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Soft anatomy of the Early Cambrian arthropod *Isoxys curvirostratus* from the Chengjiang biota of South China with a discussion on the origination of great appendages

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An updated reconstruction of the body plan, functional morphology and lifestyle of the arthropod *Isoxys curvirostratus* is proposed, based on new fossil specimens with preserved soft anatomy found in several localities of the Lower Cambrian Chengjiang Lagerstätte. The animal was 2–4 cm long and mostly encased in a single carapace which is folded dorsally without an articulated hinge. The attachment of the body to the exoskeleton was probably cephalic and apparently lacked any well-developed adductor muscle system. Large stalked eyes with the eye sphere consisting of two layers (as corneal and rhabdomeric structures) protrude beyond the anterior margin of the carapace. This feature, together with a pair of frontal appendages with five podomeres that each bear a stout spiny outgrowth, suggests it was raptorial. The following 14 pairs of limbs are biramous and uniform in shape. The slim endopod is composed of more than 7 podomeres without terminal claw and the paddle shaped exopod is fringed with at least 17 imbricated gill lamellae along its posterior margin. The design of exopod in association with the inner vascular (respiratory) surface of the carapace indicates *I. curvirostratus* was an active swimmer. Morphological comparisons demonstrate that species of *Isoxys* were diverse in feeding habits and occupied a very broad morphospace, i.e., carapace bivalved or a single shield, the pre-oral limbs antenniform or modified into great appendages, the succeeding endopods slim or stout. This casts doubt on the current taxonomy that assigns all species to a single genus, and on any presumed lifestyle of *Isoxys* extrapolated to the generic level. Finally, since *I. curvirostratus* and *I. acutangulus* carry a pair of great appendages, *Isoxys* has recently been placed into the great appendage arthropods. Such placement might be inadequate because the homology of the great appendages can not be established.

Key words: Arthropoda, *Isoxys*, soft anatomy, “great appendage”, Chengjiang biota, Cambrian, China.

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Introduction

Isoxys Walcott, 1890, a Cambrian “bivalved” arthropod with prominent antero- and postero-dorsal spines, is well known because of its widespread geographical distribution (Williams et al. 1996; Vannier and Chen 2000). Hitherto, up to 17 species have been recorded from palaeocontinental Laurentia, Siberia, Gondwana, and South China, mostly known from the empty carapaces alone (Williams et al. 1996; Vannier and Chen 2000; García-Bellido et al. 2009a). More recently, however, the soft anatomy has been revealed in eight species of *Isoxys*, particularly the visual organs and the frontal appendages (Table 1). New data obtained from two species from the Emu Bay Shale (García-Bellido et al. 2009a), one from Sirius Passet (Stein et al. 2010), two from Chengjiang (Shu et al. 1995; Vannier and Chen 2000), two from the Burgess Shale (García-Bellido and Collins 2005;

García-Bellido et al. 2009b), and one from Utah (Briggs et al. 2008) have attracted attention to the interrelationships of the species assigned to the genus. Indeed, although congeneric differences have been recognized by previous authors (Vannier and Chen 2000; García-Bellido and Collins 2005; Stein et al. 2010), deep discussion has been hampered by limited information on the soft parts. In spite of popular assignment of *Isoxys* to the great appendage arthropods in recent years (Chen et al. 2007; Waloszek et al. 2007; Vannier et al. 2009), this group as a whole remains confusing. In this context the present paper uses several lines of evidence from abundant new soft-bodied material of *Isoxys curvirostratus* Vannier and Chen, 2000, to allow a reasonable reconstruction, morphological comparison with material previously reported, detailed discussion of its ecological aspects and, finally a contribution to the on-going debate about the evolution of the great appendage arthropods.

Table 1. Previous work on *Isoxys* with soft anatomy. Y = preserved; N = not found; (n) = the number of the podomeres of frontal appendages or body segments; Fa, frontal appendage; En, endopod; Ex, exopod; Dg, digest gland or alimentary canal; Bs, segmentation of the body.

Age	Occurrence	Species	Soft anatomy					
			Eye	Fa(n)	En	Ex(n)	Dg	Bs(n)
Early Cambrian	Chengjiang, South China	<i>Isoxys curvirostratus</i> Vannier and Chen, 2000	Y	Y	N	Y	Y	Y(14)
		<i>Isoxys auritus</i> Jiang in Luo et al., 1982	Y	Y	Y	Y	Y	Y(11)
	Emu Bay Shale, Australia	<i>Isoxys communis</i> Glaessner, 1979	Y	Y	N	Y	Y	N
		<i>Isoxys glaessneri</i> García-Bellido, Paterson, Edgecombe, Jago, Gehling, and Lee, 2009	Y	N	N	N	N	N
		Sirus Passet, North Greenland	<i>Isoxys volucris</i> Williams, Siveter, and Peel, 1996	N	Y(7)	Y	Y	N
Middle Cambrian	Burgess Shale, Canada	<i>Isoxys acutangulus</i> Walcott, 1908	Y	Y(5)	Y	Y	Y	Y(13)
		<i>Isoxys longissimus</i> Simonetta and Delle Cave, 1975	Y	N	N	N	N	N
	Utah, USA	<i>Isoxys</i> sp. of Briggs et al. (2008)	Y	N	N	Y	N	N

Institutional abbreviations.—ELI, the Early Life Institute, Northwest University, Xian, China; NWU, Northwest University, Xian, China.

Other abbreviations.—as, anterior spine; co, cornea; en, endopod; es, eye stalk; ex, exopod; f1–5, podomeres of the frontal appendage from the distal to proximal; fa, frontal appendage; gl, gill lamellae of exopod; le, lateral eye; lv, left valve; ou, tooth-like outgrowth of the frontal appendage; p1–5, podomeres of endopod from the distal to proximal; pf, proximal part of frontal appendage; pr, proximal part of appendage; ps, posterior spine; ru, reticular units; rv, right valve; st, striated ornament; ta, trunk appendage; te, telson; ti, trunk inclusion; vn, vascular integumental network; 1–14, numbered trunk appendage (1 is the appendage immediately behind the frontal appendage).

