A large xenusiid lobopod with complex appendages from the Lower Cambrian Chengjiang Lagerstätte

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A large lobopod, *Jianshanopodia decora* gen. et sp. nov., with body length (excluding appendages) about 220 mm from the Lower Cambrian Haikou section, near Kunming, Yunnan, southwest China, shows a mixture of characters, including features of the lobopod *Xenusion* Pompeckj, 1927, e.g., a large cylindrical body with annulations, stout and strong lobopod appendages each bearing bases of serial tubercles, and of *Aysheaia* Walcott, 1911, i.e., a pair of large frontal appendages. This suggests that the new genus might be a connecting link between *Xenusion* and *Aysheaia*. Besides, *Jianshanopodia* shares some features with the Early Cambrian stem group arthropod *Pambdelurion* Budd, 1997, and *Kerygmachela* Budd, 1993, e.g., the pairs of mid-gut diverticula, the possible presence of tail fan, the mouth cone, the frontal pharyngeal structures and the pharynax are surrounded by the bases of the large frontal appendages. However, compared with a series of segmentally arranged, imbricating, paddle-shaped, movable lateral flaps of both *Pambdelurion* and *Kerygmachela*, *Jianshanopodia* possesses distinct complex appendages with tree-like or lamellate branches. The discovery of this rare transitional form not only throws new light on the early diversification of lobopods, and may also have significance with respect to the origin of arthropods.

Key words: Arthropoda, Lobopodia, Xenusiidae, arthropod origin, Chengjiang Lagerstätte, Cambrian, China.

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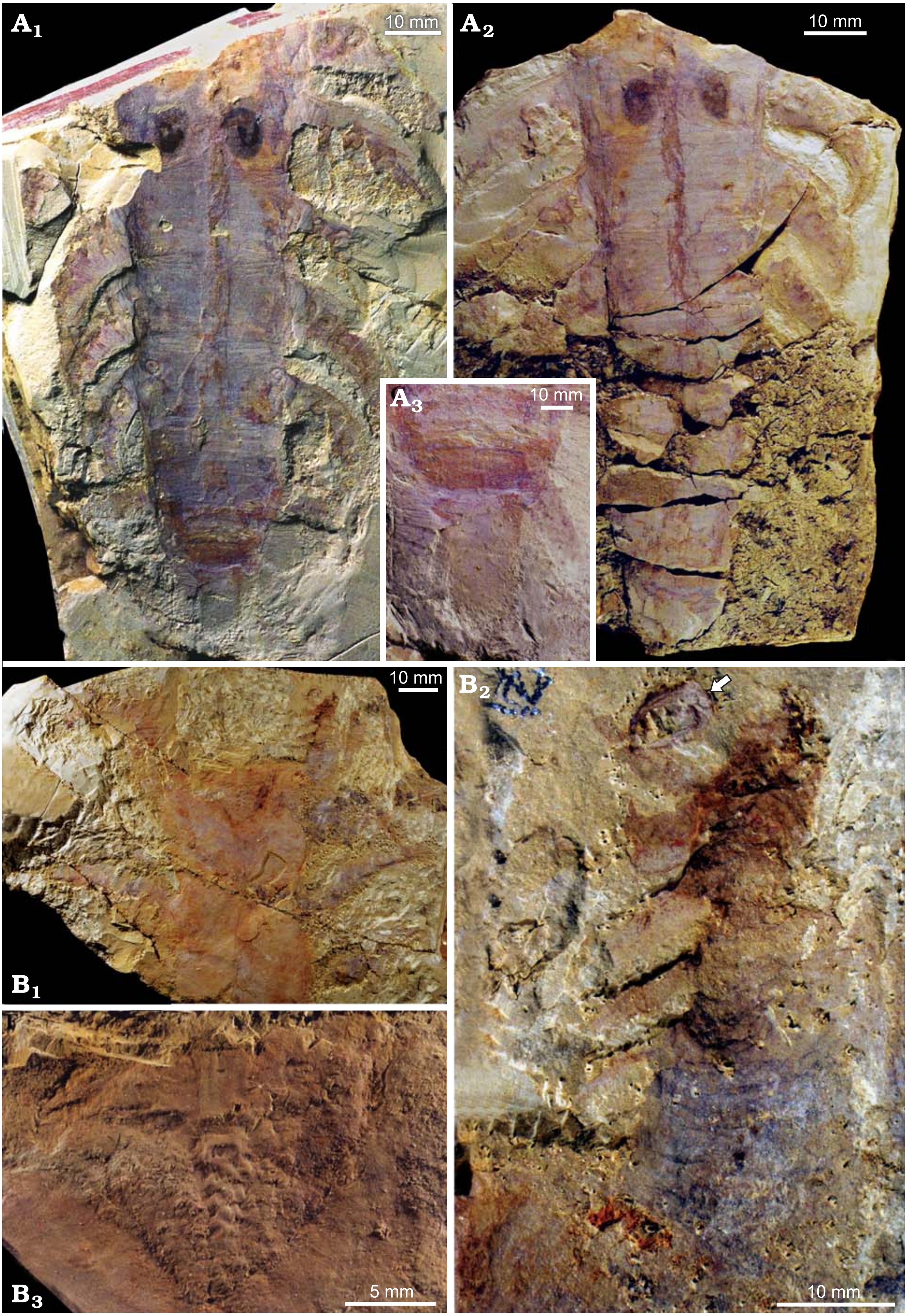
Introduction

