

The origin of crustaceans: new evidence from the Early Cambrian of China

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One of the smallest arthropods recently discovered in the Early Cambrian Maotianshan Shale Lagerstätte is described. *Ercaia* gen. nov. has an untagmatized trunk bearing serially repeated biramous appendages (long and segmented endopods and flap-like exopods), a head with an acron bearing stalked lateral eyes and a sclerite and two pairs of antennae. The position of this 520 million-year-old tiny arthropod within the Crustacea is supported by several anatomical features: (i) a head with five pairs of appendages including two pairs of antennae, (ii) highly specialized antennae (large setose fans with a possible function in feeding), and (iii) specialized last trunk appendages (segmented pediform structures fringed with setae). The segmentation pattern of *Ercaia* (5 head and 13 trunk) is close to that of Maxillopoda but lacks the trunk tagmosis of modern representatives of the group. *Ercaia* is interpreted as a possible derivative of the stem group Crustacea. *Ercaia* is likely to have occupied an ecological niche similar to those of some Recent meiobenthic organisms (e.g. copepods living in association with sediment). This new fossil evidence supports the remote ancestry of crustaceans well before the Late Cambrian and shows, along with other fossil data (mainly Early Cambrian in China), that a variety of body plans already coexisted among the primitive crustacean stock.

Keywords: Arthropoda; Crustacea; Maxillopoda; Early Cambrian; Lagerstätte

1. INTRODUCTION

The origin of one of the most diverse groups of present-day marine animals, namely the crustaceans, is still an open issue. The oldest undisputable crustaceans, which are comparable with Recent ones in key aspects of their anatomy, ontogeny and biology, e.g. three-dimensionally-preserved Orsten branchiopods and maxillopods (Walossek & Müller 1998; Walossek 1999), date back to the Late Cambrian. The phosphatocopids (Lower–Upper Cambrian), that are a group of ostracod-like bivalved arthropods and that are also well documented from the Late Cambrian Orsten fauna (Müller 1979, 1982; Hou *et al.* 1996), are assumed to represent a sister taxon of Eucrustacea (Eucrustacea = crown group crustaceans) (see Walossek 1999). Sparse and incomplete specimens with preserved soft parts attest the presence of phosphatocopids in the Middle Cambrian of Siberia (Müller *et al.* 1995) and Australia (Hinz-Schallreuter 1993; Walossek *et al.* 1993) and in the Early Cambrian of England (Hinz 1987). Although morphological evidence and molecular studies using 18S rDNA (Spears & Abele 1998, 1999, 2000) both suggest that crustaceans have an earlier origin, palaeontology has failed to confirm the presence of the group in strata older than the Late Cambrian. The existence of crustacean precursors within the diverse arthropod fauna of the Mid-Cambrian Burgess Shale fauna and the Early Cambrian Maotianshan Shale fauna has long been hypothesized. For some authors (e.g. Walossek 1999) their presence remains inconclusive because most ‘candidates’ seem to be lacking important

diagnostic features of modern crustaceans, particularly the specialized head appendages related to feeding mechanisms. Others (e.g. Chen & Zhou 1997; Hou & Bergström 1997) hold the view that the first crustaceans or the precursors of the group can be identified among the Early Cambrian arthropods and that they may be closely tied with modern crustacean lineages on the basis of their body plan (e.g. segmentation pattern). We describe here a small arthropod from the Early Cambrian Maotianshan Shale of South China that shows possible crustacean affinities.

2. NEW FOSSIL EVIDENCE

(a) Morphology

Ercaia minuscula gen. et sp. nov. differs from all Cambrian arthropods described to date. The first antenna (A1) is a long flagellum composed of 10 or 11 articulating podomeres bearing distal setae (figures 1c and 2a,c). The most distal podomere is tipped with several stiff setae. The second antenna (A2) is biramous with a relatively short endopod (approximately five podomeres). The exopod of A2 is one of the most unusual features of *E. minuscula* gen. et sp. nov. (figures 1a and 2a). It is composed of four or five podomeres, the most proximal one bearing a crescent-shaped feature from which a prominent setose fan originates (at least 24 stiff setae). Three additional pairs of head appendages occur between A2 and the first pair of biramous trunk appendages (figure 2d), but none of our specimens show the detailed structure of their basal part (e.g. basipodite). These three appendages do not seem to be specialized, and resemble the anterior trunk appendages. The lateral eyes are stalked and protrude beyond the head shield anterolaterally; they

