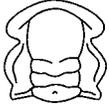


Trilobites within nautiloid cephalopods

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'Sheltered preservation' of the remains of trilobites within the shells of nautiloid cephalopods is not especially uncommon. In most cases, of course, both the trilobites and the nautiloids were dead, and the association, merely due to *post-mortem* happenstance. However, on the basis of state of preservation and occurrence, a number of live individuals of the trilobite genera *Acidaspis*, *Flexicalymene*, and *Isotelus* from the Ordovician of the United States and of *Alcymene* and *Encrinuraspis* from the Silurian of Wales and the Czech Republic seem to have entered conchs of dead cephalopods, presumably for refuge. □ Behaviour, nautiloid cephalopods, taphonomy, Trilobita.

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Empty cephalopod shells on the sea floor would have been ideal hiding places for animals in danger of predation. This would have been especially so for potential victims unable to burrow and hide in the soft sediments of a sea floor. Indeed, in some environments, empty cephalopod shells might have been the only suitable shelters from predators. On the other hand, such empty conchs might have provided ideal lairs from which a predator could have pounced on passing prey.

A number of occurrences of organisms that apparently sought shelter within conchs of Mesozoic ammonoids have been reported. For example, Matsu-moto & Nihongi (1979) and Maeda (1991) described ammonites within ammonites; Fraaye & Jäger (1995a) discussed fishes in like circumstances; and Fraaye & Jäger (1995b) reported on lobsters within ammonite conchs.

Present-day analogues involving other classes of molluscs have been reported too. Walker (1992), for example, documented hermit crabs in gastropod conchs. Schmitt (1965, p. 142) reported on amphipod crustaceans of the genus *Siphonectes* in shells of the scaphopod *Dentalium*. And reef-dwelling stomatopods commonly use empty gastropod shells as domiciles and as brooding sites (Reaka *et al.* 1989; Zuschin & Piller 1983). Moreover, Brett (1977) discussed and figured a trilobite within a closed brachiopod shell from the Devonian of New York.

There have been occasional reports of Palaeozoic orthoconic cephalopods from Europe and North America that each have one or more trilobites in the

body-chamber (or otherwise closely associated with the conch). However, examples of this phenomenon have not been extensively discussed or well illustrated. Hence, this paper.

When one is presented with specimens of trilobites in cephalopod body-chambers, the question immediately arises as to whether the trilobites were alive within the cephalopod conchs and, if so, what they were doing there.

Various kinds of organic material potentially could be found within a given cephalopod conch. The most obvious possibility, of course, is the remains of the cephalopod that secreted the shell (for example, jaw elements and radulae (Nixon 1996)) and, perhaps, its unhatched eggs or hatched progeny. Aside from such remains or products of the cephalopods themselves, there are at least six types of what has been called 'sheltered preservation' that might occur within cephalopod conchs:

1. Crop/stomach/gut contents of the cephalopod animal (e.g. Fraaye & Jäger 1996).
2. Organisms that lived within the living cephalopod (for example, as endoparasites).
3. Organisms that deliberately entered shells of dead cephalopods for food, refuge, ecdysis, reproduction, lodging, and so on (e.g. Mikulic 1994).
4. Food or other matter brought in by the organisms itemized above (e.g. Jäger & Fraaye 1997).
5. Fecal matter, shed exoskeletons, spawn, and so on, deposited or left by such organisms (e.g. Fraaye & Jäger 1995b; Kaiser & Voigt 1983).



Fig. 1. *Encrinuraspis beaumonti* (Barrande, 1846) in *Sphooceras truncatum* (Barrande, 1868) Flower, 1962. *Encrinuraspis beaumonti* horizon, Kopanina Formation (Ludfordian Stage, Ludlow Series, Silurian). Zadní Kopanina (Dlouhá Hora), Czech Republic (Národní Museum, Prague, Czech Republic, number L 16830; figured specimen [the trilobite]: Barrande, 1872, pl. 9, figs. 24–26; Šnajdr, 1990, pp. 206–207; Kríz, 1992, pl. 1, fig. 18), $\times 1.1$.

6. Organisms or parts of organisms carried into cephalopod shells by *post-mortem* transportation (e.g. Luppold *et al.* 1984, pl. 1, fig. 3).