Since the description of the first Middle Cambrian lobopod from the Burgess Shale in the last century (Walcott 1911; Whittington 1978), knowledge of Cambrian lobopods has increased dramatically, especially in recent decades (Dzik and Krumbiegel 1989; Hou and Chen 1989; Ramsköld and Hou 1991; Chen et al. 1995; Ramsköld and Chen 1998; Budd 1993, 1997, 1998, 1999; Liu et al. 2004; Xiao 2004). As they are recognized to have potential significance in tracing the origin of arthropods, these lobopods have attracted particular attention. The Lower Cambrian Chengjiang Lagerstätte, with the best preserved fossilized soft tissue, has yielded more than one third of the total species of lobopods and has contributed much to the elucidation of the origin of arthropods (Hou and Chen 1989; Ramsköld and Hou 1991; Chen et al. 1995; Ramsköld and Chen 1998; Bergström and Hou 2001; Liu et al. 2004; Xiao 2004). In this paper we report an Early Cambrian genus and species, *Jianshanopodia decora*, from the Chengjiang Lagerstätte at Haikou village of Yunnan (China) and discuss its relationships and significance for the origin of arthropod appendages.

Material and methods

The material described here was recovered from a grayish-green and grayish-yellow mudstone of the Yu'anshan Member (*Eoredlichia* Zone), Helinpu (Chiungchussu) Formation, Lower Cambrian at Haikou, Kunming, Yunnan. Details of the locality and stratigraphy were given in Zhang et al. (2001). Seven specimens (no complete specimens are known, but the fragments can be pieced together to restore a complete picture of the creature) have been collected from these localities by the work team of Early Life Institute, Northwest University. The seven specimens are preserved in fine-grained, yellowish green mudstone, and most lie parallel to the bedding plane with only one lying obliquely. The degree of compression varies among specimens. In all of the specimens we checked, the internal structures and the cuticle on the ventral side are visible as a result of exposure or seen through from the dorsal side as a result of flattening. This indicates that these specimens represent carcasses rather than moults.