Material and methods

The material described here was mainly collected from two localities (Jianshan, and Erjie) of the Chengjiang Lagerstätte in the mudstone-dominated Yu’anshan Member of the Helinpu Formation (previously Qiongzhusi Formation), Eoredlichia Zone, Stage 3, Series 2 of the Cambrian in eastern Yunnan, China, correlated with the late Atdabanian of the Siberian Cambrian sequence (Zhang et al. 2001, 2008; Hou et al. 2004). It comprises 87 specimens housed in the ELI and Department of Geology in NWU. All fossils are preserved as partly flattened impressions on slabs of mudstone, showing variable degrees of compaction. In the specimens with soft-part preservation, portions of the body lie in different laminae, allowing exposure of some hidden structures when the initial split separates two valves of the carapace into the two slabs. Digital photographs are accompanied by camera-lucida drawings to assist the morphological interpretation. Photographs were taken with tungsten lamp illumination at low angles to the plane of the specimens to enhance the relief of these highly compressed fossils. Figured and described material in this paper is identified by the prefix “JS” and “EJ”, which stands for Jianshan and Erjie localities.

For practical purposes, the morphological terms used in the description of the carapace are in general accordance

with those used by previous authors to describe the morphology of *Isoxys* (Williams et al. 1996; Vannier and Chen 2000). The term “carapace” is used in a purely descriptive meaning—to designate the exoskeleton that covers the soft body—with no phylogenetic implications. In the description of features other than the carapace we have applied the terminology that is currently used by biologists to describe the anatomical features of recent arthropods (e.g., Brusca and Brusca 2003). The gill lamellae refer to the long, narrow, flattened stiff outgrowths perpendicular to the posterior margin of the exopod shaft, which are similar to the long, flattened setae in trilobite-type exopods, although no notable constrictions (marking the position of an articulation which is by definition in a seta) have been seen at the base of each lamella due to the preservational limitations in the material at hand.

Morphological description

Carapace features of *Isoxys curvirostratus* documented to date (Vannier and Chen 2000), such as the thin, amplete valve with striated ornament and armed with a curved anterior cardinal spine, are also present in our material (e.g., Figs. 1A₁, 2A₁, B₂, 4A₁). Additionally, new evidence indicates that the carapace is composed of a single shield folded dorsally and is not truly bivalved (Fig. 3B). Similarly, cardinal spines of the “two” valves are fused into, at least at the base, a single pointed rostrum at both ends of the carapace (Fig. 3B). This indicates the absence of two units in the carapace.

Cephalon, trunk, and body attachment.—The body is preserved much darker than the surrounding areas (Figs. 2B–E, 3A₁, 4B₁) and extends from the anterior margin to the postermost part of the carapace, excluding the cardinal spines (Figs. 2C, D, 4B₁). Nearly all of the body is covered by the carapace. Any extension of the trunk beyond the carapace is probably a result of decay and displacement during the process of burial (Figs. 1A₁, 3A₁). The cephalon is poorly defined in all available specimens and the number of cephalic appendages is indeterminate (Figs. 2A, E, 3A₁). It should be noted that, the dark coloured stripes, extending ventrally along the body axis and arranged radially, represent

