

# Olenid trilobites: The oldest known chemoautotrophic symbionts?

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**Late Cambrian to early Ordovician trilobites, the family Olenidae, were tolerant of oxygen-poor, sulfur-rich sea floor conditions, and a case is made that they were chemoautotrophic symbionts. Olenids were uniquely adapted to this habitat in the Lower Paleozoic, which was widespread in the Late Cambrian over Scandinavia. This life habit explains distinctive aspects of olenid morphology: wide thoraces and large numbers of thoracic segments, thin cuticle and, in some species, degenerate hypostome, and the occasional development of brood pouches. Geochemical and field evidence is consistent with this interpretation. Olenids occupied their specialized habitat for 60 million years until their extinction at the end of the Ordovician.**

Colorless sulfur bacteria, a heterogeneous category of bacteria, are able to use reduced sulfur as a source of energy for growth and reproduction; as autotrophs, many use carbon dioxide as their sole source of carbon. They employ a variety of reactions to release this energy, reflecting a comparable variety of phylogenetic origins (1, 2). The bacteria require both a source of sulfur or sulfide and also a limited quantity of oxygen to permit oxidation. In marine environments, “the colorless sulfur bacteria are frequently found in the gradients at the interface between anoxic sulfide-containing areas and aerobic waters and sediments where, at very low oxygen and sulfide concentrations they can effectively compete with the spontaneous chemical oxidation reaction” (ref. 3, p. 400). Although hydrothermal vent environments on midocean ridges have attracted much recent attention, appropriate habitats also are widespread in shelf seas in low-oxygen environments where hydrogen sulfide accumulates.

A wide variety of metazoans, tolerant of hypoxic environments, used different biochemical adaptations to counteract the potentially lethal effect of high sulfide concentrations (4). Animals living in this habitat exhibit varying dependency on sulfur bacteria, which play a role in detoxification, when the bacteria are a source of food for animals that graze bacterial mats. The animals do not necessarily show any morphological changes related to this habitat (5). However, other metazoans have become symbiotic: They cultivate bacteria on special regions of their bodies or incorporate them in tissues such as gills. These taxa often show correlated morphological changes. Examples are known from arthropods, vestimentiferans, annelids, and several distantly related groups of bivalve mollusks (6). Among the arthropods, a variety of caridean shrimps occur around deep-sea hydrothermal vents in prodigious numbers. Some species graze directly on bacteria (7); others feed on ectosymbiotic bacteria growing on the mouthparts and the undersurface of the carapace (8). Shrimps that “cultivate” bacteria have modified mouthparts, such as dense covers of soft setae (9). Structures adapted for bacterial “gardening” have been developed on or within hypertrophied gill lamellae of bivalves (10). Both arthropods and bivalves occur often in great numbers, comprising one or a few species together. Animal taxa that have evolved dependency on chemoautotrophic symbioses tend to experience degeneration of their mouthparts.

Given the widespread occurrence and taxonomic spread of chemoautotrophic symbiosis, it is likely to have been an ancient adaptation. Because direct evidence of the fossil bacteria seldom preserves, evidence of such habits tends to be inferred from taxonomic and/or morphological data, which is not always reliable (11). The long-ranging solemyid and lucinid bivalves (10) indicate that by the Silurian (*ca.* 420 million years), this life mode already had been adopted by some groups with living descendants. Ancient vent associations have been recognized from at least the Devonian (12).

I show in this paper that even by the late Cambrian period (505 million years ago) certain extinct arthropods, trilobites belonging to the family Olenidae, evolved features best understood as evidence of sulfur chemoautotrophic mode of metabolism. If so, this finding takes the record of this type of bacterial symbiosis close to the initial radiation of large metazoans. The evidence derives from the morphological peculiarities of the trilobites themselves, including some species with reduced oral structures. Furthermore, olenid trilobites are associated with a characteristic range of lithofacies dating between Late Cambrian and Late Ordovician (*ca.* 505–445 million years ago). Some 65 genera of olenids have been named. They are worldwide in distribution, but have been particularly intensively studied from Scandinavia in the widespread late Cambrian Alum shales of Sweden and Norway.