There are many kinds of relationships between and among living things. ‘Symbiosis’, as used by Cheng (1967) and many others, has been employed for ‘all types of heterospecific associations, excluding predation, during which there exists physical contact or intimate proximity between the two members’ (Cheng 1967, p. 4). Within this general category, a significant boundary has been drawn between relationships involving metabolic dependence and those not involving such dependence (for example, mutualism and parasitism, which do, versus commensalism and phoresis, which do not). However, as Gotto (1969) noted, ‘Unfortunately, authors find the greatest difficulty in using these terms in a precisely similar manner, and the same association will often be described under different headings according to the authority consulted’ (Gotto 1969, p. 14).

This paper reports on what appear to have been live trilobites within the body-chambers of dead cephalopods. Gotto (1969, p. 15) used the term ‘inquilinism’ for ‘organisms which live together, one within the other, the former using the host animal mainly as a refuge’. Similarly, Morton (1989, p. 10) applied ‘inquilinitism’ for ‘those associations in which one animal lives within another, doing the host little or no harm, but simply using it as a place of more or less permanent refuge’. Both of these are extensions of the use of the term ‘inquiline’ by Butler (1879) for animals that live within a gall along with the insect larva that formed it (this, according to *The Oxford English Dictionary* (Simpson & Weiner 1989, 1992), is the original zoological use of the term ‘inquiline’).

An underlying assumption of all of these is that both the inquiline and the host are alive at the time of the association. However, as pointed out by Holland

(1971), in the realm of palaeontology, it commonly is a problem to establish that the ‘host’ actually was alive at the time of the association. Fraaye and Jäger (1995a, b) have described and illustrated examples of fishes and decapod crustaceans in the body-chambers of Jurassic ammonites from Germany and England. For these associations, they used the term ‘inquilinitism’. In cases like these Jurassic examples, and of those of trilobites found in the body-chambers of nautiloid cephalopods, which we describe below, it is clear that the fishes and arthropods in question were associated with the shells of dead cephalopods. Thus, strictly speaking, the term ‘inquilinitism’ is inappropriate, although it is the closest technical term in general use.

Material

Encrinuraspis beaumonti in *Sphooceras truncatum*

Specimen number L 16830 in the Národní Museum, Prague, is an orthoconic nautiloid from the *Encrinuraspis beaumonti* horizon, Kopanina Formation (Upper Silurian, Ludfordian Stage) of the Czech Republic; it is about 18 cm long (Fig. 1). The cephalopod consists of a relatively complete body-chamber (11 cm long) with an incomplete phragmocone. The trilobite is 3.4 cm long by 1.8 cm in maximum width and is located almost at the centre of the body-chamber. The trilobite is oriented with its anterior end pointed apically and with its longitudinal axis about 15° to that of the cephalopod. The thorax and the pygidium are connected. The cephalon is slightly separated from the thorax, with three segments missing; this dislocation at the cephalo-thoracic joint is indicative of a body-upright moult procedure, as described by Speyer (1985, p. 246, figs. 7h–l).

Fig. 2. ?*Treptoceras* sp. with *Flexicalymene meeki* (Foerste, 1910). No primary data, but almost certainly from the Cincinnati (Upper Ordovician) of the Cincinnati, Ohio, USA area (Orton Geological Museum, Department of Geological Sciences, Ohio State University, Columbus, Ohio, USA; OSU 50329), $\times 2$.



This specimen was reported originally by Barrande as ‘... conservé dans l’intérieur de la grande chambre d’un exemplaire de *Orthoc. truncatum*’ (1872, caption to pl. 9, figs. 24–26). However, the position of the trilobite within the cephalopod was not illustrated by Barrande or in later works (Šnajdr 1990, pp. 206–207; Kříž 1992, pl. 1, fig. 18).

Flexicalymene in ?*Treptoceras* *duseri*

Described below are three orthoconic nautiloids from the Upper Ordovician of the Cincinnati region that have trilobites of the genus *Flexicalymene* associated with them. The cephalopods are specimens of what, in the Cincinnati area, is traditionally called *Treptoceras duseri*; according to Teichert (1964, p. K214) *Treptoceras* is a junior subjective synonym of *Orthonobyoceras*, although not all workers concur (Aronoff 1979).

Specimen OSU 50329. – The cephalopod is mostly an internal mould (Fig. 2). It is about 5 cm long and is 1.4 cm in diameter at one end and 1.8 cm at the other. There are nine camerae in a length of about 4.1 cm (for an average inter-septal spacing of under 0.5 cm), but there are no septa visible in the adapertural 0.8 cm of the specimen. The septa extend only about one-half of the ‘height’ of the specimen, with the trilobites ‘above’ the edges of the septa.