The morphological terms used in the description in general are those of Dzik and Krumbiegel (1989) as far as possible. The specimens were photographed with an Olympus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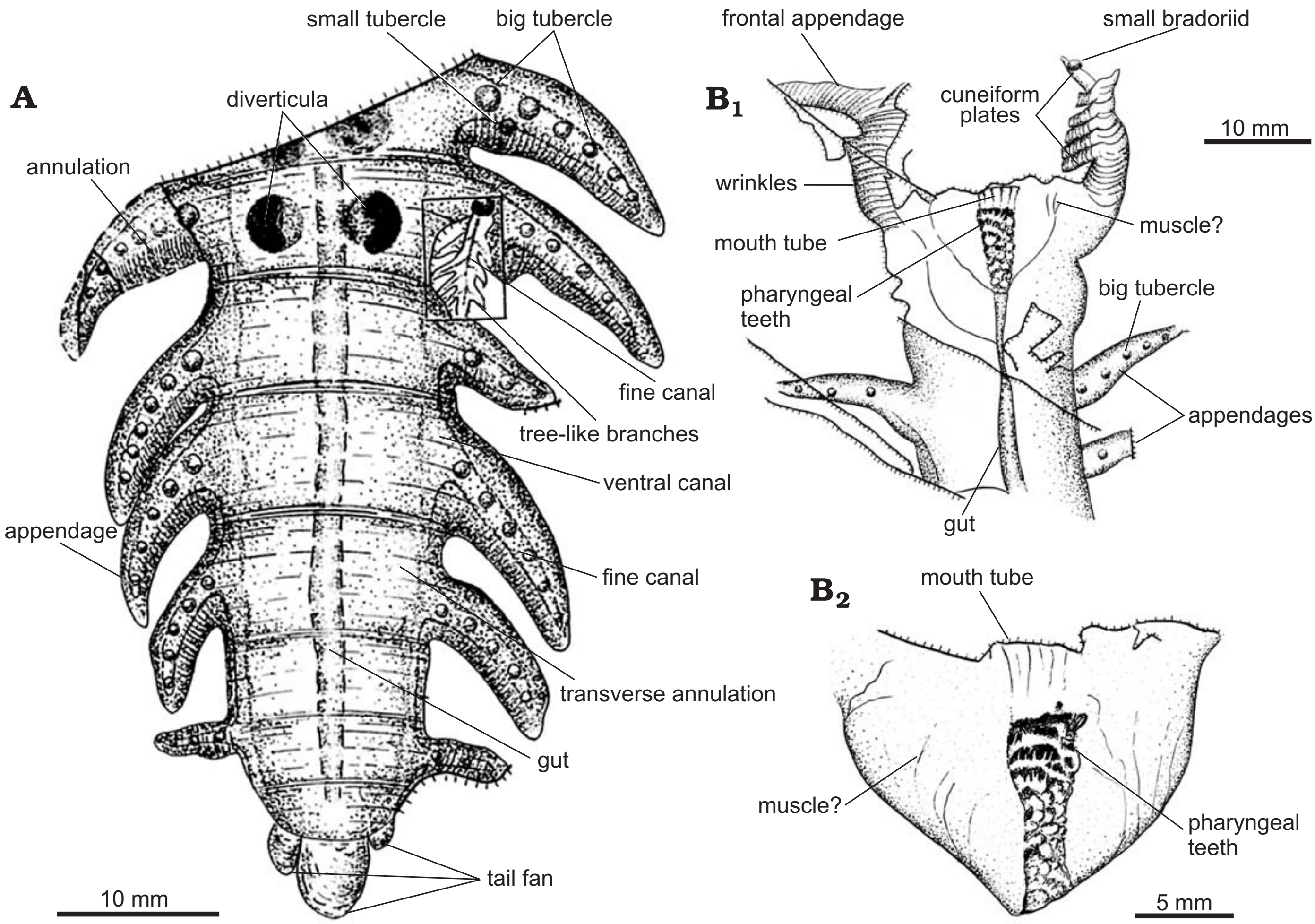


Fig. 2. Lower Cambrian xenusiid lobopod *Jianshanopodia decora* gen. et sp. nov., from Haikou, Kunming, Yunnan, China, camera lucida drawings of the specimens illustrated on Fig. 1. **A**. A sketch drawing of the specimen ELI-J0005A from Fig. $1A_1$, demonstrating all available features of a new species. **B**. ELI-J0001. B_1, the anterior part of *Jianshanopodia decora* redraw from Fig. $1B_1$, note the strongly wrinkled frontal appendages, mouth tube and funnel-like pharynx structures; B_2, enlargement of the funnel-like pharynx structures of the same specimen, from the Fig. $1B_3$.

OM-4 Ti camera. The direction of illumination was varied where necessary to illustrate different features.

Institutional abbreviation.—All specimens illustrated in this work are deposited in the Early Life Institute, Northwest University, Xi'an, China, abbreviated ELI.

Systematic paleontology

Superphylum Lobopodia Snodgrass, 1938
Class Xenusia Dzik and Krumbiegel, 1989
Order Xenusiida Dzik and Krumbiegel, 1989
Family Xenusiidae Dzik and Krumbiegel, 1989

Genus *Jianshanopodia* nov.