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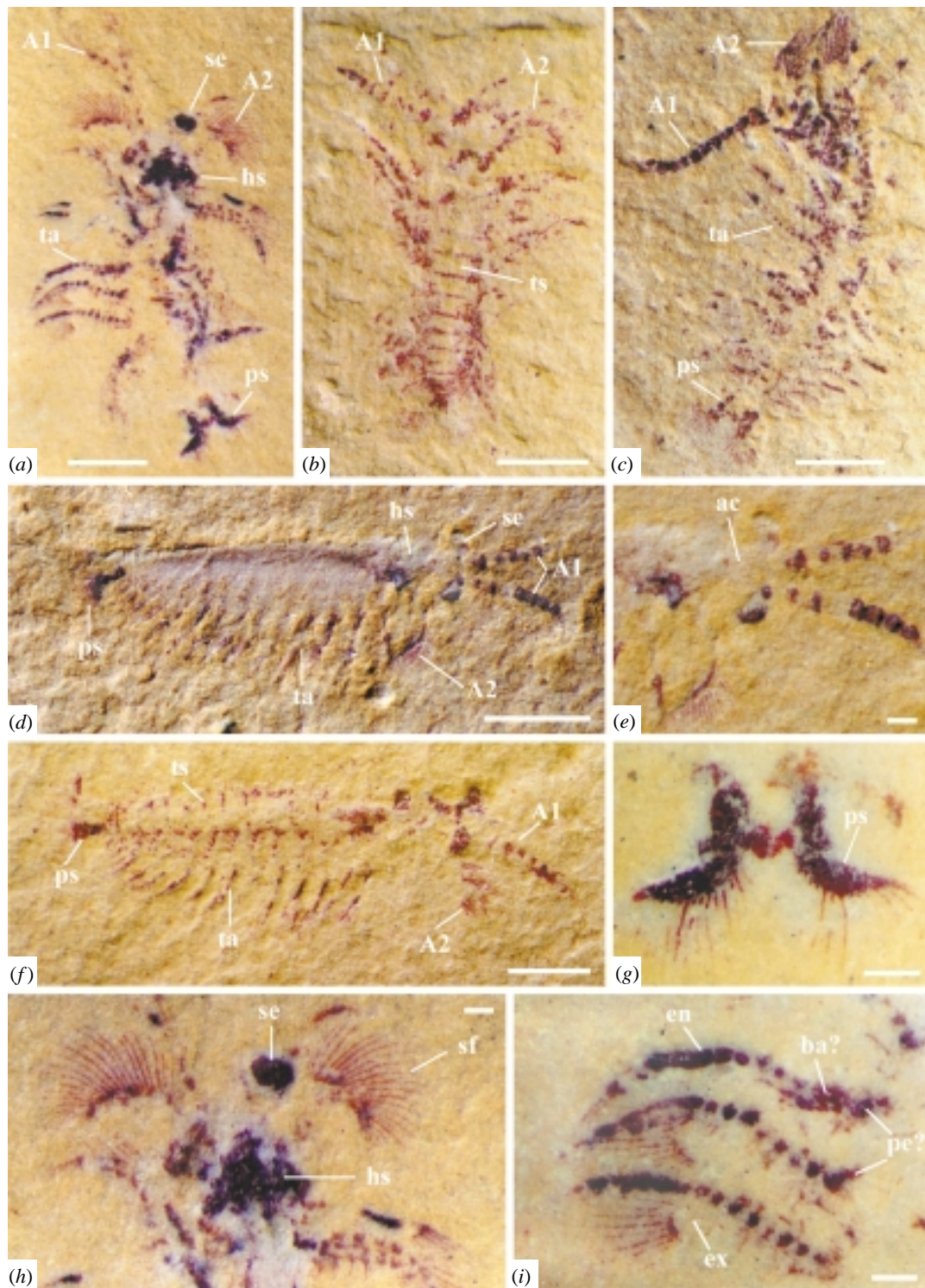