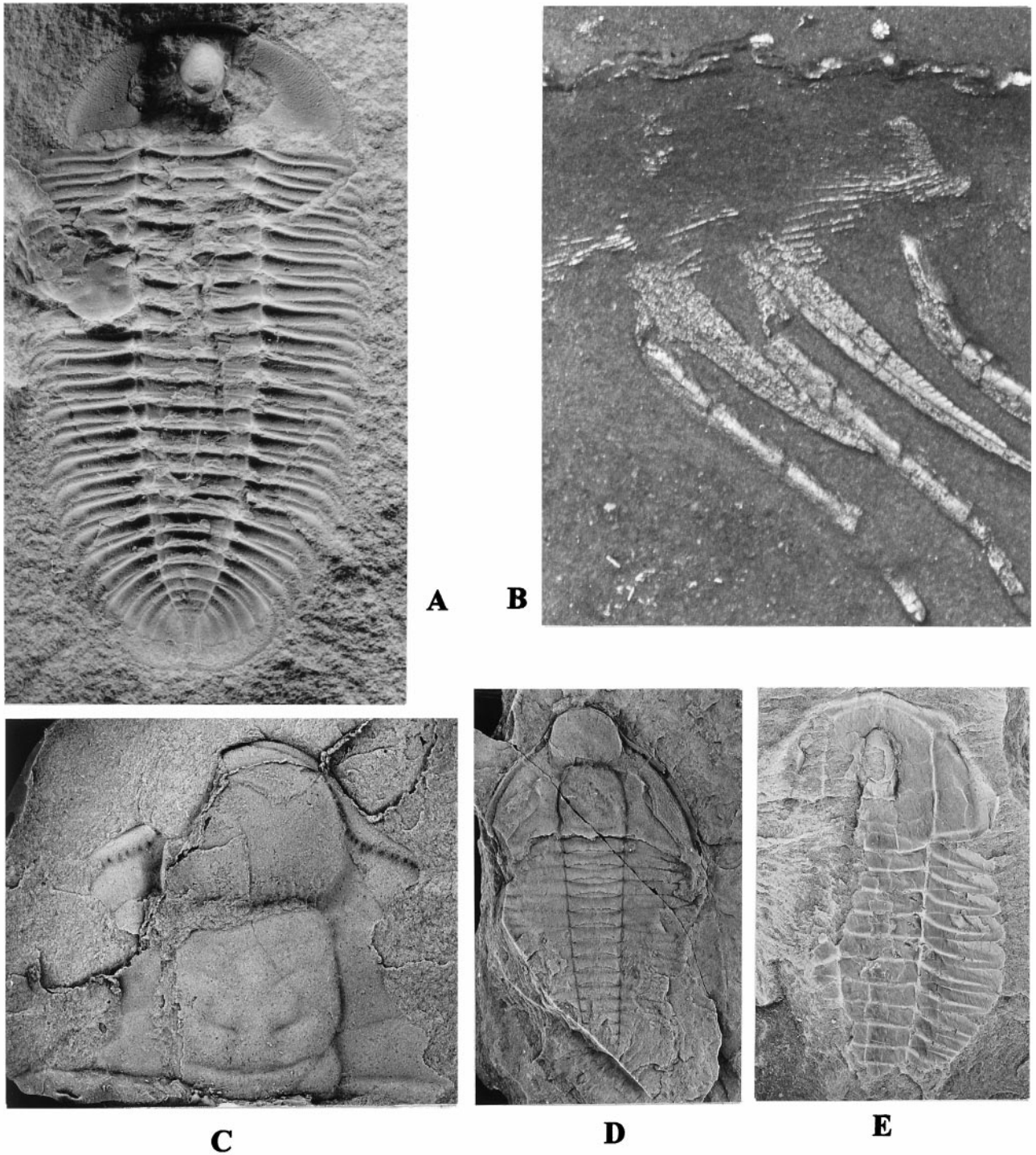
## Olenid Trilobite Morphology

Olenid trilobites (Fig. 1) are a specialized group of trilobites characterized by a remarkably thin cuticle (13). Their appendages are known pyritized in the Ordovician genus *Triarthrus* and feature large comb-like lamellate exites that usually are regarded as gill branches (14). Abundant olenid assemblages often include articulated, undisturbed molts, proving the absence of strong bottom currents in the environment they inhabited. Many species have wide, flat pleurae and frequently possess an unusually large number of thoracic segments. In the Ordovician, olenids have the most numerous segments of all their contemporaries; *Hypermeaspis* has eighteen segments, for example (see Fig. 1A). This segmentation permits both a lateral extension and multiplication of the exites, which may even overlap in echelon, thus increasing their length still further. Some olenids achieve a length of 10 cm or more. Many of the larger forms are flattened, and given their feeble axial musculature, it is extremely unlikely that they were actively swimming trilobites, and thus a sluggish benthic habit is inferred (15). Circulatory caeca have been suggested to permit increased oxygen absorption (16), and it has long been recognized that olenimorph morphology was adequate for survival in oxygen-depleted habitats (17). The outgroup of Olenidae is Ptychopariina, a conservative group of trilobites considered to have been particle feeders (18).

Given their occurrence in oxygen-poor habitats associated with sulfide-rich sediments, the peculiarities of olenid morphol-

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**Fig. 1.** Olenid trilobites. (A) Typical olenid (*Hypermeccaspis*, early Ordovician, Bolivia) preserved from underside showing “normal”-sized hypostome. Note also the large number of wide, flat segments. ( $\times 2$ .) (B) Pyritized limbs of the olenid *Triarthrus eatoni* (Green) showing filamentous gill exites. The broad hafts continuing to the lower right also would have been equipped with such filaments. Thinner jointed walking legs also are shown. [This picture is courtesy of H. B. Whittington. Beecher’s trilobite bed, Utica Shale, New York (Upper Ordovician).] (C and D) Brood pouches in olenid trilobites. *Parabolinella bolbifrons* from Fortey & Owens (Tremadoc, England) (C), cranium (D), and incomplete exoskeleton (E). ( $\times 3$  in D;  $\times 2$  in E.) Degenerate hypostome in the early Ordovician olenid from Wales *Porterfieldia punctata* (Crosfield & Skeat). ( $\times 4$ .) Specimen is preserved from underside showing reduced hypostome fallen into cephalic cavity.