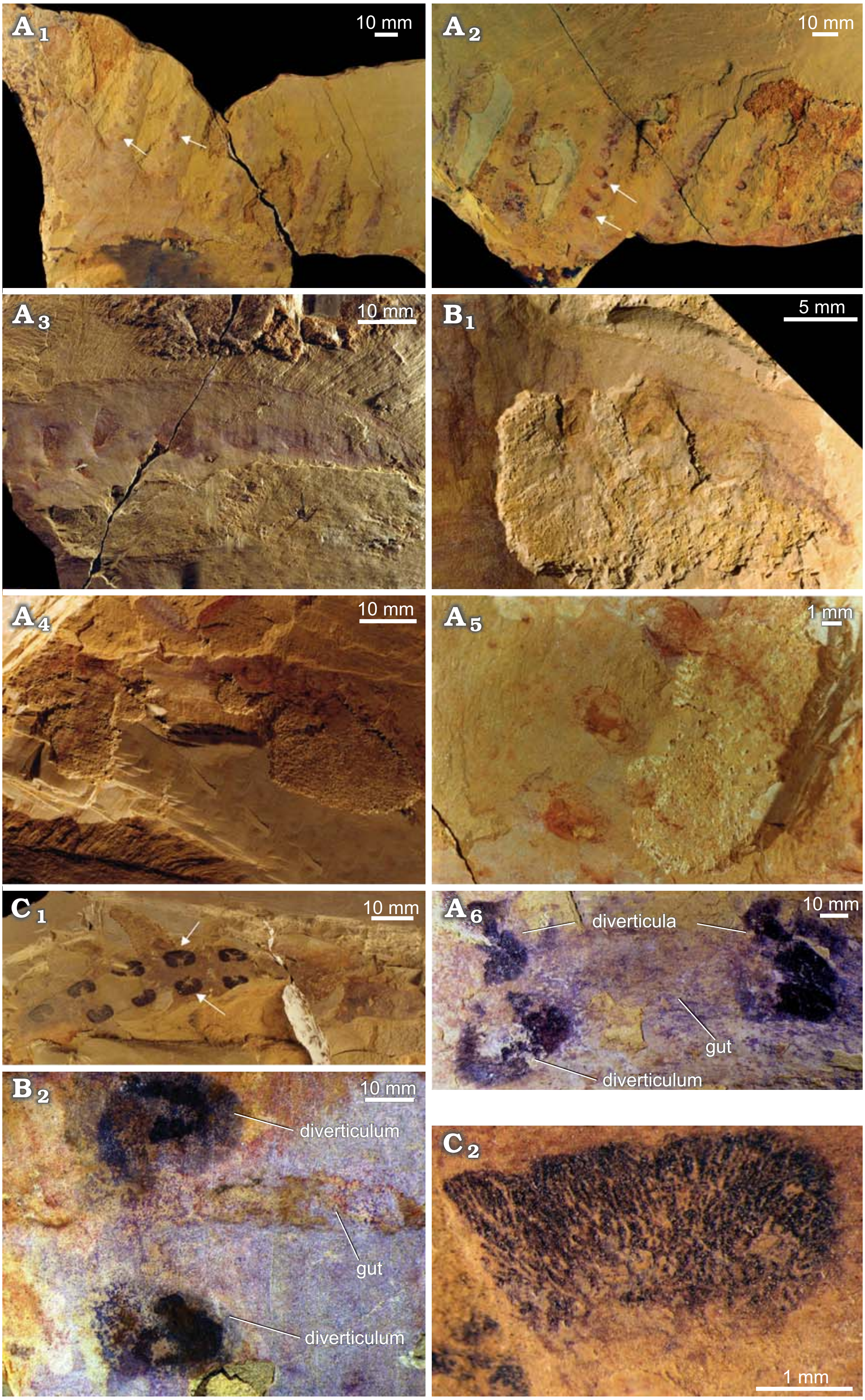
Type species: *Jianshanopodia decora* gen. et sp. nov.

Derivation of name: From Jianshan, a small mountain, alluding to the locality where the specimens are collected, and Greek *pus*, leg.

Diagnosis.—A large animal, body length (excluding appendages) probably reaching 220 mm. The mouth situated terminally; a pair of strong frontal appendages equipped with a series of cuneiform plates. The trunk region with at least nine segments, each bearing a pair of complex appendages with two rows of tubercles on their dorsal side, with tree-like or lamellate branches protruding from the tubercles. Three lobes arranged into a fan form a tail.