There are at least three specimens of *Flexicalymene* present (three cephalons are visible). The first trilobite is about 0.8 cm from the adapical end of the conch. Although both the anterior and posterior ends are slightly embedded in matrix, it is apparent that the animal is about 2.2 cm long. It is oriented dorsum-outward, with the cephalon adapertural and the plane of symmetry at about 40° to the axis of the conch. Most of the glabella and the right side of the cephalon are buried in the matrix inside the conch of the

cephalopod. The left side of the cephalon is somewhat eroded, but can be seen to overlap the first thoracic segment on that side.

The second trilobite is about 2.4 cm long and is adjacent to the adapertural end of the cephalopod. It is oriented dorsum-outward, with the cephalon adapertural and with the plane of symmetry about 50° to the axis of the conch. The pygidium is curved downward. The cephalon is fixed slightly downward and is bent to the right, so that its posterior overlaps the first two thoracic segments on that side. There is another slight bend to the right after the fourth thoracic segment. Behind the right eye are two cracks that affect the glabella, the fixigena, and the librigena; movement along one of these has resulted in a slight opening of part of the facial suture, but both facial sutures are closed at the genal angles.

The third trilobite, at first glance, appears to be an isolated cephalon lying between the other two trilobites. In fact, the thorax is buried in the matrix. The trilobite is oriented venter-outward and is fixed so that the anterior end is pointing outward. The cephalon is somewhat damaged, but the right facial suture is virtually intact at the genal angle, and the left one is intact at the anterior end (the left genal angle is not visible); the hypostoma is present and nearly in place, if not actually so. The thorax is under specimen no. 2. If the pygidium is present, it is buried in the matrix.

Specimen OSU 50330. – The cephalopod consists of part of 10 camerae and the body-chamber (Fig. 3). The ultimate camera is not as distinct as are those adapical of it, but no septal approximation is apparent. What is present of the cephalopod is about 14.5 cm long; the specimen is somewhat flattened, with maximum ‘diameters’ of about 2.5 and 4.5 cm at either end. The body-chamber appears to be slightly constricted aperturally, but no peristome is present. There is a

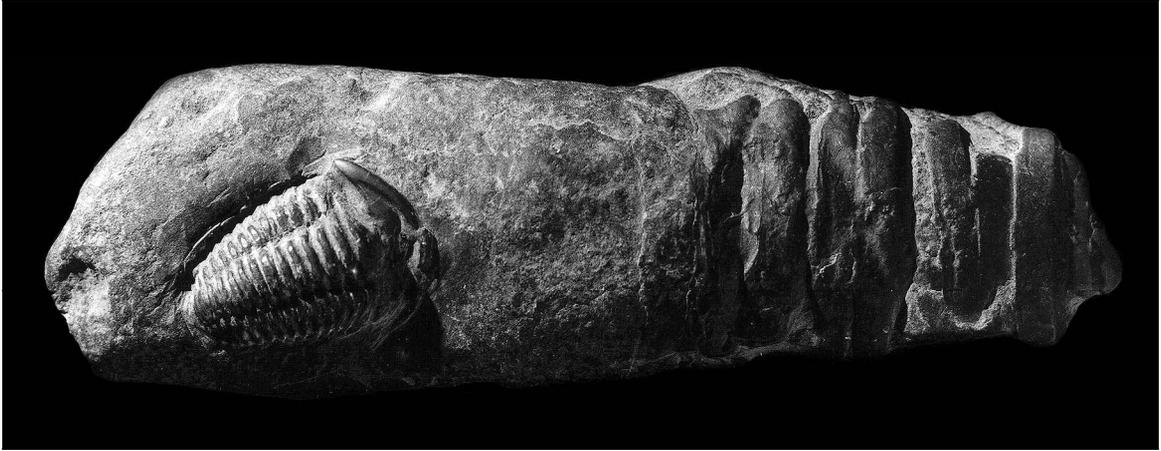


Fig. 3. ?*Treptoceras* sp. with *Flexicalymene meeki* (Foerste, 1910). No primary data, but almost certainly from the Cincinnatian (Upper Ordovician) of the Cincinnati, Ohio, USA, area (Orton Geological Museum, Department of Geological Sciences, Ohio State University, Columbus, Ohio, USA; OSU 50330), $\times 1$.

small patch of a bryozoan colony near the adapical end of the specimen.

