Soft-Part Preservation in two Species of the Arthropod Isoxys from the Middle Cambrian Burgess Shale of British Columbia, Canada

Authors: García-Bellido, Diego C., Vannier, Jean, and Collins, Desmond

Source: Acta Palaeontologica Polonica, 54(4) : 699-712

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2009.0024

Soft-part preservation in two species of the arthropod *Isoxys* from the middle Cambrian Burgess Shale of British Columbia, Canada

DIEGO C. GARCÍA-BELLIDO, JEAN VANNIER, and DESMOND COLLINS

García-Bellido, D.C., Vannier, J., and Collins, D. 2009. Soft-part preservation in two species of the arthropod *Isoxys* from the middle Cambrian Burgess Shale of British Columbia, Canada. *Acta Palaeontologica Polonica* 54 (4): 699–712. doi:10.4202/app.2009.0024

More than forty specimens from the middle Cambrian Burgess Shale reveal the detailed anatomy of *Isoxys*, a worldwide distributed bivalved arthropod represented here by two species, namely *Isoxys acutangulus* and *Isoxys longissimus*. *I. acutangulus* had a non-mineralized headshield with lateral pleural folds (= "valves" of previous authors) that covered the animal's body almost entirely, large frontal spherical eyes and a pair of uniramous prehensile appendages bearing stout spiny outgrowths along their anterior margins. The 13 following appendages had a uniform biramous design—i.e., a short endopod and a paddle-like exopod fringed with marginal setae with a probable natatory function. The trunk ended with a flap-like telson that protruded beyond the posterior margin of the headshield. The gut of *I. acutangulus* was tube-like, running from mouth to telson, and was flanked with numerous 3D-preserved bulbous, paired features interpreted as digestive glands. The appendage design of *I. acutangulus* indicates that the animal was a swimmer and a visual predator living off-bottom. The general anatomy of *Isoxys longissimus* was similar to that of *I. acutangulus* although less information is available on the exact shape of its appendages and visual organs. *I. longissimus* is characterized by extremely long anterior and posterior spines. There are now seven *Isoxys* species known with soft-part preservation, *I. acutangulus, I. longissimus* from the Burgess Shale, *I. auritus* and *I. curvirostratus* from the Maotianshan Shale of China, *I. communis* and *I. glaessneri* from the Emu Bay Shale of Australia and *I. volucris* from Sirius Passet in Greenland. The frontal appendages of *Isoxys* strongly resemble those of other Cambrian arthropods, characterized by a single pair of "great appendages" with a shared prehensile function yet some variability in length and shape.

Key words: Arthropoda, *Isoxys*, "great appendage", Burgess Shale, Lagerstätten, Cambrian.

Diego C. García-Bellido [Diego.GBC@geo.ucm.es], Departamento de Paleontología, Instituto de Geología Económica (CSIC-UCM), Facultad de Ciencias Geológicas, José Antonio Novais 2, 28040-Madrid, Spain;
Jean Vannier [jean.vannier@univ-lyon1.fr], Université de Lyon, Université Lyon 1, UMR 5125 PEPS «Paléoenvironnements et Paléobiosphère», Campus de la Doua, Bâtiment Géode, F-69622 Villeurbanne Cedex, France;
Desmond Collins [suzanne.collins029@sympatico.ca], 501-437 Roncesvalles Ave., Toronto, Ontario M6R 3B9, Canada.

Received 4 March 2009, accepted 26 August 2009, available online 3 September 2009.

Introduction

Isoxys is a worldwide distributed bivalved fossil arthropod (Williams et al. 1996) and a relatively frequent component of the middle Cambrian Burgess Shale fauna (Conway Morris 1986, Caron 2005). Since the pioneer studies of Walcott (1890), *Isoxys* has been known exclusively from its exoskeletal parts—i.e., a featureless bivalved "carapace" with cardinal spines—thus contrasting with the majority of arthropods from this famous Lagerstätte that often display a wealth of anatomical details. Although precious, the fragmentary information obtained recently from a few Chinese specimens (lower Cambrian Maotianshan Shale; Vannier and Chen 2000) has been unable to provide an accurate picture of the animal. The study of more than 40 specimens of *Isoxys* with soft part preservation, all from the ROM collections, has led to the present revision of the species *Isoxys acutangulus* (Walcott, 1908) and *I. longissimus* Simonetta and Delle Cave, 1975. This mainly descriptive account reveals key aspects of the morphology of *Isoxys* and has opened the way to new interpretations of the lifestyle and phylogenetic affinities of this enigmatic arthropod of the Cambrian seas (Vannier et al. 2009).

