1998; Garey and Schmidt-Rhaesa 1998). In these two respects, and in general body organisation, the Cambrian lobopodians to some extent resemble Recent microscopic tardigrades (Simonetta and Delle Cave 1975).

There is still some uncertainty regarding body orientation in some xenusians, which results mostly from the extreme simplicity of their body plan. The presence of a specialised pair of mouth appendages, and the terminal position of the appendage pair at the opposite end, make the orientation of the body in the Middle Cambrian *Aysheaia* indisputable (Whittington 1978). In the case of the early Cambrian *Xenusion* there is a gradient in appendage- and segment-size, which is suggestive of the presence of a posterior growth zone (Text-fig. 4A). This, together with comparison to *Aysheaia*, supports identification of the elongated legless end of the body as the animal proboscis (Dzik and Krumbiegel 1989; Ramsköld 1992). Such a position of



TEXT-FIG. 5. Sclerites of *Microdictyon effusum* Bengtson *et al.* in Missarzhevsky and Mambetov, 1981 from the base of bed 11 of the Geres Member of the Shabakhty Formation, Koksu fossil site 1239, Malyi Karatau, Kazakhstan; Late Atdabanian, Early Cambrian. A–B, sclerites ZPAL K/13 and 14 in external view. C–D, specimen ZPAL K/15 with exuviated sclerite attached to newly formed sclerite, seen from the basal side; note the basal convex surfaces closing holes of the old sclerite and rims of holes of the newly formed sclerite with empty cavities of tubercles; stereo-pair shows phosphatic external linings of a few lenticular bodies within holes of the network.

the mouth, at the terminal end of the cylindrical body, moulting of the sclerotised body covers (these characters possibly inherited from a nemathelminthan ancestor), and the lack of any well-developed body prolongation behind the last leg-pair make the xenusians closer to the tardigrades than to onychophorans. In fact, a possible juvenile xenusian from the Middle Cambrian of Siberia has been classified as the oldest known tardigrade (Müller *et al.* 1995). Antennae, jaws and oral papillae of Recent onychophorans are modified appendages (e.g. Walker 1995). This is apparently a highly derived trait. One would need more evidence than is offered by Hou and Bergström (1995) to prove the presence of so complex a head in the early Cambrian *Onychodictyon*. In *Aysheaia*, the first pair of appendages shows some modifications with respect to the others, but this was a long way towards the situation in the onychophorans, in which one pair of appendages has been transformed into a kind of antennae and two others almost completely reduced so that their claws are transformed into jaws.

In the Chengjiang xenusian *Hallucigenia*, the end opposite to the proboscis-like part of the body bears a pair of large sclerites and a crowd of appendages with a somewhat modified morphology. These have been interpreted by Hou and Bergström (1995; note the fundamentally different restoration by Chen and Zhou 1996, fig. 62) as specialised mouth appendage, similar to that in Recent onychophorans. This would make the polarity in the distribution of appendages in *Microdictyon*, *Hallucigenia*, and *Cardiodictyon* the opposite of that in *Xenusion* and *Aysheaia*. This is possible, as shown by the Early Cambrian Chengjiang probable lobopodian *Facivermis*, with a few pairs of appendages arming only one end of the body (Hou and Chen 1989), and by the pentastomids. Excellently preserved Ordovician and Late Cambrian phosphatised larvae of the pentastomids (e.g. Walossek and Müller 1994) show some similarities to *Facivermis*. However, it seems more likely that the sclerites armed mostly the central and posterior parts of the body in *Microdictyon* (Text-fig. 6c), with no correspondence to any head-like units.