There is a single specimen of *Flexicalymene* on the filling of the body-chamber, dorsum-outward. Some time in the past, some of the matrix was curatorially carved away from around the edges of the trilobite. The trilobite is oriented with the cephalon adapical and with the plane of symmetry at about 20° to the axis of the cephalopod. The trilobite is not perfectly articulated – the cephalon is flexed to the right and has been rotated so that its posterior is under the anterior end of the thorax; thus, the right side of the cephalon is mostly concealed. The left librigena, if present, is under the thorax on that side. The length of the trilobite is at least 3.4 cm (this value is somewhat low, because the cephalon is telescoped beneath the thorax).

Specimen CiMNH P193. – The cephalopod apparently is a piece of body-chamber; at least, there are no septa visible (Fig. 4). It is oval in cross-section, with major and minor axes of 3.3 and 2.2 cm, respectively; the preserved length is some 3.9 cm.

There is a single specimen of *Flexicalymene*, about 2.4 cm long, at the surface of the internal mould, oriented dorsum-outward. The long axis of the trilobite is essentially straight and is almost parallel to the length of the conch, but the condition of the cephalopod is such that it is not clear which end of the cephalopod is adapertural. The trilobite appears to be complete, although it is not totally free of matrix. The cephalon looks to be attached to the thorax, and the facial suture on the right side, to be closed; that on the left is not really visible. The pygidium seems to be attached to the thorax.

Acidaspis in ?Treptoceras duseri

Specimen CiMNH P2257. – This specimen, although lacking primary locality information, almost certainly is from the Upper Ordovician of the Cincinnati area. The cephalopod includes seven camerae and part of the body-chamber (Fig. 5). The diameter of the conch ranges from 3.5 to 4.1 cm, and the preserved length is about 11.5 cm; the body-chamber part is about 6.5 cm long.

There are two more-or-less complete specimens of *Acidaspis* plus a fragment of the pygidium of a third. Both of the first two specimens are fiat against the matrix of the cephalopod. All sutures of both are closed, including that between the cephalon and the thorax. Again the dorsal surfaces are facing outward.

The first trilobite is about 1.6 cm long, not counting the spines. It is in the phragmocone, in the adapertural-most two camerae. The cephalon is adapical, and the trilobite is oriented about 45° to the axis of the conch.

The second trilobite is about 1.3 cm long, not counting the spines. It is in the body-chamber, in the most adapical part. The trilobite is almost directly transverse to the axis of the conch. The rearmost left thoracic spine is in contact with the left pygidial spine of the other trilobite.

The third trilobite is a fragment of a pygidium, oriented venter-outward. It is about 1.5 cm adapertural of no. 2 and, like no. 1, is apparently at about 45° to the axis of the conch.

Isotelus gigas in an orthocone

Specimen SUI 9176. – This specimen is from the

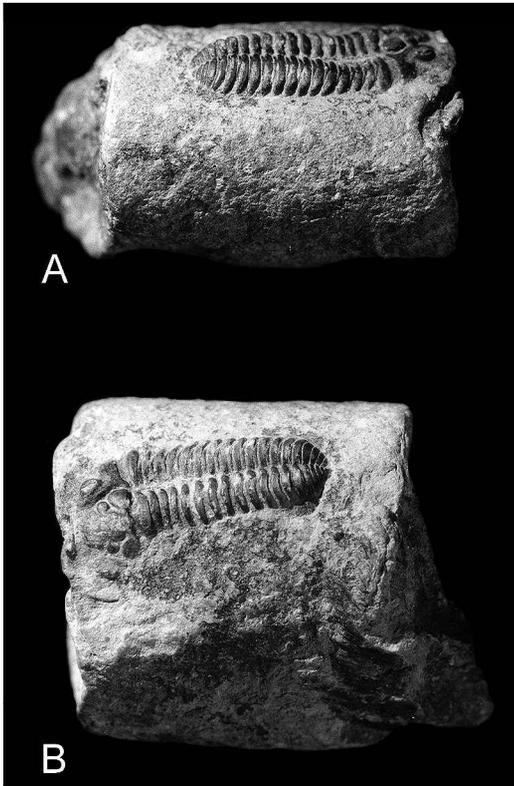


Fig. 4. Portion of a living-chamber of *?Treptoceras* sp. with *Flexicalymene meeki* (Foerste, 1910). No primary data, but almost certainly from the Cincinnatian (Upper Ordovician) of the Cincinnati, Ohio, USA, area (Cincinnati Museum Center (which includes that which formerly was the Cincinnati Museum of Natural History), Cincinnati, Ohio, USA; CiMNH P193), $\times 2$. □A. Oblique view of trilobite. □B. Dorsal view of trilobite.

