A problematical trilobite from the Lower Cambrian of Freuchen Land, central North Greenland

Philip D. Lane and Adrian W. A. Rushton

A single specimen of a remarkable trilobite is described from the Early Cambrian Buen Formation of north-east Freuchen Land, central North Greenland. It is referred with doubt to *Alacephalus* Repina, 1960, as a new species *A? davisi* sp. nov. It possibly lacked eyes, which makes it one of, if not the, earliest non-agnostoid trilobite with this adaptation. Its thoracic segments have a unique morphology. In some respects the morphology resembles that of various trilobites adapted to low-energy benthic environments of low oxygenation; such trilobites tend to be widely distributed, and in agreement with this *Alacephalus* appears to be interprovincial.

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The trilobite described below was collected by Neil C. Davis from laminated, locally bioturbated, mudstones in north-east Freuchen Land (Fig. 1; Geological Survey of Greenland collection 319544) which are estimated to be not more than 5 m from the top of the Buen Formation. This formation has been interpreted as a siliciclastic shelf deposit forming part of the sequence on the southern margin of the Franklinian Basin in Greenland. In its typical development, in southern Peary Land to the south-east of the present locality, the Buen Formation has two units and varies in thickness from about 425–500 m (Jepsen, 1971; Peel, 1982; Higgins *et al.*, 1991). The lower unit is sand-dominated and is considered to have been deposited under high energy, inshore conditions; bioturbation is common, and there is a large ichnofauna (Bergström & Peel, 1988; Bryant & Pickerill, 1990). This unit is succeeded by an upper mud-dominated unit, deposited in a lower energy, outer-shelf environment. It is from this latter unit that the trilobite described below was collected, although the bipartite division of the formation is not clearly expressed in north-eastern Freuchen Land.

Age of the specimen

The Early Cambrian age is inferred from the presence elsewhere in Peary Land of olenellid trilobites within and immediately above the Buen Formation (Palmer & Peel, 1979; Higgins *et al.*, 1991). About 20 km to the north-east, in Sirius Passet across J. P. Koch Fjord, the olenellid trilobite *Buenellus higginsi* Blaker, 1988 (Family Nevadiidae) is associated with an abundant soft-bodied fauna (Conway Morris *et al.*, 1987; Conway Morris & Peel, 1990; Peel, 1990), together with large articulated sponges such as the demosponge *Choia hindei* Rigby, 1986; the same kinds of sponges are associated with the new trilobite in GGU collection 319544. However, the soft-bodied fauna from Sirius Passet appears to be derived from near the base of the Buen Formation, in contrast with the collection described here from the upper beds of the formation.

Preservation

The specimen, preserved in laminated mudstones, is flattened but not tectonically deformed. The poor state of preservation of the specimen makes interpretation of the morphology difficult; our interpretation of the various structures seen on the cranidium is shown in Fig. 3a. Diagenetic flattening has removed the original convexity, although this could not have been great since the pleural portions of the specimen, including genal and pleural spines, are stretched out in a single plane and not (even partially) folded under, as would be expected in a trilobite with a very convex cross-section. The anterior, longer pleural spines, as preserved, have longitudinal cracks, which indicates that they may have been oval or circular in cross-section. In addition they have creases at their bases which suggest that they were in life directed somewhat down and have been rotated up-