ogy also are plausibly explained as adaptation to chemoautotrophic symbiosis. The extended pleural areas are available for cultivation of sulfur bacteria. It is possible that the bacteria were grown on the ventral membrane beneath the extended pleurae and/or on the appendages. However, the lamellate respiratory

exites of the limbs (Fig. 1B) invite comparison with the gills of bivalves or the appendages of carideans among those living fauna that are modified in chemoautotrophic symbionts for bacterial growth. Then multiplication of thoracic segments is readily explained by the same life habit: to provide as extensive an area

as possible for bacterial cultivation. In such a specialized habitat few predators ventured, and exceptionally thin cuticle combined with poor streamlining was not disadvantageous.

Direct evidence of mode of feeding is elusive in fossils; however, there is evidence that advanced olenids may have been able to dispense with the normal trilobite feeding apparatus. Autotrophic bacteria would have precluded any need for prey or other form of organic compounds. In virtually all trilobites a stout ventral plate, the hypostome, covers the foregut, and the mouth lies behind it. The hypostome functioned in the manipulation of food (19). However, in olenids such as *Peltura* and *Porterfieldia*, the hypostome has become atrophied (Fig. 1E); this modification had been mentioned (18), but previously was inexplicable. In the context of chemoautotrophic symbiosis, it can be taken as evidence of either direct ingestion of bacteria or absorption of fixed organic carbon into the hemocoel. Primitive olenids such as *Olenus* have normal hypostomes, and degeneration of the hypostome is characteristic of one subfamily, Pelturinae, which may have carried dependence on their bacterial symbionts furthest.

*Olenus*-like morphology persisted in the Olenidae from the late Cambrian to near the end of the Ordovician, a period of 60 million years. During the same period, the rest of the Trilobita underwent a profound morphological radiation (20), and the conservatism of these olenids is attributed to the persistence of their habitat. However, within the family Olenidae as a whole there is considerable morphological variety, reflecting different life habits within the olenid biotope, details of which remain to be investigated.