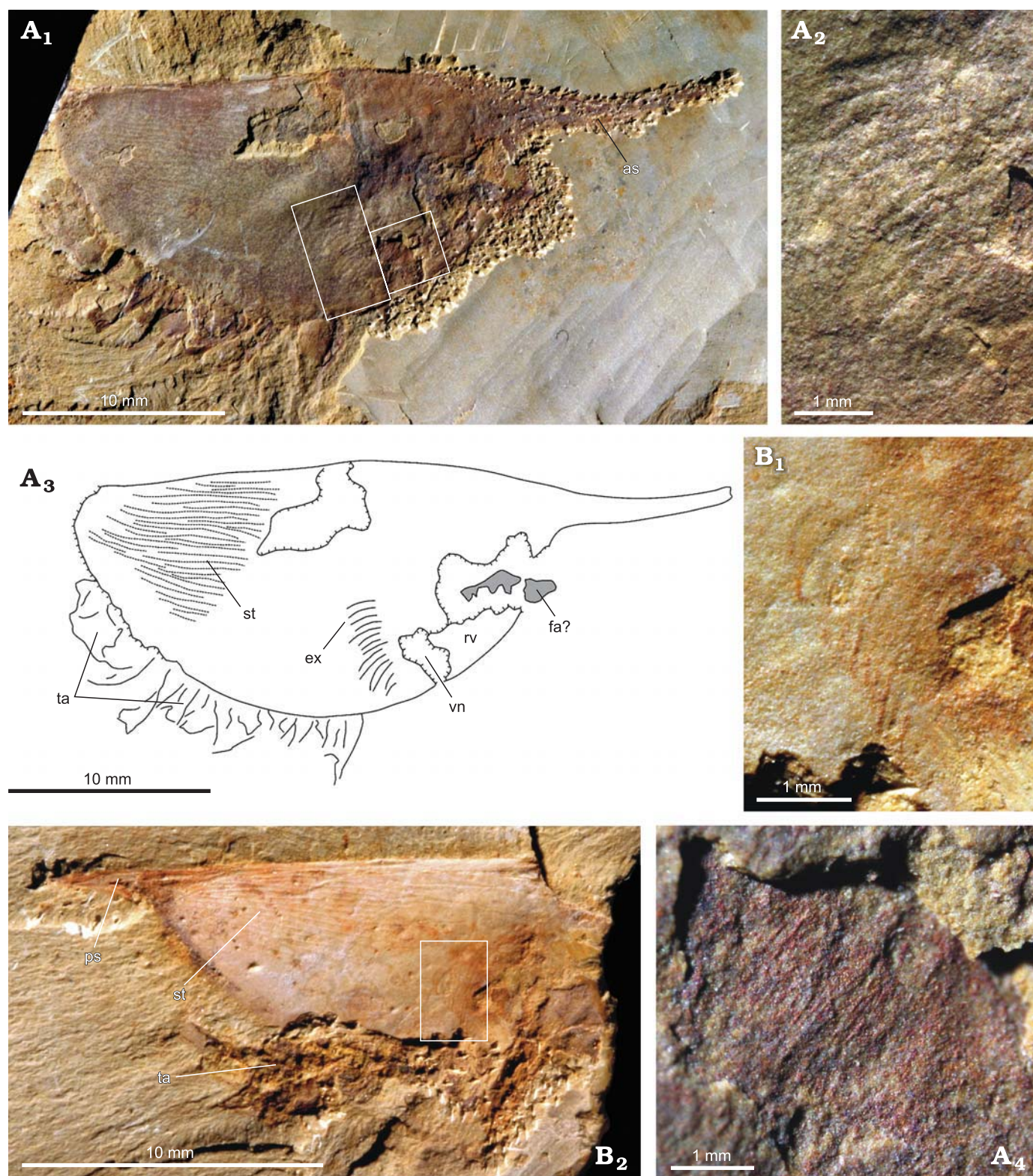


Fig. 1. An early arthropod *Isoxys curvirostratus* (Vannier and Chen, 2000) from the Lower Cambrian Chengjiang biota, South China. **A.** JS0010 from Jianshan section; A₁, showing the outline and the striated ornament of the carapace; A₂, detailed view of exopod, showing the gill lamellae; A₃, camera-lucida drawing of A₁; A₄, detailed view of vascular integumental network. **B.** JS172 from Jianshan section; B₁, detailed view of exopod, showing the gill lamellae; B₂, showing the striated ornament on the posterior of the carapace and exopod. Abbreviations: as, anterior spine; ex, exopod; fa, frontal appendage; ps, posterior spine; rv, right valve; st, striated ornament; ta, trunk appendage; vn, vascular integumental network.

organic stains of the decayed trunk rather than limbs as was assumed by Vannier and Chen (2000). Limbs are, in fact,

preserved in relief and are pale in colour (Figs. 2A₁, E₁, 4B₁). The trunk part is, however, visible as dark coloured stripes in

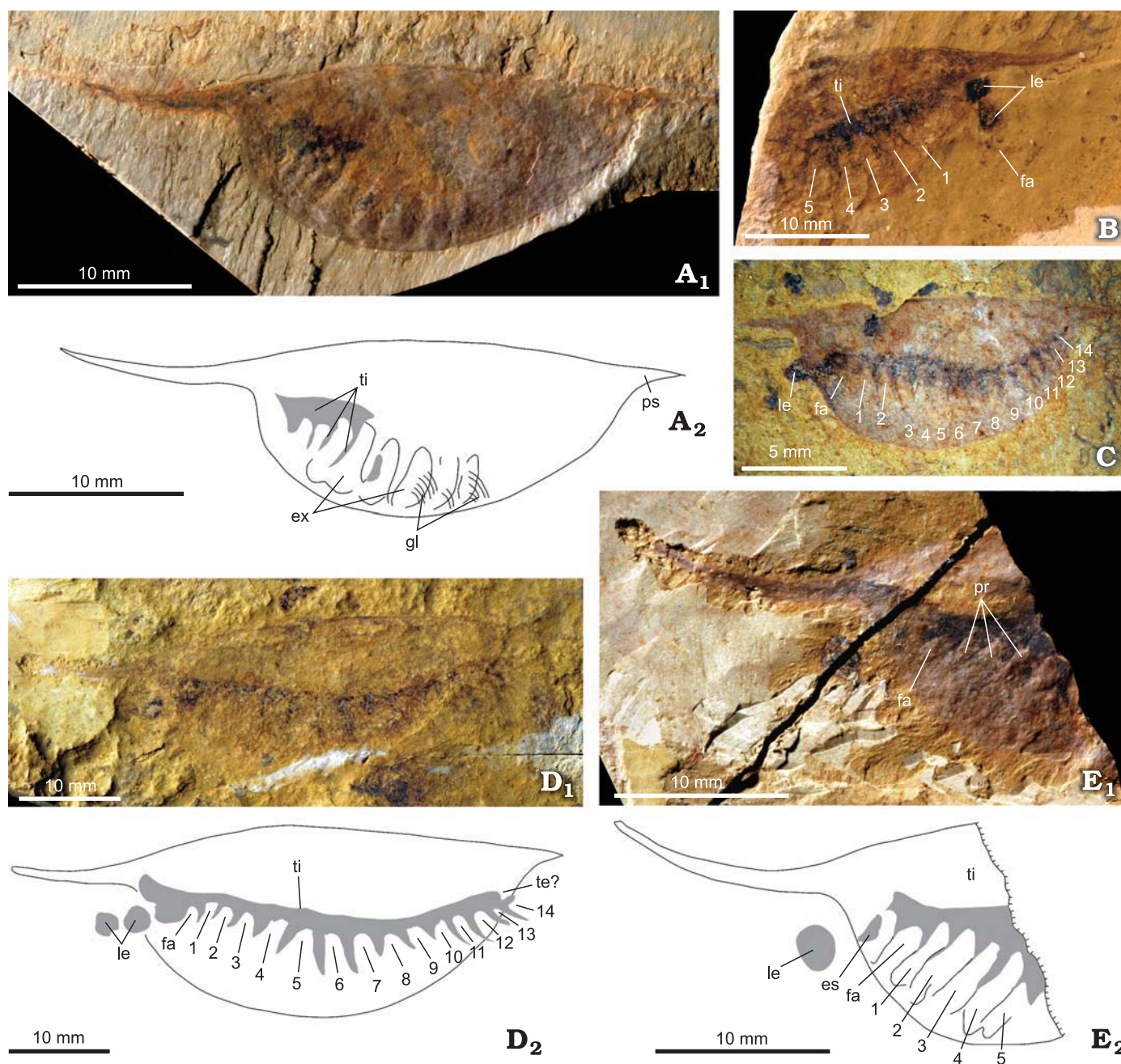


Fig. 2. An early arthropod *Isoxys curvirostratus* (Vannier and Chen, 2000) from the Lower Cambrian Chengjiang biota, South China from Erjie section (A–C, E) and from Jianshan section (D). **A.** EJ0423; **A₁**, complete specimen showing the outline of carapace, lamellae of the exopod; **A₂**, camera-lucida drawing of **A₁**. **B.** EJ0424, showing the eye spheres, frontal appendage, trunk and the traces of trunk appendages. **C.** EJ0422, immature specimen showing 14 trunk somites. **D.** JS154; **D₁**, showing eye spheres, the number of the trunk somites and location of appendages; **D₂**, camera-lucida drawing of **D₁**. **E.** EJ0407; **E₁**, showing the eye sphere and stalk, appendages in relief and the trunk; **E₂**, camera-lucida drawing of **E₁**. Abbreviations: es, eye stalk; ex, exopod; fa, frontal appendage; gl, gill lamellae of exopod; le, lateral eye; pr, proximal part of appendage; ps, posterior spine; te, telson; ti, trunk inclusion; 1–14, numbered trunk appendage.

the gaps between two adjoining appendages (see Fig. 2E₁). Accordingly, the number of somites can be estimated at 14 on the basis of limbs which are evident in JS154 and the counterpart of JS0014 (Fig. 2C, D), although the intersomitic boundaries of the trunk are not evident in *Isoxys curvirostratus*.

