

# The Early Cambrian origin of thylacocephalan arthropods

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*Zhenghecaris shankouensis* gen. et sp. nov. is one of the largest “bivalved” arthropods of the Lower Cambrian Maotianshan Shale fauna. Its non-mineralized carapace was dome-like, laterally compressed, armed with rostral features, and probably enclosed the entire body of the animal. *Zhenghecaris* was provided with elliptical stalked lateral eyes. The carapace design, external ornament and visual organs of *Zhenghecaris* suggest affinities with the Thylacocephala, an extinct (Lower Silurian to Upper Cretaceous) group of enigmatic arthropods whose origins remain poorly understood. The bivalved arthropods *Isoxys* and *Tuzoia* (Lower and Middle Cambrian) are two other potential thylacocephalan candidates making this group of arthropods a possible new component of Cambrian marine communities. *Zhenghecaris*, *Isoxys*, and *Tuzoia* are interpreted as nektonic animals that probably inhabited the lower level of the water column in shallow shelf settings at depths of perhaps 100–150 m or less. Their feeding mode either in the water column (e.g., mesozooplankton) or on the substrate (e.g., small epibenthos, detritus) is uncertain, although some of these arthropods were possibly mid-water predators (e.g., *Isoxys* with raptorial appendages).

Key words: Arthropoda, *Zhenghecaris*, Lagerstätte, Cambrian, Maotianshan Shale, China.

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## Introduction

The thylacocephalans are “bivalved” arthropods with a long fossil record (Lower Silurian to Upper Cretaceous; Mikulic et al. 1985; Schram et al. 1999), a worldwide distribution (Europe, North America, Australia, China and South America) and a distinctive morphology exemplified, in some Mesozoic species, by hypertrophied visual organs and long raptorial appendages (e.g., Secrétan 1985; Fig. 1). Despite substantial information obtained over the years from several fossil Lagerstätten (Solnhofen, Germany; Mazon Creek, Illinois, USA; La Voulte-sur-Rhône, France), the Thylacocephala remain an unusual group of animals whose origin and affinities within the Arthropoda, particularly their relationship to crustaceans, remain unresolved. In this paper we describe a new bivalved arthropod, namely *Zhenghecaris shankouensis* sp. nov., from the Lower Cambrian Maotianshan Shale of SW China and analyze its possible thylacocephalan affinities. We also discuss the possibility that other Cambrian bivalved arthropods such as *Tuzoia* Walcott, 1912 and *Isoxys* Walcott, 1890 may belong to the Thylacocephala, making the group a possible new arthropod constituent of Cambrian communities.

*Institutional abbreviations.*—Sk, Early Life Research Centre, Chengjiang, Yunnan Province, China; FSL, Faculty of Sciences, Université Claude Bernard Lyon 1, France; IPMR, Museum d’Histoire Naturelle, Paris.

## Material and methods

The specimens were recovered from excavations made near the Shankoucun Village (near Anning, ca. 40 km SW of Kunming City, Yunnan Province; Peng et al. 2001; Huang, 2005) by J.-Y. Chen, D.-Y. Huang, and their collaborators. The excavated horizons belong to the Maotianshan Shale Member of the Yu’anshan Formation, assigned to the Lower Cambrian by trilobite zonation (for general stratigraphy, see Hou et al. 2004). As in other localities of Yunnan Province where the Maotianshan Shale crops out, the host rock of the fossils consists of three different facies: background mudstones containing organic-rich laminae (Fig. 2B), single-event mudstones resulting from rapid deposition of suspended mud (microturbiditic events possibly generated by storms and bioturbated mudstones (see Zhang et al. 2001; Zhu et al. 2001, 2003; Hu 2005). Exceptionally preserved

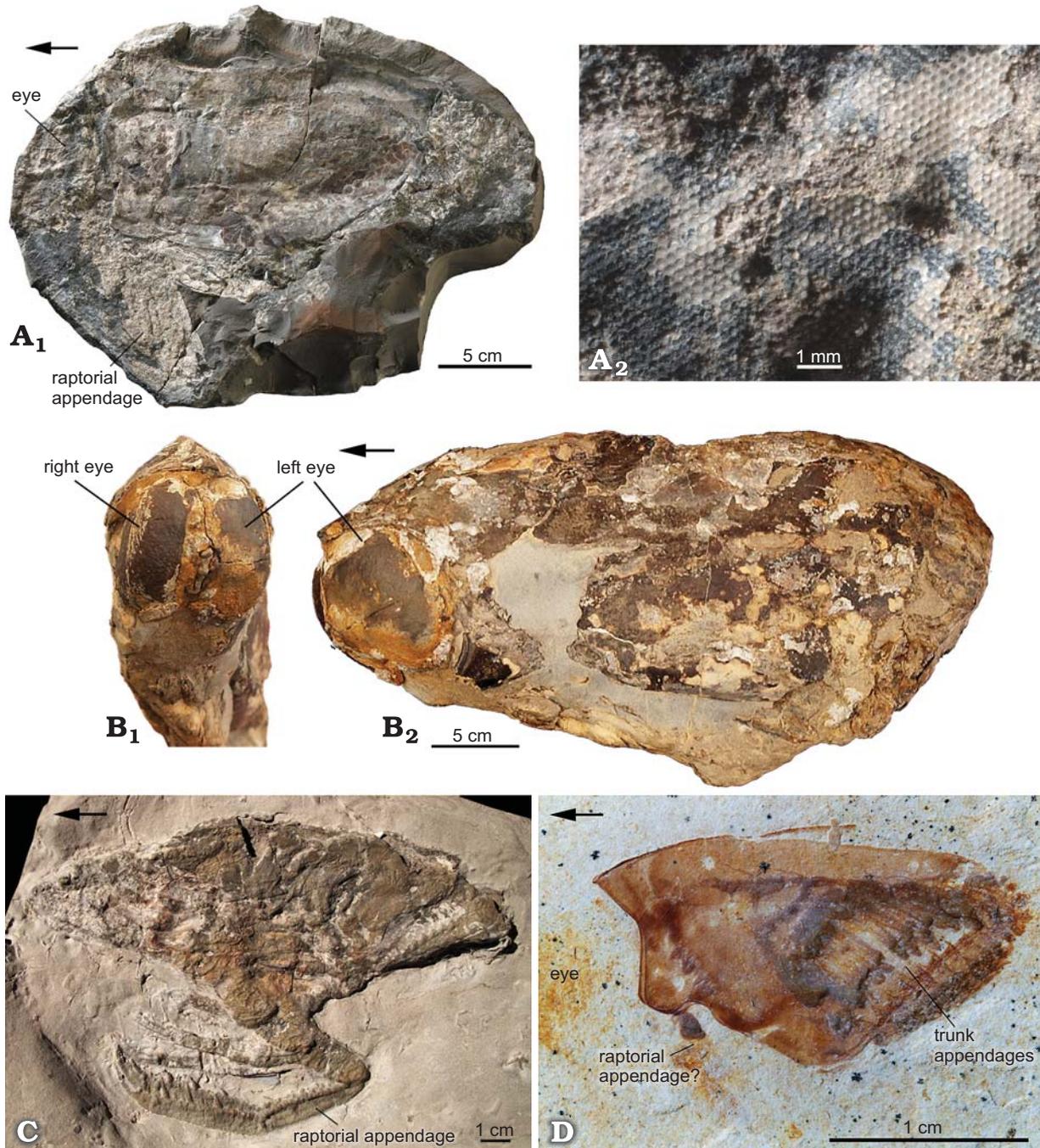


Fig. 1. Mesozoic thylacocephalans. **A–C.** *Dollocaris ingens* Van Straelen, 1923, Callovian, La Voulte, France. FSL 170759, general view (**A<sub>1</sub>**) and detail (**A<sub>2</sub>**) of visual surface. **B.** Three-dimensionally preserved specimen showing a pair of bulbous eyes, in left lateral (**B<sub>1</sub>**) and frontal (**B<sub>2</sub>**) views (collection of the Musée d'Histoire Naturelle, Lyon, specimen number in-progress). **C.** IPM R 62002, specimen showing well-preserved raptorial appendages. **D.** *Mayrocaris bucculata* Polz, 1994, general view of paratype (specimen 93032701 from Polz 1994: pl. 1: 3, courtesy S. Secrétan).

soft-bodied fossils (e.g., worms, non-mineralized arthropods) and high faunal diversity generally characterize the single-event mudstones whereas lower diversity assemblages of carcasses, exuviae, and lightly sklerotized organisms are more frequent in background mudstone (Hu 2005). *Zhenghecaris* gen. nov. is rare. Its bivalved carapace is typically covered with thin brownish amorphous Fe-rich aluminosilicate (Zhu et al. 2005) contrasting with the greenish

mudstone matrix. Although flattened by compaction, part of its three-dimensional aspect is preserved. The fauna associated with *Zhenghecaris* gen. nov. consists of numerous priapulid worms (Huang 2005), Porifera, Cnidaria, Lobopodia, Hyolitha, Arthropoda (e.g., trilobites, naraoides, *Fuxianhuia*, *Acanthomeridion*, *Retifacies*, *Xandarella*, *Urokodia*, *Alalcomenaeus*, waptiids, *Isoxys*, bradoriids, anomalocaridids), Mollusca, Sipuncula, Brachiopoda, Urochordata, and organ-