Figure 1. *Ercaia minuscula* gen. et sp. nov. (Ercaicun, Haikou near Kunming, Yunnan Province, South China), an Early Cambrian Maotianshan Shale member, middle part of Yu'anshan Formation (*Eoredlichia*–*Wudingia* Zone). (a) General view of holotype EC 10001. (b) General view of EC 10002. (c) General view of EC 10003. (d) General view of EC 10004. (e) Detail of the posterior half of EC 10004. (f) General view of EC 10005. (g–i) Detailed views of the caudal pediform structures (g), antennal setose fans (h) and biramous trunk appendages (i) of holotype EC 10001. All light colour micrographs. (a–d, f) Scale bar = 500 μ m. (e, g–i) Scale bar = 100 μ m. A1 and A2, first and second antennae; ba?, possible basis; en, endopod; ex, exopod; hs, head shield; pe?, possible proximal endite; ps, pediform structure; se, stalked lateral eyes; ta, thoracic appendages; ts, trunk segment.

are inserted on the anteriormost, possibly acron-like section of the head. The morphology of the mouth region (e.g. feeding apparatus with a labrum and atrium oris) is unknown. The head shield is narrow with an overall

elliptical shape (length less than 25% of the animal's length) and is armed with marginal spines. The trunk segments are all similar to each other and form a set of 13 cylindrical elements (T1–T13) that show a gradual

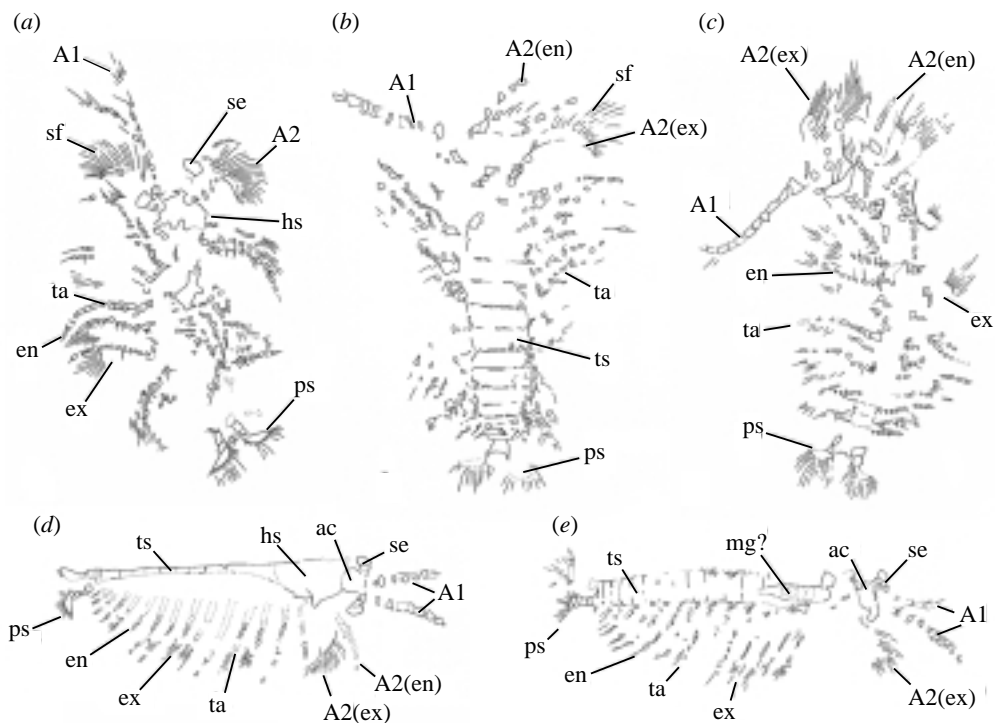


Figure 2. *Ercaia minuscula* gen. et sp. nov. Line drawings of the same specimens as shown in figure 1. (a) EC 10001, (b) EC 10002, (c) EC 10003, (d) EC 10004 and (e) EC 10005. ac, acron; A1, first antenna; A2(en), endopod of the second antenna; A2(ex), exopod of the second antenna; en, endopod; ex, exopod; h, head; hs, head shield; mg?, possible midgut; ps, pediform structure; se, stalked lateral eye; sf, antennal setose fan; ta, thoracic appendage; ts, trunk segment.