Ordovician of Iowa (Fig. 6). The cephalopod is a poorly preserved piece of what appears to be an annulate orthocone. There are no septa visible, and it is not clear which is the adapertural end. The preserved part is about 15 cm long and 5.6 cm in diameter.

The trilobite is virtually complete and intact and is about 3.3 cm long. It is in the middle of the matrix and is oriented parallel to the axis of the conch. It is slightly flexed longitudinally, with its dorsum concave.

Phacops *in* *Acleistoceras*

Specimen SUI 94473. – This specimen was collected from the Middle Devonian of Iowa. The cephalopod has a maximum diameter of about 8 cm and is about the same length (Fig. 7). The specimen consists of body-chamber and parts of two camerae.

The trilobite is a solitary cephalon about 2.7 cm wide. It is located some 3.5 cm from the last septum and about the same distance from the adapertural end of the cephalopod. There is no sign of the thorax, but beneath the cephalon and separated from it by about 0.7 cm there is a piece of what may be a pygidium.

Alcymene puellaris *in* *an orthocone*, *cf.* *Polygrammoceras bullatum*

Specimen number TCD 35928 in the Trinity College Geological Museum, Dublin, consists of the body-chamber only of a cephalopod with two trilobites. When it was discovered during a meeting of the Ludlow Research Group in 1992 in Upper Silurian rock of South Wales, only one trilobite was visible; Dr. Derek Siveter developed the specimen; in so doing, he was obliged to destroy a small, enrolled specimen of the same trilobite, but revealed beautifully the two individuals shown in Fig. 8.

The body-chamber is partially preserved as the convex surface of an internal mould in siltstone. The preserved length of the body-chamber is 9.0 cm. Its width, seen centrally, is 2.9 cm. The rate of increase in diameter, as seen, is slight. Although unimpressive, the mould is recognisable as almost certainly belonging to

Fig. 5. *?Treptoceras* sp. with *Acidaspis* sp. No primary data, but almost certainly from the Cincinnatian (Upper Ordovician) of the Cincinnati, Ohio, USA, area (Cincinnati Museum Center (which includes that which formerly was the Cincinnati Museum of Natural History), Cincinnati, Ohio, USA; CiMNH P2257 [formerly accession no. 1228]), $\times 1$.