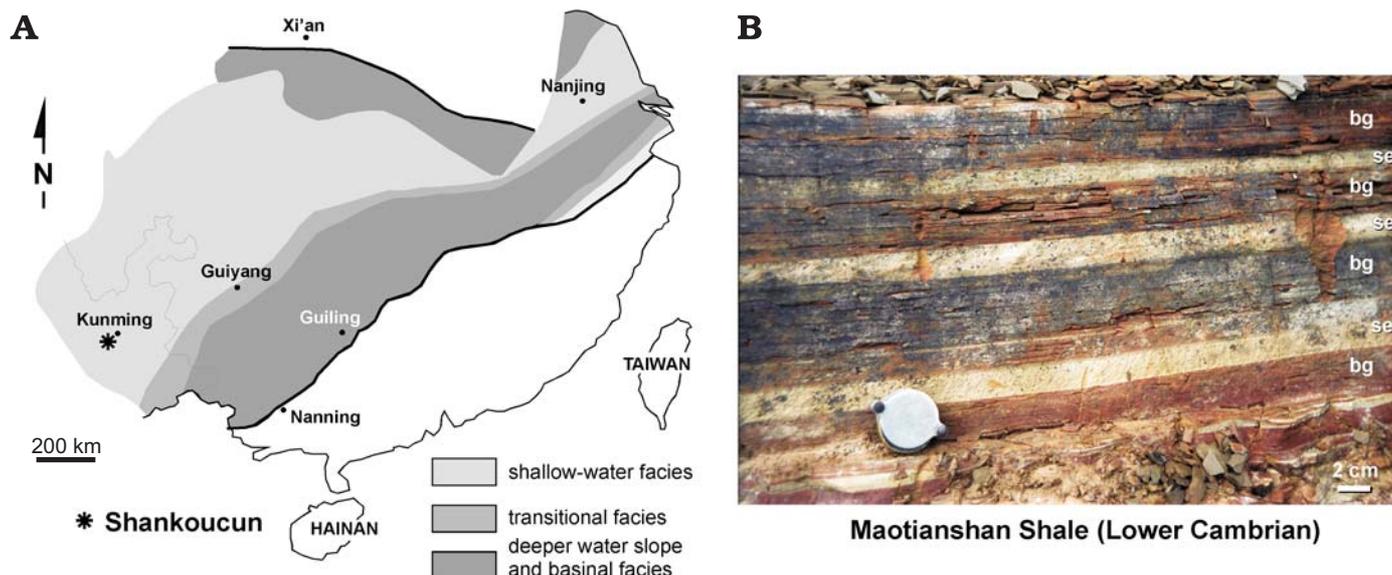


Fig. 2. Fossil locality and depositional environment. **A**. Simplified paleogeographic map of the Yangtze Platform during the Sinian–Cambrian boundary showing main facies distribution (asterisk for fossil locality). **B**. Alternating siltstones-mudstones layers at Shankoucun (Maotianshan Shale, Lower Cambrian). Map after Zhu et al. (2003; simplified). bg, background mudstone ; se, single-event mudstone (see explanation in text).

isms with uncertain affinities such as chancelloriids and edloniids (Vannier and Chen 2005).

Line-drawings were made from colour photographs. The mydocopid ostracod *Leuroleberis surugaensis* from the Pacific Coast of Japan (see Vannier et al. 1996) is used for comparisons with *Zhenghecaris* gen. nov. from the Lower Cambrian of China. Both are laterally compressed bivalved arthropods with an ovoid carapace and rostral features. The carapace architecture and internal anatomy of *Leuroleberis* were studied by means of X-ray microtomography (Skyscan, Antwerp), Scanning Electron Microscopy (SEM) and micro-tome sections.

## Systematic paleontology

Class Thylacocephala Pinna, Arduini, Pesarini, and Teruzzi, 1982

Order and Family uncertain

*Diagnosis* (modified after Schram 1990).—Arthropods with a laterally compressed shield-like carapace (length from ca. 15 to 250 mm long) enclosing the entire body. No prominent abdominal feature (e.g., tail with telescopic elements, telson, and furcae) emerging from the carapace posteriorly. Carapace ovoid with typically an anterior rostrum-notch complex; posterior rostrum may be present. Lateral surface evenly convex or with longitudinal ridge(s). External ornament (e.g., striated, pitted, corrugated, terrace-like structures). Eyes well-developed, situated in optic notches, either spherical or drop-shaped (possibly stalked), in some species hypertrophied (i.e. filling the optic notches or forming a paired, frontal globular structure) with numerous small om-

matidia. Possibly five cephalic appendages (short A1 and A2, Md, Mx1, Mx2). Well-marked trunk tagmosis. Anterior trunk with, in some forms, three segments bearing very long geniculate and chelate appendages protruding beyond the ventral margin of the carapace. Posterior trunk with a series of 8, possibly more, styliform and filamentous pleopod-like appendages decreasing in size posteriorly. Eight pairs of well-developed gills in the trunk region.

*Genera*.—A total of 21 genera and one described in open nomenclature are included within the Thylacocephala (Table 1 and Fig. 3).

*Discussion*.—This Class of arthropod was erected by Pinna et al. (1982) on the basis of *Ostenia cypriformis* from the Lower Sinemurian of Osteno (Italy). The authors distinguished five diagnostic features but gave no formal definition of the Thylacocephala. These features were: (1) the hyper-development of the anterior part of the cephalon that, according to them, lacked eyes but, curiously, housed ovaries; (2) an univalved cephalic shield encapsulating the trunk region of the animal; (3) a set of three pairs of well-developed “uniramous” appendages recognized as A1, A2, and maxillipeds (Mxp), with an assumed locomotory function; (4) a feeding apparatus that comprised the mandible (Md) and a pair of maxillae with an assumed filtering function; (5) a relatively reduced thoracic section (first segment bearing Mxp attached to cephalon followed by a series of 8 segments with thoracopods; (6) a very reduced abdomen with no apparent segmentation. Since this pioneer work, detailed studies have been carried out in a wide range of stratigraphical horizons and depositional environments and under various taphonomic conditions and have considerably improved our knowledge of the thylacocephalan animals (Fig. 4; see Secr-

Table 1. Age, occurrence, and key-references of thylacocephalan genera.

Genera	Age	Occurrence	References
<i>Ainiktozoon</i> Scourfield, 1937	Lower Silurian	Scotland	Scourfield 1937; Van der Bruggen et al. 1997
<i>Ankitokazocaris</i> Arduini, 1990	Lower Triassic	Italy	Arduini 1990
<i>Atropicaris</i> Arduini and Brasca, 1984	Upper Triassic	Italy	Arduini and Brasca 1984; Arduini 1988
<i>Austriocaris</i> Glaessner, 1931	Upper Triassic	Austria	Glaessner 1931; Rolfe 1969
<i>Clausocaris</i> Polz, 1989	Upper Jurassic (Tithonian)	Germany	Polz 1989, 1990, 1992, 1993
<i>Concavicaris</i> Rolfe, 1961	Devonian (Eifelian)-Carboniferous (mid-Pennsylvanian)	France, Czech Rep., Australia, USA	Chlupac 1963; Briggs and Rolfe 1983; Schram 1990
<i>Convexicaris</i> Schram, 1990	Carboniferous (mid-Pennsylvanian)	USA	Schram 1990
<i>Coreocaris</i> Kobayashi, 1937	Lower Permian	South Korea	Kobayashi 1937
<i>Dollocaris</i> Secrétan and Riou, 1983	Middle Jurassic (Callovian)	France	Secrétan 1983, 1985; Secrétan and Riou 1983; Fröhlich et al. 1992
<i>Harrycaris</i> Briggs and Rolfe, 1983	Upper Devonian (Frasnian)	W. Australia	Briggs and Rolfe 1983
<i>Kilianicaris</i> Van Straelen, 1923	Middle Jurassic (Callovian)	France	Van Straelen 1923
<i>Mayrocaris</i> Polz, 1994	Upper Jurassic (Tithonian)	Germany	Arduini 1990; Polz 1994
<i>Microcaris</i> Pinna, 1974	Upper Triassic	Italy	Pinna 1974
<i>Ostenocaris</i> Arduini, Pinna, and Teruzzi, 1984	Lower Jurassic (Sinemurian)	Italy	Pinna 1974; Arduini et al. 1980, 1984; Alessandrello et al. 1991
<i>Paraostenia</i> Secrétan, 1985	Middle Jurassic (Callovian)	France	Fröhlich et al. 1992
<i>Protozoa</i> Dames, 1886	Upper Cretaceous (Santonian)	Lebanon	Schram et al. 1999
<i>Pseudericthus</i> Dames, 1886	Upper Cretaceous (Santonian)	Lebanon	Schram et al. 1999
<i>Thylacocephalus</i> Lange, Hof, Schram, and Steeman, 2001	Upper Cretaceous (Santonian)	Lebanon	Lange et al. 2001
<i>Rugocaris</i> Tintori, Bigi, Crugnola, and Danini, 1986	Lower Jurassic (Pliensbachian)	Italy	Tintori et al. 1986
<i>Yangzicaris</i> Shen, 1983	Middle Triassic	China	Shen 1983
Unnamed form (in Mikulic et al. 1985)	Silurian (Llandovery)	USA	Mikulic et al. 1985
<i>Zhenghecaris</i> gen. nov.	Lower Cambrian	China	this paper

