4. M. L. Schlossman *et al.*, *Phys. Rev. Lett.* **66**, 1599 (1991).
5. K. Kjaer *et al.*, *J. Phys. Chem.* **93**, 3200 (1989).
6. R. M. Kenn *et al.*, *J. Chem. Phys.* **95**, 2092 (1991).
7. D. Jacquemain *et al.*, *J. Am. Chem. Soc.* **113**, 7684 (1991).
8. B. Lin *et al.*, *Phys. Rev. Lett.* **111**, 191 (1990).
9. F. Leveiller *et al.*, *Science* **252**, 1532 (1991).
10. J. Garnaes, D. K. Schwartz, R. Viswanathan, J. A. N. Zasadzinski, *Nature* **357**, 54 (1992).
11. D. K. Schwartz, J. Garnaes, R. Viswanathan, J. A. N. Zasadzinski, *Science* **257**, 508 (1992).
12. D. K. Schwartz *et al.*, *Phys. Rev. E* **47**, 452 (1993).
13. J. Garnaes, D. K. Schwartz, R. Viswanathan, J. A. N. Zasadzinski, *Synth. Met.* **55–57**, 3795 (1993).
14. I. R. Peterson, R. Steith, H. Krug, I. Voight-Martin, *J. Phys.* **51**, 1003 (1990).
15. The floating monolayer was studied with the liquid surface diffractometer on wiggler beamline BW1 at HASYLAB, DESY, Hamburg, Germany. A beam of wavelength 0.1351 nm was incident on the surface at an angle $\alpha = 0.85\alpha_c$ to enhance surface sensitivity, where α_c is the critical angle for total external reflection, giving a footprint of 50 by 5 mm. The background level of scattering was reduced by the maintenance of a He atmosphere inside the trough. Detection was done by a vertically oriented PSD with 256 channels mounted behind a Soller collimator, giving a horizontal resolution (full width at half maximum) of $0.114\ \text{nm}^{-1}$ and a vertical resolution of $0.050\ \text{nm}^{-1}$ per channel.
16. The water phase was Millipore filtered water with resistivity >18 M ohm · cm and thermostated at 20.0° ± 0.1°C. Chloroform was of analytical grade purchased from Merck (Rahway, NJ). The monolayer was compressed at a rate of $0.009\ \text{nm}^2$ per molecule per minute. After compression, the surface pressure was kept constant by the adjustment of the barrier position.
17. J. Als-Nielsen and K. Kjaer, in *The Proceedings of the NATO Advanced Study Institute, Phase Transitions in Soft Condensed Matter*, T. Riste and D. Sherrington, Eds. (Plenum, New York, 1989), pp. 113–137; K. Kjaer; *Physica B*, in press.
18. J. Garnaes, T. Bjørnholm, M. Jørgensen, J. A. N. Zasadzinski, *J. Vac. Sci. Technol.*, in press.
19. Spreading and compression were done in a manner similar to the procedure in the synchrotron study (*15*). The silicon wafer was cleaned in a solution of H_2O_2 and H_2SO_4 and then etched in hydrofluoric acid to make it hydrophobic. The LB films were transferred by the use of KSV-5000-3 (KSV Instruments, Helsinki) deposition equipment at a deposition speed of 1 mm/min. Cadmium behenate was transferred from a floating monolayer of behenic acid (>99%, Aldrich) with a subphase containing 5×10^{-4} M $CdCl_2$ (99.99%, Aldrich) and with the pH adjusted to 6.5. For both the cadmium behenate and the acceptor, the amount of film transferred was 1.0 ± 0.1 of a monolayer at both the downstroke and upstroke.
20. T. Bjørnholm *et al.*, *Synth. Met.* **57**, 3807 (1993).
21. For imaging, we used a Nanoscope III FM (Digital Instruments, Santa Barbara, CA) and microfabricated Si_3N_4 tips formed on cantilevers with a spring constant of 0.1 to 0.6 N/m. The *x* and *y* (horizontal) calibration was performed from 28 images of mica [absolute uncertainty 1.7% (*12*)]. The *z* calibration was calculated from bilayer step heights on LB films of fatty acids (*13*). We did not apply image processing or on-line filtering to any of the images of molecules. Unit-cell parameters were calculated from images of five domains recorded with two different tips.
22. A. I. Kitaigorodskii, *Organic Chemical Crystallography* (Consultant Bureau, New York, 1961).
23. ______, *Molecular Crystals and Molecules* (Academic Press, London, 1973).
24. S. Abrahamson, B. Dahlén, H. Löfgren, I. Pascher, *Prog. Chem. Fats Other Lipids* **16**, 125 (1978).
25. B. T. G. Liesner and G. Wegner, *Thin Solid Films* **68**, 77 (1980).
26. K. B. Blodgett, *J. Am. Chem. Soc.* **57**, 1007 (1935).
27. A. S. Maryin, J. R. Sambles, G. J. Ashwell, *Phys. Rev. Lett.* **70**, 218 (1993).
28. A. S. Dhindsa, M. R. Bryce, J. P. Lloyd, M. C. Petty, *Thin Solid Films* **165**, L97 (1988).
29. I. R. Girling *et al.*, *J. Opt. Soc. Am. B* **4**, 950 (1987).
30. We thank K. Bechgaard, K. Carneiro, T. Geisler, L. Nielsen, K. Schaumburg, and P. Sommer-Larsen for useful discussions; S. Munk for technical assistance; and HASYLAB at DESY, Hamburg, Germany, for beam time. Supported by the Danish Materials Technology Development Program, the Danish Natural Science Research Council (grant 3.70.01-08/93), the U.S. Office of Naval Research (grant N00014-90-J-1551), and the NSF (grants CTS 9Z12290 and CTS 91-02719).