Institutional abbreviations.—ROM, Royal Ontario Museum, Toronto, Canada; USNM, United States National Museum, Smithsonian Institution, Washington D.C., USA.

Other abbreviations.—a1, first crustacean antenna, at, attachment area; an, anus; ar, anterior rostrum; as, anterior spine; db, dorsal part of body; dm, dorsal margin of headshield; e, eye; en, endopod; es, eye stalk; ex, exopod; fa, frontal appendage; fm, fecal material; fo, median headshield fold; gt, gut; Hmax, greatest height of headshield; hs, headshield; l, left; L1, length

doi:10.4202/app.2009.0024

of headshield excluding cardinal spines; L2, length of headshield including cardinal spines; mg, midgut glands; ms, marginal setae; os, ocular segment; pb, posterior part of body; pe, peduncle; pf, pleural fold of headshield; pr, posterior rostrum; ps, posterior spine; r, right; ro, rostrum; ta1–13, trunk appendage, 1^{st} to 13^{th} pair; te, telson; tf, telson flap; tr, trunk; vm, ventral margin of headshield.

Previous work on *Isoxys* from North America

The genus was introduced by Walcott (1890) from carapaces recovered from the lower Cambrian Chilhowee Group of Tennessee, USA. The type species *Isoxys chilhoweanus* Walcott, 1890 has a very simple morphology with short, almost equal, cardinal spines (Williams et al. 1996: fig. 7-2). The first record of *Isoxys* in the Burgess Shale is also due to Walcott (1908), who created a second species, *Isoxys acutangulus* (Walcott, 1908), based on specimens from the "Great Fossil Bed-*Ogygopsis* Shale" of Mount Stephen (also known as the "Trilobite Beds"). It is now certain that the latter species does not belong to *Anomalocaris*, as was tentatively proposed by Walcott at the time (Briggs et al. 1994). *Isoxys acutangulus* appears in Walcott's (1908: 13) faunal inventory as a "new, very rare species" but lacks any description and holotype designation. The single figured specimen shows strong resemblances, mainly the lateral outline, with *Isoxys chilhoweanus* from Tennessee. A second species from the Burgess Shale, *Isoxys longissimus* was described by Simonetta and Delle Cave (1975). It differs markedly from both *Isoxys chilhoweanus* and *Isoxys acutangulus* by its extremely long spines projecting from the anterior and posterior cardinal corners of the carapace. More recently, Briggs et al. (2008) described *Isoxys* sp. from the middle Cambrian of Utah (Langston Formation, Spence Shale Member). One specimen shows eyes and homonomous appendages concealed under the carapace, but its state of preservation does not allow a more detailed description. Other possible occurrences of *Isoxys* in North America and other regions are summarized in Williams et al. (1996) and Vannier and Chen (2000).