tan and Riou 1983, Secrétan 1985, Pinna et al. 1985 for the Jurassic of La Voulte and Osteno; Briggs and Rolfe 1983 for the Upper Devonian of Australia; Polz 1990, 1992, 1993, 1994, 1997 for the Upper Jurassic of Solnhofen; Schram 1990 for the Upper Carboniferous of Mazon Creek; Schram et al. 1999 and Lange et al. 2001 for the Cretaceous of Lebanon). The updated definition of Thylacocephala presented here and modified from Schram (1990) is an attempt to synthesize the paleontological information obtained over the last 20 years concerning the group. Schram (1990) suggested that the Thylacocephala should be separated into two orders, the Concavicarida Briggs and Rolfe, 1983 and the Conchyliocarida Secrétan, 1983. The Concavicarida were defined (Schram 1990: 2) as thylacocephalans with a carapace armed with prominent rostral features that, anteriorly, overhangs a well-defined optic notch. By contrast, the Conchyliocarida (Schram 1990: 10) are characterized by a carapace lacking a clearly delineated optic notch and a rostrum and typically have eyes situated on the surface of a large protruding so-called "cephalic sac". The subdivision of Thylacocephala proposed by Schram (1990) stresses differences in the development of eyes and their encapsulating exoskeletal structure (rostrum-notch complex) but underlines no other anatomical differences (e.g., segments, appendages) between the two or-

ders. In recent crustaceans, the size, shape, and structure (e.g., density and number of ommatidia) of eyes express the various responses of animals to capture and utilize light in their respective environments. These features have a strong environmental control and, to us, cannot be used alone to distinguish higher taxa. For this reason, we do not maintain here the order-level distinction of Thylacocephala proposed by Schram (1990).

*Age and occurrence.*—See (Table 1 and Fig. 3).

### Genus *Zhenghecaris* nov.

*Type species:* *Zhenghecaris shankouensis* sp. nov., by monotypy.

*Derivation of the name:* In honour of the great Chinese mariner Zheng He (1371–1435) who was born near the study area. He sailed from China to many places throughout the South Pacific, Indian Ocean, and distant Africa, some 80 years before Columbus' voyages.

*Diagnosis.*—Thylacocephalan with long, strongly, and evenly convex dorsal outline. Stout anterior and posterior pointed rostrum. Broad concave optic notch anteroventrally situated. Ventral margin truncated medioventrally. Narrow rim running parallel to ventral margin. No lateral ridge. External surface of carapace with fine corrugated and tuberculated micro-ornament. "Teardrop"-shaped stalked eyes protruding from the carapace beyond the anteroventral margin.

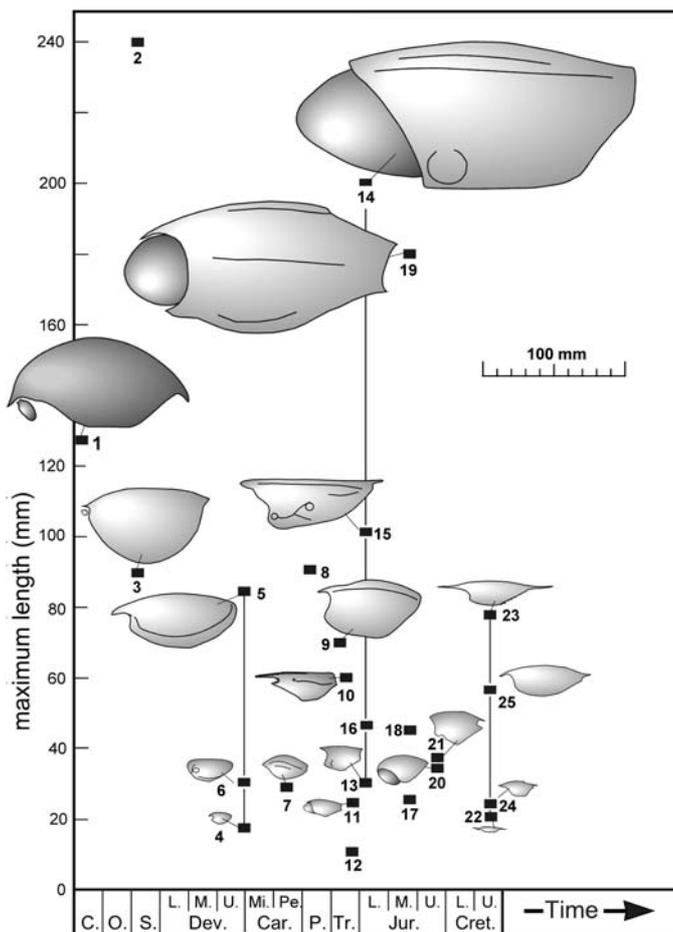


Fig. 3. Size range of thylacocephalans (Lower Cambrian to Upper Cretaceous). 1, *Zhenghecaris* gen. nov.; 2, *Ainiktozoon*; 3, undescribed thylacocephalan (Mikulic et al. 1985); 4, 5, *Concavicularis* (2 different species represented); 6, *Harrycaris*; 7, *Convexicaris*; 8, *Coreocaris*; 9, *Ankitokazocaris*; 10, *Yangzicaris*; 11, *Atropicaris*; 12, *Microcaris*; 13, 14, *Ostenocaris* (2 different species represented); 15, *Austriocaris*; 16, *Rugocaris*; 17, *Parostenia*; 18, *Kilianocaris*; 19, *Dollocaris*; 20, *Clausocaris*; 21, *Mayrocaris*; 22, 23, *Protozoa* (2 different species represented); 24, *Pseuderichthus*; 25, *Thylacocephalus*. C., Cambrian; Car., Carboniferous; Cret., Cretaceous; Dev., Devonian; Jur., Jurassic; L., Lower; M., Middle; Mi., Mississippian; O., Ordovician; P., Permian; Pe., Pennsylvanian; S., Silurian; Tr., Triassic; U., Upper. Carapace outlines from original publications (see references in Table 1).

**Age.**—Lower Cambrian (*Eoredlichia*–*Wutingaspis* trilobite Zone).

**Discussion.**—*Zhenghecaris* gen. nov. is by far the largest bivalved arthropod (holotype ca. 125 mm long) ever found within the Maotianshan Shale biota (Hou et al. 2004; Chen 2004). The unusually large bivalved arthropods claimed by Hou (1987, 1999) also from the Maotianshan Shale biota (Xiaolantian section) are much smaller than *Zhenghecaris* gen. nov. The length of the carapace reaches 7.7 mm in *Occacaris oviformis* (holotype), 15 mm in *Forfexicaris valida* (holotype), and 71 mm in *Yunnanocaris megista* (paratype). *O. oviformis* is known from a single specimen

with relatively well-preserved appendages, eyes and posterior trunk. Although definitely ovoid, the exact lateral outline of its carapace is unclear (Hou et al. 2004: fig. 16.24), especially anteriorly (Fig. 5A). Both *F. valida* and *Y. megista* (Fig. 5A, B) have sub-oval valves with a postplete lateral outline (greatest height posterior to the mid-length; see Scott 1961). They lack external ornament except numerous concentric wrinkles and irregular ridges that result from compaction of the vaulted non-mineralized carapace. The pustulose/corrugated external features of the holotype of *Y. megista* are irregular and most probably artefacts (diagenetic mineralization?; see Hou 1999: fig. 1.4). *Pectocaris spatiosa* Hou, 1999 and *Pectocaris eurypetala* (Hou and Sun, 1988) are two additional large bivalved arthropods from the Chengjiang biota (max. size 90 mm and 35 mm, respectively). Both forms have a carapace with a sub-elliptical lateral outline devoid of cardinal processes. *Pectocaris eurypetala* has numerous branchiopod-type appendages, an elongate telson with fluke-shaped rami. In summary, none of these 4 large bivalved arthropods (*Occacaris*, *Yunnanocaris*, *Forfexicaris*, *Pectocaris*) resembles *Zhenghecaris* gen. nov.