A few olenids recently have been shown to carry spectacular brood pouches (Fig. 1C and D). Given the stringencies of the olenid environment, it is plausible that the brood pouch maintained a steady level of oxygenation for the larval trilobites until they too could begin a symbiotic existence. Experiments on living bivalves (21) have shown that they are not chemoautotrophic throughout life, but acquire their bacteria from the sediment at an early stage of growth. A survey of brood pouches in other trilobites—overwhelmingly Cambrian (22)—shows that the majority bearing these pouches is convergent on olenids and may be evidence that these trilobites, too, adopted a similar life habit.

### The Olenid Paleoenvironment

The best-preserved trilobite specimens occur in sulfur-rich “stinkstone” nodules, which occur scattered through a highly condensed and generally laminated black shale sequence. In the Upper Cambrian part of the Alum shales, the macrofauna is dominated almost entirely by trilobites belonging to the family Olenidae (23). By contrast, contemporary shelf faunas in North America may have representative species of 20 or more trilobite families (24) and the lithologies are not sulfide-rich. In certain calcareous nodules from the Alum shales, an “orsten” fauna of minute, meiofaunal-sized arthropods and arthropod larvae also has been recovered by dissolution (25). These animals have been described mostly as being nekto-benthic deposit feeders (26). The other common component of the fauna, agnostid trilobites, is considered by many specialists to have been planktonic (27).

There is considerable evidence for low oxygen concentrations in rocks deposited in the “olenid sea” environment. Henningsmoen (23) originally suggested a comparison with the Black Sea. He pointed out that the unbioturbated, laminated sediments indicated complete anoxia subsurface. Sulfur in the form of pyrites has long been known to be abundant in the sediments themselves (28), which are also high in radioactive trace elements and organic matter, both features of low-oxygen sites of sediment accumulation (29). The sea floor conditions have been described as “dysaerobic with alternating anoxic and more oxic conditions”

(30), exactly those conditions favored by colorless sulfur bacteria. In Ordovician examples of the olenid environment, the occurrence of the typical lithologies and fauna has been associated with the oxygen minimum layer as it approached the continental shelf or with marginal basins having limited circulation induced by a volcanic barrier (31). However, the Cambrian olenid sea in Scandinavia occupied much of the Baltic craton and may have been consequent on poorly circulated stratified water across this relatively isolated paleocontinent (32). Certain bedding planes are covered with the remains of olenids generally belonging to one or two species (33), which supports the idea that although olenid sea conditions may have been inimicable to most benthic macrofaunal life, it was beneficial to appropriately specialized trilobites. Such high concentrations of a few specialists are typical of chemosymbiotic biotopes. Alum shales higher in the geological column (e.g., in the Jurassic) have comparable sedimentary and geochemical signatures (34) and similarly specialized faunas.

### Field Evidence

A section in the “Great Quarry” at Andrarum, Sweden, through the Alum shales of the Upper Cambrian *Olenus* Zone, has been studied in great detail by Clarkson *et al.* (35). A centimeter-scale log through the 1.5 m of the section shows a correlation between the presence and abundance of pyrite and the abundance of *Olenus truncatus* and *Olenus wahlenbergi* (Fig. 2). Where pyrite disappears altogether so do olenids, and their place is taken by an ostracod, *Cyclotron*. There is one pyritic interval from which olenids are absent, but agnostid trilobites are particularly abundant. This finding is consistent with the latter as being planktic, and therefore unaffected by a period of complete sea floor anoxia exceeding the marginal conditions under which olenids could prosper. To offer more secure proof of olenid habits, future studies might focus on rock sections in which olenid biofacies alternates with that carrying a different *benthonic* fauna; under these field conditions it should be possible to prove cooccurrence of the olenids alone with high pyrite and evidence of dysoxia.