Body attachment is highly hypothetical since no direct evidence of adductor muscle scars has been found. Speci-

mens preserved in lateral aspect, whose posterior trunk hung down and protruded from the ventral margin of the carapace, while the anterior trunk was not displaced (e.g., Figs. 1A₁, 3A₁) in association with the much darker expanded area at the anterior half of the trunk (Figs. 2A, C), indicate that the trunk was attached to the carapace at the anterior region. Telson and rami are hardly discernible due to the poor preservation in the present material.

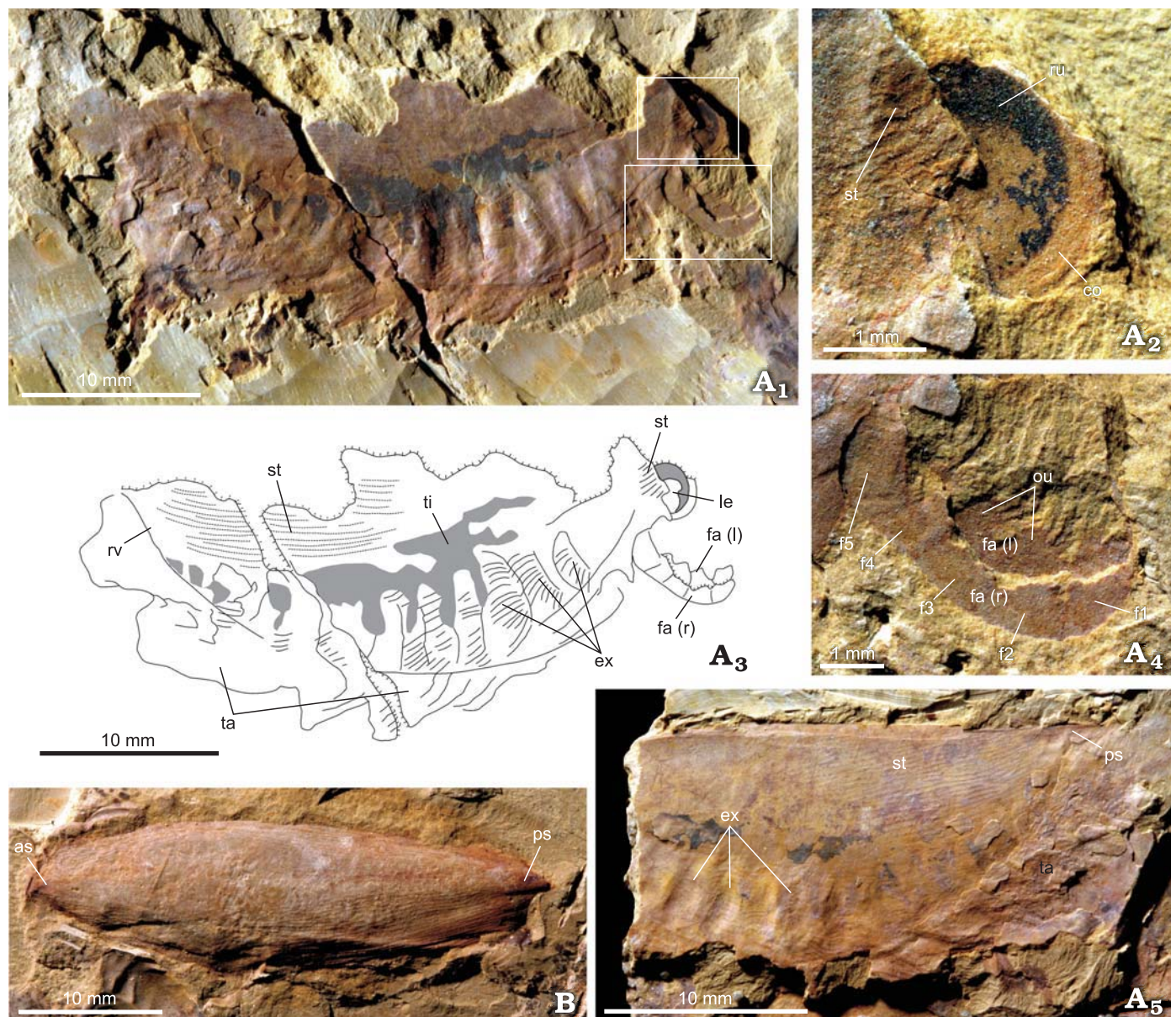


Fig. 3. An early arthropod *Isoxys curvirostratus* (Vannier and Chen, 2000) from the Lower Cambrian Chengjiang biota, South China. **A.** JS0014 from Jianshan section; **A**₁, specimen showing the striated ornament of the carapace, eye, frontal appendages, exopod and trace of the trunk; **A**₂, detailed view of eye sphere, showing two individual layers, the light external cornea and the dark internal core; **A**₃, camera-lucida drawing of **A**₁; **A**₄, detailed view of frontal appendages, showing the intersegmental membranes, five podomeres and tooth-like outgrowths; **A**₅, the counterpart of JS0014, showing the posterior part of specimen. **B.** EJ0417 from Erjie section, dorsal view showing the single shield carapace and unsplit base of anterior or posterior spines. Abbreviations: as, anterior spine; co, cornea; ex, exopod; f1–5, podomeres of the frontal appendage from the distal to proximal; fa, frontal appendage; ou, tooth-like outgrowth of the frontal appendage; ps, posterior spine; ru, reticular units; st, striated ornament.