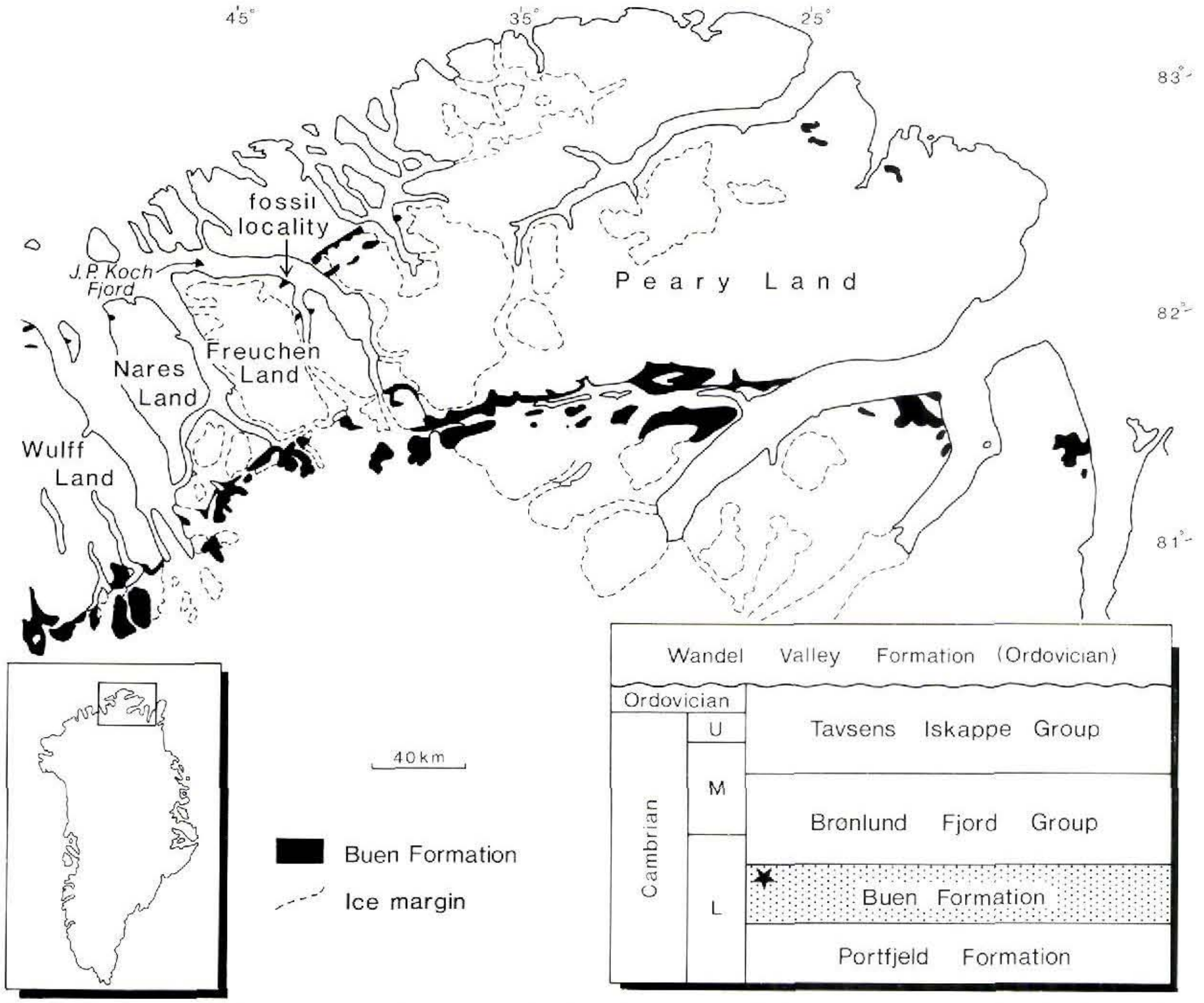


Fig. 1. Locality in central North Greenland from which *Alacephalus? davisi* was collected. The occurrence of the trilobite near the top of the Buen Formation is indicated in the inset which shows a representation of stratigraphic classification in southern Peary Land.

wards on compaction of the sediment; such an orientation of the anterior pleural spine is also indicated on a detached thoracic segment, which is preserved in cross-section and shows it directed downwards at about 25° (Fig. 3b). The shorter posterior pleural spines have a very weak crease at their bases, or lack this feature, so that it is possible that they were more nearly horizontally directed. The convexity of the thoracic axis was considerable, as also shown by the detached segment. The unusual thoracic axial lobes may have been emphasised by the flattening.