1 February 1994; accepted 4 April 1994

Evidence for Monophyly and Arthropod Affinity of Cambrian Giant Predators

Jun-yuan Chen, Lars Ramsköld,* Gui-qing Zhou

The Chinese Early Cambrian Chengjiang fauna includes three different anomalocaridids, a globally spread, extinct marine group including the largest known Cambrian animals. Anomalocaridids were active predators, and their presence implies that a complex ecosystem appeared abruptly in the earliest Phanerozoic. Complete specimens display several sets of characters shared only with some other exclusively Cambrian forms. This evidence indicates that anomalocaridids, *Opabinia*, and *Kerygmachela* form a monophyletic clade. Certain features indicate arthropod affinities of the clade, and for this group an unnamed (sub)phylum-level taxon within an arthropod (super)phylum is proposed.

The rapid diversification of animal life near the base of the Phanerozoic Eon is unparalleled in the history of life, but researchers are far from reaching a consensus on the origin of animal phyla or how they are related. This early radiation of the Metazoa produced perhaps all animal phyla extant today and some additional, extinct groups. In this report we discuss one such group, composed of large predators. Their presence in the Early Cambrian is important for the understanding of early metazoan evolution, trophic levels, and life habits. The diversity of the group implies that considerable evolution took place during a time interval even shorter (*1*) than previously suspected. This pattern parallels that of other Early Cambrian groups and is at the heart of two questions: the "Cambrian explosion" and the early evolution of the largest animal group on Earth, the arthropods.

Fossils usually preserve only hard or mineralized parts, and as most early metazoans lack such parts, the rare early Palaeozoic occurrences of soft tissue preservation are crucial for our knowledge of metazoan early evolution. For 75 years the Canadian Middle Cambrian Burgess Shale fauna provided most data on soft-bodied animals, but similar preservation is now known to be widespread in Cambrian rocks (2). An important site was discovered in 1984 (3) in Chengjiang, Yunnan, south China, and is approximately late Atdabanian (about 525 to 530 million years old). The Chengjiang fauna (*4*) may have lived only 5 million years (*1*) after the "Cambrian explosion" began at the onset of the Tommotian age. The superb preservation and high diversity (*5*) (now close to 100 known species) equal those of the Burgess Shale fauna which is ~10 million years younger.

Mineralized parts in both metazoans, protists and cyanobacteria (*6*), as well as a diverse macrofauna producing varied trace fossils (*7*), appear abruptly close to the Precambrian-Cambrian boundary. This major diversification of life forms is known as the "Cambrian explosion." The biotic system appears to have quickly reached a level of complexity not far from that present in modern oceans. As today, suspension feeding and deposit feeding were the dominant means of primary consumption (*8*). As long as evidence to the contrary was lacking, macrophagous predators were thought to have evolved much later in the Cambrian. With the redescription of the Burgess Shale fauna, several such predators were recognized (*9–11*). These predators occupied a primary level, but *Anomalocaris* also possessed at least the size and physical ability to exploit a secondary level.

Our excavations of 1990–92 at Chengjiang yielded fossils of giant predators of three different kinds, including complete specimens of *Anomalocaris* and a related form. *Anomalocaris* was initially described on the basis of isolated frontal appendages. These, the disassociated jaws, and a body found later were interpreted as three separate animals until such parts were found together in a nondisarticulated specimen from the Burgess Shale (*12*). However, this *Anomalocaris canadensis* specimen lacked the posterior part. A tapering, blunt body

---

J.-y. Chen and G.-q. Zhou, Nanjing Institute of Geology and Palaeontology, Academia Sinica, Chi-Ming-Ssu, Nanjing 210008, People's Republic of China.
L. Ramsköld, Museum of Palaeontology, University of Uppsala, Norbyvägen 22, S-752 36 Uppsala, Sweden.

*To whom correspondence should be addressed.

end was suggested (*11*) on the assumption that *A. canadensis* was closely related to *Peytoia nathorsti*, a second, more common anomalocaridid also included in *Anomalocaris*. The Chengjiang material reveals major differences between *Anomalocaris* and *Peytoia*, and we therefore revive the genus *Peytoia* for *P. nathorsti* (*13*).