### Discussion

The field occurrence, morphology, and paleoenvironment of olenid trilobites are consistent with their specialized adaptation to a low-oxygen, high-sulfur benthic marine habitat. The wide thoracic pleurae, weak musculature, and multiplication of thoracic segments of many olenids further suggest that they may have developed a symbiotic relationship with sulfur bacteria; degeneration of the hypostome in advanced olenids is hard to explain any other way. This development would be the earliest occurrence of this form of symbiosis in the fossil record; olenids typically are found in late Cambrian strata. Olenids were derived from benthic, particle-feeding ancestors, exhibiting progressive morphological specializations that are suggestive of obligate adaptations to the dysaerobic environment of the olenid sea. Other forms of symbiosis may be much older, if the claims of Ediacaran animals as examples of photosynthetic symbionts are to be credited (36). However, the environmental indicators of the olenid habitat, and the constraints on the lifestyle of these undoubted arthropods, are more critically constrained than is the case with the late Precambrian enigmatic metazoans.

The main difficulty with the proposal is how the olenids performed the delicate maneuver between the sulfur-rich sedimentary surface layer and the marginally oxygenated bottom waters that is necessary for the completion of the bacterial metabolic cycle. Some indirect evidence comes from trace fossils. Birkenmajer and Bruton (37) have suggested that very shallow trace fossils that they associate with olenids “were made by animals which swam above the bottom and occasion-