Eye.—In five specimens, pairs of large lateral eyes are preserved in life position as dark, round impressions, about one seventh of the valve height in diameter, extending beyond the anterior margin of carapace (Figs. 2B–E, 3A₁, 4B₁). In JS0014, two individual layers can be recognized from a single eye sphere (Fig. 3A₂); the light external layer probably represents the cornea, and the dark internal core is best interpreted as the remains of retinulae units. The eye stalk, unsegmented, is visible in two specimens, unequivocally in EJ0404 (Fig. 4B₁). The length of the stalk is equal to the diameter of the eye and its width is about one fifth of the eye

sphere, with an equal dimension from the proximal to the distal part. The proximal part of the stalk is located at the presumed cephalon (ocular segment).

Frontal uniramous appendage.—The antermost pair of appendages is present in six of our specimens (e.g., Figs. 1A₁, 2B, E₁, 3A₁, 4A₁, B₁), and are uniramous, curved and protrude beyond the anteroventral margin of the carapace. In specimen JS0014 the frontal appendage is almost 7 mm in length and 1 mm in diameter, consisting of five segments suggested by the four well-developed intersegmental mem-

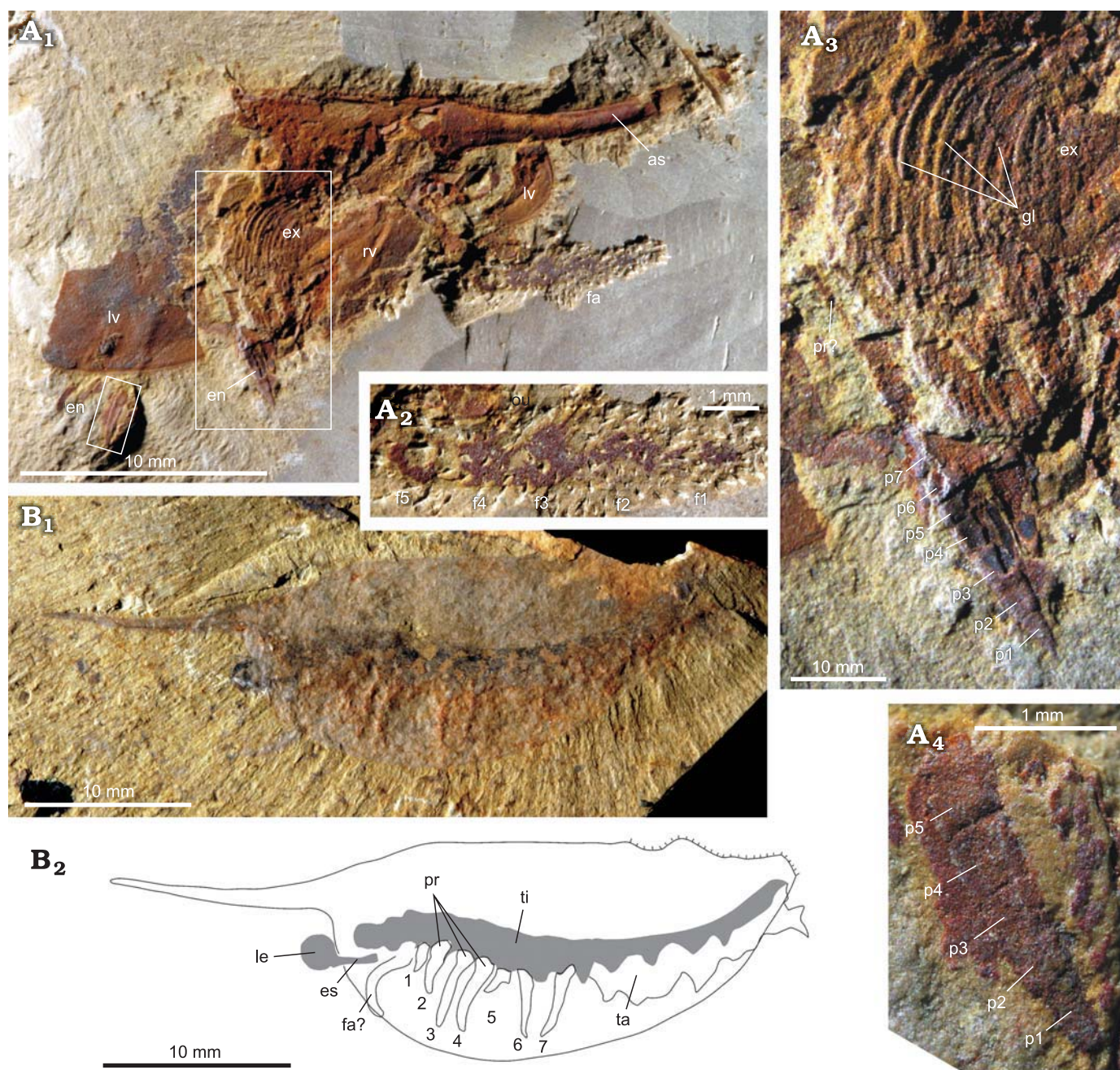


Fig. 4. An early arthropod *Isoxys curvirostratus* (Vannier and Chen, 2000) from the Lower Cambrian Chengjiang biota, South China. **A.** JS0008 from Jianshan section; A₁, posterior part of an incomplete specimen showing the frontal appendage, exopod, endopod; A₂, detailed view of the frontal appendage, showing five podomeres and tooth-like outgrowths; A₃, detailed view of exopod and endopod, showing the gill lamellae of exopod and the podomeres of endopod; A₄, detailed view of endopod, showing its podomeres. **B.** EJ0404 from Erjie section; B₁, showing the location of the eye stalk, trunk, proximal part of appendages and the outline of endopod; B₂, camera-lucida drawing of B₁. Abbreviations: as, anterior spine; en, endopod; es, eye stalk; ex, exopod; f1–5, podomeres of the frontal appendage from the distal to proximal; fa, frontal appendage; gl, gill lamellae of exopod; lv, left valve; p1–5, podomeres of endopod from the distal to proximal; pr, proximal part of appendage; rv, right valve; st, striated ornament; ta, trunk appendage; ti, trunk inclusion; 1–7, numbered trunk appendage.

branes on the right appendage (Fig. 3A₄). The proximal segment seems different from the distal ones in shape, possibly representing the basal segment. Stout tooth-like outgrowths are visible in the segments of the left appendage (Fig. 2A₄). In JS0008, five segments of the frontal appendage are also indicated by the indisputable outgrowths (Fig. 3A₁). The outline of the frontal appendage, followed by the eyes, is preserved in EJ0424 (Fig. 4B). The proximal part of the frontal

appendage is present in some specimens, for example in EJ0407, and apparently shows no sign of significant post-mortem displacement. Therefore, the frontal appendage is likely inserted into the cephalon immediately posteroventral of the eye stalk (Fig. 4E). A similar orientation also occurs in JS0010 (Fig. 1A₁) and EJ0404 (Fig. 3B). Note also that the frontal appendage is located very close to the succeeding limbs with no gap between them (Fig. 4E).