Towards the front of the cephalon what appears to be some portion of the exoskeleton (since it bears a similar sculpture to the rest of the specimen) lies across the glabella. It seems most likely that it is the right librigena displaced but not inverted (as indicated by the matching sculpture of the rest of the dorsal surface of the cephalon), possibly during moulting.

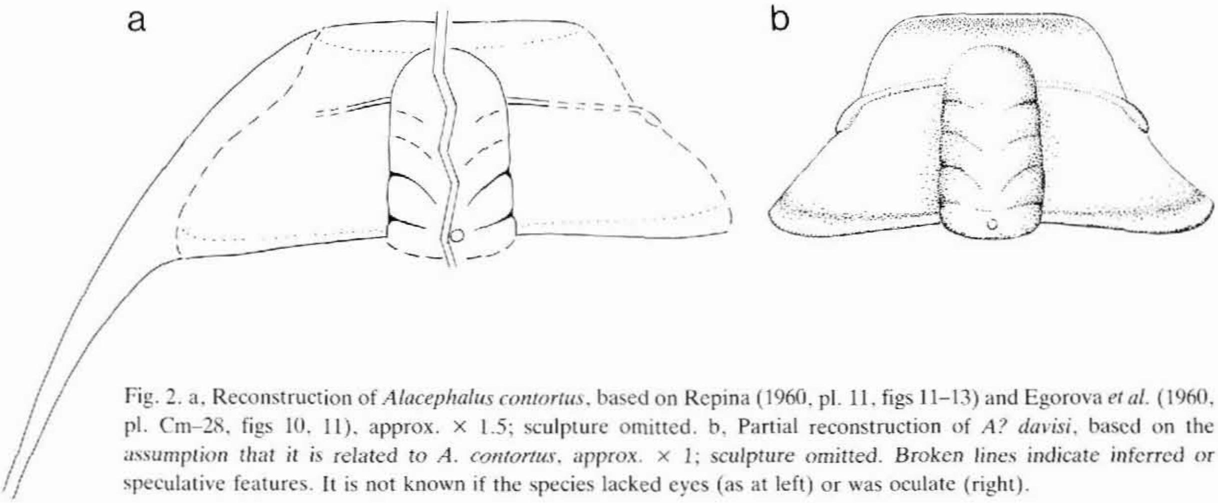


Fig. 2. a, Reconstruction of *Alacephalus contortus*, based on Repina (1960, pl. 11, figs 11–13) and Egorova *et al.* (1960, pl. Cm–28, figs 10, 11), approx. × 1.5; sculpture omitted. b, Partial reconstruction of *A? davisi*, based on the assumption that it is related to *A. contortus*, approx. × 1; sculpture omitted. Broken lines indicate inferred or speculative features. It is not known if the species lacked eyes (as at left) or was oculate (right).

Systematic description

Family unknown

Genus *Alacephalus?* Repina, 1960

Type species. Alacephalus contortus Repina, 1960, p. 222, pl. 11, figs 11–13, from the Lower Cambrian of Tuva, western Sayan, Russia (see also Egorova *et al.*, 1960 p. 247, pl. Cm–28, figs 10, 11).

Discussion. Alacephalus is a relatively large trilobite, unusual among Early Cambrian trilobites in having wide fixigenae (and thus long eye ridges), and relatively small palpebral lobes. A reconstruction of the type species (known only from the cranidium) is shown in Fig. 2a, based on Repina (1960, pl. 11, figs 11–13) and Egorova *et al.* (1960, pl. Cm–28, figs 10, 11). *Alacephalus* resembles the supposed solenopleurid *Rimouskia typica* Resser, 1938 (see Rasetti, 1955, pl. 1, fig. 10, pl. 5, figs 1–5) from the Early Cambrian of Quebec, Canada; the former, though, has oblique rather than transverse glabellar furrows, a less distinctly marked and more transverse anterior border and considerably wider fixigenae.

Alacephalus? davisi sp. nov.

Plate 1; Figs 2b, 3

Derivation of name. For Neil Davis, the collector of the specimen.