The complete *Anomalocaris* specimen from Chengjiang (Figs. 1 and 2) represents a new species closely related to *A. canadensis*. The individual is a juvenile, 111 mm long plus furcae adding at least 35 mm. The two raptorial appendages (Fig. 1C), based preorally near the front, are stretched out anteriorly. The paired, stalked eyes are set dorsolateral to the mouth, not far posteriorly as in *Peytoia*. The jaw apparatus is composed of four larger and many smaller, elongate plates set in a circle (Fig. 1E). It differs from *Peytoia* in having tuberculated plates and a diagonal rather than sagittal and transverse arrangement of the four large plates. The body is elongate, with 11 imbricating, paired lateral flaps, each with a canal system (Fig. 1D) (see animal 2 below). Posteriorly is a tail fan, composed of three partly overlapping blade pairs. Two long, slender furcae extend posteriorly. Traces of gills are present between the lateral flaps, and more adaxially are segmentally arranged, large, rounded dark spots similar to in *Peytoia*, composed of bunches of fine, curved threads. Some transverse lines cross the trunk, connecting the inner anterior extremities of the lateral flaps. Their dorsoventral position is uncertain, but in a few places (Fig. 2, arrows) the lines pass dorsal, but not ventral, to the alimentary canal in places where it is three dimensionally preserved. They may indicate dorsally expressed segmentation, but irregularities and wrinkling of the lines complicate their interpretation as tergite boundaries. However, evidence of at least a separately articulating head tergite in animal 2 (see caption of Fig. 3A) indicates the presence of tergites also in *Anomalocaris*. Previous suggestions (*14, 15*) of tergites in *Anomalocaris* were based on misinterpreted structures unrelated to the above; they were also interpreted as legs (*14*). There is no evidence of legs in the Chengjiang material. Nine disarticulated anterior appendages of *Anomalocaris* indicate total body lengths (excluding furcae) between 60 and 320 mm; an isolated jaw apparatus evidently belonged to an *Anomalocaris* individual about 1 m long.

The second anomalocaridid from Chengjiang, animal 2, is represented by two complete specimens (Figs. 3 and 4), about 40 isolated anterior appendages (Fig. 4A), and several parts of jaw apparatuses (Fig. 5C). Animal 2 resembles *Anomalocaris* in the number of lateral flaps, the flap venation, tail fan, and long furcae, but it has smaller and differently built anterior appendages, large and anteriorly set eyes, a wider trunk with much larger flaps (Fig. 3A versus Fig. 2), and a different jaw apparatus. Isolated appendages indicate a complete length, excluding furcae, of up to 1 m. Animal 2 is broadly similar to *Peytoia*, having anteriorly set eyes and a wide trunk with large flaps, but *Peytoia* has very short furcae and lacks a tail fan (both may be due to either preservation or real absence), and

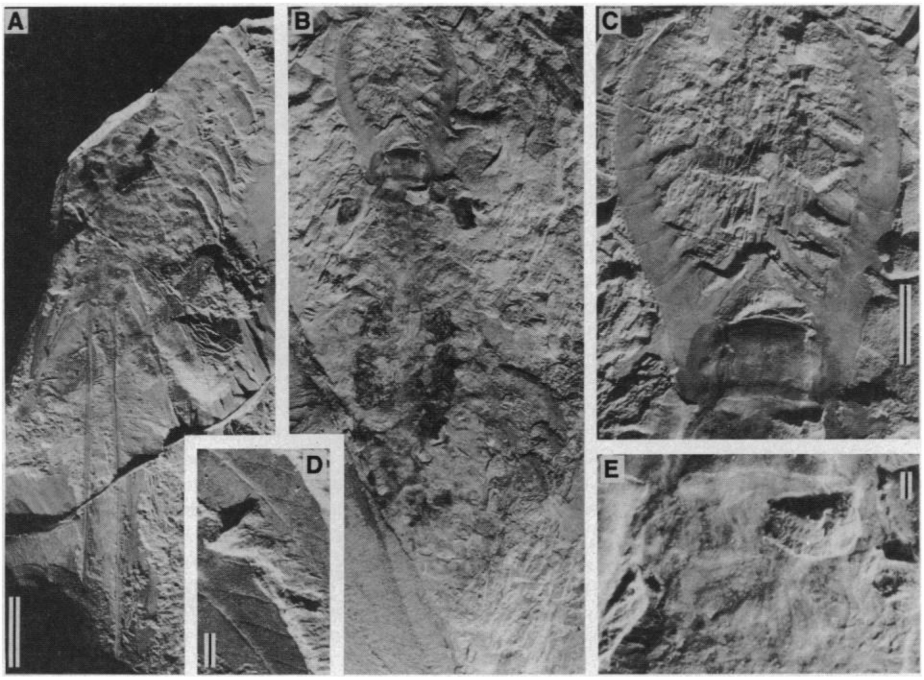

Fig. 1. *Anomalocaris* n. sp. from Chengjiang. Specimen ELRC 20001a-b, complete, young individual exposed from the ventral side (part: B, C, and E) and dorsal side (counterpart: A and D), respectively. (**A**) Overall view showing imbricating flaps, tail fan, and furcae [scale bar 10 mm, applies also to (B)]. (**B**) Overall view. (**C**) Detail of head and frontal appendages (scale bar 5 mm). (**D**) Detail showing veins in flaps (scale bar 1 mm). (**E**) Detail showing jaw apparatus (scale bar 1 mm).