The Burgess Shale specimens

Fossil localities.—The type locality of *Isoxys acutangulus* is the Trilobite Beds on Mount Stephen (Fig. 1A, B, loc. 6; Walcott 1908). The *Isoxys* specimens studied here are those from the ROM collections and were collected at various localities and horizons within the Burgess Shale Formation: the Walcott Quarry, the Raymond Quarry, the "*persephone* layer" (RQ +20 to +23), the "*Tuzoia* layer" (TZ) and two layers of the Collins Quarry (UE and EZ), all on the west slope of Fossil Ridge (Fig. 1A, loc. 1a to 1e), the south face of Mt. Field (Fig. 1A, loc. 2), the ESA and ESB sites on the north shoulder of Mt. Stephen (Fig. 1A, loc. 3), south along the west slope of Mount Stephen to just south of the Fossil Gully fault at the S7 locality (Fig. 1A, loc. 4), and further south still to the Mt. Stephen "Collins Quarry" (WS; Fig. 1A, loc. 5) and the Mt. Stephen Trilobite Beds (ST; Fig.1A , loc. 6). Two specimens come from the west side of Stanley Glacier, about 50 km southeast of Fossil Ridge (Fig. 1A, loc. 7). *Isoxys longissimus* was found at three localities, all of which are on the west slope of Fossil Ridge: the Raymond Quarry, the "*Tuzoia* layer" and the Collins Quarry (Fig. 1A, locs. 1b, 1c, and 1e). In total, there are 295 catalogued *Isoxys* specimens available for study in the ROM collections, 14% of them (41 specimens) having soft parts preserved (typically eyes, frontal appendages, trunk appendages with flap-like exopods, midgut glands, and more rarely trunk end). *Isoxys* occurs throughout the Burgess Shale Formation, with *I. acutangulus* having the widest range (Fig. 1B). This species is present at 9 levels, within the Kicking Horse Shale Member (WS locality), the Campsite Cliff Shale Member (S7 and ST localities), the Walcott Quarry Shale Member (Greater Phyllopod Bed), the Raymond Quarry Shale Member (Raymond Quarry, "*persephone* layer", TZ levels and ESB locality), the Emerald Lake Oncolite Member (EZ and UE) and the Waputik Member (Stanley Glacier locality) of the Stephen Formation, equivalent to the Burgess Shale Formation's Marpole Limestone Member (Fletcher and Collins 1998). *Isoxys longissimus* is known only from the middle part of the Burgess Shale Formation: the Walcott Quarry Shale Member, the Raymond Quarry Shale Member and the Emerald Lake Oncolite Member. The detailed abundance of *Isoxys acutangulus* and *Isoxys longisssimus* throughout the Burgess Shale Formation is given in Table 1 (Jean-Bernard Caron, personal communication 2008). About 62% of the *Isoxys* specimens are from the Walcott Quarry Shale Member.

Preservation.—The majority of specimens with soft part preservation are laterally compacted (Figs. 2–4) with eyes and distal parts of appendages protruding beyond the margins of the headshield. Torn-off or folded parts of the flaps often reveal internal organs (e.g., digestive system) and segmented body features (e.g., Fig. 4). Dorso-ventrally compacted specimens are much rarer and show details of the tail fan (Fig. 5). It is important to note that most of our specimens with soft body preservation show no important disarticulation. This indicates that the time interval between the death of the animal and its burial was probably short and that carcasses were rapidly subtracted from the action of currents, scavenging and strong decay. Experiments with Recent shrimps have shown that, as soon as decay commences, the slightest disturbance caused major disarticulation (Allison 1986; Briggs and Kear 1994). Although limited, traces of decay-induced physical fragmentation in *Isoxys* do occur and concern mainly the degree of attachment of the body with the headshield (Fig. 3B) and the trunk appendages (e.g., exopods missing). The most advanced stage of decay was observed in one specimen (Fig. 3D) where the body forms an indistinct mass of appendages and organs, almost totally detached from the headshield. The most de-