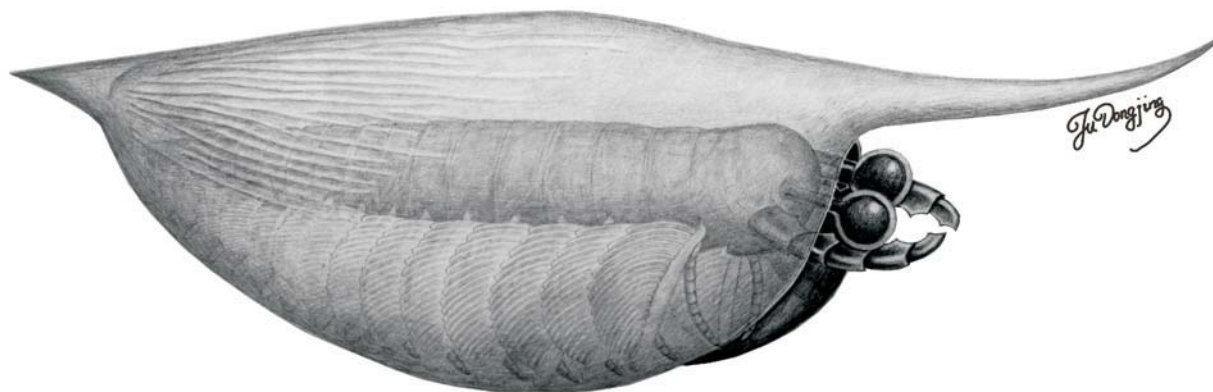


Fig. 5. An early arthropod reconstruction of *Isoxys curvirostratus* (Vannier and Chen, 2000). The animal was covered by the carapace. The trunk length, which consists of 14 somites varies from 2 to 3 cm in adults. Large stalked eyes and a pair of uniramous prehensile appendages (5 podomeres) bearing stout inner outgrowths protruded anteriorly. The following appendages are biramous and uniform—i.e., a slender endopod with many podomeres and an exopod fringed with many long lamellae.

Biramous appendages.—Following the frontal appendage is a series of 14 pairs of uniform biramous appendages. They seem to reach maximum size in the anterior half of the body and dwindle towards each end (e.g., Figs. 2C, 3A₁, 4B₁). The exopod is elliptical in outline and slightly inclined to the sediment surface in a consistent way, overlapping the posterior one (Figs. 2A₁, 3A₁, 4A₁). The ratio of length to width is about 2:1. Some specimens, though scarce, reveal the detailed structures of the exopod. In the initial split of specimen JS0008 (Fig. 4A₁), the exopod is fringed with a series of long and narrow lamellae along its posterior margin, which extend backwards and downwards, each overlapping the succeeding one (Fig. 4A₃). Extrapolation indicates that each exopod bears at least 17 lamellae; it is not possible to determine whether or not this number varied among all of the exopods. Similar features can be recognized in JS0014 (Fig. 3A₁, A₃) and JS0010 (Fig. 1A₁, A₂), and are also found in JS172 (Fig. 1B₁, B₂) and EJ0423 (Fig. 2A₁). The separated setae around the exopod in EJ0423 (Fig. 2A₁) is the trace of the inadequately preserved flat lamellae.

The endopod is slender (0.3 mm in diameter) and segmented. Podomere boundaries are evident in JS0008, in which the endopods extend beyond the ventral margin of the carapace (Fig. 3A₁). Two endopods show the distal podomeres; 5 in the posterior endopod (Fig. 4A₄) and 7 in the anterior endopod (Fig. 4A₃). We infer that the endopod contains more than 7 podomeres, but the precise number is unknown since podomere boundaries in the proximal part of the anterior endopod are hardly discernible (Fig. 4A₃). Neither a claw nor endites occur in the endopods. Several reddish tubular objects, extending ventrally along the body axis and arranged radially, also represent the endopods in EJ0404 (Fig. 4B). The anterior seven endopods, especially the third and fourth one are evident. The swollen basal part indicates attachment to the body and the distal part nearly reaches the ventral margin of the carapace. Accordingly, the endopods must have been equal to the exopods in length.

Internal organs.—A dark coloured band along the midline of the trunk, typically black or brown, possibly represents the

alimentary canal and/or digestive glands, although no three-dimensional structures like those in Burgess Shale specimens have been found. The alimentary canal is entirely sediment—free and lacks any bodily material inside (Figs. 2B–E, 3A₁, 4B₁).

Apart from the alimentary canal, an additional soft anatomical structure has also been found in our material. In specimen JS0010, whose right anteroventral valve was removed and the internal structure exposed (Fig. 1A₁), there are many elongate, anastomosing ridges over the entire surface of the internal mould. The ridges are very fine, each 50 µm in diameter, and are reddish in colour (Fig. 1A₄). These structures are reminiscent of the vascular integumental network of Recent myodocopes and are thus interpreted as analogues. Similar structures were also described from other fossil groups, such as Middle Cambrian bradoriid *Anabaroichilina* Linnarsson, 1869 (Vannier et al. 1997: fig. 7A).