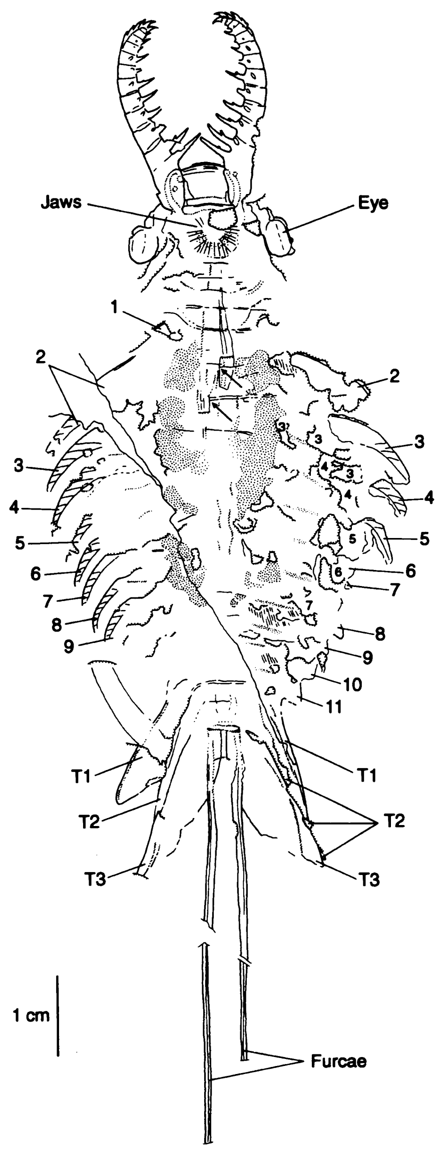

Fig. 2. Camera lucida drawing of *Anomalocaris* n. sp., specimen of Fig. 1. Features below the oblique line bisecting the specimen are from the counterpart, seen in dorsal view and mirrored; features above are from the part and seen in ventral view. Lateral flaps are numbered 1 to 11, blades of the tail fan are designated T1 to T3. Striated structures, possibly gills, are seen associated with flaps 2, 8, and 10 on the (animal's) left side. Arrows indicate where possible tergite boundaries pass dorsal to the three dimensionally preserved gut. The stippled areas represent paired, segmentally arranged structures equaling 2X to 4X of Fig. 3A. The unidentified object between flap 9 and T1 is probably not part of the individual.

its anterior appendages, although poorly known, were smaller than in animal 2 or *Anomalocaris*.

In the anterior appendages of animal 2, there are 12 podomeres distal to one large one bearing a long pincer spine, which clearly could interact with the spines on the inner side of the appendage. The podomeres articulate by means of pivot joints (Fig. 4, A and C); more proximal articulations are different but not yet analyzed. The pivotal axes are situated toward the outer appendage margin and thus permit considerable flexure inward, but only limited outward curvature, a range of flexibility confirmed by preserved postures of anomalocaridid appendages.

The well-preserved flap venation in animal 2 somewhat resembles the wing venation of insects. Similar canals in *Peytoia* were previously interpreted as strengthening rays (*11*). Our interpretation as veins is supported by the wrinkled, three dimensionally preserved structure in one specimen (Fig. 4E). A series of subparallel veins (Fig. 3) branch, occasionally with anastomoses (Fig. 4D), from a central vein and curve laterally to meet a vein running along the flap margin (Fig. 4B). One or two veins cross at least parts of the posterior extension to join the central vein (Fig. 4D). The blades of the tail fan, well preserved in a large incomplete individual, lack veins.

The complicated jaw apparatus (Fig. 3B) consists of large, elaborate teeth, apparently set symmetrically in a plate circle. Circle fragments include several smooth, elongated plates and some tuberculated, occasionally oval ones. There are at least six teeth, perhaps eight, possibly set in pairs. Each tooth has a row of four major claw-shaped cusps (Fig. 5C). The two largest cusps appear to be single, but the smaller may be paired.

The third Chengjiang anomalocaridid is represented exclusively by large (up to 25 cm across), *Peytoia*-like jaw apparatuses (Fig. 5B). There is an outer circle of elongate plates, each with one or a few broad-based spines pointing inward. Inside the outer plate circle, numerous teeth are set in rows radiating from the mouth center, presumably lining the mouth cavity; each row has at least eight teeth increasing in size peripherally. Each tooth is broad-based and cap-shaped and bears a horizontal row of four to six spines directed inward. Comparison with complete anomalocaridid specimens indicates that the jaws belonged to a species that reached 2 m in length.

Anomalocaridids were active predators, as indicated by the raptorial anterior appendages. The hydrodynamic profile would allow fast swimming to persue and capture prey. Because of the supposed lack of tail fins, the animals have been thought to use the lateral flaps for swimming. The complete Chengjiang specimens show a tail fin, as does the first, as yet undescribed, Burgess Shale *Anomalocaris* specimen that is nearly complete (*16*, *17*). This fan tail may indicate an alternative fish-like, or carangiform, locomotion through undulation of the body, with the tail used for steering and stabilizing, aided by the apparently relatively stiff furcae. Cuticular segmentation, if present, would provide sufficient flexibility to the exoskeleton. The morphology also suggests that anomalocaridids may have spent much time partly buried or camouflaged in the bottom sediment, with the stalked eyes protruding over the bottom and scanning the surroundings for swimming prey, being prepared for attacks on prey coming within range.

The alimentary canal in Chengjiang anomalocaridid specimens is preserved as a black film or a mud infilling, without identifiable gut contents. Predation by *Anomalocaris* has been inferred from healed injuries in trilobites (*18*) [wounds are compatible with jaw morphology (*11*)] but is still unproven from gut contents. Trilobites have been found in the gut of the arthropod *Sidneyia* (*10*), a 13-cm-long Burgess Shale predator, and in the smaller arthropod *Utahcaris* (*19*).