reduction in size towards the posterior end of the animal (figures 1*b*, 2*b,e* and 3). Each segment bears a pair of biramous appendages. The appendages of T1–T12 consist of a slender endopod with at least 12 articulated podomeres, each bearing one or two setae on a tiny expansion (figure 1*h,i*). The endopod is flanked by an elongate paddle-like exopod attached to a possible basis (figure 1*i*) and lined with numerous fine setae along its distal margin. The last endopodial segment is longer and bears terminal setae. The most proximal element of the appendage is interpreted here as a possible proximal endite (*sensu* Walossek 1999) and bears a row of stiff setae (figure 1*i*). The appendages gradually decrease in relative size towards the posterior end of the trunk (figure 1*f*). The last trunk segment (T13) is provided with a pair of slightly divergent pediform structures, that are each composed of four segments and terminated by a setose blade (figure 1*g*) that recalls the setose fans of A2, as if the same features were repeated at both ends of the animal. Possible endopodial remnants pointing inwards may be present (figure 1*g*). The appendage of T13 is superficially more similar to the uropods of modern crustaceans than to any other simple caudal features such as furcal-like rami. The exact morphology of the trunk end is unknown. All specimens distribute within a narrow size range (1.2–3.3 mm with 75% of specimens between 2.3 and 3.0 mm) and presumably belong to the adult and pre-adult stages.

(b) Inferred lifestyle

The body design and appendage distribution (figure 1*d,f*) of *Ercaia* indicate poor abilities for crawling, in

contrast with numerous dorsally flattened arthropods of the Maotianshan Shale biota (e.g. Hou & Bergström 1997). More probably, *Ercaia* was using its trunk appendages (paddle-like exopods) and the multidirectional flexions of its slender body for stirring up flocculent material in the water–sediment interface and for swimming close to the bottom (possibly with a metachronal rhythm as in a variety of modern crustaceans such as remipeds) (Felgenhauer *et al.* 1992). The setose fans of A2 may have acted as sweeping combs that were capable of generating feeding currents and trapping suspended particles such as organic detritus, algae or bacteria. The second antenna of numerous Recent copepods plays this role (Boxshall 1986, 1992). The setose fans of *Ercaia* probably functioned at low Reynold's number (there are analogues in Recent copepods) (Koehl & Strickler 1981) and were therefore possibly acting as solid rakes rather than actual filters. The paddle-like pediform structures may have served in locomotion (vertical movements). Although *Ercaia* does not conform to the strict definition of the meiofauna, i.e. animals passing through a sieve of 1 mm mesh but being retained on sieve of 0.1 mm mesh, this tiny arthropod is likely to have occupied an ecological niche similar to those of some Recent meiobenthic organisms (e.g. copepods living in association with sediment) (see Coull 1988). Meiofaunal arthropods are known to have occurred in the Upper Cambrian (fig. 2 in Walossek 1993). The small macrobenthos of the Maotianshan Shale biota is also represented by prolific bivalved arthropods such as bradoriids (Hou 1997; Shu *et al.* 1999; Hou *et al.* 2001) and the larval stages of larger organisms (e.g. naraoides) (Chen *et al.* 1996).

3. EVOLUTIONARY IMPLICATIONS

Our knowledge of the early history of crustaceans is based almost exclusively on the study of Upper Cambrian three-dimensionally-preserved minute fossils that have been chemically extracted from phosphatic limestones (e.g. Swedish Orsten material). This exceptional and abundant material has led authors (Walossek 1999) to recognize (i) representatives of eucrustaceans (=crown group Crustacea containing all the living crustaceans) such as maxillopods (e.g. *Dala*, *Bredocaris* and *Skaracarida*) (Müller 1983; Müller & Walossek 1985*a,b*, 1988; Walossek & Müller 1992, 1998) and branchiopods (e.g. *Rehbachella*) (Walossek 1993, 1999), (ii) a sister group of Eucrustacea represented by the ostracod-like Phosphatocopida (Müller 1979, 1982), and (iii) several isolated forms interpreted as derivatives from the stem line Crustacea (e.g. *Martinssonina*, *Goticaris*, *Cambropachycope* and *Henningsmoenicaris*) (fig. 5 in Walossek 1999). The phosphatocopids most probably lie at an evolutionary level close to the crown group Crustacea (Hou *et al.* 1996). The presence of eucrustaceans earlier in the fossil record is often considered as uncertain (Walossek 1999) on the assumption that early and middle Cambrian arthropods (e.g. those from Burgess and Maotianshan Shale Lagerstätten) lack some essential characteristics of the crustacean body plan (e.g. no specialized exopods, no proximal endites on the post-antennular limbs and head and trunk tagmosis different from that of Crustacea). *Canadaspis* (Early and Middle Cambrian), which was first believed to represent an early malacostracan (Phyllocarida) (Briggs 1978, 1992), is rejected from the Crustacea by several authors (Dahl 1984; Hou & Bergström 1997; Walossek 1999) on the basis of its peculiar limb morphology, although its segmentation pattern (five presumed head segments, eight thoracic and seven limbless abdominal segments plus a telson) is comparable with that of Recent phyllocarids. With regard to Cambrian arthropods in general, much stress has been placed on the presence or absence of limb specialization (typically head appendages involved in feeding mechanisms) and perhaps more attention should be paid to essential characteristics of the body plan such as the segmentation pattern.