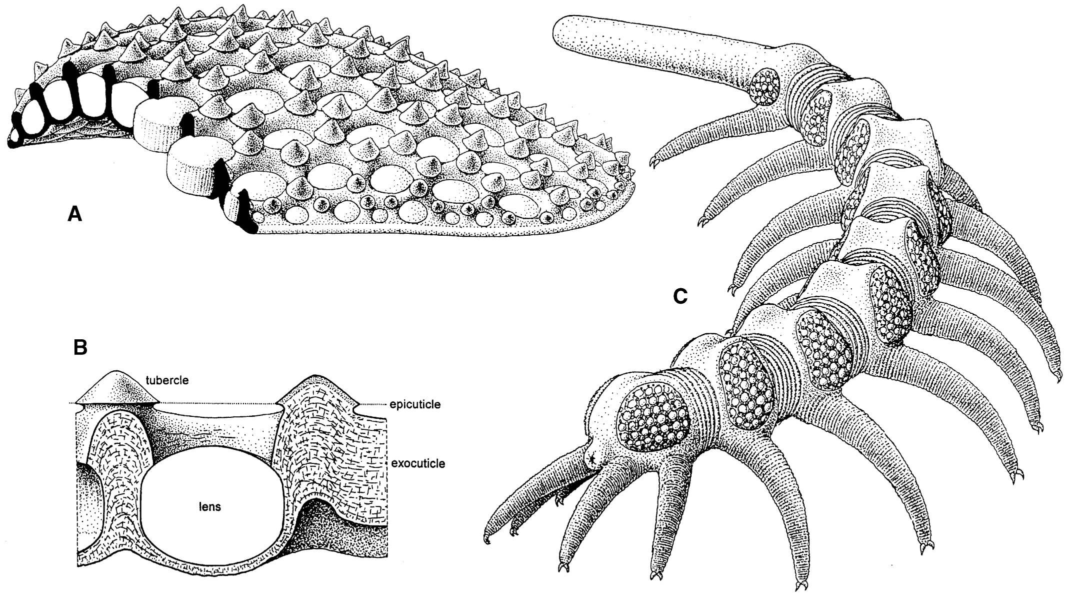
Sclerite development and exuviation

The xenusiids exuviated. The earliest Cambrian Baltic *Xenusion* and some specimens of the Middle Cambrian *Aysheaia* are represented by exuvia. There is also evidence of exuviation in the Chengjiang *Microdictyon* (Chen *et al.* 1995; Chen and Zhou 1998). This, as well as the geometrically simple body form, its annulation resembling that of the cuticle of Cambrian priapulid worms, and the annulation of appendages similar to that of the basal parts of appendages in the most primitive arthropods, was used to suggest a transitional position of the xenusians between the nemathelminthan worms and the arthropods (Dzik and Krumbiegel 1989). The evolutionary continuity between lobopodians and arthropods is supported by homology of the segmental homeobox genes of the onychophorans (paralogues 1–8, from lab to Abd-A) and those of *Drosophila* (Grenier *et al.* 1997).

The conical tubercles at the junction of the walls of the holes of *Microdictyon* resemble the circular sclerites at the cuticle surface of the early Palaeozoic palaeoscolecid nemathelminthan worms (Bengtson 1977; Conway Morris 1997; Müller and Hinz-Schallreuter 1993). Homology is possible, although at least late palaeoscolecids had cuticle of much more derived structure. In the Ordovician palaeoscolecid *Milaculum* collagen cords typical of the Recent nematomorphs (Bresciani 1991) were already established (Dzik 1986, fig. 7).

The structurally closest Recent homologue of the xenusiid cuticle is probably the cuticle of the priapulids. The priapulid cuticle consists of an external, very dense, thin, proteinaceous layer (epicuticle), a dense proteinaceous middle layer (exocuticle) with some chitin content in deeper sublayers, and a fibrillar chitin-rich inner layer (endocuticle), which can be sclerotised in the teeth (Lemburg 1998). Also the tardigrade epithelium is structurally and functionally complex enough to produce cuticular plates of complexity comparable with *Microdictyon*, though of much smaller size. In some of them a complex system of lacunar spaces within the cuticle occurs (see Kinchin 1994, p. 47). The complex internal structures in sclerites of their much larger Cambrian relatives presumably originated in a similar way.