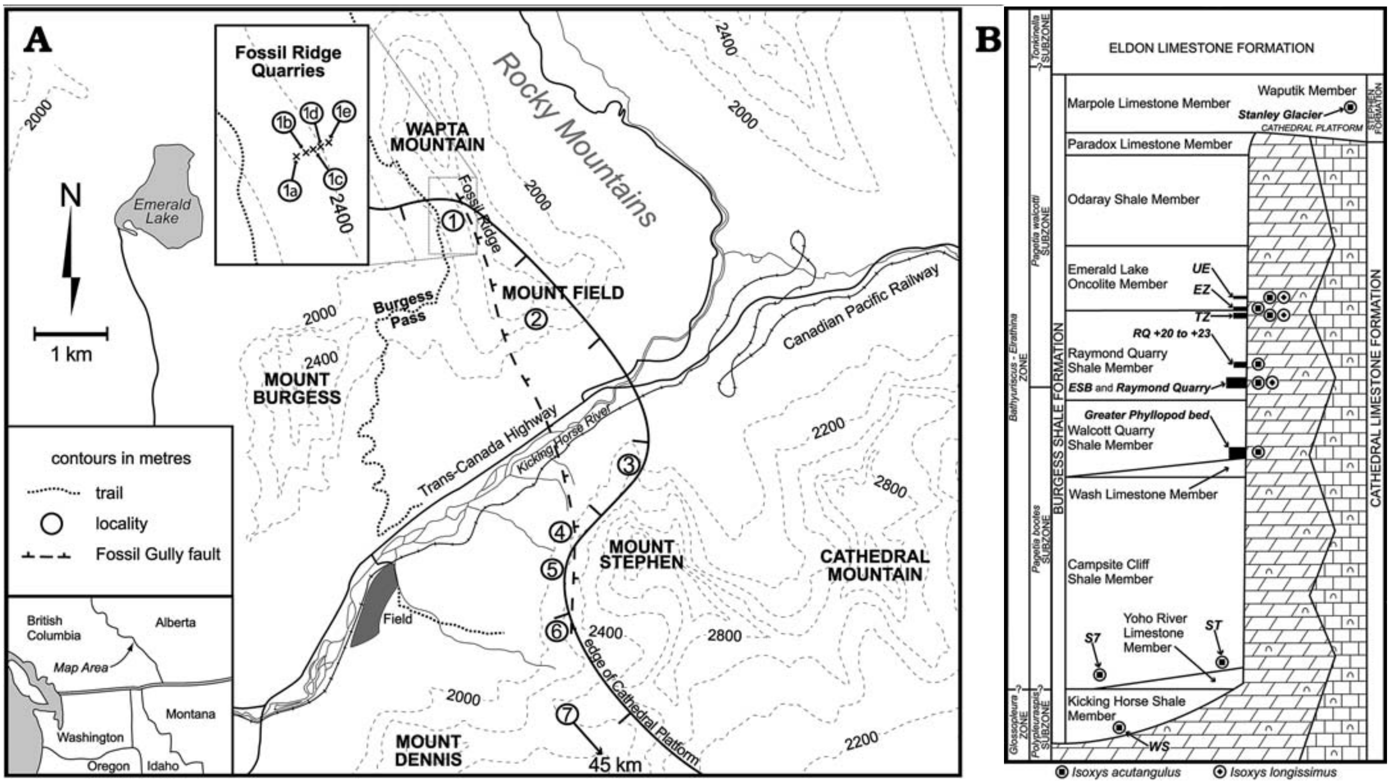


Fig. 1. **A**. Topographic map of the Burgess Shale area near Field, British Columbia (Canada). The numbers indicate localities where specimens of *Isoxys acutangulus* (Walcott, 1908) and *Isoxys longissimus* Simonetta and Delle Cave, 1975 were collected by ROM parties. 1. West slope of Fossil Ridge: 1a, Greater Phyllopod bed, Walcott Quarry; 1b, Raymond Quarry; 1c, "*persephone* layer" (RQ +20 to +23); 1d, "*Tuzoia* layer" (TZ); 1e, Collins Quarry—"*Ehmaniella* Zone" (EZ) and "Upper *Ehmaniella*" (UE); 2, South face of Mt. Field; 3, North shoulder of Mt. Stephen (ESA, ESB); 4, S7 locality; 5, Mt. Stephen Collins Quarry (WS); 6, Mt. Stephen Trilobite Beds (ST); 7, Stanley Glacier. **B**. Stratigraphic section of the Burgess Shale and Stephen Formations (modified from Fletcher and Collins, 1998). Circles indicate the levels where specimens of *Isoxys acutangulus* (Walcott, 1908) and *Isoxys longissimus* Simonetta and Delle Cave, 1975 from the seven localities in A were collected.

cay-resistant non-exoskeletal parts seem to have been the eyes, which always keep their spherical shape, and the frontal appendage, that may have been more strongly sclerotized than the other appendages. Contrasting with the majority of soft-bodied features that have no relief, the midgut glands are three-dimensionally preserved. The preservation of such fragile organs is not specific to *Isoxys* and has been observed in other arthropods from the Burgess Shale (Butterfield 2002; Vannier and Chen 2002) and other Cambrian Lagerstätten (e.g., Kaili: Zhu et al. 2004). It is due to the early phosphatization (apatite) of soft tissues immediately after the animal's death and burial. This may be the most reliable indicator of the absence of slow post-mortem sinking or drifting of carcasses in the water column.

Material and methods

Digital photographs were taken under different light conditions (low and high angles, non-polarized and polarized light, with specimens immersed in water or dry). We used the crossed polarizing method of photographing Burgess Shale fossils described in Boyle (1992) and Bengtson (2000). Composite line drawings were made of the part and counterpart (when available) of selected specimens and combined with information obtained via the aforementioned photographic techniques.

Systematic palaeontology

Phylum Arthropoda Siebold and Stannius, 1845

Class, order, and family uncertain

Genus *Isoxys* Walcott, 1890

Type species: *Isoxys chilhoweanus* Walcott, 1890, by original designation; from the lower Cambrian (*Bonnia–Olenellus* Zone) Chilhowee Group, Tennessee, USA.