Holotype. Geological Museum of the University of Copenhagen (MGUH) 21.143 (cephalon and ?partial thorax, from GGU collection 319544); monotype.

Description. Cephalon transverse. Width (tr.) of cranidium at posterior margin appears to be nearly three times the length (sag.). Glabella apparently subparallel-sided, broadly rounded in front, apparently reaching the indistinct anterior border furrow, nearly one-fifth of cranidial width at occipital ring. Occipital ring is poorly preserved so that its length is unknown; a median occipital tubercle (or spine base) interrupts the occipital furrow. S1 narrow but distinct, inclined back and inwards at about 45°; L1 subtriangular, nearly one-third of preoccipital glabellar length. Preservation is such that S2 and S3 are not seen. Axial furrow narrow and rather less distinct than S1; preglabellar furrow indistinctly seen. Fixigena relatively very broad, posteriorly at least one and three-quarters as wide as glabella at L1. No eye has been detected but a short section of an ocular ridge is preserved; it cannot be traced far abaxially. No facial suture is seen, but it evidently lay at least as far out as the trace of the doublure. The lateral margin of the specimen is interpreted as a slightly displaced pair of librigenae of which only the doublure is evident in the form of a furrow-like structure parallel to the lateral margin. Posterolaterally, the adaxial part of a stout genal spine is preserved; it is directed out and back, extending back at least as far back as the axial ring of the 7th thoracic segment. An area occupying the midpart of the glabella which lacks the sculpture of the dorsal surface of the exoskeleton is interpreted as the trace of the inner surface of the hypostome (Plate 1c). It

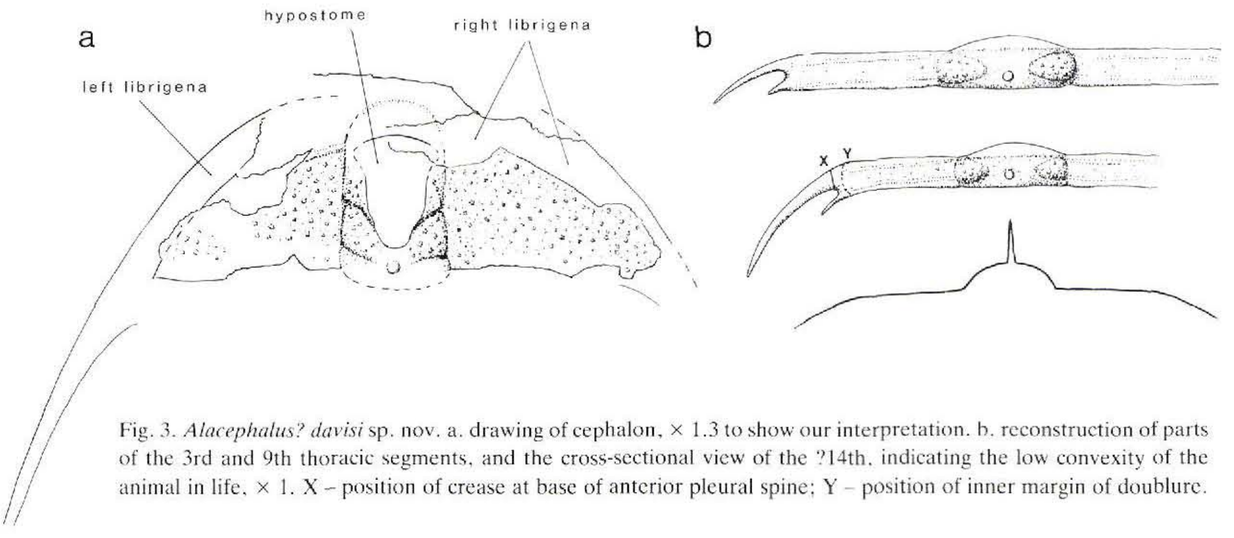


Fig. 3. *Alacephalus? davisi* sp. nov. a. drawing of cephalon, × 1.3 to show our interpretation. b. reconstruction of parts of the 3rd and 9th thoracic segments, and the cross-sectional view of the ?14th, indicating the low convexity of the animal in life, × 1. X – position of crease at base of anterior pleural spine; Y – position of inner margin of doublure.

is more or less parallel-sided, with small wings anteriorly and with semicircular outline posteriorly; it is one-half the width and about two-thirds the length of the pre-occipital glabella, and has evidently been displaced backwards, its posterior margin now arrested against the S1 furrows, so that its anterior margin is well posterior of the front of the anterior lobe of the glabella.