The walls of *Microdictyon* sclerites show an internal structure (Bengtson *et al.* 1986) suggestive of a stepwise way of secretion. There is also a series of levels in the external morphology of the sclerite which may correspond to successive stages in sclerite formation. The external-most level is marked by the location of the sharp edges of tubercles in the same plane. This suggests that originally an organic membrane that has not been preserved connected them, at least in the early stages of their development. Such a location is occupied by epicuticle in the priapulids (Text-fig. 6b). The tubercles are built of a distinctive capping tissue, which continues to the rim of the hole and terminates at the sharp edges marking the orifices of the holes (Bengtson *et al.* 1986, p. 99). At this level the external surface of the lenticular



TEXT-FIG. 6. Restoration of sclerite structure of *Microdictyon effusum* Bengtson *et al.* (*in* Missarzhevsky and Mambetov 1981). A, diagrammatic representation of a section across the lens with proposed interpretation of its structure. B, hypothetical epicuticle membrane is proposed to explain the morphology of tubercles. C, body appearance of *Microdictyon* as seen from its posterior end. All based on the Chengjiang specimens (Chen *et al.* 1995) and new data on the sclerite organisation.

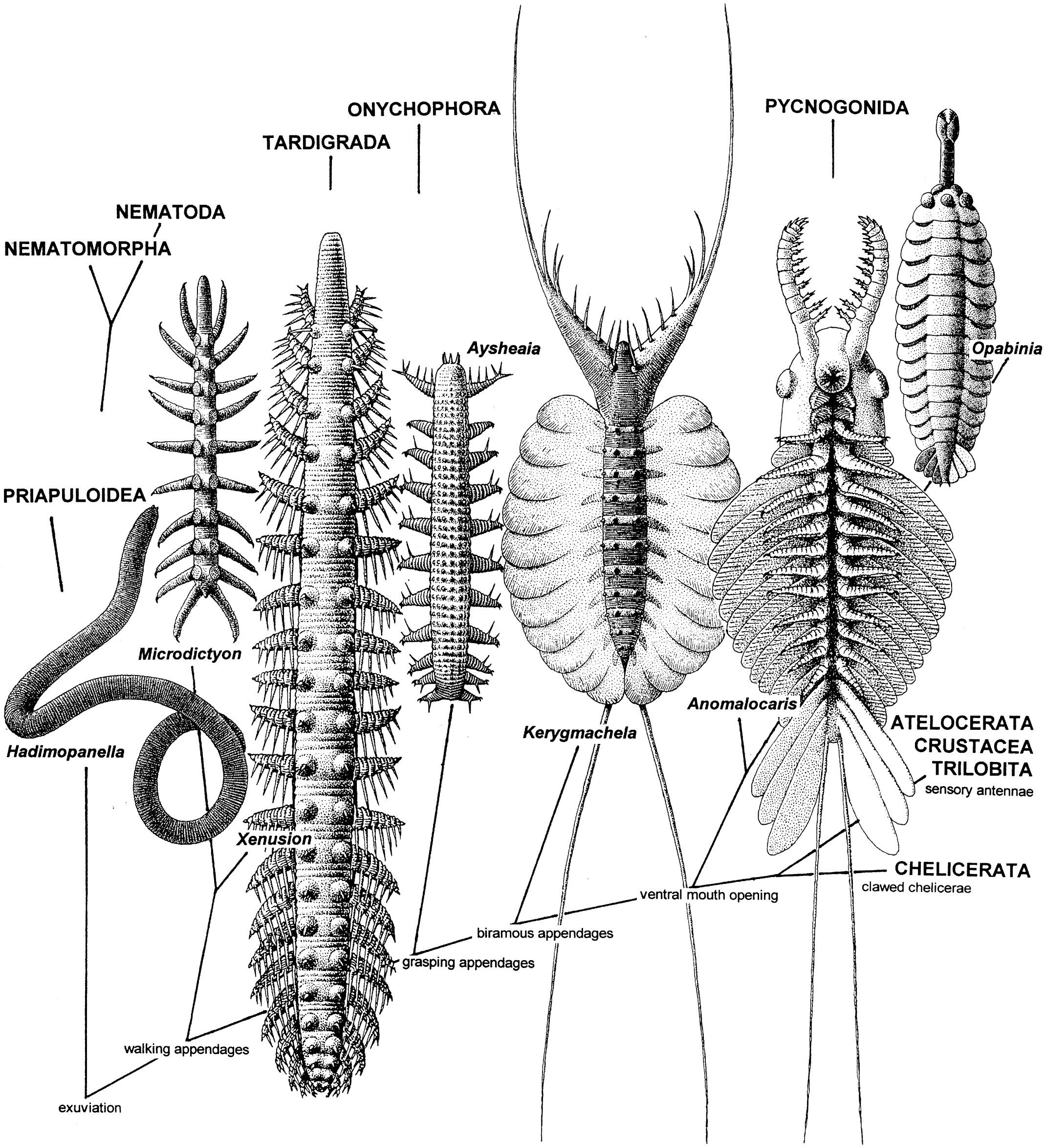
body, as preserved in the incompletely shed out specimen, contacted the hole wall, which narrows steeply below and continues to cover the lower convex surface of the lens. The sclerite interior is built of laminated tissue (Bengtson *et al.* 1986), which indicates that it was secreted basally, like exocuticle of the priapulids and other ecdysozoans.