Morphological and functional comparisons with other species of *Isoxys*

Carapace.—Variation of carapaces on the basis of spine length and valve shape among species in *Isoxys* should be employed with caution in taxonomy, though both are very useful as diagnostic qualitative characters. Because the cardinal spines in *Isoxys* specimens are fragile, their true length may not be preserved (Williams et al. 1996). Valve shape, for example, the ratio of length to height varies between juvenile and mature specimens of *I. auritus* Jiang 1982 (for mature individuals see Shu et al. 1995: fig. 1C; for juveniles see Vannier and Chen 2000: fig. 3E; Hu et al. 2007: fig. 1D; and Vannier et al. 2009: fig. 3i). Therefore, intraspecific variation of carapace outline appears to be present at least in some species of *Isoxys*. This, again, diminishes the diagnostic importance of the carapace configuration. Micro-ornamentation of

the carapace occurs in three species, while carapaces in other species are smooth. Only *I. curvirostratus* bears a striated ornament, which is different from the reticulate pattern shared by *I. auritus* and *I. communis* Glaessner, 1979 (García-Bellido et al. 2009a). Note also that, the “bivalved” carapace is, in fact, a single shield in *I. curvirostratus* and *I. volucris* Williams, Siveter, and Peel, 1996 (Stein et al. 2010), rather than a truly bivalved carapace found in *I. auritus* (Shu et al. 1995). The spine was split into two halves along the entire dorsal line of *I. auritus* (clear in Vannier and Chen 2000: fig. 2F, G; Shu et al. 1995: fig. 1C), while *I. curvirostratus* obviously bears a single anterior or posterior spine, which also indicates the absence of two units. The fact that the carapace of *I. auritus* bears two units can be also supported by the presence of adductor muscles, which are used for opening and closing the bivalved carapaces (Shu et al. 1995: 337, fig. 1C). *I. communis* and *I. acutangulus* Walcott, 1908 (García-Bellido et al. 2009b) have a median headshield fold. The anteriorly splayed-out valves in some specimens of *I. acutangulus* (see Briggs et al. 2004: fig. 102) are most probably an artifact produced by compression since the dorsal line is slightly convex in lateral views (García-Bellido et al. 2009b). There is no information about the other three species because of the lack of dorso-ventrally compressed specimens.

The presumed pelagic lifestyle of *I. curvirostratus* is deduced from structural comparisons with Recent crustaceans (Williams et al. 1996; Vannier and Chen 2000). However, this assumption does not need to apply to all the species of *Isoxys*. Stein et al. (2010) stated that a pelagic lifestyle could not be assumed in *I. volucris* because the associated characters of the carapace presumed by Vannier and Chen (2000) were absent. Similarly, the thick and stiff carapace of *I. auritus* is rather inconsistent with such a pelagic lifestyle.

Eye.—Eyes are by far the most frequently preserved organs in the specimens with soft-part preservation. They have been described in nearly all species, except *I. volucris* (Stein et al. 2010). The eye spheres do not differ significantly from each other in shape and position, and indicate excellent vision (García-Bellido et al. 2009b; Vannier et al. 2009). The complicated structures occur only in *I. curvirostratus* (see also Vannier et al. 2009: figs. 3g, h), making further comparisons impossible. However, variations in the length and location of the eye stalk indicate interspecific variation. For example, the eye spheres of *I. acutangulus* are very close to the front part of the head (ocular segment); thus the stalk is too short to recognize, in contrast to the longer eye stalk of *I. curvirostratus*.

Frontal appendage.—The frontal appendage has been recognized as being of vital importance in resolving the feeding issue in *Isoxys*, but the reported differences in morphology have not yet received the treatment they deserve. The stout frontal appendage of *I. curvirostratus* described above most closely resembles that of *I. acutangulus* (García-Bellido et al. 2009b; Vannier et al. 2009) in having five podomeres and an obvious inner outgrowth with spines instead of the slender antenna illustrated by Vannier and Chen (2000). The raptorial function

of the latter has been proposed by García-Bellido et al. (2009b) and Vannier et al. (2009). It is also worth noting that the frontal appendage of *I. curvirostratus* was the only food gathering structure and all the succeeding appendages have no median enditic protrusions and are not armed with setae or spines for food gathering and manipulation. We are convinced that *I. curvirostratus* was a predator rather than a filter feeder. In contrast, the first appendage of *I. auritus* is antenniform in morphology, and composed of multiple podomeres with numerous setae and directs anteroventrally (Vannier et al. 2009: figs. 3i, j). Such a design is similar to the sensory antennae of many arthropods and may not have grasping function. Indeed, interspecific differentiation of the frontal appendage has been also documented in *I. volucris*, which has at least seven podomeres, instead of five or nine, and the distal podomere carries two spines (Stein et al. 2010). The frontal appendage was also reported in *I. communis*, in which it curves upwards but lacks evidence of the inner outgrowth and robust spines seen in *I. curvirostratus* and *I. acutangulus* (García-Bellido et al. 2009a). In addition, the gap between the frontal appendage and succeeding limbs, which might have borne several additional head appendages in *I. acutangulus*—as assumed by Vannier et al. (2009)—is absent in *I. curvirostratus*.

Biramous appendage.—Predation is usually associated with strong locomotion. In addition to the nature of the carapace recognized previously (Vannier and Chen 2000), active swimming and adaptation to a predatory lifestyle can be supported by powerful swimming appendages: the comb-like structure of the exopod (posterior margin fringed with numerous gill lamellae)—which is a common design of exopods in Cambrian arthropods—and the combination of locomotory and respiratory functions. The well developed lamellae of the exopods substantially increase the effective surface of the appendage, consequently improving the ability of movement as well as respiration. Exopods were also observed in four other species of *Isoxys*. They have an identical structure, being paddle shaped and fringed with setae. However, the fact that numerous long and narrow lamellae (possibly flat setae) overlap mutually along the posterior margin of the exopod in *I. curvirostratus* is undisputed. It is remarkably different from the separated filament setae around the exopod known from *I. acutangulus*, *I. auritus*, and *Isoxys* sp. (Briggs et al. 2008). Thus, exopod morphology may vary interspecifically, as is the case for frontal appendages.