Associated with the Chengjiang fauna are locally common coprolites up to 4.5 cm by 6.5 cm across. Most contain hard parts of either bradoriids or hyolithids, but some display a mixture of bradoriids, hyolithids, and trilobites. Soft-bodied animals dominate the Chengjiang fauna and must, as in the Burgess Shale fauna (*11*), have been important prey for the anomalocaridids but would leave no trace in the coprolites, and no soft-bodied individuals have yet been

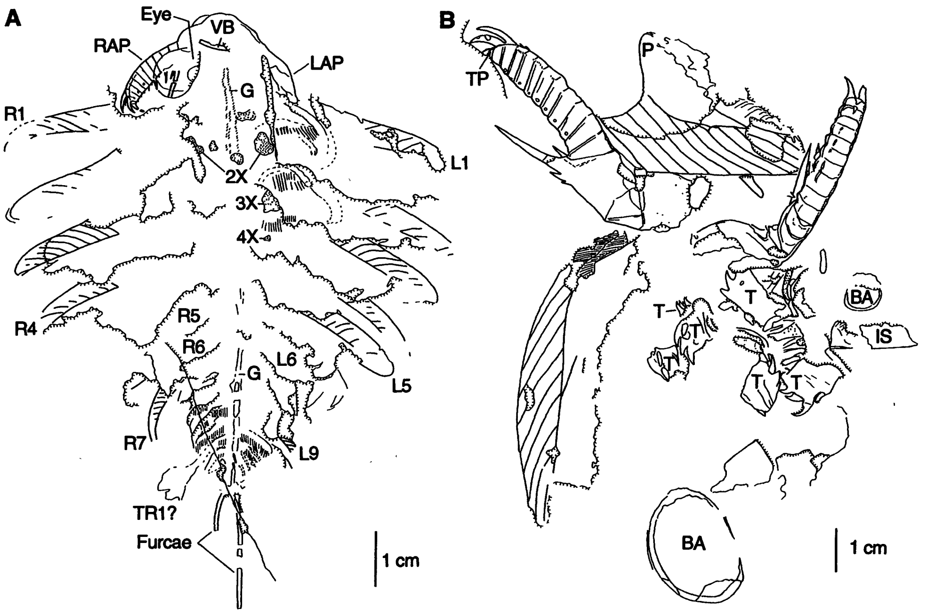

Fig. 3. New anomalocaridid animal 2 from Chengjiang. (**A**) Camera lucida drawing of specimen ELRC 21002a, a complete, young individual exposed from the ventral side, with minor parts added from the counterpart ELRC 21002b. The large right eye is at the lowest (most dorsal) level of bedding. The right anterior appendage (RAP) is partly added from the counterpart, as is the ventral bar (VB). The three distal, spine-bearing podomeres of RAP are preserved in a position dorsal to R1. The incomplete left appendage (LAP) lies ventral to L1. Postures of RAP, LAP, and VB show that the head is rotated anticlockwise relative to R1-L1, indicating a separate exoskeletal head tergite. All preserved lateral flaps (right side R1 to R7; left side L1 to L9) carry vein patterns. R1, R2, and distal part of R3 added from counterpart. Lamellate gill-like structures are set adaxially on all flaps (only shown for L1 to L3 and most posteriorly). R7 and L9 show that the flaps extend well outside the "gills." The gut (G) is partly preserved in relief. The designations 2X to 4X indicate segmentally arranged structures equaling the "nodular mineralized areas" described (*11*) in *Anomalocaris nathorsti*. Most of 4X is covered by L3. Parts of first tail fan blade (TR1?) tentatively identified, added from counterpart. (**B**) Camera lucida drawing of specimen ELRC 21001a, an anterior part of a carcass with disarticulated parts preserved in various orientations; some minor areas added from counterpart ELRC 21001b. One anterior appendage is preserved in parallel aspect, showing 12 podomeres distal to the large, spine-bearing one, the distal three including the terminal (TP) each carrying an outer spine. The boundaries between the podomeres are flexed posteriorly near the pivotal points of articulation (see also Fig. 4A). The other anterior appendage is detailed in Fig. 4C. Two lateral flaps remain of the four present before preparation revealing six teeth (T) and other parts of the jaw apparatus. One flap shows the end of its posterior extension (P), the other shows near its base two striated blades of feathery appearance. An *Isoxus* (IS) and two bivalved arthropods (BA) are associated with the carcass.

found exhibiting healed injuries conceivably inflicted by predators. All previously reported Cambrian coprolites (*19–21*) are North American. In no cases has the producer been positively identified. The large sizes and the lack of burrows of anemones, conceivable Cambrian coprolite producers (*22*), have pointed to *Anomalocaris* or other even larger unknown predators (*19, 21*). The gut of an *Anomalocaris* individual 0.5 m long may have reached 20 mm in diameter (*19*). The third Chengjiang form possibly reached 2 m, and by scaling, its gut may have been 80 mm in diameter, so the large coprolites from Chengjiang are within the possible range.