This, taken together with histological evidence (Bengtson *et al.* 1986), allow a reconstruction of the origination of the sclerite. The lenticular structures of the *Microdictyon* sclerite possibly developed as spherical cisterns filled with a fluid. The soft tissue could freely penetrate the surface only at junctions between each of three cisterns and this is the place where tubercles developed, which initially had their own internal cavity, as suggested by the distribution of laminae in the framework tissue (Bengtson *et al.* 1986, fig. 3). The tissue was subsequently withdrawn from near the surface, leaving behind the first lamella of the exocuticle. The sclerotisation of the regions separating cisterns resulted in their shrinking and opening the holes above the cisterns. The shrinking cuticle was raised up to form strongly convex rims. Finally, a contraction of its whole volume drew together the margins of the cisterns horizontally, forcing them to attain a lenticular instead of spherical shape (Text-fig. 5C).

There is no strict analogue among Recent ecdysozoans of such formation of lens-like structures and a sclerotic network separating them. In the fossil material only the cornea of the trilobite eye is known well enough to offer an analogy. This poses the question of whether the similarity of the *Microdictyon* sclerites to compound eyes of early arthropods is not an expression of evolutionary continuity.

Implications for the evolution of arthropod compound eyes

The possibility that the compound eye originated within the xenusians is strengthened by Budd's (1999) interpretation of the Early Cambrian *Kerygmachela*, an animal that shares some xenusian and anomalocaridid arthropod traits (Text-fig. 7). He proposed that the oval bases of paired spines in the cephalic region represent eyes. Other anomalocaridids had large, thus probably compound, eyes, either pedunculate



TEXT-FIG. 7. Probable relationships of the Cambrian ecdysozoans showing the position of *Microdictyon* in the morphogic series connecting the xenusians and anomalocaridids. A possibility which emerges from these data is that the compound eye-like sclerites of *Microdictyon* are homologous with the compound eyes of the anomalocaridids and the arthropods.

or partially incorporated into the head shield. *Opabinia*, probably the most bizarre of the Burgess Shale arthropods, was equipped with five stalked compound eyes (Whittington 1975). The serial distribution of compound eye-like sclerites in *Microdictyon* was thus not unique in the Cambrian. A mechanism of induction of homeotic genes responsible for the appearance of the ectopic eyes in *Drosophila* (see Halder *et al.* 1995) can be invoked to explain the origin of such serial arrangement.

Growing palaeontological evidence seems to support the idea that the compound eye originated only once in the evolution of arthropods although there are various opinions on the homology of compound eyes in different groups of arthropods (reviewed by Fryer 1996). Large compound eyes were probably typical for the oldest Atelocerata. Among the myriapods, the scutigerid centipeds, the only ones having compound eyes, were already represented in the Silurian, and the Palaeozoic millipedes had generally larger eyes than their Recent relatives (Shear 1997). The similarity in organisation and morphogenesis of the primitive insect and crustacean ommatidium is so close that homology between them is likely (Melzer *et al.* 1997, 2000). Compound eyes thus had to be present in the common ancestor of the Atelocerata and Crustacea, which lived not later than Early Cambrian. In fact, virtually all primitive-looking Cambrian arthropods had well-developed compound eyes, and the case of *Xandarella* shows how the primitive stalked eyes could attain a dorsal position, being incorporated in the cephalic shield (Hou and Bergström 1997).