Ercaia has several plesiomorphic characters that are inherited from more ancestral arthropod lines and exemplified by its prominent stalked eyes, its repeated series of trunk appendages and the uniform-like design of its post-A2 appendages (a multisegmented endopod and paddle-like exopod). Such characters are found in numerous arthropods of the Maotianshan Shale biota, e.g. *Fortiforceps foliosa* (Hou & Bergström 1997) and *Jianfengia multisegmentalis* (Hou 1987; see Chen & Zhou 1997; Hou & Bergström 1997). *Ercaia* also has an eye-bearing acron (figures 1*d,e*, 2*d* and 3) that appears to represent a primitive character that also occurs in adult forms of Cambrian *Fuxianhuia* and *Kuamaia* (Early Cambrian) (Chen *et al.* 1995) and *Helmetia* (Middle Cambrian). However, *Ercaia* possesses a set of original features that may indicate crustacean affinities. These are: (i) a head with five pairs of appendages (A1 + 4 patterns and not A1 + 3 patterns as in most Early Cambrian arthropods), (ii) highly specialized biramous antennae with setose fans, and (iii) similarly modified uropod-like appendages

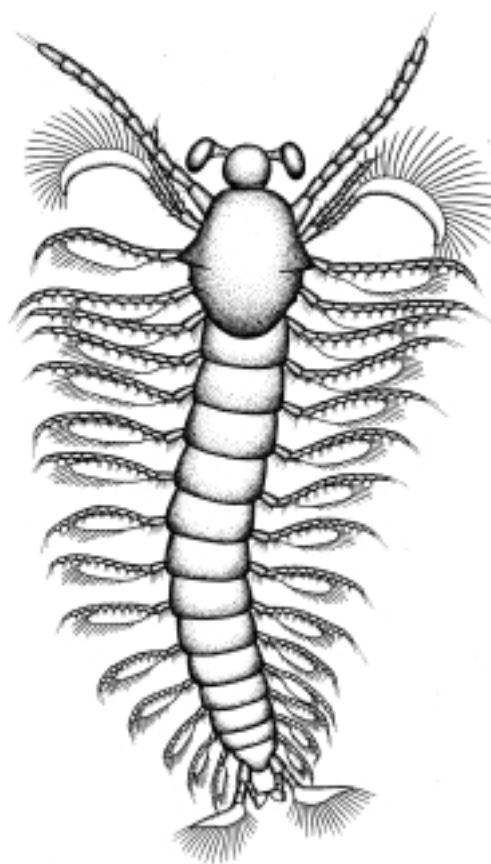


Figure 3. Reconstruction of the dorsal view of *E. minuscula* gen. et sp. nov.

(pediform structures fringed with setae) at the end of the trunk. However, anatomical features that were considered by Walossek (1999) to be characteristic of the ground pattern of the stem species of Eucrustacea (a fourth head appendage specialized for food transport, a mouth region with fine hairs and an orthonauplius larval stage with three pairs of limbs) could not be observed in *Ercaia*. These features may have been originally absent in *Ercaia* or are not preserved. Important preservational differences between the Orsten material and the fossils from other Cambrian Lagerstätten (Maotianshan, Burgess, Sirius Passet) often hinder detailed comparisons.