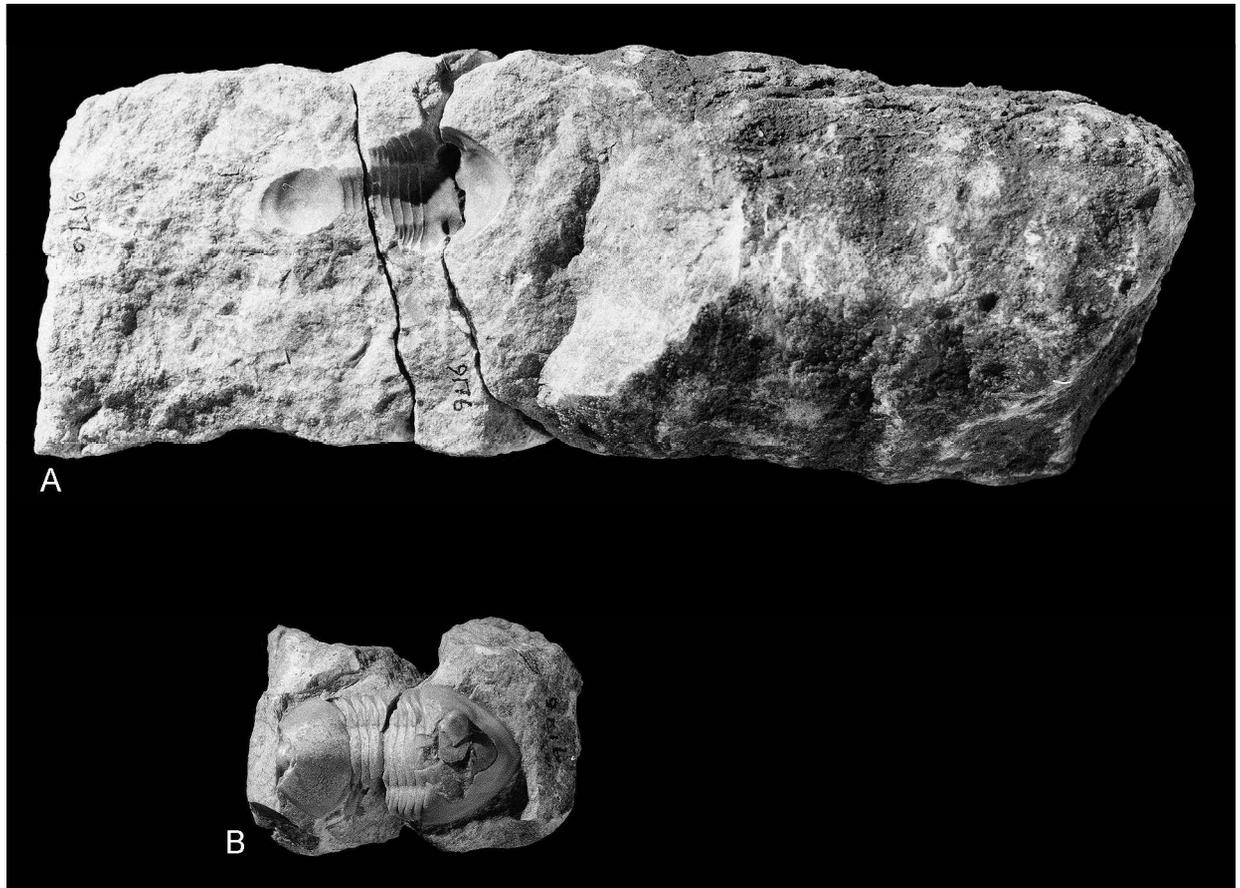


Fig. 6. *Isotelus gigas* DeKay, 1824 in a cephalopod. Plattville Fm. (Ordovician). Guttenberg, Clayton County, Iowa, USA. Collected by A. O. Thomas (The Department of Geology, University of Iowa, Iowa City, Iowa, USA; SUI 9176; figured specimen [the trilobite]: Walter, 1926, pl. 27, fig. 21), $\times 1$. □A. The cephalopod with the 'negative' of the trilobite; note that no septa are visible. □B. The trilobite.

the very common Silurian orthocone *Polygrammoceras bullatum*.

The two largely complete trilobites measure 1.75 and 1.4 cm in length, and their widths at the anterior end of the thorax are 1.0 and 0.85 cm, respectively. Both are situated at the adapical end of the body-chamber and, although facing in opposite directions, are nearly parallel to its length. It seems likely that they entered the cavity when alive. Possibly the shell was already partially filled with sediment, resulting in the fact that they are not centrally placed. In any case, the body-chamber became filled with silt like that of the matrix of the whole specimen, presumably by gentle influx. The enrolled trilobite no longer extant reinforces the view that the associated trilobites entered the orthocone when alive.

Discussion

When one is presented with specimens such as those

described above, the question immediately arises as to whether the trilobites were alive within the cephalopod conchs and, if so, what they were doing there.

In some instances, the answer seems obvious. For example, if only fragments of trilobites are present, a post-mortem accumulation seems highly likely. Even in the case of more-or-less complete, but isolated trilobite parts (like the cephalon of SUI 94473), no real case can be made for the trilobite having been alive whilst within the body-chamber.

Intact or virtually intact specimens would seem to indicate that the trilobites were alive or that the specimens are exoskeletons left *in situ* by live trilobites. The latter is not a new idea, of course. In a discussion of trilobites of the genus *Vogdesia* in the Upper Ordovician of Iowa, Ladd (1928, p. 387) stated:

Evidently the dead shells of the large cephalopods served as retreats or molting places for *Vogdesia* because rolled specimens of the trilobite can frequently be obtained by breaking the body-chambers of the cephalopods. Indeed the surest way to obtain perfect specimens is to traverse one of the small stony creek beds and crack open all the water worn cephalopods encountered.