The homology of the compound eye, however, does not necessarily imply homology of corneal structures. In the living fossil *Limulus* corneal lenses are frequently absent (e.g. Fahrenbach 1969, fig. 1; Passaglia *et al.* 1997) and light is condensed solely by the crystalline cone (e.g. Elofsson and Odselius 1975; Caveney 1998). Apparently, lenses developed sporadically and independently in the evolution of arthropods as additional optical devices. If the *Microdictyon* sclerites had anything to do with the compond eye, this was just another case of formation of corneal lenses within a cuticular framework.

The *Microdictyon* sclerites resemble the schizochroal eyes of post-Cambrian phacopid trilobites in that particular lenses were separated by a kind of interlensar sclera. The shape of the possible lenses in *Microdictyon*, however, is much closer to that of typical trilobite eyes with densely packed ommatidia (holochroal; see Clarkson 1979, fig. 1D) than to structurally and geometrically complex eye lenses of the phacopids (see Miller and Clarkson 1980, fig. 3). Schizochroal eyes may have arisen from a holochroal precursor by paedomorphosis (Clarkson and Zhang 1991). A similar organisation of eyes developed independently in the eodiscid trilobites (Jell 1975), and perhaps also in *Microdictyon*.

The common origins of eyes may extend even further, to non-ecdysozoan phyla. Homologous homeotic genes are responsible for the morphogenesis of eyes in arthropods and vertebrates (Quiring *et al.* 1994; Oliver and Gruss 1997; Pan and Rubin 1998; Chow *et al.* 1999). A possible explanation for this is that their common ancestor also had eyes (Halder *et al.* 1995) or at least some eye components (Nielsen 1998). However, homology at molecular level may be misleading in this particular case. Some of these genes have also been identified in molluscs and nematodes. As no eyes are present in nematodes and it is unlikely that their ancestors ever had any eyes, such genes had to be originally involved in functions not related to vision, with recruitment for visual system formation and function occurring later (Duncan *et al.* 1997).

No doubt compound eyes can originate independently. They are known to occur in organisms so basically unrelated to the arthropods as the chaetognaths. In *Eukrohnia hamata* the eye is composed of about hundred ‘ommatidia’, each photoreceptive cell being armed with a lens (Bone and Goto 1991) of virtually the same shape as the lenses in the *Microdictyon* sclerites.

The xenusians commonly possessed spiny sclerites arranged metamerically at the dorso-lateral surface of the body (Hou and Bergström 1995). The homology between the eye-like sclerites of *Microdictyon* and spiny sclerites of *Hallucigenia* (Bengtson 1991) makes it likely that the dorsal spines of another Cambrian lobopodian, *Xenusion*, also belong to the same series of homologous structures. One may propose that polarity of this series is such that the ancestral shape was spine-like. The sclerotisation of the cuticle around a soft tissue projection is a widespread phenomenon among ecdysozoans. The scalids of the priapulids (see Storch 1991) and sensory hairs of the tardigrades (see Kinchin 1994) are formed in such way. These analogies also suggest that the original function could have had both protective and sensory functions. A change in their function from sensory tactile to photosensitive would require transformation of the ciliate sensory cells, known to be present inside such organs in Recent ecdysozoans (e.g. Kristensen 1981). Some genes may keep silent expression of other genes that originated earlier in the evolution and may emerge suddenly (Rutherford and Lindquist 1998). This makes it potentially possible that the genetic information used by the xenusians to construct their eyes was used again later by the arthropods.

The compound eye interpretation of the sclerites of *Microdictyon* remains far from being proven.

However, it is not incompatible with current knowledge of ecdysozoan relationships and it may serve as a working hypothesis to explain the complex organization of the sclerites.