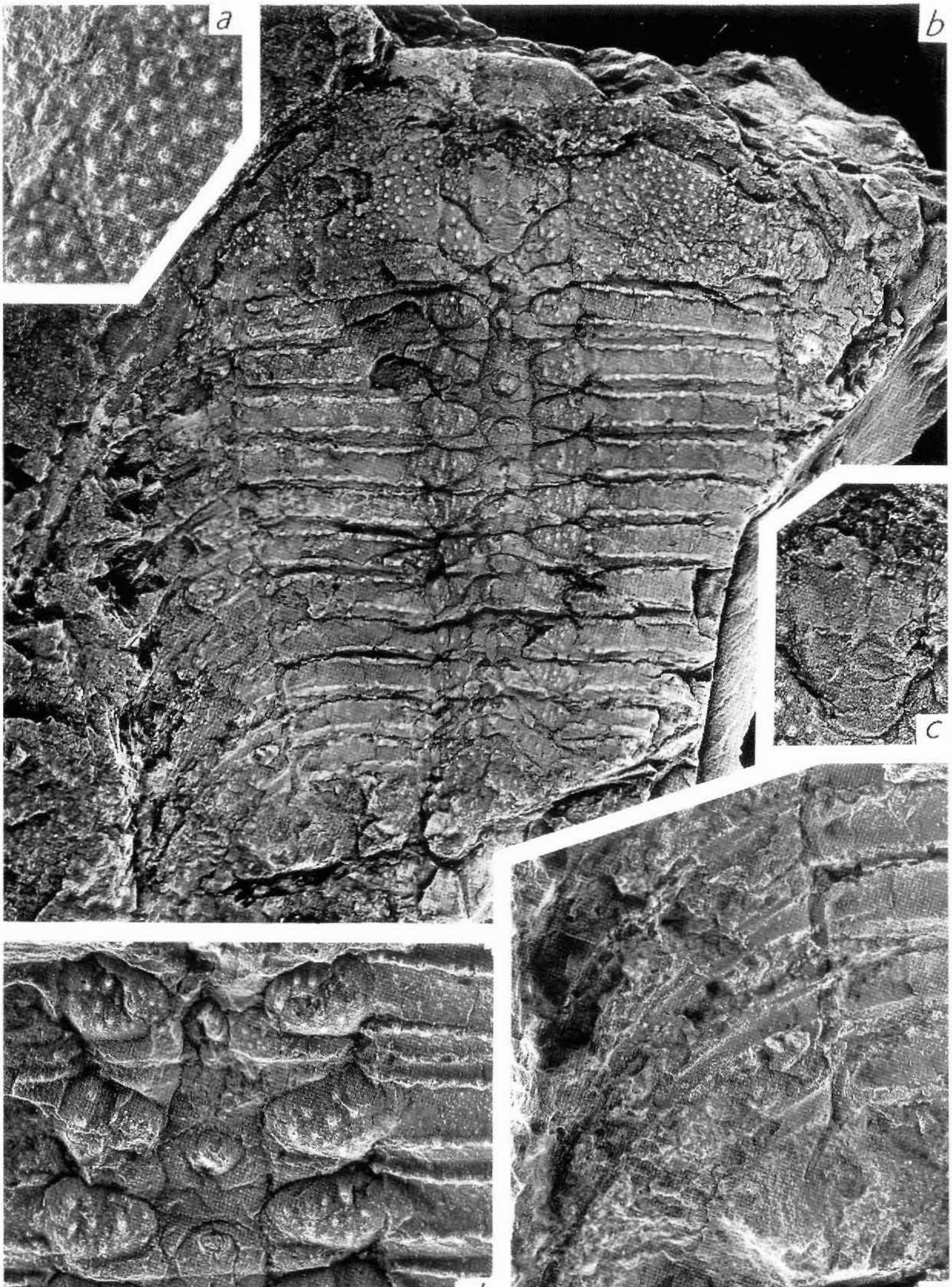
Thorax of at least 12 segments, which have an axial ring less than one-third the total width (excluding pleural spines). Each ring (Plate 1d) appears to have lateral, paired, transversely elongate, oval lobes which occupy nearly the full length (exsag.) of the ring abaxially, and taper to cover the lateral one-third of the ring (Plate 1d; Fig. 3b). Articulated portion of pleural part of segment, each of which is a little wider (tr.) than the axis, is transverse. Pleural furrow wide (exs.) and transverse, and delimited by two very narrow (exsag.) ridges placed close to the segmental boundary; these are in the position of, and may have accommodated, the pleural veins (Öpik, 1961). Each segment possesses a concave anterior flange which underlies the posterior flange of the segment in front (e.g. Plate 1, right pleura of sixth, and left pleura of seventh segments (cf. Whittington, 1990, p. 40). The abaxial end of each pleura has two spines (Plate 1e; Fig. 3b); the anterior arises from the anterior half of the pleura and is the longer, being of length equal to or greater than the width of the axis; these longer, anterior spines curve back and gently outwards at about 35° to the transverse direction. The posterior spines are much shorter, perhaps one-third or one-quarter the length of the anterior, and are straighter; they appear to arise from the abaxial end of the articulating ridge. Both spines progressively become longer and more backwardly-directed towards the posterior of the thorax. The inner margin of the thoracic doublure lies just abaxial to the bases of the pleural spines (Fig. 3b).