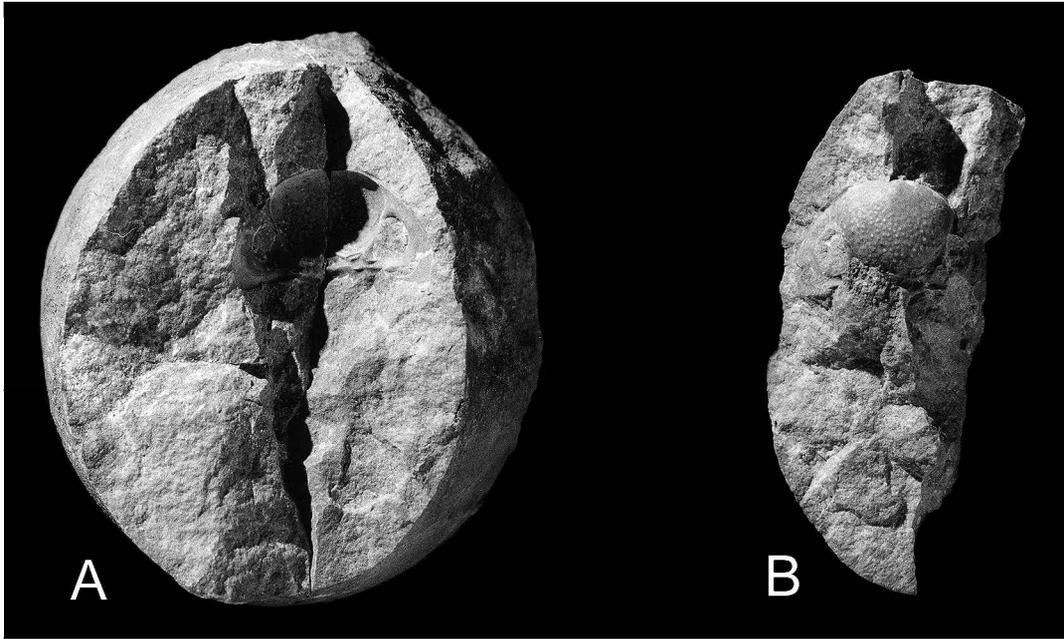


Fig. 7. *Acleistoceras* sp., with the cephalon of a *Phacops* sp. Upper part of the Solon Member, Little Cedar Formation, Cedar Valley Group (Givetian, M. Devonian). Fossil Point Locality, Coralville Lake area, near Iowa City, Iowa, USA. Collected by James E. Preslicka (The Department of Geology, University of Iowa, Iowa City, Iowa, USA; SUI 94473), $\times 1$. □A. Transverse view, looking adapically, showing the 'negative' of the cephalon of the trilobite. □B. 'Positive' of the cephalon of the trilobite.

And, nearly seven decades later, Mikulic (1994) discussed at somewhat greater length the possibility that trilobites used cephalopod conchs as refuges in which to perform ecdysis. (Unfortunately, there are no illustrations of the phenomenon in Ladd's paper, nor is a repository cited. There is a collection of his material at the University of Iowa, but there do not seem to be any of the trilobite-bearing nautiloids to which he referred.)

The Barrande specimen of *Encrinuraspis beaumonti* described above supports the moulting-refuge hypothesis. The dislocation at the cephalo-thoracic joint in this specimen is indicative of a body-upright moult procedure, as described by Speyer (1985, p. 246, figs. 7h-l).

In three of the specimens described here, the cephalopod is associated with more than one individual of the same species of trilobite (CiMNH P2257 with *Acidaspis*, OSU 50329 with *Flexicalymene*, and TCD 35928 with *Alcymene*). Such occurrences would seem to support the suggestion of Speyer & Brett (1985) that, in analogy with at least some present-day marine arthropods, trilobites assembled in monospecific, age-segregated clusters and moulted prior to *en masse* copulation.

Among the specimens discussed here, there is a great range in variation in the attitude of the trilobites within the matrix and in their location with respect to the walls of the nautiloid conchs. If there were an

empty cephalopod-shell lying on the sea floor, and a trilobite crawled in, one would expect the fossil trilobite to be found lying with its venter close to the inside of the cephalopod shell (for example, the specimen of *Isotelus gigas*, Fig. 6). That this is not the common occurrence in the specimens here presented is probably due to the original position the trilobites having been disturbed by later movement of the dead orthocone, by disturbance when sediment came into the conch, or both.

Of especial concern, however, are the instances of complete trilobites at the surface of the internal moulds of cephalopods, and even of the phragmocone-portion of the cephalopods. In OSU 50329, for example, there are two specimens of *Flexicalymene* at the surface of the specimen, one of them clearly in the phragmocone-portion. The fact that the septa extend only one-half of the 'height' of the cephalopod conjures up the image of a damaged conch lying partially filled with sediment and embedded in the sea floor, with the upper portions of the septa breached – leaving enough of a cavity to provide shelter for the trilobites. Casting doubt on this interpretation is the fact that the larger trilobite of this specimen is very large relative to the size of the cephalopod and to any opening that might have existed between the edges of the broken septa and the wall of the conch. Indeed, it looks more as though the trilobite is *on* the mould, rather than having been *within* it. In any case, the third