Jianshanopodia differs from all other representatives of the Xenusiidae by having the complex appendages and the tail

← Fig. 1. Lower Cambrian xenusiid lobopod *Jianshanopodia decora* gen. et sp. nov., from Haikou, Kunming, Yunnan, China. **A**. Holotype ELI-J0007; A_1, the part (ELI-J0007A); A_2, counterpart (ELI-J0007B), which was unfortunately broken into pieces during preparation; A_3, enlargement of the tail fan from A_1. **B**. Specimen ELI-J0001; B_1, anterior part of *Jianshanopodia decora*; B_2, enlargement of the right frontal appendage showing the five cuneiform plates and the most anterior frontal plate with a probable captured victim (indicated by an arrow), a small bradoriid; B_3, enlargement of the pharynx.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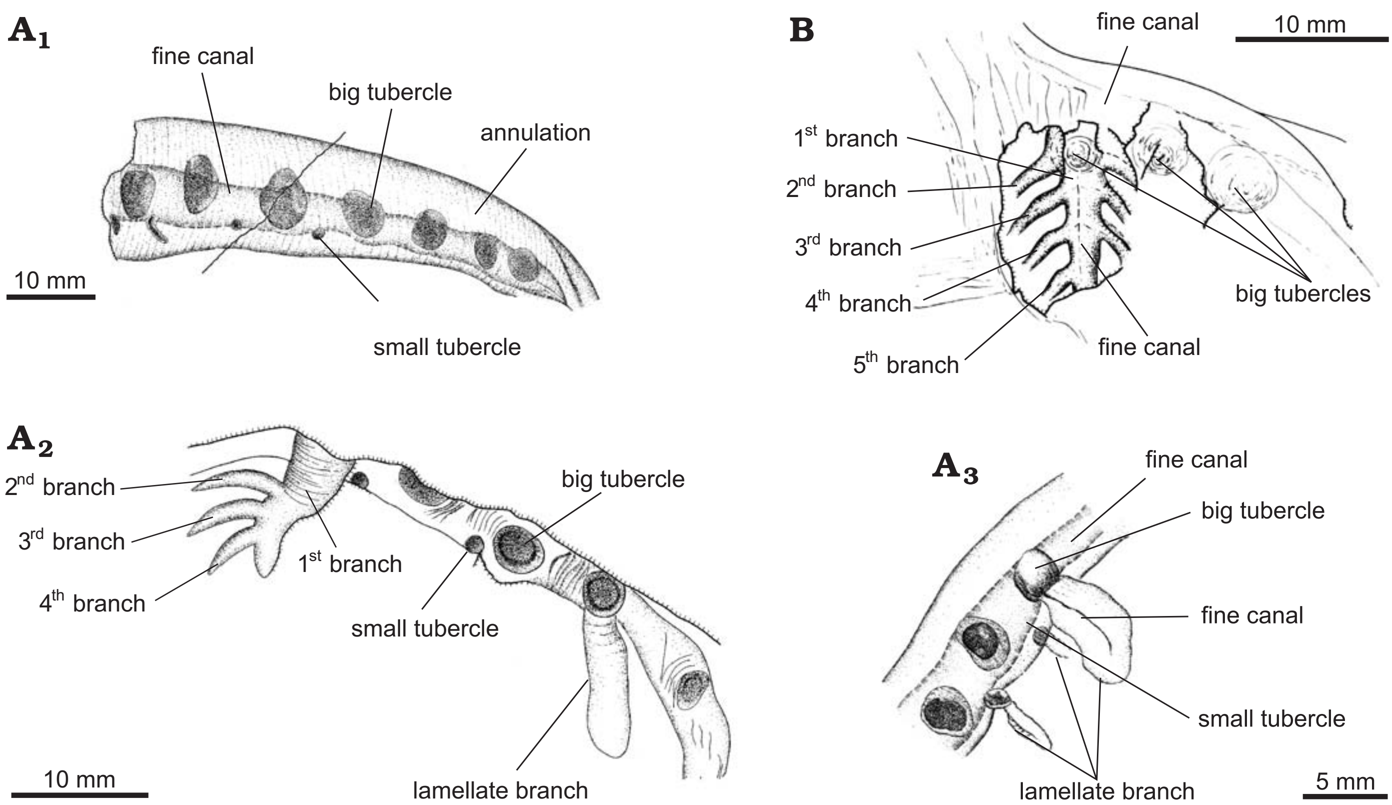