*Zhenghecaris* displays some important thylacocephalan features (Figs. 6, 7), such as: (1) a dorsally fused laterally compressed carapace with a rostrum-notch complex present at both the anterior and posterior ends of the carapace, and (2) well-developed stalked eyes protruding through the anterior notch. *Zhenghecaris* falls within the size range of the majority of thylacocephalans (carapace length between 15 and 250 mm; Fig. 3). Other resemblances with Palaeozoic and Mesozoic representatives of the group should be noted, too. For example, the truncated midventral margin of *Zhenghecaris* recalls that of *Concavicularis milesi*, *Harrycaris*, *Ostenocaris*, *Protozoa damesi*, and *Pseuderichthus* (Arduini et al. 1980; Briggs and Rolfe 1983; Schram et al. 1999). Its marginal rim (Fig. 6A<sub>5</sub>, A<sub>7</sub>) is similar to that of *Mayrocaris* (Polz 1997), *Protozoa* and *Pseuderichthus* (Schram et al. 1999). Its corrugate and tuberculate ornament (Fig. 6A<sub>8</sub>, B<sub>2</sub>, B<sub>3</sub>) is comparable with that of *Protozoa* and *Pseuderichthus* (regularly spaced pits) and *Mayrocaris* (terraced lines). It is also reminiscent of myodocope ostracodes (short crescent-like ridges sheltering sensory setae; Fig. 8). *Zhenghecaris* differs from all other thylacocephalans by its most peculiar long vaulted dorsal margin and its drop-shaped eyes. These two original features justify the erection of a new genus.

**Occurrence.**—Yunnan Province, South China, Lower Cambrian (*Eoredlichia*–*Wutingaspis* trilobite Zone).

### *Zhenghecaris shankouensis* sp. nov.

Figs. 4C, 6, 7.

**Holotype:** Sk010120a, b, part and counterpart of an almost complete specimen (Figs. 6A, 7A). **Paratype** Sk010121a, b, part and counterpart of a smaller incomplete specimen with well-marked external ornament (Figs. 6B, 7B).

**Type locality:** Shankoucun Village, Anning City, 40 km SW of Kunming, Yunnan Province, SW China; Yu'anshan Formation, Maotianshan Shale Member, Lower Cambrian (*Eoredlichia*–*Wutingaspis* trilobite Zone).

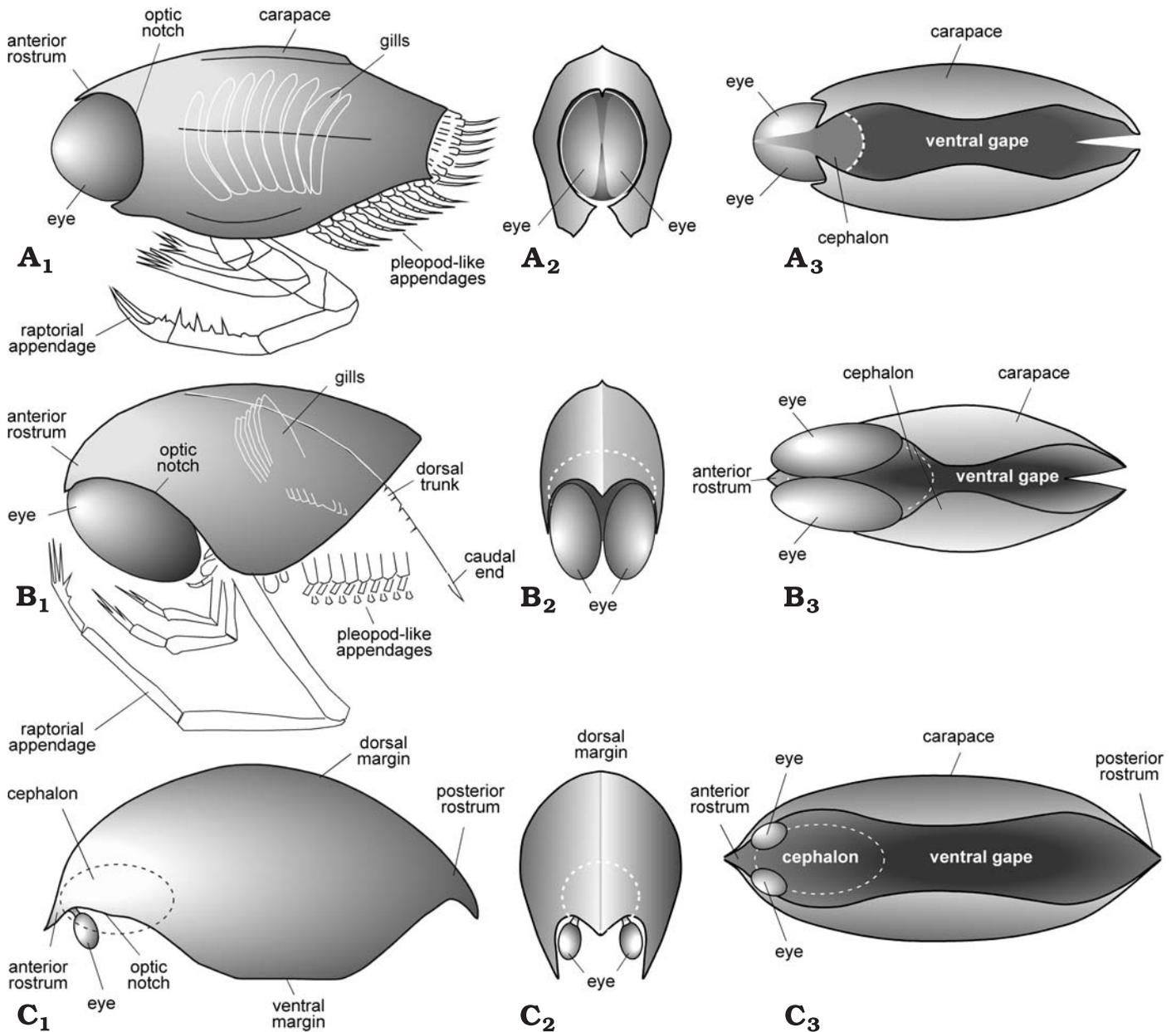


Fig. 4. Simplified reconstructions showing the general morphology of thylacocephalan arthropods in left lateral (subscripted with "1"), frontal (subscripted with "2"), and ventral (subscripted with "3") views. **A.** *Dollocaris ingens* (Middle Jurassic, La Voulte, France; modified from Secrétan 1985). **B.** *Clausocaris lithographica* (Upper Jurassic, Solnhofen, Germany). **C.** *Zhenghecaris shankouensis* gen. et sp. nov. (Lower Cambrian, Maotianshan Shale biota, China). Not to scale. A and B modified from Secrétan 1985 and Polz 1990, respectively.

*Derivation of the name:* From Shankou, the type locality.

*Material.*—In addition to the holotype and paratype, three incomplete specimens all preserved laterally compressed.

*Diagnosis.*—as for genus.

*Description.*—The lateral outline is almost elliptical with L:H = 1.87 (holotype), the dorsal margin being remarkably long and evenly convex. The ventral margin is divided into three sections of almost equal length; the anteroventral and posteroventral sections are slightly concave, whereas the midventral one is flat. A pointed rostrum is present anteriorly

and posteriorly (Fig. 7A<sub>1</sub>, A<sub>2</sub>). A narrow ridge runs parallel to the ventral margin (Fig. 6A<sub>6</sub>, A<sub>7</sub>). The lateral surface of the carapace bears no other ridge, its convexity being even. Dorsal views of the holotype do not show any obvious hinge line or groove between the two lateral flaps. The original shape of the carapace was probably that of a laterally compressed shield with no external dorsal splitting. Post-mortem lateral compaction enhanced the dorsal convexity of the dorsal area and flattened out the lateral flaps. Part of the anterior rostrum may have been topped by a narrow strengthening carina (Fig. 7A<sub>3</sub>). The carapace is almost entirely covered with elongated

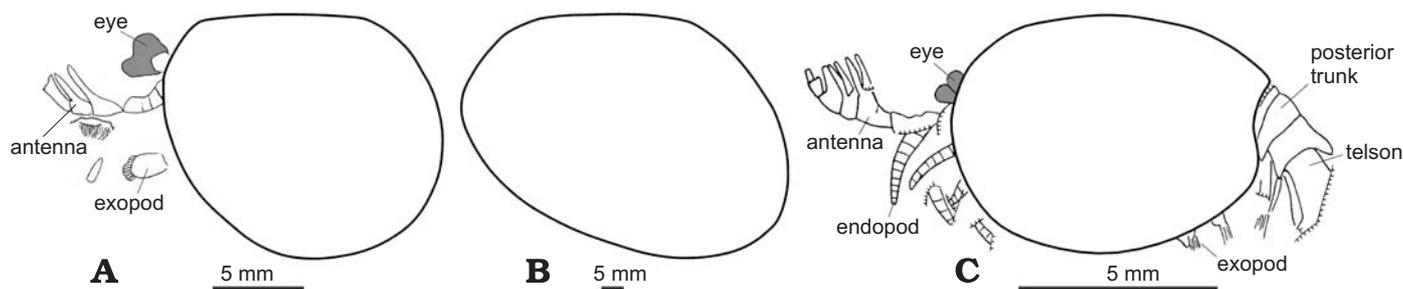


Fig. 5. Hou (1999)'s "large" bivalved arthropods from the Lower Cambrian Maotianshan Shale, China). A. *Forfexicaris valida* with soft parts. B. *Yunnanocaris megista* (soft anatomy unknown). C. *Occacaris oviformis* with soft parts. Simplified after Hou (1999: figs. 2, 4) and Hou et al. (2004: fig. 16.17). Eyes in dark grey.

and rounded tubercles that give the external ornament a corrugated aspect. The tubercles of the paratype show a concentric arrangement (Figs. 6B<sub>3</sub>, 7B<sub>1</sub>). The concentric pattern is slightly deflected posterodorsally and adjacent to a smooth area (Fig. 6B<sub>2</sub>). These two features remain enigmatic (muscle attachment?). No soft parts (e.g., appendages) are preserved except an elliptical feature interpreted as an eye. This assumed eye is situated below the rostrum and protrudes through the anterior notch of the carapace. It bears a small stalk. Its surface does not show ommatidia-like structures.