Species included: *Isoxys acutangulus* (Walcott, 1908); *Isoxys carbonelli* Richter and Richter, 1927; *Isoxys longissimus* Simonetta and Delle Cave, 1975; *Isoxys communis* Glaessner, 1979; *Isoxys auritus* Jiang, 1982 (in Luo et al. 1982); *Isoxys paradoxus* Hou, 1987; *Isoxys bispinatus* Cui, 1991 (in Huo et al. 1991); *Isoxys zhurensis* Ivantsov, 1990; *Isoxys volucris* Williams, Siveter, and Peel, 1996; *Isoxys curvirostratus* Vannier and Chen, 2000; *Isoxys wudingensis* Luo and Hu, 2006 (in Luo et al. 2006); *Isoxys glaessneri* García-Bellido, Paterson, Edgecombe, Jago, Gehling, and Lee, 2009.

Emended diagnosis.—Headshield thin, nonmineralized, flexible, folded dorsally into two equal hemispherical flaps that

doi:10.4202/app.2009.0024

covered most of the body features. No true articulated hinge, pleural folds being possibly conjoined dorsally by a narrow band of cuticle. Each pleural fold with two prominent spines of variable length extending antero- and posterodorsally. Dorsal outline straight or slightly convex to form a weak to well-developed cusp anterior of headshield mid-length. Weak lateral sculpture; a small circular node and/or a chevron-like shallow furrow may be present anteriorly. Entire lateroadmarginal ridge swollen to extremely narrow. When present, external ornament is uniform micro-reticulation or longitudinal striae. Narrow to broad doublure may be present. Long segmented body attached to headshield by its most anterior part. Bulbous ocular segment bearing a pair of large spherical eyes that protrude slightly antero-ventrally. One pair of frontal appendages, long, curved, extend beyond the flap margins; possibly flexible with prehensile function; divided into a possible proximal peduncle followed by a short-segmented claw-like unit with spiny outgrowths along its anterior margin. Homonomous series of 13 pairs of biramous appendages, each with short endopods and large flap-like exopods fringed with setae. Trunk end has a tail fan formed by the flattened telson with a pair of lateral flaps and the posteriormost pairs of exopods. Tube-like midgut flanked with numerous pairs of glands. (Modified from Williams et al. 1996: 950; Vannier and Chen 2000: 311).

Discussion.—*Isoxys* is an arthropod known from the early and middle Cambrian of North America, South China, Siberia, South Australia and North Gondwana (Spain: Richter and Richter 1927; France: Vannier et al. 2005). Its wide distribution is, however, restricted to tropical and subtropical regions, indicating possible temperature control on its distribution (Williams et al. 1996). *Isoxys* is unique among the so-called bivalved arthropods by its stout, in some cases extremely long, cardinal spines and the lack of strong lateral relief. The majority of bivalved arthropods known from the Cambrian of various regions have either featureless rounded shields (e.g., waptiids; Taylor 2002) or shields with a strong lobation (e.g., most bradoriids; Hou et al. 2002). *Isoxys* differs from them in having prominent cardinal spines and no long telescopic trunk extending behind the shield thus contrasting with, for example, *Waptia* Walcott, 1912, *Clypecaris* Hou, 1999, *Canadaspis* Novozhilov, 1960, *Occacaris* Hou, Bergström, Wang, Feng, and Chen, 1999, and *Forfexicaris* Hou, Bergström, Wang, Feng, and Chen, 1999 (Briggs et al. 1994; Hou et al. 2004).

Isoxys is regarded here as having a short head bearing eyes and a single pair of frontal appendages. However, uncertainties remain concerning the number of head segments of this arthropod. Numerous specimens of *Isoxys acutangulus* (Fig. 2A–C) clearly show a gap between the segment that bore the frontal appendage and the presumed first trunk segment that bore a biramous appendage and the first pair of midgut glands. Our material does not allow us to determine whether there were other additional head segments that may have filled this gap and if these carried any kind of (reduced?) appendages. The "bivalved carapace" of *Isoxys* is likely to be a headshield—i.e., a cuticular fold originating from the head section and extending laterally and posteriorly into large flap-like extensions (pleural folds).