Fig. 4. Camera lucida explanatory drawings of the specimens of *Jianshanopodia decora* gen. et sp. nov. from Fig. 3. **A**. ELI-J0005A; A_1, enlargement of tubercles of one of the appendages (see Fig. 3A_3); A_2, different branches of the appendages (see Fig. 3A_4); A_3, the lamellate branches (see Fig. 3A_5). **B**. ELI-J0007A, the tree-like branches of the holotype (see Fig. 3B_1).

fan. It differs from *Xenusion* Pompeckj, 1927 in its frontal appendages, the pharyngeal structure, and the complex appendages; and from *Hadranax* Budd and Peel, 1998 in its appendages with branches, the pairs of diverticula instead of large trunk nodes, and the tail fan; *Jianshanopodia* shares with the stem group arthropods *Kerygmachela* Budd, 1993, *Pambdelurion* Budd, 1997, and *Anomalocaris* Chen, Ramsköld, and Zhou, 1994 the presence of similar frontal appendages, but easily distinguishable from them in its appendages without lateral flaps, and *Jianshanopodia* differs from *Aysheaia* Walcott, 1911 in having complex appendages and the tail fan.

Jianshanopodia decora sp. nov.

Figs. 1–4.

Derivation of the name: *Decora* Latin, alluding to its beautiful and splendid appearance.

Holotype: ELI-J0007, part and counterpart (Figs. 1A, 2A, 3B, 4B).

Type locality and horizon: Helinpu (Chiungchussu) Formation, Yu'anshan Member (*Eoredlichia* Zone), Lower Cambrian. All specimens were collected from Haikou Village, Kunming, Yunnan.

Material.—The material came exclusively form the type locality and all seven specimens were extracted from a grayish-green and grayish-yellow mudstone there. No complete specimens are known, but the fragments can be pieced together to restore a complete picture of the creature.

Diagnosis.—As for genus.

Description.—The body of *Jianshanopodia decora* comprises three regions: the head, the trunk and the tail. Specimen ELI-J0001 shows the morphology of the head region clearly. It consists of a pair of stout, strongly wrinkled appendages about 40 mm long flanking the anterior, with five cuneiform plates attached along the inner margin of the appendages (Figs. 1B_1, B_2, 2B_1). A small bradoriid can be observed located on the most anterior frontal plate, in terms of the direction of the cuneiform plate and the location spot of the bradoriid, it is likely to be a captured prey rather than just a chance superimposition (Figs. 1B_1, B_2, 2B_1). The structure of the anterior gut is noteworthy, appearing to consist of a short, dilatable mouth tube that leads into a funnel-like pharynx surrounded by the bases of the large frontal appendages.

← Fig. 3. Details of Lower Cambrian xenusiid lobopod *Jianshanopodia decora* gen. et sp. nov. from Haikou, Kunming, Yunnan, China. **A**. Specimen ELI-J0005; A_1, part ELI-J0005A showing appendages with tubercle structures, the arrows point to the big and small tubercle structures; A_2, counterpart ELI-J0005B showing appendages with tubercle structures, shown with arrows; A_3, enlargement of tubercles of one of the appendages of A_1; A_4, different branches of the appendages of A_1; A_5, lamellate branches of A_1; A_6, enlargement of the diverticula of A_2. **B**. Part of the holotype ELI-J0007A; B_1, tree-like branches; B_2, enlargement of the diverticula. **C**. Specimen ELI-J0006; C_1, pairs of diverticula; C_2, tube-like internal structures.

Irregularly-placed wrinkles in the pharynx appear to be muscles. In the middle of the pharynx there is a mass of prominent circular structure, a structure is similar to the pharyngeal teeth of the tardigrade *Echiniscoides* (Barnes et al. 1993), and here interpreted as such (Figs. $1B_1$, B_3, $2B_2$).