Eleven thoracic segments remain articulated with the cephalon; a twelfth segment appears to lie on its posterior edge with its axial spine in the plane of the bedding. The trace of the pleural regions of this segment lies almost in a straight line, suggesting that in life they were nearly flat and horizontal (Fig. 3b) with the pleural spines gently declined. The width of the axis of this segment is rather narrower than that of the eleventh, and suggests that this may be the fourteenth segment or thereabouts.

Pygidium and other parts of the exoskeleton not known. The whole surface is covered by irregularly-spaced granules. These granules vary greatly in size, but the appearance is dominated by the larger ones (Plate 1a).

Plate 1.

Alacephalus? davisi sp. nov.
MGUH 21.143 from GGU collection 319544, from the Early Cambrian Buen Formation of Freuchen Land, central North Greenland. a. sculpture of right fixigena, × 4. b. the incompletely-preserved holotype, dorsal view × 1.5. c. sculptureless imprint of ventral(?) surface of hypostome; the strong oblique furrows are due to the posterolateral margin of the hypostome resting against the S1 lateral glabellar furrows, × 3. d. axial rings of thoracic segments 1–3, × 3. e. paired left pleural spines of segments 8–11, × 3.


a
b
c
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e

Discussion. As discussed below, the new trilobite *Alacephalus? davisi* is of particular interest on two counts. First, it is one of the earliest occurrences of a small eyed or eyeless trilobite; perhaps only the Early Cambrian *Atops* is of similar antiquity (Howell & Stubblefield, 1950). Second, features of the construction of the thoracic segments make a unique combination amongst trilobites, though individually the features are known in other unrelated groups. The taxonomic position of this specimen, therefore, is unclear not only because of the uncertainties caused by the poor preservation of such critical features as the glabellar furrows and facial suture, but also because of some of the observed morphological characters which are unusual amongst trilobites.

1) The long glabella reaching the anterior border furrow, coupled with the oblique glabellar furrows.

2) Among Lower Cambrian trilobites, the lack of long eyes.

3) The lobate structure of the thoracic axis.

4) The two pairs of pleural spines on each thoracic segment, of which the anterior are longer than the posterior.