The pair of frontal appendages of *Isoxys* shows strong similarities with the so-called "great appendage" of other Cambrian arthropods such as *Leanchoilia* Walcott, 1912, *Alalcomenaeus* Simonetta, 1970, *Yohoia* Walcott, 1912, *Jianfengia* Hou, 1987, *Haikoucaris* Chen, Waloszek, and Maas, 2004, and *Fortiforceps* Hou and Bergström, 1997 (see Vannier et al. 2009). These resemblances concern the structure of the appendage itself, especially the small number of podomeres bearing outgrowths, its frontal location and prehensile shape. The presence of a smooth peduncle similar to that of other great appendage arthropods cannot be ascertained: whereas some specimens have a great appendage with its proximal part lacking endite-like projections or spines (e.g., Fig. 2B), others do show outgrowths along the entire length of their appendage (e.g., Fig. 3A, B). Contrasting with *Isoxys*, "great appendage" arthropods have a tiny cap-like headshield with no lateral/posterior extensions covering the animal's body. A headshield comparable with that of *Isoxys* is found in only two forms from the Chengjiang biota, namely *Occacaris* and *Forfexicaris* (see Hou et al. 2004). Both have stout "great appendages" pointing forwards and upwards, which may suggest possible relations of *Isoxys* with these two bivalved arthropods. "Great appendage" (or megacheiran) arthropods encompass a wide range of Cambrian forms from smaller epibenthic predators that do not exceed 10 cm in length to, according to some authors, much larger anomalocaridids (Chen et al. 2004). Among the latter, the one that shows the closest resemblances to megacheirans based on its appendages is *Parapeytoia*. However, other anomalocaridids (e.g., Maas et al. 2004) have multisegmented frontal appendages curved posteriorwards and no true peduncle, which does not support a placement with the megacheirans.

The definition and status of megacheirans as a whole remains uncertain, even their monophyly. They have been assigned by some authors (e.g., Wills et al. 1998; Cotton and Braddy 2004) to the Arachnomorpha (= chelicerate-allied and trilobite-allied clades). Chen et al. (2004) tentatively placed them in the stem-lineage Chelicerata on the basis of presumed homologies between the "great appendage" and the chelicera of the crown-group Chelicerata (e.g., Recent spiders, scorpions, and horseshoe crabs). These hypotheses require more character support.

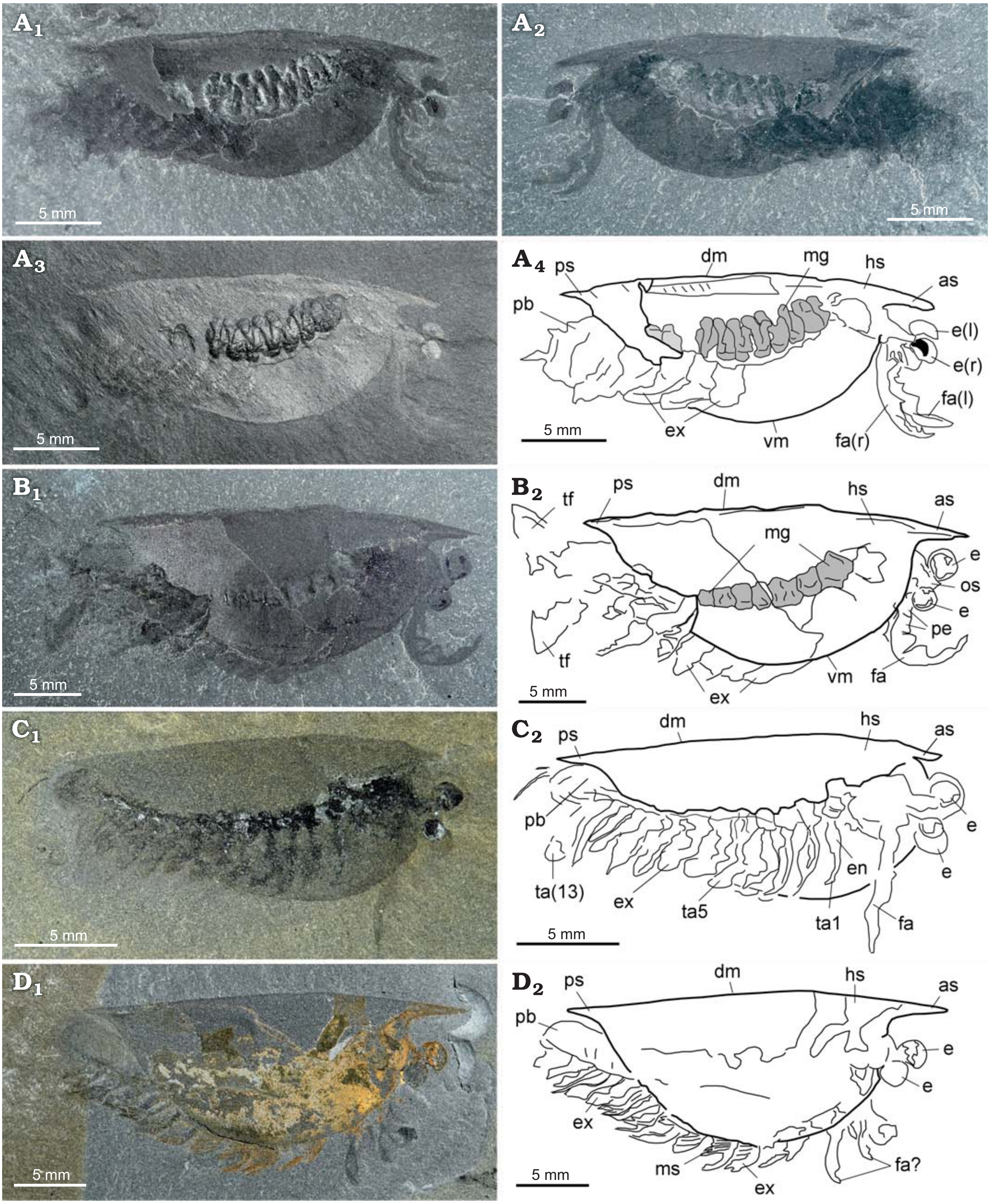
Stratigraphic and geographic range.—Lower middle Cambrian, cosmopolitan.