The worm-like trunk region seems sub-cylindrical in cross-section. It is composed of at least nine segments, and in terms of the whole morphology of the trunk, probably the number of segments was as many as up to 12, each segment bears traces of transverse broad annulations with a density of 80 mm^{-1} (Figs. 1A, 2A). The segments become narrower in the posterior portion of the trunk. Nearly all specimens exhibit stout, sub-triangular appendages that probably projected ventro-laterally from both sides of each segment (Figs. 1A, 2A, B_1). The appendages are similar in form but decrease in size toward the rear. Two rows of prominent tubercle structures lie on the inferred dorsal side of the appendage from the base to the tip (Figs. $1A_1$, A_2, $3A_1$–A_3, A_5, $4A_1$, A_3). The axial row of tubercle structures is bigger than the lateral ones. Seven big tubercles and four small ones at most are preserved (Figs. $3A_1$–A_3, $4A_1$, A_3). The most striking character of *Jianshanopodia decora* is the tree-like or lamellate structures projecting from the tubercles. The holotype ELI-J0007A exhibits tree-like branches projecting from the first big tubercle of one appendage (Figs. $1A_1$, 2A, $3B_1$, 4B). The tree bears five branches. The first branch, 10 mm long, is the main body of the tree and it tapers toward the tip. The 2nd, 3rd, 4th, and 5th pairs of branches all project from the lateral margin of the first branch, there is nearly the same distance between them, about 3 mm long. Similar tree-like branches also occur in the first big tubercle of one appendage of ELI-J0005A; there are also four branches, but the branches are only preserved on one side (Figs. $3A_4$, $4A_2$). Most likely because of different preservation, the lamellate branches occur on the 4th large tubercle and the 3rd small tubercle of the same appendage of ELI-J0005A (Figs. $3A_5$, $4A_3$). All the appendages of *Jianshanopodia decora* possess narrow, transverse annuli. The number of annuli is proportional to the length of appendages (Figs. $1A_1$, A_2, 2A, $3A_3$, $4A_1$). The tips of the appendages are moderately pointed, but there is no convincing evidence for the presence of terminal claws.

As in most lobopods (Chen et al. 1995; Bergström and Hou 2001), there is a fine canal running centrally through the entire length of each appendage in *Jianshanopodia decora*. In specimens ELI-J0005A and ELI-J0007A, the fine canal extends centrally to the branches of appendages (Figs. $1A_1$, 2A, $4A_1$, A_3, B). The fine canal branches out from the ventral canal of the body cavity, which is expressed in the body as a dark-brown tube (Figs. $1A_1$, 2A).

The gut appears to run through the entire trunk region (Figs. $1A_1$, A_2, B_1, 2A, B_1), usually preserved as a flattened band lying near the ventral margin. No evidence for the anus is present. In most specimens, two rows of prominent, dark, reniform structures with internal anastomoses are situated on either side of the gut (Figs. $1A_1$, A_2, 2A, $3A_6$, C). In specimen ELI-J0004B, linear and elongate tube-like internal structures are observed (Fig. $3C_2$). Given their association with the gut (Figs. $1A_1$, A_2, 2A, $3A_6$, B_2), they are likely to represent mid-gut diverticula, as occur in the stem group arthropod *Pambdelurion* (Budd 1997, 1999) and many Cambrian arthropods such as *Naraoia* (Whittington 1977).

The tail region of *Jianshanopodia decora* is not well preserved. After careful preparation, we were able to observe the outline of three lobes arranged into a tail fan, one is located in the midline, the two others on both sides. The middle one is bigger and stronger than the others (Figs. $1A_1$, A_3, 2A).

Comparisons

As a rare lobopod, *Jianshanopodia* shows most similarities with xenusiid lobopods such as the *Xenusion* and *Hadranax* of the Early Cambrian, and also shares some features with *Aysheaia* of the Middle Cambrian. Features indicating such similarities and possible affinities include: (i) the big body size; (ii) a large cylindrical body with annulations; (iii) stout and strong lobopod appendages each bearing bases of serial tubercles; (iv) terminal mouth; and (v) a pair of frontal appendages. This last feature is also similar to the anterior grasping appendages of anomalocaridid arthropods that were proposed to be homologous between the lobopod *Aysheaia* and the anomalocaridids (Dzik and Krumbiegel 1989; Budd 2002; Dzik 2003). Accordingly, *Jianshanopodia* based on its morphology and geological age is probably a xenusiid lobopod intermediate between *Xenusion* and *Aysheaia*. Besides, *Jianshanopodia* shares some features with the Early Cambrian stem group arthropod *Pambdelurion* (Budd 1997, 1999) and *Kerygmachela* (Budd 1993, 1999). The shared features between *Jianshanopodia* and *Pambdelurion* are the pairs of mid-gut diverticula and the possible presence of tail fan. Especially the pairs of mid-gut diverticula, which are (i) located in nearly the same regions on both sides of the gut and connected to it; (ii) both of them are reniform in shape; (iii) they both bear the same internal structures, e.g., linear or elongate radiating tubes. The similarities between *Jianshanopodia* and *Kerygmachela* are the frontal pharyngeal structures, both of them bear a mouth cone and a muscular pharynx, and the pharynx is surrounded by the bases of the large frontal appendages. However, *Pambdelurion* and *Kerygmachela* possesses a series of segmentally arranged, imbricating, paddle-shaped, movable lateral flaps, whereas *Jianshanopodia* bears distinctive complex branched lobe-like appendages. Taken together, these features suggest that *Jianshanopodia* is not only a probable xenusiid lobopod intermediate between *Xenusion* and *Aysheaia*, but also suggest that this is a xenusiid of rare transitional form between lobopods and arthropods.