The glabellar form and S1 furrows, and the lack of long eyes, are features that induce us to refer *davisi* to *Alacephalus?* It differs from *A. contortus* in having a much longer L1 and a wider interocular area of the fixigena (i.e. it is wider to the posterior of the eye ridge); in *A. contortus* the interocular area of the fixigena is about equal in width to the width of the glabella in the same line, whilst in *A? davisi* it appears to be not less that one and a quarter times as wide as the glabella. The wide fixigenae resemble those of *A. latus* Romanenko (1978, pl. 32, figs 16–19) which is from the Early Cambrian of Altai, Russia. In this latter species, however, the glabella tapers anteriorly somewhat and the ocular ridges are not oblique but nearly transverse. The librigenae of *A. latus* lack the strong spine of *A? davisi*. The pygidium assigned to *A. latus* has a few thoracic segments attached and these have normal pleurae, resembling, for example, *Solenopleura*, and not resembling those of *A? davisi*.

The shape of the glabella and its contact with the anterior border furrow, and the thin transverse eye-ridges recall *Atops* and *Pseudatops* (Howell & Stubblefield, 1950, pl. 1, fig. 3; pl. 2, figs 1, 2). *A? davisi* differs in having the glabellar furrows more oblique and in its thoracic structure. *Gelasene acanthinos* Palmer (1968, pl. 2, figs 1–3, 5, 6; text-fig. 6) differs in having a tapered glabella that is pointed in front, and a definite (though short) preglabellar field. The anterior segments of the thorax show some resemblance to that of *A? davisi* in having two spines on each pleura; it differs in that the base of the smaller (posterior) spine is not terminal but is situated adaxially (arising near the pleural fulcrum) compared with that of the larger spine.

The eyes of *A? davisi* may have atrophied entirely, but if eyes were present, they were positioned well out from the glabella and well forward of the posterior margin (Fig. 2b). As described above, it is thought that the facial suture must have been largely marginal or intramarginal. This type of morphology is homoeomorphic with that of trilobites which occur in offshore, mudstone-dominated facies; examples include *Lehua* (see Whittington, 1963, p. 84, pl. 23, figs 1–12; Lane, 1971, p. 36, pl. 7, fig. 17) certain olenids (e.g. Henningsmoen, 1957, pls 3–8; Fortey, 1974, p. 11) and the eyeless dalmanitid *Mucronaspis (Sonxites) cellulana* (Siveter *et al.*, 1980, p. 201, figs 4, 5). Although distinctive, it is not a morphology likely to aid taxonomic placement.

Remarks on the thoracic structure

The structure of the thorax bears similarities to a range of genera. The bilobed axial rings are, however, unusual. Henningsmoen (1957) referred to the structure of an occipital ring of the same general form as that of *davisi* as 'composite', as in for example *Ctenopyge (Ctenopyge) affinis gracilis* Henningsmoen (1957, p. 201, pl. 19, figs 20, 21); that such a structure may have been present in *A? davisi* is inferred from the structure of the thoracic axial rings. Its function is unknown, but insertions for musculature is an obvious possibility. Oblique apodemes on the axial rings of *Ceratocephala barrandii* were described by Thomas (1981, p. 95). These occupy a similar position to the furrows bounding the lateral axial bilobes in *davisi*, but the homology of the structures cannot be assumed.

The thoracic pleurae of *A? davisi* are wide (tr.) and flat and the pleural ridges may have accommodated well-developed propleural and opisthopleural veins. This structure is similar to certain trilobites which, though not closely related, are all thought to be adapted to conditions of low oxygenation, e.g. *Papyriaspis lanceola* (see Öpik, 1961, pl. 68, figs 1, 2), *Parabolina heres* (Rushton, 1982, pl. 2, figs 15–18) and *Hedinaspis regalis* (Palmer, 1968, pl. 15, figs 21, 22).