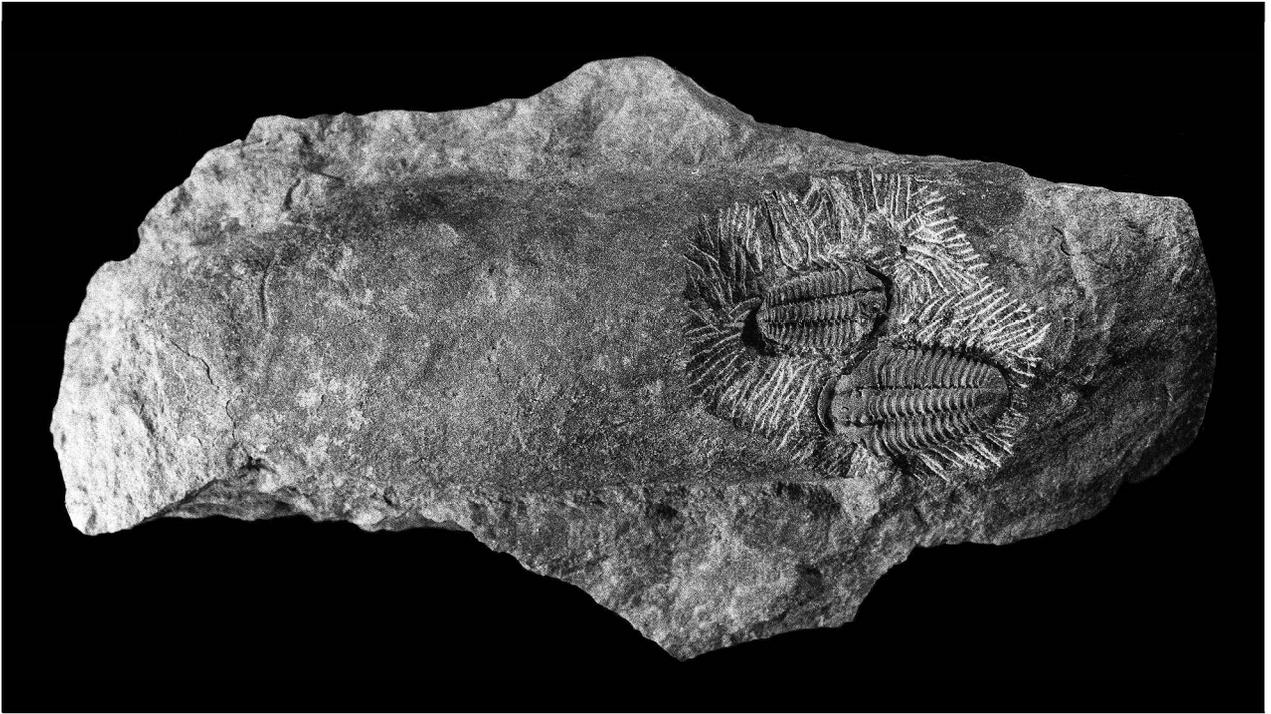


Fig. 8. *Alcymene puellaris* (Reed, 1920) in a specimen of what is almost certainly *Polygrammoceras bullatum* (J. de C. Sowerby, 1839). Lower Llangibby Beds, *Saetograptus leintwardinensis* Biozone (Ludfordian Stage, Ludlow Series, Silurian). Old quarry (ST 3650 9729), immediately south of the ruins of Llangibby Castle, Gwent, Wales. (Geological Museum, Trinity College, Dublin, Ireland; TCD 35928), $\times 1.5$.

trilobite, buried upside-down in the matrix beneath the second trilobite, but with the hypostoma in place, is puzzling, unless it is the result of prior filling of the conch, perhaps with *post-mortem* movement of the nautiloid shell. Ironically, CiMNH P2257 presents a similar picture, although involving *Acidaspis* rather than *Flexicalymene*. Again, there is a third individual oriented venter-outward – perhaps part of a shed exuvium.

The apparently frequent use of cephalopod conchs by moulting arthropods in the Mesozoic, with the arthropods sometimes becoming long-term residents, is supported by the common occurrence of their droppings. In some cases, the body-chambers of the cephalopods contain large numbers of these millimeter-sized fecal pellets shaped like grains of rice (Fraaye & Jäger 1995b). Unfortunately, to date, no examples of any Palaeozoic microcoprolite–trilobite–cephalopod relationships have been reported.

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