Ercaia superficially resembles remipedes (Carboniferous–Recent), which have been considered as the most primitive of all crustaceans by several authors (Schram 1986; Schram & Hof 1998). Indeed *Ercaia* and Recent remipedes both possess a long untagmatized trunk region flanked by serially repeated biramous swimming appendages, but the trunk of remipedes display many more segments (up to 36) (Felgenhauer *et al.* 1992; Cals 1996) than *Ercaia* (13 segments). Moreover, Recent and Carboniferous remipedes have a fully developed set of specialized head appendages, which are not found in *Ercaia*. These major differences do not support the idea that *Ercaia* might be a remiped. Neither Cambrian evidence nor molecular data recently obtained from 18S rDNA (Spears & Abele 1998) credit the supposedly primitive status of remipedes. Their morphology may be merely the result of relatively Recent adaptations to very specialized lifestyles and habitats (anchihaline cave systems) (Felgenhauer *et al.* 1992).

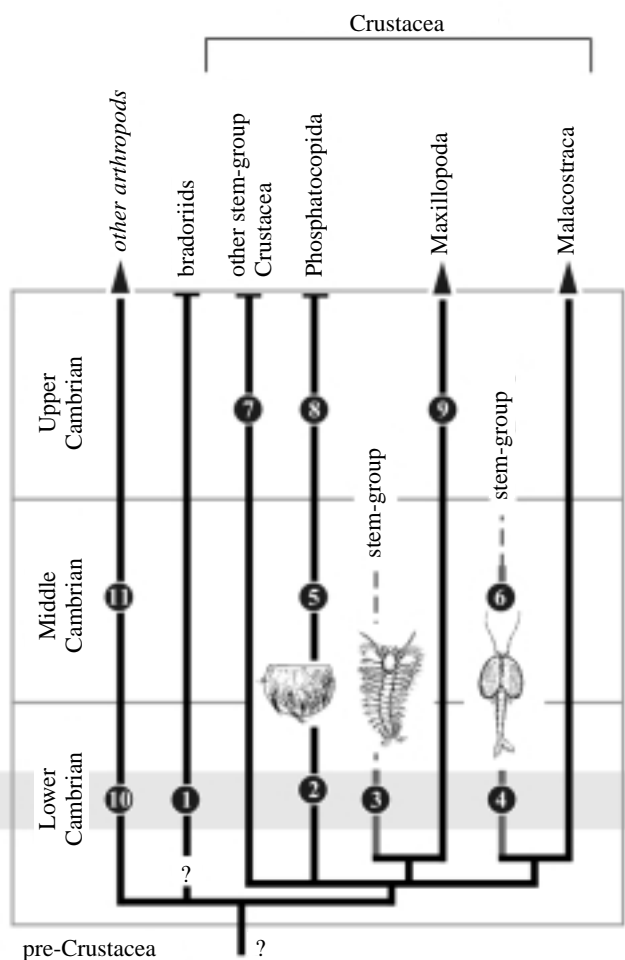


Figure 4. Tentative phylogenetic tree of the Crustacea focusing on the early history of the group. Partly based on fig. 11 in Walossek (1999) (branchiopod, cephalocarid, phyllocarid and eumalacostracan lineages not represented here). The relation of bradoriids to Crustacea is uncertain (Shu *et al.* 1999). The Precambrian history of arthropods is hypothetical. The numbers are occurrences of taxa not nodes or characters. 1, *Kunmingella* (Shu *et al.* 1999); 2, Vestrogothiicopina (Hinz 1987); 3, *Ercaia* gen. nov.; 4, *Canadaspis*, waptiid *Chuandianella* and *Clypecaris* (Chen & Zhou 1997; Hou & Bergström 1997; Chen *et al.*, unpublished data); 5, undetected Phosphatocopina (Müller *et al.* 1995); 6, *Canadaspis* and *Waptia* (Briggs *et al.* 1994); 7, *Henningsmoenicaris*, *Martinssonina*, *Cambrocaris*, *Cambropachycope* and *Goticaris* (Walossek 1999); 8, *Hesslandona* and *Vestrogothia* (Müller 1982); 9, *Bredocaris*, *Skara* and *Dala* (Walossek & Müller 1998); 10 and 11, other arthropods from the Maotianshan Shale (Lower Cambrian) and Burgess Shale (Middle Cambrian) biota. The horizontal shaded band represents the Maotianshan Shale fauna of early Atdabanian (Chen & Zhou 1997). The time is not to scale.