Double pleural spines are present in various unrelated trilobites including Xystriduridae, ?Solenopleuridae, ?Dorypygidae and Odontopleuridae. In some Xystriduridae (*Polydinotes* and *Galahetes*; Öpik, 1975, p. 30, figs 7B, C) the pleural tips have two spines of which the anterior is larger, as in *A? davisi*. The differences in the cranidia indicate that *A? davisi* is not closely related to the Xystriduridae. Double marginal spines occur on a *Dorypyge* pygidium (Fortey & Rushton, 1976, pl. 11, fig. 2). The anterior spine is the smaller; this structure may prove to be repeated on the thoracic segments as is the case in the thoracic and pygidial spines of *Galahetes fulcrosus* Öpik (1975, text-figs 7c, 13; pls 16–20). As noted above, the solenopleurid? *Gelasene* (Palmer, 1968, p. 81, fig. 6) has pleural spines and spines on the fulcra of each thoracic segment.

Double pleural spines occur commonly also in odontopleurid trilobites; Chatterton & Perry (1983) described such spines in 21 species belonging to 10 genera and subgenera of the family. In some, anterior and posterior pleural spines occur on all thoracic segments (e.g. *Odontopleura brevigena* Chatterton & Perry (1983, text-figure 13). In every case the anterior spine is shorter than the posterior; the opposite of the case in *davisi*, and each increases in size in more posterior segments. In some cases the posterior spine is longer than the articulated portion of the same segment. For example, the posterior pleural spine of the posterior segment of *Diacanthaspis (Diacanthaspis) hollandi* Chatterton & Perry (1983, text-fig. 36) is more than twice as long as its articulated portion. Both these characters, i.e. the progressive increase in size of spines posteriorly and the consequent greater relative length of the (posterior) pleural spine compared to the articulated portion of its pleura, are particularly well displayed by the widespread *Odontopleura ovata* Emmrich, 1839 (see Prantl & Přibyl, 1949, p. 138, pl. 1, figs 1–4, pl. 7, fig. 1; Whittington, 1956, p. 197, fig. 4). This species, originally described from the Late Wenlock of Czechoslovakia, also occurs in the *murchisoni* biozone (Sheinwoodian, Early Wenlock) of North Wales, and the Wenlock to Early Ludlow of Silesia, Poland. In other forms, twin pleural spines occur on the posterior segment only; *Ceratocephala barrandii* (see Thomas, 1981, p. 95, pl. 25, fig. 2b; text-fig. 10) is one such.

Functional morphology

The functional significance of double pleural spines remains uncertain. As those species which possess this feature all have relatively wide pleural regions of low convexity, some correlation with the character of the substrate might be expected to be reflected in the occurrence of these forms in similar lithofacies, possibly deposited in similar sedimentary environments. The majority of the instances given above which have true double pleural spines (*A? davisi, O. ovata* and the odontopleurids described by Chatterton & Perry) occur in sediments interpreted on other grounds to have been deposited in outer shelf to slope environments; *post mortem* transport can be ruled out since articulated specimens occur in all three examples. The dorypygid and *Galahetes* both occur in carbonate sequences, the latter deposited in "euphotic and eutrophic waters habitable down to the sea floor" (Öpik, 1975, p. 5). The only similarity of all the cases is the fine grained nature of the matrix in which the specimens occur; this provides no explanation of the double spine as a structure, nor lends any clues to an explanation of their function.

Significance in provinciality

In reconstructions of Early Cambrian faunal provinces (e.g. Pillola, 1990) North Greenland lies in the faunal province characterised by olenellid trilobites whereas the Altai-Sayan fold belt of Siberia, from which *Alacephalus cortortus* and *A. latus* come, lies in the Bigotinid Province (which also contains redlichiids). Generally speaking, there are few or no genera of trilobites in common between these provinces; if *A? davisi* proves to be correctly assigned to *Alacephalus* it constitutes an exception. However, trilobites which occupied outer-shelf and slope habitats are those most likely to cross provincial boundaries (e.g. Fortey & Owens, 1978; Cocks & Fortey, 1990), and it is postulated that *A? davisi* is an example of such a trilobite.

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