POSSIBLE *MONGOLITUBULUS-MICRODICTYON* RELATIONSHIP

A morphologic series connects the simple spines of the *Mongolitubulus* morphology with the most complex of the *Microdictyon* type. Among the co-occurring Chengjiang xenusians, *Onychodictyon* sclerites show similar shapes and location on the body. The oval convex sclerite plate with poorly preserved, virtually smooth, surface morphology, is supplemented by a prominent, dorsally oriented spine (Ramsköld 1992; Hou and Bergström 1995). Such a spine dominates over the base in a sclerite from the Early Cambrian of Greenland illustrated by Bengtson (1991). The sclerite has a sharply pointed, smooth apex and the rest of its surface is also smooth. Its base is surrounded by a rim and contains deep depressions that are closely similar to the holes in *Microdictyon*. These sclerites are thus morphologically and structurally transitional between the 'eyes' of *Microdictyon* and the dorsal spines of *Hallucigenia*. If, as suggested above, the *Mongolitubulus* sclerites were xenusian spines, they would form the end of this morphologic series. Some other types of sclerite may belong to the same group, based on their reticulate to scaly surface ornamentation.

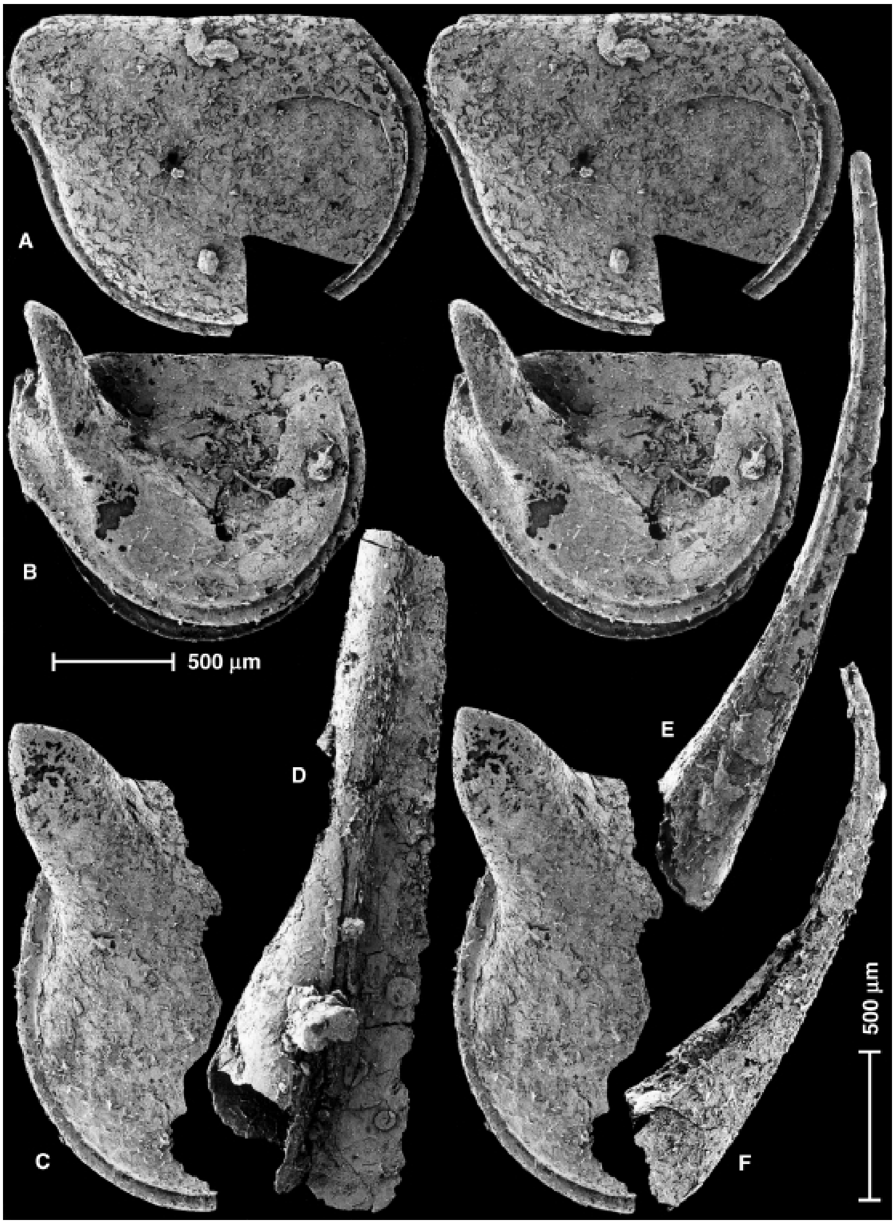
Judging from illustrations in Esakova and Zhegallo (1996, pl. 7, figs 14–16), the low-conical sclerites of *Cambrocassis verrucata* Missarzhevsky, 1977 (co-occurring with *Mongolitubulus* in its type area) show a network of ridges connecting tubercles with flat tips. A network of ridges connecting scales can also be found in sclerites of the *Mongolitubulus* type. The numerous minute scales on the surface of sclerites of *Rushtonites spinosus* Hinz, 1987 from the Lower Comley Limestone of England (Hinz 1987) are connected by a network of ridges forming an incipient reticulate-rhombic pattern. This pattern is much more regular in an unnamed species of *Rhombocorniculum* illustrated by Landing (1988, fig. 11.6). Early *Rhombocorniculum* has sclerite shapes that are closely similar to those of *Mongolitubulus* (compare Text-fig. 2 with Brasier 1986, fig. 5L–Z). The transition from *Mongolitubulus* to *Rhombocorniculum* in general shape, surface ornamentation, and internal organisation (Wrona 1989), is thus relatively complete. The shape, with the base narrowed with respect to the main sclerite body and oval, remains similar to *Mongolitubulus* in even more advanced *Rhombocorniculum* (Missarzhevsky and Mambetov 1981, pl. 15, fig. 7; Hinz 1987). Brasier (1989, p. 126) suggested an evolutionary transformation of *Rhombocorniculum* towards a wider and more twisted appearance, thus departing from the simple shapes typical of *Mongolitubulus*. The strongly asymmetric *Rhombocorniculum* sclerites were undoubtedly paired, arming the body of their bearer with at least two rows. There are clearly two discrete types of sclerites, one relatively narrow with the sharp edge only on one side, the other widely triangular with edges on both sides (see Hinz 1987). The double-edged sclerites are much less numerous in samples and not so variable in cross-section, curvature and twisting. The wall structure of advanced *Rhombocorniculum* has a highly ordered organisation (Landing *et al.* 1980), with longitudinal prisms arranged more or less parallel to the sclerite surface. Some of the *Rhombocorniculum* sclerites show possible retention of exuviated older sclerites (see Hinz 1987, pl. 10, figs 1–2) which proves its ecdysozoan nature. This is consistent with the idea that these were xenusian spines.