Isoxys acutangulus (Walcott, 1908)

Figs. 2–6.

1908 *Anomolocaris* (?) *acutangulus* sp. nov.; Walcott 1908: 13, pl. 2: 5.
1928 *Anomalocaris* ?? *acutangula* Walcott, 1908; Walcott 1928: 320.

Fig. 2. Bivalved arthropod *Isoxys acutangulus* (Walcott, 1908), Raymond Quarry Shale Member, Burgess Shale Formation, middle Cambrian, near Field, British Columbia, Canada (see Fig. 1), general morphology. **A**. ROM 57912A, B; A_1, part of specimen with eyes, frontal appendages and well →



developed midgut glands; A_2, counterpart; A_3, specimen with high reflection of carbonaceous surfaces; A_4, line drawing of specimen. **B**. ROM 57900; B_1, specimen with well preserved posterior end, including telson with flaps; B_2, line drawing of specimen. **C**. ROM 57903A; C_1, specimen showing both endopod and exopod of body appendages; C_2, line drawing of specimen. **D**. ROM 57913A; D_1, specimen with marginal setae on exopods; D_2, line drawing of specimen. All laterally compressed specimens and polarized light except A_3. Midgut glands in gray tone.

doi:10.4202/app.2009.0024

1975 *Isoxys acutangulus* (Walcott, 1908); Simonetta and Delle Cave 1975: 6, pl. 5: 6, pl. 54: 3, 4, 6–9 [*non* 1 (= *Burgessia bella*)].
1986 "shrimp"; Collins 1986: 37, fig. 4.
1991 *Isoxys acutangulus* (Walcott, 1908); Delle Cave and Simonetta 1991: fig. 20F.
1991 "shrimp"; Delle Cave and Simonetta 1991: fig. 23D.
1994 *Isoxys acutangulus* (Walcott, 1908); Briggs et al. 1994: 149, pl. 102.
2001 *Isoxys acutangulus* (Walcott, 1908); Donovan and Lewis 2001: fig. 1F.

Type material: The type-material consists of two specimens from the Mt. Stephen Trilobite Beds (Fig. 1A, loc. 6,), which occur within the Campsite Cliff Shale Member (ST, Fig. 1B), Burgess Shale Formation (Fletcher and Collins 1998). These are USNM 56521 (part and counterpart) and USNM 56521B. No holotype was designated in the original description by Walcott (1908: 13).