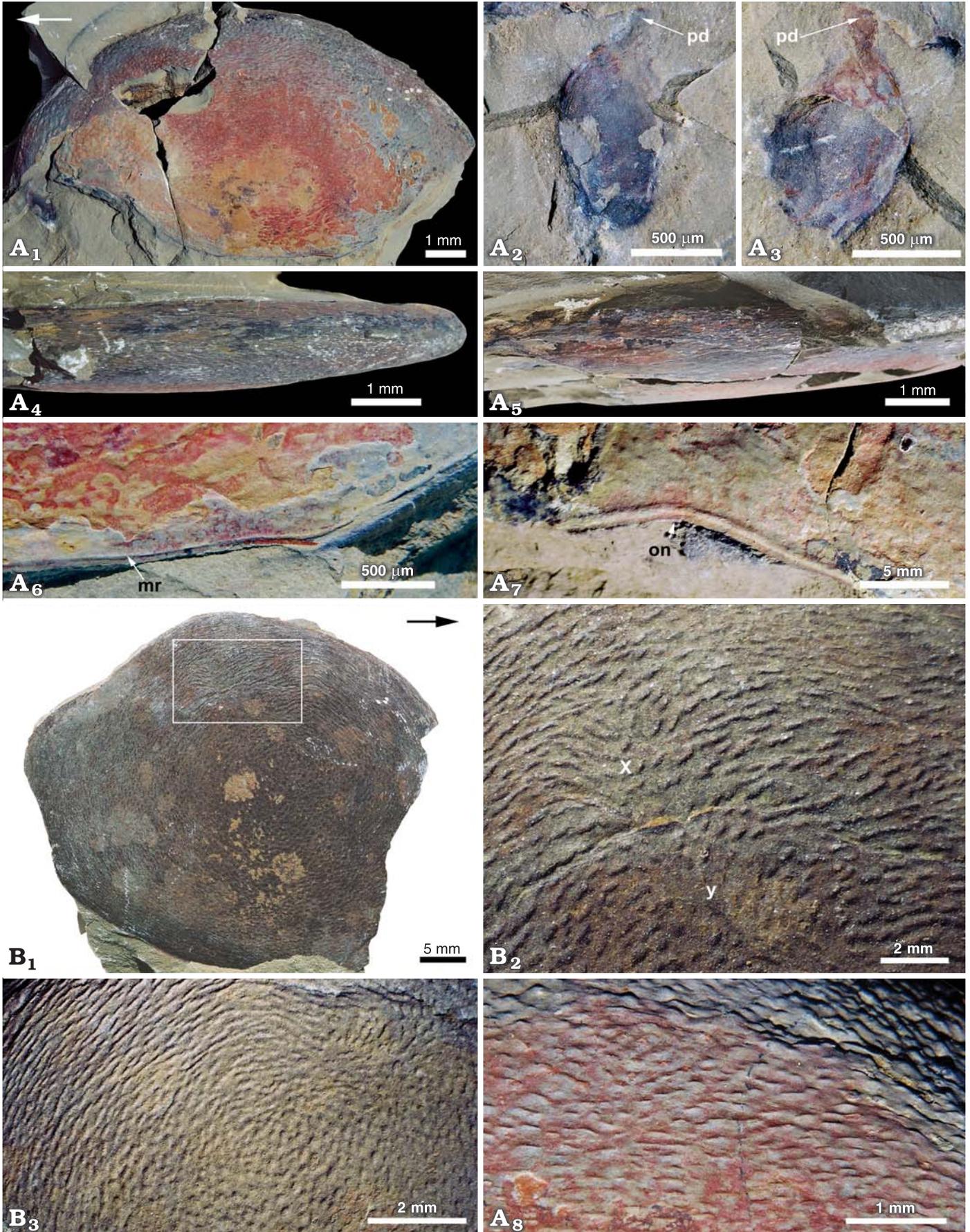
*Occurrence.*— Only known from type locality.

## Thylacocephalans: body plan and lifestyles

The thylacocephalans were relatively large bivalved arthropods (size from ca. 15 mm up to possibly 250 mm; Figs. 1, 3) whose segmented body was almost entirely enclosed within a laterally compressed carapace. There is no fossil evidence of any abdominal termination emerging from the carapace posteriorly such as for example in fossil and Recent phyllocarid crustaceans (typically a "tail" complex with abdominal telescopic segments, telson, and furcae; Vannier et al. 1997). The sclerotized, possibly weakly mineralized carapace of thylacocephalans superficially resembles that of myodocope ostracods (Ordovician–Recent) in having a prominent anterior notch-rostrum complex and an overall elliptical shape (Fig. 8). However, thylacocephalans were much larger than the average myodocope ostracods (Recent forms range from most commonly 1–3 mm, to 35 mm in rare gigantic deep-sea species) and differ markedly from them in important aspects of their segmentation and appendage structure. Anteroventral raptorial appendages are absent in ostracods. The notch-rostrum complex of thylacocephalans was associated with highly developed visual organs. These lateral eyes were either "tear-drop-shaped" and pedunculate (e.g., *Zhenghecaris* gen. nov., Early Cambrian; Fig. 4) or, in numerous species, formed huge, globular, and faceted organs (e.g., *Dollocaris*, *Clausocaris*, Middle Jurassic; Fig. 1A–D) that superficially resemble the

hypertrophied eyes of some modern pelagic hyperiid crustaceans (Bowman and Gruner 1973). The eyes of *Dollocaris ingens* were paired (Fig. 1C, D; see also Secrétan and Riou 1983 and Fröhlich et al. 1992) and possessed numerous ommatidia (ca. 15 per mm<sup>2</sup>; Fig. 1B).

The segmentation pattern of thylacocephalans has been the subject of debate since the mid-1980's (Rolfe 1985; Secrétan 1985; Polz 1993; Schram 1990; Schram et al. 1999) and there is still an important lack of knowledge concerning the number and the exact morphology of cephalic appendages. However, several specimens with preserved soft parts from Palaeozoic and Mesozoic Lagerstätten provide very useful information on the general body plan of thylacocephalans. In addition to prominent eyes, the cephalon of thylacocephalans was probably fitted with two pairs of short antennae (A1, A2) and, a set of 3 appendages (Md, Mx1, Mx2) and a labrum which altogether formed the mouth parts of the animal [(see fossil evidence from *Dollocaris* (Secrétan and Riou 1983) and *Thylacocephalus* (Lange et al. 2001)]. Computerized reconstructions of 3D-specimens preserved in nodules (e.g., by using X-ray-microtomography or the new method advocated by Sutton et al. 2001) are expected to reveal the actual segmentation of thylacocephalans. No specimen shows evidence of long multisegmented flagellum-like antennules (A1) that are frequent in fossil and Recent arthropods. *Thylacocephalus* from the Upper Cretaceous of Lebanon has two pairs of apparently short antennae (A1 and A2 bearing at least 5 and 11 segments, respectively; Lange et al. 2001). Rolfe (1985) noted that, in modern crustaceans, the hypertrophy of lateral eyes is often accompanied by the sharp reduction of antennae (e.g., hyperiid amphipods such as *Hyperia*; Bowman and Gruner 1973). It might have been the case in thylacocephalans, too. *Concavicaris georgeorum* had mandibles armed with a molar process (Schram 1990) but very limited information is available concerning the mandibles of other taxa. One of the most conspicuous metameric features of thylacocephalan trunk is a series of 8 gills (e.g., Secrétan 1985; Schram et al. 1999) which were possibly attached to the anterior segments of the trunk as possible epipodites or exopodites. However, the exact location of their attachment area remains unclear. In *Dollocaris ingens*, the gills form two symmetrical fan-like structures on both