Admittedly, the evidence offered by the morphology of these spinose sclerites alone is too weak to prove their zoological affinity. Until complete body fossils of a *Mongolitubulus*-like animal is found, its lobopodian nature will remain only a working hypothesis.

THE KOKSU LOBOPODIAN COMMUNITY

The assemblage from the sandy limestone of the Geres Member is unusual in being almost completely dominated by only two kinds of sclerites, one of proven (*Microdictyon*), the other of possible (*Mongolitubulus*) lobopodian nature. Their abundance and the very low contribution of other fossilisable animals suggests that this was the kind of environment which was the most suitable for, even if not exclusive to, them. This offers an opportunity to identify their habitat.

The studied sample of 3988 specimens is of very low diversity, being totally dominated by



TEXT-FIG. 8. Non-lobopodian members of the fossil assemblage from the base of bed 11 of the Geres Member of the Shabakhty Formation, Koksu fossil site 1239, Malyi Karatau, Kazakhstan, Late Atdabanian, Early Cambrian. A, bradoriid species 1, stereopair of the carapace valve ZPAL K/16. B–C, bradoriid species 2, stereopairs of the complete deformed carapace ZPAL K/17 and incomplete non-deformed valve ZPAL K/19. D, possible grasping spine ZPAL K/22 of the chaetognath (?) *Protohertzina cultrata* Missarzhevsky, 1977. E, spine ZPAL K/20 of *P. triangula* (Missarzhevsky and Mambetov, 1981). F, spine ZPAL K/24 of *P. anabarica* Missarzhevsky, 1973.