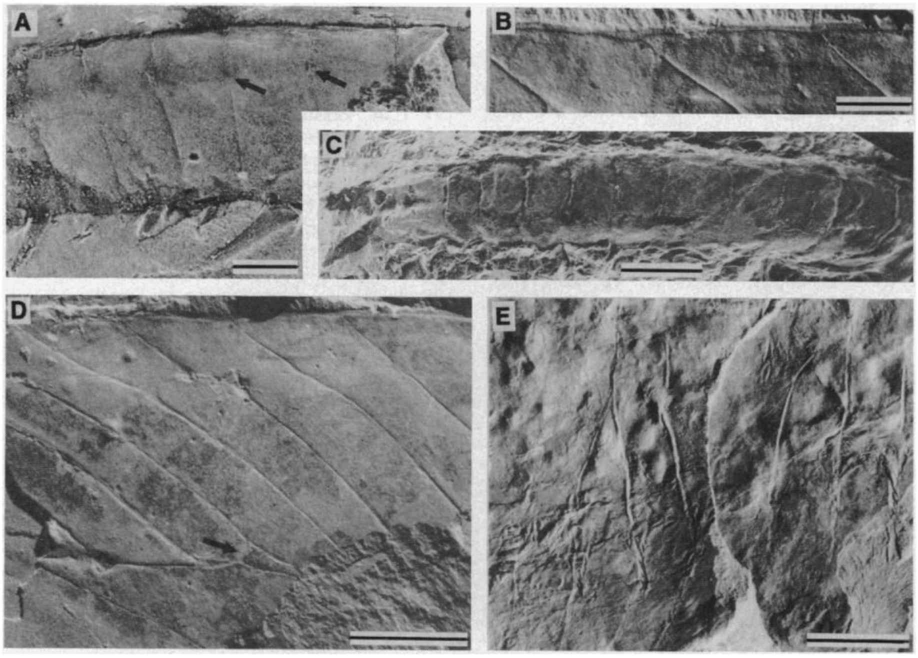

Fig. 4. New anomalocaridid animal 2 from Chengjiang. (**A**) Anterior appendage of ELRC 21003, detail. Two pivot points of articulation between podomeres arrowed; scale bar 2 mm. (B to D) Details of ELRC 21001a, see Fig. 3B. (**B**) Anterior margin of flap showing oblique veins joining marginal vein; scale bar 2 mm. (**C**) Anterior appendage (to right in Fig. 3B) oriented with its outer curvature toward the observer, showing articulating devices and anterior median groove between paired spine rows; scale bar 5 mm. (**D**) Central part of flap (between anterior appendages in Fig. 3B); an anastomosing vein between the central vein and one oblique vein is arrowed; scale bar 5 mm. (**E**) Detail of incomplete, articulated specimen ELRC 21050, showing the wrinkled surface of two successive flaps, anterior to right; scale bar 5 mm.

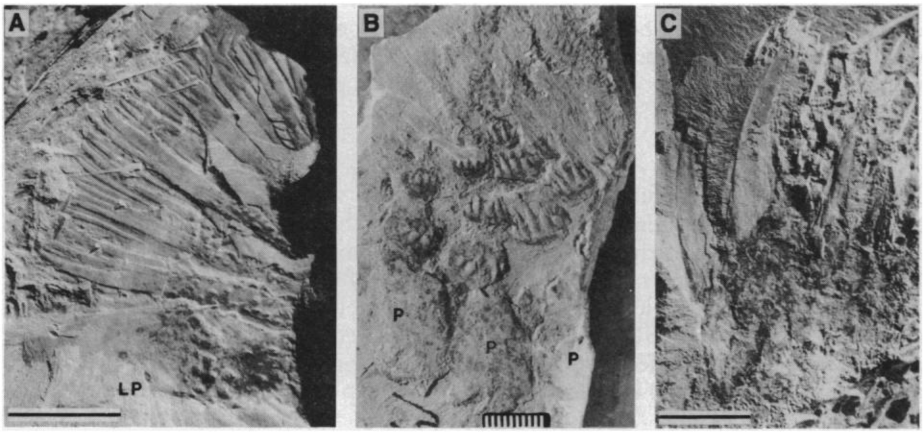

Fig. 5. Anomalocaridid jaw parts from Chengjiang. (**A**) *Anomalocaris*. ELRC 22020b, a quarter of a jaw circle, center at right, with one large plate (LP) followed above by a series of smaller plates. The next large plate borders (in part ELRC 22020a) to the margin at the upper right. Light from south. (**B**) Incomplete jaw apparatus of *Peytoia* type, center at top, ELRC 22002a. Inside three large plates (P) of the outer circle are about 15 teeth, each with five pointed cusps directed adcentrally. (**C**) Incomplete, isolated tooth of animal 2 with four long, claw-shaped cusps preserved, ELRC 21040. All scale bars 1 cm.

Anomalocaridids share the following characteristic features: (i) highly movable and flexible, jointed preoral appendages with double spine rows; (ii) a strong, multielement jaw apparatus including a circle of plates with spines pointing centrally; (iii) large, globular, stalked, dorsal eyes; (iv) ventrally based, imbricating flaps, each overlying its anterior neighbor; (v) a vein system in the flaps; (vi) configuration and position of the gill-like structures; (vii) lack of antennae and jointed postoral appendages; probably (viii) the presence of a composite caudal fin; and (ix) long furcae. We regard these features as synapomorphies defining a monophyletic group. To this group of anomalocaridids may be added the poorly known Polish Lower Cambrian *Cassubia* (*23*) and the Burgess Shale *Hurdia* (*16*).