Discussion

Arthropods are a predominant group in both the living animal kingdom (accounting for ~80% of the total species) and in the

Cambrian animal community (about half of the total species), and they play a very important role in the ecological system (Ruppert and Barnes 1994). The origin of arthropods has been hotly debated (Willmer 1990; Fortey and Thomas 1997; Edgecombe 1998) and it is generally held by paleontologists that arthropods should be rooted in the early lobopods, and some intermediate forms have been found to bridge them (Dzik and Krumbiegel 1989; Budd 1997, 1999; Dzik 2003; Liu et al. 2004; Xiao 2004). The similarity of the segmental homeobox genes of the onychophorans and those of *Drosophila* give strong support for this hypothesis (Grenier et al. 1997). The annulation of xenusiid is similar to that of the basal part of appendages in most primitive arthropods, a feature used to suggest a transitional position of the xenusiid between lobopods and arthropods (Dzik and Krumbiegel 1989; Dzik 2003). The strong annulation of appendages of *Jianshanopodia* offers a new support for this hypothesis. In terms of the frontal appendages, Budd (2002) has hypothesized that it was primitively innervated from the protocerebrum, and recent date on the developmental neuroanatomy of the pycnogonids gave support to this hypothesis and suggests that the pycnogonid chelifores are homologous to the frontal appendages of certain Cambrian forms (Maxmen et al. 2005; Budd and Telford 2005). Alternatively, Chen et al. (2004) preferred to regard the frontal appendages as equivalent to the antennae of insects and crustaceans presenting some paleontological evidence to support this view. The evaluation of these and many other possibilities is beyond the scope of this paper. However, no matter which hypothesis is favored, the frontal appendages of the xenusiid *Jianshanopodia*, *Hadranax* and *Aysheaia* are crucial to elucidate the origin of the arthropods.

The most obvious feature of arthropod diversity is manifested in the number, morphology and function of their appendages. Antennae, mouthparts, walking legs, grasping and swimming appendages are all modifications of the basic jointed-leg structure that defines the phylum (Budd 1996; Shubin et al. 1997). It is generally held that jointed legs evolved from simple unjointed appendages of Cambrian lobopods. Cambrian taxa with different types of "arthropodization" and limb morphology can be identified (Robison 1990; Hou and Bergström 1997; Zhang et al. 2003). Some paleontologists have hypothesized that fusion between the lateral lobes and ventral lobopodia might have given rise to the biramous limb (Shubin et al. 1997; Budd 1999). It is one evolutionary possibility. However, comparison of *Dll* expression and limb outgrowth in various types of crustaceans and insects suggests that uniramy, biramy and polyramy are the products of shifts in signals along the dorso-ventral axis of the body wall and those additions or reductions in branch number might have evolved readily (Panganiban et al. 1995). Corresponding with this idea, the complex branches of *Jianshanopodia* appendages are likely to represent another variant. Kukalova-Peck (1992) has proposed that both uniramy and biramy are evolved from the reductions of polyramy. This speculation is consistent with the complex appendages of *Jianshanopodia*.

Taken together, *Jianshanopodia*, with its mosaic features of *Xenusion*, *Hadranax*, and *Aysheaia*, strongly support the unity of the lobopods. Furthermore, the similarities between *Jianshanopodia* and the stem group arthropod *Pambdelurion* and *Kerygmachela* present new evidence for the idea that a transitional position of the xenusiids between lobopods and arthropods. Besides, *Jianshanopodia* possesses distinct complex appendages with tree-like or lamellate branches, which not only suggest that there were various diversifications of lobopods at the early stage of their evolution, but that they are also crucial to any exploration of the origin of appendages in the arthropods.

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