The phylogenetic relationships of *Ercaia* with other extant crustacean groups are difficult to establish, mainly because of the lack of detailed information concerning its ventral anatomy. However, its segmentation pattern suggests affinities with maxillopodan crustaceans that are abundantly represented in the Recent and recognized in the Upper Cambrian (Walossek & Müller 1998). The 5 head and 13 trunk segmentation of *Ercaia* is close to that of Maxillopoda (5 head and 11 trunk segmentation),

although no subdivision of the trunk into well-delineated thoracic and abdominal units (6 thoracic and 5 abdominal or 7 thoracic and 4 abdominal units) (see Newman 1983; Walossek & Müller 1998) is distinguishable in *Ercaia*. Maxillopods with a relatively advanced trunk tagmosis (seven thoracic and four abdominal units) are known from the Upper Cambrian Orsten of Sweden (*Dala*) (Walossek & Müller 1998). We propose the challenging hypothesis that *Ercaia* and the Maxillopoda may have a common ancestor (figure 4). The maxillopod lineage may have evolved from ancestors comparable with *Ercaia* (i) by the loss of trunk segments as a possible result of paedomorphosis, and (ii) by the loss of posterior appendages leading to the maxillopodan tagmosis (thorax/abdomen) to ultimately give rise to the maxillopodan lineages that form a large part of the modern microcrustacean biodiversity (e.g. copepods, ostracods, cirripeds and branchiurans). The origin of Ostracoda from one of the bivalved arthropod groups present in the Cambrian (e.g. phosphatocopids or bradoriids) is controversial (Hou *et al.* 1996; Chen & Zhou 1997; Shu *et al.* 1999). An alternative to this model is that the body plan of ostracods may have arisen from tiny non-bivalved animals comparable to *Ercaia* via the loss of trunk appendages and the encasement of the body by the head shield. The bilamellar furcal complex of myodocopid (Parker 1997) and platycopid (Schulz 1976) ostracods may have evolved from appendage structures such as the pediform structures of *Ercaia*. In our tentative evolutionary scenario (figure 4), early Cambrian crustaceans are represented by at least three types of body plans, which are exemplified by bivalved phosphatocopids, *Ercaia* and phyllocarid-like animals (e.g. *Canadaspis* and waptiids).

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APPENDIX A: SYSTEMATIC PALAEOLOGY

Superclass Crustacea Pennant, 1777

? Class Maxillopoda Dahl, 1956

Ercaia gen. nov.

Derivation of the name

From the type locality Ercaicun (Ercai Village), Yunnan Province, China.

Type species

Ercaia minuscula gen. et sp. nov.

Diagnosis

A small (*ca.* 2–4 mm long) elongate arthropod. Head with an acron bearing a pair of stalked lateral eyes and a sclerite and five pairs of appendages. An elliptical head shield. Al with a long and segmented flagellum. Biramous

A2 (endopod short and segmented and exopod bearing a scale-like feature fringed with a setose fan). Post-antennular head appendages similar to anterior trunk appendages. Trunk with 13 articulated segments all similar in shape. One pair of biramous appendages per trunk segment (a slender multi-articulated endopod and flap-like exopod fringed with setae) all similar in shape except the last pair (short segmented pediform structures with a setose fan).

Ercaia minuscula gen. et sp. nov.

Derivation of the name

Alluding to the small size of this arthropod.

Material

One hundred and thirty-two specimens typically preserved isolated, either laterally compressed or dorsoventrally flattened and, more rarely, as small clusters of individuals. Appendage remains typically preserved as reddish aluminosilicate films in weathered mudstones. Exoskeletal elements rarely disarticulated. All the material is deposited in the collections of the Early Life Research Centre, Chengjiang, Yunnan Province, China.

Holotype

EC 10001, a dorsoventrally flattened specimen (figures 1a, g–i and 2a).

Paratypes

EC 10002 (figures 1b and 2b), 10003 (figures 1c and 2c), 10004 (figures 1d, e and 2d) and 10005 (figures 1f and 2e).

Type locality

Ercaicun, Haikou near Kunming, Yunnan Province, South China; Early Cambrian Maotianshan Shale member in the middle part of the Yu'anshan Formation (*Eoredlichia*–*Wutingaspis* Zone).

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.