The closest relative of the anomalocaridids is *Kerygmachela* (*24*), a 20-cm-long animal from the Lower Cambrian Sirius Passet fauna (*25*) of Greenland. Features indicating such affinity include (i) a pair of stout, movable anterior appendages, each with (ii) a double spine row along the inner side and about four terminal spines; (iii) a central body of 11 segments; (iv) imbricating lateral flaps with (v) associated gill-like structures; and (vi) a pair of long furcae.

Kerygmachela was allied with the recently recognized (*26*) group of onychophora-like Cambrian lobopods by splitting the clade and placing anomalocaridids, myriapods, and biramous arthropods as ingroup taxa in the resulting phylogram (*24*). The four characters stated to ally *Kerygmachela* with the lobopods are questionable for the following four reasons: Character 1, the reported "lobopod legs" in the animal may not be legs because (i) the structures are preserved in positive relief in both dorsal and ventral views, indicating strong sclerotization and stiffness; (ii) they span only about 30% of the body width, far too little to provide stability; and (iii) they may be based laterally on both sides of the axial region, a position incompatible with a leg interpretation, whereas the legs of Cambrian lobopods are based ventrally (90° apart). Character 2, the "circular body musculature" structures are too large and wrongly situated to be comparable with lobopod musculature. Character 3, "appendages with spines" apparently denote the frontal appendages in *Kerygmachela* but the trunk legs in lobopods, two incomparable structures. Character 4, the "transverse axial wrinkling" merely reflects an analogous accordion-like trunk, necessary for flexure of an exoskeleton undivided into tergites.

Opabinia (*27*), a Burgess Shale conundrum conventionally unassigned to phylum, also resembles the three anomalocaridids. Shared features are: (i) preoral, spine-bearing frontal appendages; (ii) apparent absence of other jointed appendages including antennae; (iii) large, stalked, dorsally set eyes; (iv) a mouth set ventrally, distant from the anterior margin; (v) a series of ventrally based, segmentally arranged, imbricating, paddle-shaped, movable lateral flaps; (vi) comb-like gills positioned between the flaps; (vii) two exsagittal rows of segmentally repeated ventral or internal structures of unknown function, preserved as black or light-reflective patches; (viii) a telson-like structure composed of two or three pairs of large flaps; and (ix) furcae, at least in some forms. *Kerygmachela* shares most of these characters, besides general similarities including overall appearance and inferred predatory mode. Features (i) through (ix) are regarded here as synapomorphies indicating a monophyletic origin for the forms. Some of the structures are considerably modified in *Opabinia*: There are five eyes rather than two, the lateral flaps usually imbricate in a reversed direction, and the single preoral appendage is apparently formed by fusion of the pair present in anomalocaridids (*14*, *28*)—an intermediate stage may be represented by *Kerygmachela*.

These differences, and, for example, the sclerotized mouth apparatus in anomalocaridids, indicate considerable evolution between the common ancestor and its descendants. The assignment (*24*) of *Kerygmachela* to the lobopods is regarded here as erroneous, and the concomitant suggestion of lobopod legs in *Opabinia* is incompatible with the Chengjiang anomalocaridid evidence, showing the fibrous nature of these structures [character (vii) above]. We therefore reject assignment (*24*) of these taxa to the Lobopodia. We regard the anomalocaridids, *Kerygmachela*, and *Opabinia* as representing a group of phylum-level rank, and propose an unnamed phylum-level taxon, defined by characters (i) through (ix).

Several features indicate affinities of the group to accepted arthropods: the presence of a tough exoskeleton, growth by moulting, true segmentation, comb-like gills, and pivot joints in the appendages. The (super)-phylum Arthropoda also embraces the groups from the dismantled (*29*) Uniramia, and evidently also the Onychophora, after recent molecular work (*30*). If a superphylum level is used for this revived arthropod concept, the group is a phylum, whereas if the phylum level is chosen, the group is a subphylum of the Arthropoda.