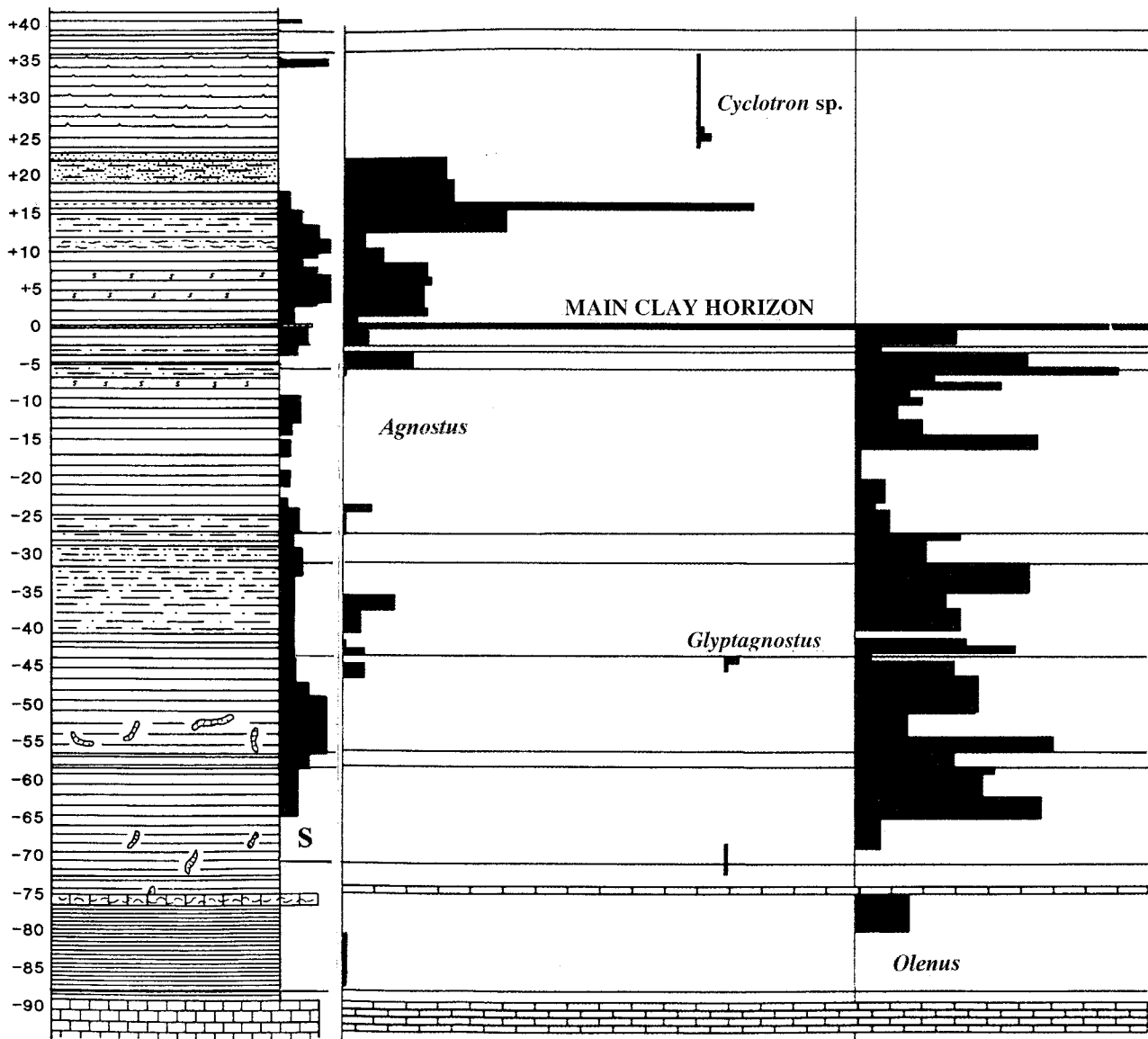


Fig. 2. Section through late Cambrian *Olenus* Zone Alum Shale at Andrarum, Sweden, showing sulfide occurrence (S on left) with occurrence of the supposed chemoautotrophic symbiont *Olenus*, which is replaced by the ostracod *Cyclotron* when sulfide is absent. Planktonic agnostids (*Agnostus* and *Glyptagnostus*) can extend beyond the tolerance range of benthic olenids. Data from Clarkson *et al.* (35), redrawn with permission. Contemporaneous sections on Cambrian platforms lack both olenids and high concentrations of sulfide.

ally darted down to it and up again” (ref. 37, pp. 308–309). If this statement is correct, it suggests that some olenids spent much of their time hovering on the edge of the sulfide-rich zone, moving up or down to balance their own need for respiration and/or the completion of the bacterial metabolic cycle. This habit may be analogous to the recent lucinid *Solemya* in which such a balance is achieved by movement of the animal between anoxic sulfide-rich sediment and the oxygenated zone (38). Details of bacterial cultivation can only be speculated on. However, if olenids were like recent analogues from several phyla, their long “gill” filaments could have provided a suitable area for bacterial growth. Typical olenid multiplication of thoracic segments, and increase in their width, would increase the area available for bacterial growth.

Olenids may not be the only trilobites that became chemoautotrophic symbionts: There are several convergent “oleni-

morphs” in other trilobite families (39). Their associated geochemistry would repay investigation. The most striking example is the Silurian genus *Aulacopleura* (40) in which the thoracic segments are unusually numerous, wide, and variable in number as compared with its contemporaries. It too is found in dark shales. There are still more olenimorphs of Cambrian age in which brood pouches have been identified (22). It is possible that a symbiotic lifestyle will prove to be widely distributed among ancient arthropods.