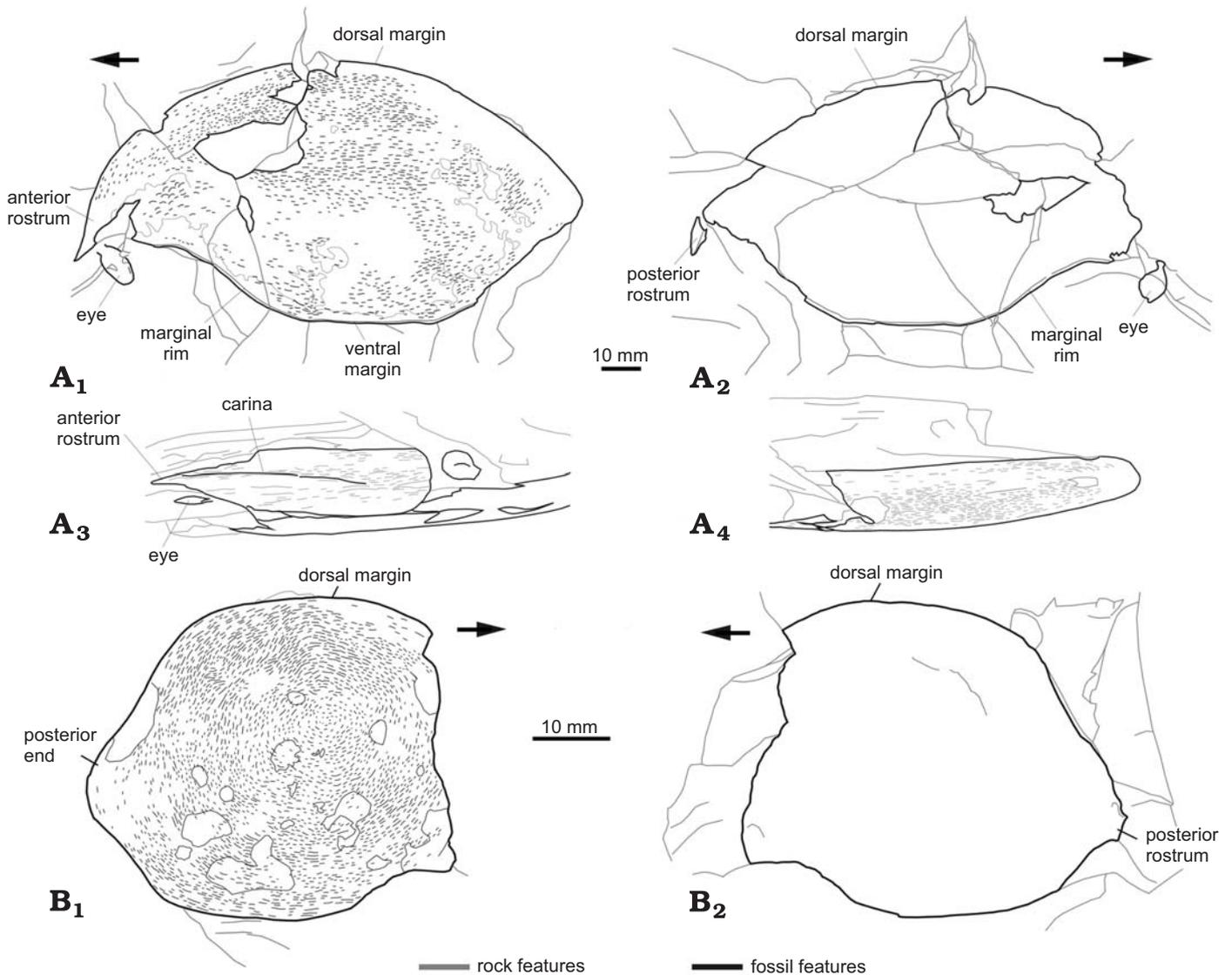


Fig. 7. *Zhenghecaris shankouensis* sp. nov. from Shankou, Yunnan Province, South China, Maotianshan Shale, Lower Cambrian. Line drawings from photographs of the same specimens as shown in Fig. 6. **A.** Holotype Sk010120, lateral views of part (A<sub>1</sub>) and counterpart (A<sub>2</sub>), anterodorsal (A<sub>3</sub>), and posterodorsal (A<sub>4</sub>) views. **B.** Paratype Sk010121, lateral views of part (B<sub>1</sub>) and counterpart (B<sub>2</sub>). Arrows point anteriorly.

sides of the trunk. Excellently preserved specimens from La Voulte (Charbonnier and Vannier, unpublished information) reveal fine details such as secondary lamellae, afferent, and efferent canals (Secrétan 1985) that recall the structure of gills (e.g., phyllobranchiate; Taylor and Taylor 1992) in modern decapod crustaceans. Another major feature of the anterior trunk of thylacocephalans (e.g., *Concavicaris*, *Dollocaris*, *Clausocaris*, *Protozoa*, *Thylacocephalus*) are the so-called “long appendages” (typically 3 pairs; Figs. 1,

4A<sub>1</sub>) designed for an evident prehensile function (geniculate shape and spiny features as in Recent stomatopod crustaceans) in relation with predatory or scavenging habits (mechanical handling/breakdown of carcasses or prey; Secrétan 1985; Rolfe 1985). The posterior section of the trunk had a completely different anatomy. It bore a battery of at least 8 homonomous styliform and filamentous pleopods (long protopods obliquely aligned; e.g., Fig. 4A<sub>1</sub>) that seem to have had a locomotory function, possibly similar to that of pleo-

← Fig. 6. *Zhenghecaris shankouensis* sp. nov. from Shankoucun, Yunnan Province, South China, Maotianshan Shale, Lower Cambrian. **A.** Holotype Sk010120; lateral view (A<sub>1</sub>); close-up of lateral eye, part (A<sub>2</sub>) and counterpart (A<sub>3</sub>); posterodorsal view showing convex dorsal area (A<sub>4</sub>); anterodorsal view (A<sub>5</sub>); marginal rim (posteroventral, A<sub>6</sub>) and anterior notch area (A<sub>7</sub>); details of corrugated micro-ornament in posterodorsal area (A<sub>8</sub>). **B.** Paratype Sk010121. General lateral view (B<sub>1</sub>), close-ups of micro-ornament in mediodorsal (B<sub>2</sub>), and central areas (B<sub>3</sub>), counterpart of paratype. All light colour micrographs. Abbreviations: mr, marginal rim; pd, peduncle of eye; on, “optic notch”; x, micro-ornamented area with converging corrugae; y, area with attenuated micro-ornament. Arrows point anteriorly.