Mongolitubulus spines, which contribute 95·7 per cent to it. The lobopodian *Microdictyon*, with only 15 specimens, contributes just 0·4 per cent to the assemblage. Hou and Bergström (1995) suggested that xenusian claws may correspond to the phosphatic Early Cambrian microfossil *Mongolodus*, but no such claws have been found in the Koksu fossil assemblage.

Enigmatic protohertzinids are represented at Koksu by at least three species, namely *Protohertzina anabarica* Missarzhevsky, 1973, *P. cultrata* Missarzhevsky, 1977, and *P. triangula* Missarzhevsky and Mambetov, 1981 (see Missarzhevsky and Mambetov 1981; Missarzhevsky 1989), but by only 2–3 poorly preserved specimens of each (Text-fig. 8D–F). Qian and Bengtson (1989, p. 67) and Brasier (1989, p. 125) suggested that several kinds of sclerites were represented in the same protohertzinid animal but this cannot be tested with such a small sample.

There are also two unnamed species of bradoriids represented in the sample (Text-fig. 8A–C). Bradoriids were ostracod-like early arthropods with poorly differentiated tagmation. One of the Koksu species had a prominent tubercle close to the anterior margin of the valve which, being more strongly scleritised, is better represented in the residue than the complete thin phosphatic lining of the whole valve. The tubercles probably housed eyes (Shu *et al.* 2000). The other species had completely smooth valves. The carapace structure is not similar to that of associated sclerites of *Mongolitubulus*. Together, although well preserved, the bradoriids represent only 1 per cent of the assemblage. These disparities in number and structure disprove any *Mongolitubulus*-bradoriid relationship proposed by Melnikova (2000).

Trilobites are represented by only small pieces of internal moulds of pleurae and spines (six specimens). Fossils of sessile benthic organisms are very rare. The apparently originally phosphatic *Hyolithellus* tubes (they occur in Cambrian samples with no signs of secondary phosphatisation) are represented by 53 fragmentary specimens. This amounts to only 1·3 per cent of the sample, and if *Mongolitubulus* and the other fossils noted above are secondarily phosphatised, this is a taphonomic over-representation anyway. Fragmentary acrotretid (1 per cent) and lingulid (0·2 per cent) brachiopod shells were also originally organo-phosphatic. No doubt the brachiopods and *Hyolithellus* tubes, represented by small pieces of shell, were transported from somewhere else to their final resting place at Koksu. This was probably also the case with the trilobites.

The most obvious specific characteristic of the Koksu community is, thus, the lack of any indigenous passively benthic or infaunal organisms. The original community was composed almost exclusively of vagile benthos living above the sediment surface. The sediment was thus probably not hospitable for any infaunal or epifaunal life. The Koksu lobopodians, which presumably had a predatory life, could have preyed on completely soft-bodied organisms, not represented in the fossil assemblage even by sclerites.

CONCLUSIONS

The Early Cambrian phosphatic sclerites covering dorso-lateral sides of segments of the xenusian lobopodian *Microdictyon* originally contained non-phosphatised lenticular bodies within each of the holes of their network. This makes their similarity to arthropod compound eyes plausible. If the spinose sclerites in *Kerygmachela*, the Early Cambrian fossil transitional between the xenusians and anomalocarididids, were truly eyes, the gap between the *Microdictyon* ‘compound eyes’ and the real compound eyes of *Anomalocaris* narrows considerably, making homology of the xenusiid and arthropod structures likely. The *Microdictyon* sclerites are end-members of a morphologic series leading to the dorsal spines of another xenusian, *Hallucigenia*, and possibly to even more prominent spines of the problematic *Rhombocorniculum* and *Mongolitubulus*. *Microdictyon* and *Mongolitubulus* sclerites co-occur in several localities, and in the Koksu locality are associated with other rare organisms that actively moved above the sediment surface. They were thus possibly ecologically related. If truly a lobopodian, *Mongolitubulus* would resemble the most generalised and probably the oldest member of those Cambrian articulates, *Xenusion*.

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