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1. Bos, P. & Kuenen, J. G., eds. (1983) in *Microbial Corrosion* (Metals Society, London), pp. 18–27.
2. Kelly, D. P. (1988) in *Autotrophic Bacteria*, eds. Schlegel, H. G. & Bowien, B. (Science Tech, Madison, WI), pp. 193–218.
3. Robertson, L. A. & Kuenen, J. G. (1992) in *The Prokaryotes*, eds. Balows, A., Trüper, H. G., Dworkin, M., Harder, W. & Schliefer, K.-H. (Springer, Heidelberg), 2nd Ed., pp. 385–413.
4. Vetter, R. D., Powell, M. A. & Somero, G. N. (1991) in *Metazoan Life Without Oxygen*, ed. Bryant, C. (Chapman & Hall, London), pp. 109–128.
5. Vetter, R. D., Wells, M. E., Kurtzman, A. L. & Somero, G. N. (1987) *Physiol. Zool.* **60**, 121–137.
6. Fisher, C. R. (1990) *Rev. Aquatic Sci.* **2**, 399–436.
7. Van Dover, C. L., Fry, B., Grassle, J. F., Humphris, S. & Rona, P. A. (1988) *Mar. Biol. (Berlin)* **98**, 209–216.
8. Gebruk, A. V., Pimenov, N. V. & Savvichev, A. S. (1992) *Mar. Ecol. Prog. Ser.* **98**, 247–253.
9. Segonzac, M., de Saint Laurent, M. & Casanova, B. (1993) *Cah. Biol. Mar.* **34**, 535–571.
10. Distel, D. L. (1998) *Bioscience* **48**, 277–286.
11. Powell, E. N., Callender, W. R. & Stanton, R. J. (1998) *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **144**, 85–114.
12. Campbell, K. A. & Bottjer, D. J. (1995) *Geology* **23**, 321–324.
13. Fortey, R. A. & Wilmot, N. V. (1991) *Palaeontol. Zeitschr.* **65**, 141–151.
14. Whittington, H. B. & Almond, J. E. (1987) *Philos. Trans. R. Soc. London B* **317**, 1–46.
15. Fortey, R. A. (1974) *Skr. Nor. Polarinst.* **160**, 1–129.
16. Jell, P. A. (1978) *Alcheringa* **2**, 251–260.
17. Fortey, R. A. (1985) *Trans. R. Soc. Edinburgh Earth Sci.* **76**, 219–230.
18. Fortey, R. A. & Owens, R. M. (1999) *Palaeontology* **42**, 429–465.
19. Fortey, R. A. & Owens, R. M. (1999) in *Functional Morphology of the Invertebrate Exoskeleton*, ed. Savazzi, E. (Wiley, New York), pp. 77–98.
20. Foote, M. (1991) *Palaeontology* **34**, 461–485.
21. Gros, O., Frankiel, L. & Moueza, M. (1998) *Invert. Reprod. Dev.* **34**, 219–231.
22. Fortey, R. A. & Hughes, N. C. (1998) *J. Paleontol.* **72**, 639–649.
23. Henningsmoen, G. (1957) *Skr. Nor. Vidensk.-Akad. Kl. 1: Mat.-Naturvidensk. Kl.* **1**, 1–304.
24. Ludvigsen, R., Westrop, S. R. & Kindler, C. H. (1989) *Palaeontogr. Can.* **6**, 1–175.
25. Müller, K. J. & Walossek, D. (1985) *Trans. R. Soc. Edinburgh Earth Sci.* **76**, 161–172.
26. Walossek, D. (1998) in *Arthropod Relationships*, eds. Fortey, R. A. & Thomas, R. H. (Chapman & Hall, London), pp. 139–153.
27. Robison, R. A. (1972) *24th Int. Geol. Congr. Montreal* **7**, 33–40.
28. Westergaard, A. H. (1944) *Sver. Geol. Under. C* **459**, 1–45.
29. Thickpenny, A. (1987) in *Marine Clastic Sedimentology*, eds. Leggett, J. K. & Zuffa, G. G. (Graham & Trotman, London), pp. 156–171.
30. Thickpenny, A. (1984) in *Fine Grained Sediments: Deep Water Processes and Facies*, eds. Stow, D. A. V. & Piper, D. J. W. (Geological Society, Oxford), pp. 511–526.
31. Fortey, R. A. & Owens, R. M. (1978) *Bull. Br. Mus. Nat. Hist. Geol.* **30**, 225–294.
32. Andersson, A., Dahlman, B., Gee, D. G. & Snäll, S. (1985) *Sver. Geol. Under. C* **56**, 1–50.
33. Clarkson, E. N. K., Taylor, C. M. & Ahlberg, P. (1997) *Trans. R. Soc. Edinburgh Earth Sci.* **88**, 69–89.
34. Raiswell, R. & Berner, R. A. (1985) *Am. J. Sci.* **285**, 710–724.
35. Clarkson, E. N. K., Ahlberg, P. & Taylor, C. M. (1998) *Geol. Foeren. Stockholm Foerh.* **120**, 257–267.
36. McMenamin, M. A. S. (1998) *The Garden of Ediacara* (Columbia Univ. Press, New York).
37. Birkenmajer, K. & Bruton, D. L. (1971) *Lethaia* **4**, 303–319.
38. Reid, R. G. B. (1990) in *The Bivalvia*, ed. Morton, B. (Hong Kong Univ. Press, Hong Kong), pp. 127–140.
39. Fortey, R. A. & Owens, R. M. (1990) in *Evolutionary Trends*, ed. McNamara, K. J. (Belhaven, London), pp. 121–142.
40. Hughes, N. C. & Chapman, R. E. (1995) *Lethaia* **28**, 333–353.