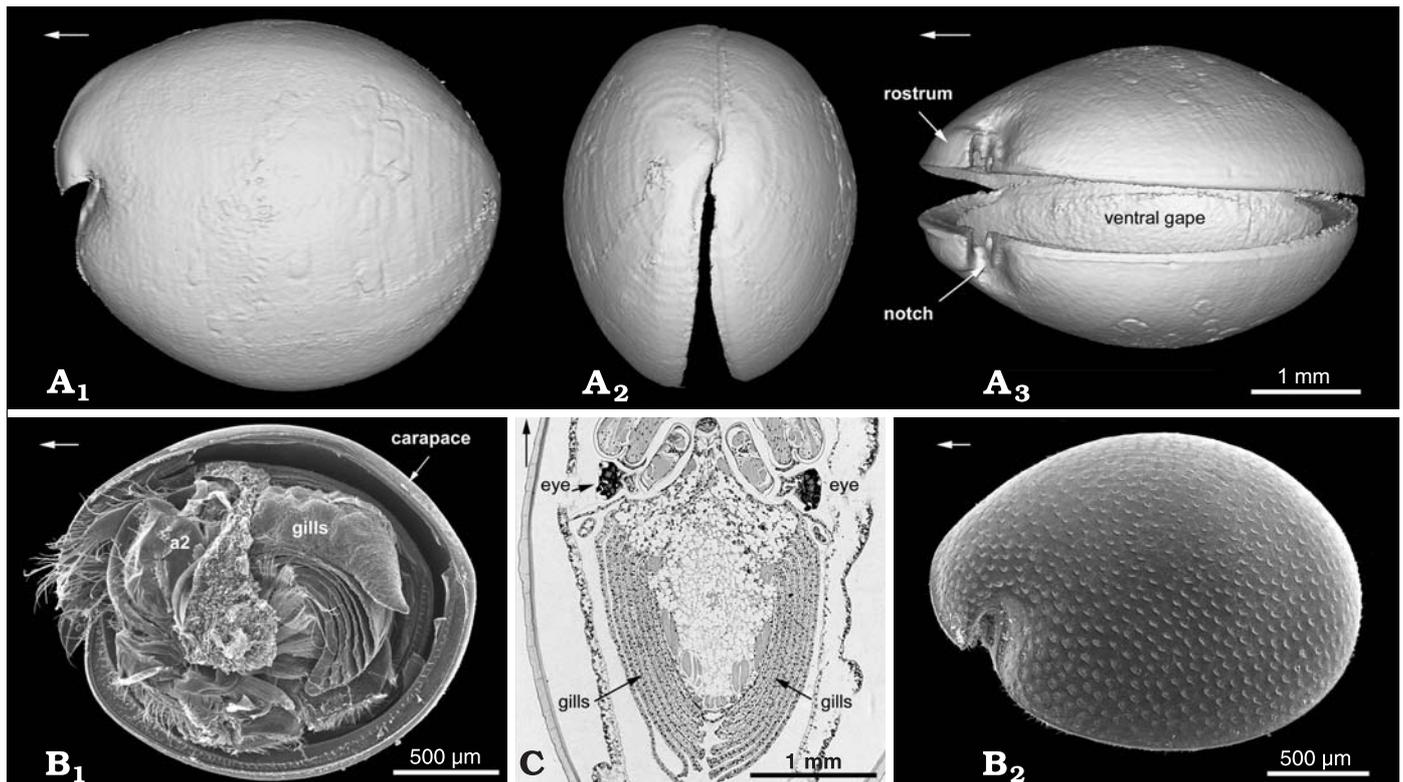


Fig. 8. General morphology of a present-day bivalved arthropods exemplified by the mydocopid ostracod *Leuroleberis surugaensis* (Cylindroleberididae) from the Pacific coast of Japan. *L. surugaensis* buries itself in sediment and can swim in the water column. **A.** X-Ray Microtomographs of the animal (specimen FSL 526005) in left lateral (**A<sub>1</sub>**), posterior (**A<sub>2</sub>**), and ventral (**A<sub>3</sub>**) views, complete specimen observed in life-position, immersed in 70% alcohol; body and appendages present but not detected by X-rays. **B.** SEM micrograph of body (**B<sub>1</sub>**, left valve removed) and external ornament (**B<sub>2</sub>**, left valve) of specimen FSL 526006. **C.** Longitudinal section through lateral eyes and gills (microtomized paraffin section); specimen FSL 526007. Abbreviation: a2, second antenna.

pods in Recent phyllocarids (Rolfe 1985; Vannier et al. 1997). The number of segments of the posterior region of the trunk may not have exceeded 8. The apparent series of 16 appendages that protrudes beyond the posterior margin of *Dollocaris* (Fig. 4A<sub>1</sub>) may actually be an artefact possibly produced by the post-mortem slippage of the two sets (right and left) of appendages along the same plane. This hypothesis needs to be confirmed by detailed observations of the three-dimensionally preserved specimens from La Voulte. The caudal termination of thylacocephalans is poorly documented. In some species (e.g., *Ainiktozoon*; Van der Bruggen et al. 1997) it may have borne a small caudal ramus.

The internal organs of thylacocephalans are rarely preserved except the foregut and a possible stomach pouch situated within the cephalic protuberance (e.g., *Ostenocaris*, *Protozoa*). The stomach contents of *Ostenocaris* (Pinna et al. 1985) preserves identifiable remains of fish (both Selachii and Teleostei), hooks of cephalopods, and carapaces of unidentified crustaceans and small thylacocephalans. Added to the presence of long chelate appendages, these gut contents clearly point to a predatorial or a scavenging feeding mode. The supposed ovarian eggs of *Ostenocaris* (Pinna et al. 1982) are actually vertebral elements of fish (see Rolfe 1985) making the hypothesis of reproductive organs located in the head highly improbable. Linear series of tubercles along the

lateral surface of the carapace of numerous species (Rolfe 1985) may suggest the presence of light organs (epidermal glands) comparable with those of modern deep-sea bioluminescent ostracods (Angel 1993). Some thylacocephalans may have used these supposed bioluminescent organs as lures (predatory or anti-predatory behaviour?) or for sexual communication.

Although a benthic mode of life for thylacocephalans has been envisaged by some authors (Secretan 1985, Schram 1990), the arthropods possess a number of features that would suggest capabilities for swimming and adaptation to dim-light environments. These are (1) the relatively thin non-mineralized carapace, (2) the well-developed rostral spines in some forms (e.g., *Protozoa*, *Pseuderichtus*; Schram et al. 1999) for possible buoyancy control (Vannier and Chen 2000), (3) the battery of pleopods for swimming, and (4) the remarkably large and prominent eyes that provided some species with a panoramic field of vision. Concerning vision, the presence of numerous small ommatidia distributed over huge eyes (e.g., *Dollocaris*; Fröhlich et al. 1992) reduces the interommatidial angle and possibly improved the ability of thylacocephalans to detect small objects (Land 1981; Rolfe 1985). The hypertrophy of eyes in numerous thylacocephalans may be interpreted as an adaptation to vision at low light intensities.

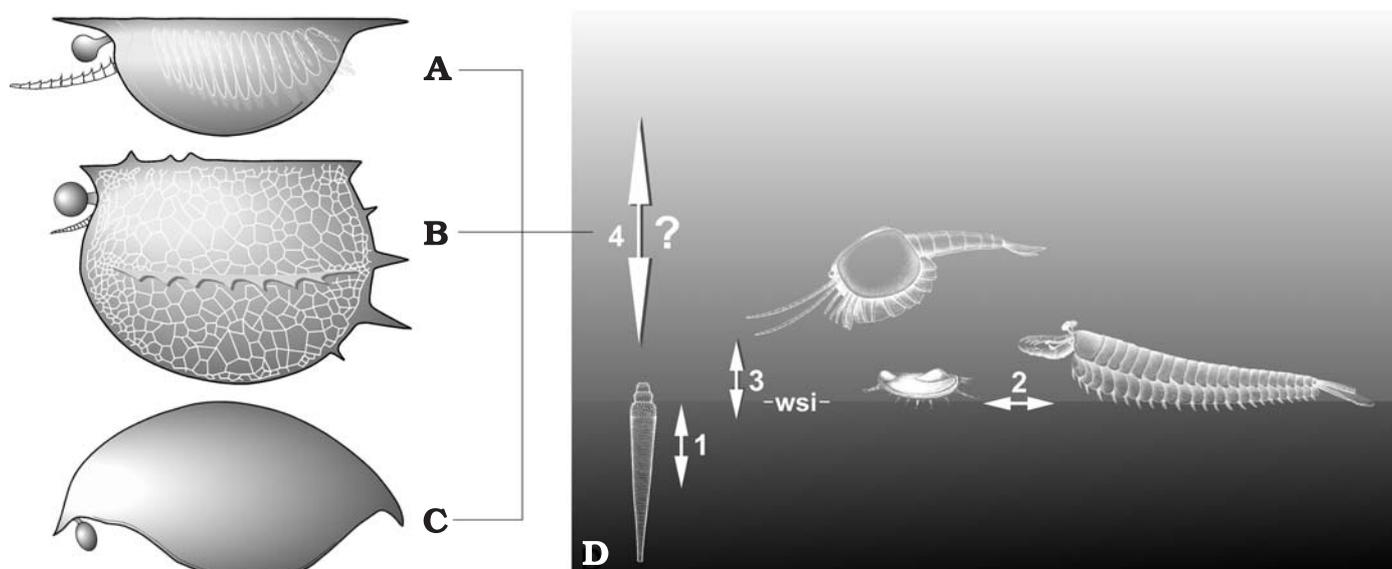


Fig. 9. Interpretation of possible Early Cambrian thylacocephalans as nektonic organisms living in the lowermost levels of the water column in a shelf marine habitat (max. bottom depth ca. 100–150 m). **A.** *Isoxys* (after Vannier and Chen 2000, modified; possible prehensile appendages after Hu 2005). **B.** *Tuzoia* (after Vannier et al. in press). **C.** *Zhenghecaris* gen. nov. Members of the benthic (1; selkirkiid worms), epibenthic (2; arthropods *Fortiforceps* and *Kunmingella*) and nektobenthic communities (3; waptiids); wsi, water-sediment interface. Not to scale.

## Affinities of thylacocephalans

The assumed relation of Thylacocephala to Crustacea has been the focus of different hypotheses including the cirriped, phyllocarid, malacostracan (hoplocarid), branchiopod, and maxillopod options (e.g., Briggs and Rolfe 1983; Schram 1990; Schram et al. 1999) but none of them brings conclusive arguments. Some anatomical features of the thylacocephalans may indeed indicate crustacean affinities. These are: (1) the two pairs of antennae of *Thylacocephalus* (Lange et al. 2001) that is the most satisfactory fossil evidence to date of a close relationship between the thylacocephalans and crustaceans, (2) the globular compound eyes with preserved ommatidia, crystalline cones, and retinula cells, that resemble modern hyperiid eyes, (3) the radial series of 8 pairs of probably phyllobranchiate gills attached to the trunk, (4) the body tagmosis (anterior trunk with prehensile limbs and gills; posterior trunk with serially repeated pleopod-like appendages), and (5) the crustacean-like design of the prehensile limbs. However, it is difficult to ascertain whether thylacocephalans are indeed crustaceans because of the lack of firm evidence concerning their post-antennal cephalic appendages. The carapace architecture of thylacocephalans (e.g., shield enclosing the body almost completely; anterior rostrum-notch complex) is close to that of Recent aquatic crustaceans such as Maxillopoda (typically Ostracoda, Ascothoracica and larval cirripeds) and Branchiopoda (e.g., Martin 1992). External resemblances between thylacocephalans, especially the Devonian concavicularids (Briggs and Rolfe 1983), and myodocopid ostracods are also worth mention (Fig. 8). However, it is highly probable that most of these resemblances are due to convergent evolu-

tion. The segmentation pattern of Recent crustaceans such as Maxillopoda (5-6-5 or 5-7-4; see Newman 1983; Waloszek and Müller 1998) seems to be fundamentally different from that of thylacocephalans (probably 5-3-8). No decision concerning the placement of thylacocephalans within or outside the Crustacea can be envisaged until detailed information on head appendages is made available (number, structure).