Endopods are rarely preserved in *Isoxys*. Three species are known to display only their outlines, while their detailed morphology is known only in *I. curvirostratus* and *I. auritus*. Endopods of *I. curvirostratus* are preserved as slender rods, each bearing more than 7 podomeres but no distal claw, which may not be adapted to walking habits. Endopods of *I. auritus* are relatively stout, which is three times the diameter of *I. curvirostratus* and bears fewer podomeres (DF and XZ unpublished material). It is likely that the endopod of *I. auritus* is fit for crawling on the substrate surface intermittently instead of free swimming. Furthermore, in contrast to the early view

of the dwarf endopod in *Isoxys*, new data at least from *I. curvirostratus* and *I. volucris* indicate that the endopods must have reached at least the length of the exopods. The endopod of *I. acutangulus* appears to be slim and elongate (García-Bellido et al. 2009b), but no details are known.

Other soft parts.—The inner vascular (respiratory) surface of the carapace also supports the inferred swimming habit of *I. curvirostratus*. The oldest record of such a structure is in a bradoriid from the early Cambrian of Greenland and consistent features are also recognized from a range of Cambrian bivalved arthropods (see Vannier et al. 1997). This feature suggests that the animal probably had an integrated circulatory system (including a heart) similar to Recent crustaceans, as well as branchial circulation (via the thoracopods) to improve respiratory ability. Additional internal organs, like the three dimensional preserved mid-gut gland—commonly observed in *I. acutangulus* and *I. communis*—are not evident in *I. curvirostratus* although organic-rich deposits in the trunk are clearly recognizable.

Discussion

It is evident that species assigned to the genus *Isoxys* occupy a quite broad morphospace. At least two morphotypes of carapace can be recognized, i.e., the bivalved carapace with a dorsal hinge in *I. auritus*, and the single shield carapace in *I. curvirostratus*. This, as well as the reported differences in limb morphology, has cast a doubt on the close relationship between all *Isoxys* species (see also Stein et al. 2010). Similarly, any presumed lifestyle of *Isoxys* at the genus level is questionable. In such terms, the widespread distribution of the genus cannot be used to indicate a pelagic habit for particular species since geographical distribution at the species level might be relatively provincial. The conspicuous interspecific morphological differences necessitate interpretation of the ecology of *Isoxys* at the species level.

The information on soft part anatomy of *Isoxys* has been much refined since its first description, but the placement of the genus within the Arthropoda remains ambiguous. Recently, several authors have assigned *Isoxys* to the “great-appendage” arthropods (Chen et al. 2007; Waloszek et al. 2007; Vannier et al. 2009) even though there is still a lack of consensus over the concept of the great-appendage group. Hou and Bergström (1997) erected the Class Megacheira to include a group of arthropods bearing the pre-oral “great appendage” (e.g., *Leanchoilia* Walcott, 1912, *Jianfengia* Hou, 1987b, and *Fortiforceps* Hou and Bergström, 1997). They stated that the “great appendage” corresponded to the second antenna of crustaceans, and the antennule was commonly reduced or lost. This opinion was based on a single specimen of *Fortiforceps foliosa* (Hou and Bergström 1997: 26, 45) bearing a pair of uniramous antennules in front of the “great appendage”. Accordingly, the “great appendage” should be innervated from the tritocerebrum (like the second antenna of crustaceans).

Cotton and Braddy (2004) also proposed that the “great appendage” was a tritocerebral appendage.

In contrast, Chen (2004: 294) doubted the presence of the first antenna in *Fortiforceps*. Instead, Chen et al. (2004, 2007) referred the “great appendage” to the first (deutocerebral) limb homologous to the chelicera of Chelicerata, thus placing *Fortiforceps* in the stem-lineage of Chelicerata. This single pre-oral capturing appendage is indeed similar to the chelicera of Chelicerata functionally, although the presumed homology between them requires confirmation (Chen et al. 2007; Waloszek et al. 2007; Köhl et al. 2009; Vannier et al. 2009). However, this hypothesis excludes anomalocaridids and *Occacaris* Hou, 1999/*Forfexicaris* Hou, 1999 (with two pre-oral appendages) from the “great appendage” arthropods even though all of these bear raptorial appendages. Alternatively, some authors have accepted that an antenna occurs anterior to the great appendage in some instances, but have different views about the location of the great appendage. Budd (2002) stated that the great appendage was positioned on the protocerebrum and then changed to the labrum. However, Scholtz and Edgecombe (2006) proposed that the feeding great appendage should be innervated from the deutocerebrum, and the frontal antenna as a “primary antenna” associated with the protocerebral region was lost or modified.

García-Bellido et al. (2009b) and Vannier et al. (2009) proposed that *Isoxys* and two other “bivalved” arthropods, *Occacaris* and *Forfexicaris*, may belong to the same clade as they share a similar huge carapace within the “great appendage” group. Superficial resemblances in “bivalved” carapaces are, however, probably due to convergent evolution, which may also be true for the characteristic feature of *Isoxys* (prominent spines). Additionally, the “great appendage” is evidently a modified 1st antenna in the former but a 2nd appendage in the latter (Bergström and Hou 2005). Further evidence from the shield of *Fuxianhuia* Hou, 1987 (Hou 1987a, see also *Cindarella eucalla* Chen, Ramsköld, Edgecombe, and Zhou, 1996 (Chen et al. 1996; Ramsköld et al. 1997) is worth mentioning. The medium-sized shield of *Fuxianhuia* is also free from the anterior thoracic segments. Budd (2002) recognized a median crease in its cephalic shield, which folded along a straight line during lateral compression (Budd 2002), although it is usually not known to be bivalved. The cephalic shield of *Fuxianhuia* (possibly representing an intermediate between the two styles: a cephalic shield and a large “bivalved” carapace) helps us to understand that the large carapace of *I. curvirostratus* was modified no more than through posterior extension and ventrolateral folding of the cephalic shield. Thus, it is difficult to determine the taxonomy on the basis of the convergent “bivalved” carapace.

Many arthropods share a functionally raptorial “great appendage”, but the assumption of homology is disputable. We are convinced that *I. curvirostratus* has only one pair of frontal great appendages immediately following the ocular segment, and thus is presumably innervated from the deutocerebrum. On the contrary, *Occacaris* and *Forfexicaris* share two pre-oral appendages, and thus their great appendages

(corresponding to the second antenna) might have originated from the tritocerebral segment. The great appendages of anomalocaridids were considered to be deutocerebral in origin because the second appendage might be modified into a labrum (Zhang 2009). Therefore, the great appendage itself is a functional adaptation rather than a synapomorphic character defining a monophyletic group.

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