REFERENCES AND NOTES

1. S. A. Bowring *et al.*, *Science* **261**, 1293 (1993).
2. S. Conway Morris, *Trans. R. Soc. Edinb. Earth Sci.* **80**, 271 (1989).
3. W.-t. Zhang and X.-g. Hou, *Acta Palaeontol. Sin.* **24**, 591 (1985).
4. J.-y. Chen and B.-D. Erdtmann, in *The Early Evolution of Metazoa and the Significance of Problematic Taxa*, A. M. Simonetta and S. Conway Morris, Eds. (Cambridge Univ. Press, New York, 1991), pp. 57–76.
5. X.-g. Hou, L. Ramsköld, J. Bergström, *Zool. Scr.* **20**, 395 (1991).
6. S. Bengtson, in *The Proterozoic Biosphere—A Multidisciplinary Study*, W. J. Schopf and C. Klein, Eds. (Cambridge Univ. Press, New York, 1992), pp. 397–411.
7. M. A. Fedonkin and B. N. Runnegar, in (*6*), pp. 389–395.
8. S. Conway Morris, *Palaeontology* **29**, 423 (1986).
9. ______, *Spec. Pap. Palaeontol.* **20**, 1 (1977).
10. D. L. Bruton, *Philos. Trans. R. Soc. London Ser. B* **295**, 619 (1981).
11. H. B. Whittington and D. E. G. Briggs, *ibid.* **309**, 569 (1985).
12. ______, in *Proceedings of the Third North American Paleontological Convention, Montreal*, B. Mamet and M. J. Copeland, Eds. (Business and Economic Service Limited, Toronto, 1982), vol. 2, pp. 573–575.
13. The combination of the anterior appendage "F" [D. E. G. Briggs, *Paleontology* **22**, 631 (1979)] with *P. nathorsti* (*11*) was recently rejected (*16*), and much other Burgess Shale material previously assigned (*11*) to the species *nathorsti* may belong to yet another anomalocaridid, *Hurdia* (*16*).
14. J. Bergström, *Lethaia* **19**, 241 (1986).
15. L. Delle Cave and A. M. Simonetta, in (*4*), pp. 189–244.
16. D. H. Collins, in *Fifth North American Paleontological Convention, Chicago, Abstracts and Program*, S. Lidgard and P. R. Crane, Eds. (The Paleontological Society, Lawrence, KS, 1992), p. 66.
17. R. Gore, *Natl. Geogr. Mag.* **184**, 120 (October 1993).
18. D. M. Rudkin, *R. Ontario Mus. Life Sci. Occas. Pap.* **32**, 1 (1979); G. R. Vorwald, *Geol. Soc. Am. Abstr. Programs* **14**, 639 (1982); D. E. G. Briggs and J. D. Mount, *J. Paleontol.* **56**, 1112 (1982); S. Conway Morris and R. J. F. Jenkins, *Alcheringa* **9**, 167 (1985); L. E. Babcock and R. A. Robison, *Nature* **337**, 695 (1989); L. E. Babcock, *J. Paleontol.* **67**, 217 (1993).
19. S. Conway Morris and R. A. Robison, *Univ. Kans. Paleontol. Contrib. Pap.* **122**, 1 (1988).
20. G. F. Matthew, *Proc. Trans. R. Soc. Can. Sect.* **48**, 123 (1891); J. W. Durham, *Geol. Soc. Am. Abstr. Programs* **3**, 114 (1971); S. Conway Morris, *Annu. Rev. Ecol. Syst.* **10**, 327 (1979); ______ and R. A. Robison, *Univ. Kans. Paleontol. Contrib. Pap.* **117**, 1 (1986); J. Sprinkle, *Mus. Comp. Zool. (Harv. Univ.) Spec. Publ.* 1–283 (1973).
21. R. A. Robison, in (*4*), pp. 77–98.
22. S. P. Alpert and J. N. Moore, *Lethaia* **8**, 223 (1975).
23. J. Dzik and K. Lendzion, *ibid.* **21**, 29 (1988).
24. G. Budd, *Nature* **364**, 709 (1993).
25. S. Conway Morris *et al.*, *ibid.* **326**, 181 (1987).
26. L. Ramsköld and X.-g. Hou, *ibid.* **351**, 225 (1991).
27. H. B. Whittington, *Philos. Trans. R. Soc. London Ser. B* **271**, 1 (1975).
28. J. Dzik, in *Evolutionary Biology Volume 27*, M. K. Hecht, R. J. Macintyre, M. T. Clegg, Eds. (Plenum, New York, 1993), pp. 339–386.
29. J. Kukalová-Peck, *Can. J. Zool.* **70**, 236 (1992); W. A. Shear, *Nature* **359**, 477 (1992).
30. J. W. O. Ballard *et al.*, *Science* **258**, 1345 (1992); W. C. Wheeler, P. Cartwright, C. Y. Hayashi, *Cladistics* **9**, 1 (1993).

31. Supported by the Chinese Academy of Science and the National Geographic Society (grant no. 4760-92). L.R. acknowledges support in China by the Wenner-Gren Foundation.

27 December 1993; accepted 15 March 1994

Reconciling Short Recurrence Intervals with Minor Deformation in the New Madrid Seismic Zone

Eugene S. Schweig* and Michael A. Ellis

At least three great earthquakes occurred in the New Madrid seismic zone in 1811 and 1812. Estimates of present-day strain rates suggest that such events may have a repeat time of 1000 years or less. Paleoseismological data also indicate that earthquakes large enough to cause soil liquefaction have occurred several times in the past 5000 years. However, pervasive crustal deformation expected from such a high frequency of large earthquakes is not observed. This suggests that the seismic zone is a young feature, possibly as young as several tens of thousands of years old and no more than a few million years old.

Over the past decade, conflicting evidence has been mounting regarding the recurrence intervals of large earthquakes in the New Madrid seismic zone of the Central United States, the site of at least three great earthquakes in 1811 and 1812. Seismological, geodetic, and some paleoseismological data suggest a relatively short recurrence interval, on the order of 1000 years or less, and deformation rates comparable with those at plate margins. Yet, other data indicate that these rapid strain rates cannot have been constant for geologically long periods of time.

Seismological evidence for a short recurrence interval is in the form of earthquake frequency-magnitude relations. Johnston and Nava (*1*) analyzed the historical and instrumental record and determined that earthquakes of surface-wave magnitude, M_S, ≥ 8.3 should recur every 550 to 1100 years on average in the New Madrid seismic zone.

Liu *et al.* (*2*) reoccupied a 1950s triangulation network in the southern New Madrid seismic zone using the global positioning system (GPS). Their data indicate

---

E. S. Schweig, U.S. Geological Survey and Center for Earthquake Research and Information, University of Memphis, Memphis, TN 38152, USA.
M. A. Ellis, Center for Earthquake Research and Information, Memphis, TN 38152, USA.

*To whom correspondence should be addressed.