## Other Cambrian thylacocephalans?

It is becoming clear that several Cambrian taxa of uncertain systematic position and affinities such as *Isoxys* Walcott, 1890, and *Tuzoia* Walcott, 1912, may find their place within the Thylacocephala. For example, the larger representatives of *Isoxys* (e.g., from the Maotianshan Shale biota; Vannier and Chen 2000; size frequently over 50 mm) have two pointed rostra, large spherical eyes, no projecting abdominal termination but instead a series of filamentous trunk limbs used for swimming. Small spiny lightly sclerotized forms such as *I. volucris* from the Sirius Passet Lagerstätte, Greenland (Williams et al. 1996) and similar unnamed arthropods from the Lower Cambrian deeper water black shales of South China (Zhu and Vannier, unpublished information) are convergent with *Isoxys* and most likely belong to a different group of possibly pelagic animals.

*Tuzoia* is a typical mid-Cambrian bivalved arthropod (size up to 180 mm long) with a non-mineralised dome-like carapace strengthened by prominent pointed features and often flanked by a spiny frill (Resser 1929; Briggs et al. 1994; fig. 6a; Lieberman 2003; Vannier et al. in press). It occurs also in the Lower Cambrian of China. *Tuzoia* had a pair of

large, stalked, spherical possibly compound eyes facing forward, comparable with those of *Isoxys*. Unfortunately, there is a lack of information concerning the anatomy of *Tuzoia*, particularly whether it possessed filamentous appendages or not. No trace of a posteriorly protruding segmented trunk was found in *Tuzoia*, whereas this feature is typical of numerous Lower Paleozoic bivalved arthropods (e.g., phyllocarid-like waptiids or *Yunnanocaris*; Fig. 5B). The major part of the body of *Tuzoia* is likely to have been enclosed within the carapace. The hypothesis that *Isoxys*, *Tuzoia*, and *Zhenghecaris* gen. nov. may belong to the same group of large bivalved arthropods, possibly the Thylacocephala, needs confirmation from soft part evidence.

Thylacocephala or bivalved arthropods that could be interpreted as such have no record in the Ordovician (see Table 1). The earliest post-Cambrian representatives of Thylacocephala are Silurian [*Ainiktozoon loganense* Scourfield, 1937 from Lower Silurian of Scotland (Scourfield 1937; Van der Bruggen et al. 1997) and an unnamed form from the Llandoverly of Wisconsin (Mikulic et al. 1985)]. Bivalved arthropods such as *Caryocaris* are recurrent faunal components of Ordovician graptolitic black shales (Vannier et al. 2003). Their abdominal morphology (flattened furcal rami, telescopic segments) suggests possible affinities with the crustacean phyllocarids. These phyllocarid features are present neither in *Ainiktozoon* nor in the unnamed form from Wisconsin (Mikulic et al. 1985) that has three geniculate, probably raptorial appendages comparable to those of some Mesozoic thylacocephalans (Fig. 3A, D). The absence of Thylacocephala in the Ordovician remains an enigma but may have a taphonomic origin such as the absence of fossil site in shallow water settings with suitable conditions for their preservation.

## Early Cambrian nektonic arthropods

The presumed pelagic lifestyle of *Isoxys* is deduced from its carapace design and appendage structure (Fig. 9A) and from comparisons with Recent pelagic crustaceans (e.g., halocypridid ostracods; Vannier and Chen 2000). However, the notion of a pelagic lifestyle needs to be clarified. By definition, planktonic organisms are too small for their own intrinsic movements to be able to overcome the dispersive effects of water movements (Reynolds 2001). The size of most modern zooplankton such as copepods, ostracods, and chaetognaths rarely exceeds 20 mm (mesozooplankton). Although many of them are capable of vertical migration through the water column, their movement is strongly constrained by viscosity. By contrast with plankton, nektonic organisms can swim and overcome the normal movement of water. Typical Recent nektonic crustaceans are the euphausiaceans (e.g., Antarctic krill; adult size ca. 50 mm) that are provided with powerful swimming appendages. Relatively large swimming arthropods such as *Isoxys* sensu stricto (see section on “Other Cam-

brian thylacocephalans?”) probably belong to this ecological category of animals, the nekton. Similarly, *Tuzoia* (Vannier et al. in press) and *Zhenghecaris* gen. nov. may have had a similar nektonic lifestyle although the presence of swimming appendages is not confirmed in these two arthropods. The presence of a pair of large, stalked, spherical possibly compound eyes facing forward (*Isoxys*, *Tuzoia*) or downward (*Zhenghecaris*) is consistent with a nektonic lifestyle that requires multidirectional vision (e.g., for food search and predator avoidance). Defining the exact habitat and bathymetry of *Zhenghecaris* and its allies within the water column remains speculative. “Bivalved” arthropods such as waptiids and numerous other forms present in the Maotianshan Shale biota (e.g., *Occacaris*, *Forfexicaris*, Fig. 9; *Clypecaris*, *Branchiocaris*, *Pectocaris*, *Oddaraia*, *Canadaspis*, see Hou et al. 2004), all provided with a flexible abdomen and paddle-like furcal rami, had obvious capabilities for swimming in the water column and possibly stirring up the sediment for food search or protection in a similar way to present-day phyllocarids (Vannier et al. 1997; Vannier and Chen 2005). Some of them had prehensile antennae and were probably predators (e.g., *Occacaris*, *Forfexicaris*). The large size and carapace design of *Zhenghecaris*, *Isoxys*, and *Tuzoia* are poorly consistent with such a “nektobenthic” lifestyle (e.g., sheltering in the flocculent layer at the water-sediment interface). Instead, we interpret these forms as free-swimmers possibly living in the lowermost levels of the water column. Recent taphonomical and sedimentological studies (Hu 2005) indicate that the Yu’anshan Formation was deposited under an approximate 50 to 200 m water depth along a NW-SE gradient (Eastern Yunnan). The localities where *Zhenghecaris*, *Isoxys*, and *Tuzoia* occur have an intermediate position along the gradient and are likely to have been within a bathymetrical range of 100–150 m. These estimates would suggest that the arthropods were living in the photic zone where, by definition, primary productivity occurs.

Relatively little is known of the functioning of the Early Cambrian pelagic ecosystem (Butterfield 1994, 1997, 2001) although potential inhabitants of the water column are diverse (e.g., phytoplankton, ctenophores, chaetognaths, medusa-like eldoniids, arthropods, chordates). Evidence for a mesozooplankton in the Early Cambrian are sparse however, and limited to rare chaetognaths (Chen and Huang 2002; Chen 2004; Chen et al. 2002; Hu 2005) and possible filter-feeding crustaceans (filter apparatuses from the Lower Mount Cap Formation, NW Canada; Butterfield 1994). Indeed this crucial ecological category in modern marine ecosystems (e.g., food source for nekton) is virtually absent from the major Lower Cambrian Lagerstätten, most probably due to unfavourable preservational conditions (e.g., small size, decay in the water column). The feeding mode of large bivalved arthropods such as *Zhenghecaris*, *Isoxys*, and *Tuzoia* remains hypothetical. It is uncertain whether these animals were feeding in the water column or on the substrate. However, the presence of a strong protruding, spiny, anterior appendage in *Isoxys* from both the Chengjiang (Hu 2005: pl. 12: 2) and the Burgess (Garcia-Bellido and Collins 2005) Lagerstätten support the hypothesis

that *Isoxys* was a pelagic predator and not a filter feeder. These appendages indeed resemble the typical “great appendages” of numerous Cambrian arthropods with assumed predatory habits (Maas et al. 2004). In addition, the hyper-developed spherical eyes of *Isoxys* (Vannier and Chen 2000) and *Tuzoia* (Vannier et al. in press) are also consistent with predatorial strategies that would have necessitated the detection and capture of mesozooplanktonic prey. However, at present, no such evidence from preserved prehensile appendages is available in *Tuzoia* and *Zhenghecaris*. Similar to modern environments, it is clear that the Early Cambrian water-sediment interface housed a diverse and potential food source (e.g., small prey, carcasses of various animals, detritus sinking down through the water column) for a variety of animals, amongst them numerous predators/scavengers (see Vannier and Chen 2005). Large arthropods such as *Zhenghecaris* and its allies, even though we suppose they were nektonic swimmers, may have found adequate amounts of food on the bottom and thus matching the definition of demersal animals.

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