Material.—295 catalogued specimens in the ROM collections, 41 of them with preserved soft parts (Table 1). 62 and 29% of specimens were collected from the Walcott Quarry Shale Member and the Raymond Quarry Shale Member, respectively. 83% of the specimens with soft parts are from Raymond Quarry.

Emended diagnosis.—Pleural folds of headshield with an hemielliptical lateral outline tapering posteriorly and short cardinal spines; anterior one ca. 0.2L1 (L1= shield length excluding spines), slightly droopy; posterior one very short; angle between anterior spine axis and anterior margin between 90° and 110°, between posterior spine axis and posterior margin ca. 40°; L1:H ca. 2. Cardinal spines of each pleural fold joined to form a strong anterior and posterior rostrum. No sculpture or lobation on lateral flaps. Dorsal margin slightly convex. Very narrow latero-admarginal ridge. Large spherical eyes (diameter up to ca. 0.1L1) protruding on both sides of anterior rostrum and directed slightly anteroventrally. Ocular segment bulbous, eye stem very short. First pair of appendages adjacent to ocular segment, uniramous, long, curved with a serrated inner margin; consists of a proximal, possibly 2-segmented peduncle followed by a 4-segmented claw-like unit (3 podomeres bearing a conical tooth-like outgrowth + a terminal subchelate element). Following 13 appendages biramous with a simple endopod and a large elliptical exopod bearing numerous marginal setae. Size of exopods decreasing towards the telson. Telson bearing lateral flaps. Tubular midgut flanked with at least 8 pairs of bulbous digestive glands.

Table 1. Number of *Isoxys* specimens of both species collected by ROM crews according to stratigraphic levels within the Burgess Shale Formation. Abbreviation: SSP, specimens with soft-part preservation.

Burgess Shale Formation Members	*Isoxys acutangulus*		*Isoxys longissimus*	
	total	SSP	total	SSP
Waputik Member	2	0	0	0
Emerald Lake Oncolite Member	4	2	2	1
Raymond Quarry Shale Member	87	35	2	0
Walcott Quarry Shale Member	185	1	1	0
Campsite Cliff Shale Member	15	0	0	0
Kicking Horse Shale Member	1	1	0	0
Talus specimens or specimens from localities with poor stratigraphic constraints	1	2	0	0
Total	295	41	5	1

Description.—The total length of the headshield (L2) of the laterally preserved specimens varies from ca. 10 to almost 40 mm (H between 4 to 16 mm), L1:H being almost constant at about 2. The outline of juveniles and presumed adults is virtually identical with the anterior and posterior cardinal spines equalling ca. 0.2L1 and 0.15L1, respectively. In most laterally preserved specimens, Hmax lies at 0.5L1 (amplete outline) or slightly anterior to it (preplete outline). Dorso-ventrally compacted specimens show a symmetrical headshield with no splitting area (i.e., groove) between the right and the left flaps. The cardinal spines of the two pleural folds are fused into a single pointed rostrum at both ends of the shield (Fig. 5A). This indicates the absence of a true dorsal hinge as, for example, in ostracods. The headshield of *Isoxys acutangulus* was obviously thin, flexible and folded dorsally, resulting in two lateral pleural folds. These folds may have been joined by a relatively resistant ligament of the same composition as the headshield itself which would explain the lack of external suture. By contrast, headshields with the two folds splayed open on the sediment surface ("butterfly" orientation; Vannier et al. 2007) are clearly split into two halves along their entire dorsal line including spines (e.g., Briggs et al. 1994: fig. 102). These dorso-ventrally compressed specimens lack soft parts and are most probably molted shields, the dorsal split being possibly an artifact produced during the molting process and emphasized later on after burial. The dorsal outline is slightly convex with a maximum elevation lying anteriorly at ca. 0.3–0.4L1 (e.g., Figs. 2C, 4B). The ventral outline is tapering regularly beyond the mid-length line towards the posterior cardinal angle. No micro-ornament is visible on the external surface of the headshield. The dorsal attachment of the headshield to the body was probably very narrow (Fig. 3A, B, D) and limited to the head part. Indeed, most of the body—i.e., beyond the segment bearing the frontal appendages—seems to have been free and not attached to the shield. This is shown at various stages of the decay process (Fig. 3B, D).

Eyes are by far the most frequently preserved organs in *Isoxys acutangulus*, being present in more than 90% of specimens with soft-part preservation. They consist of a pair of spherical bulbs attached to the front part of the head (ocular segment) through a very short stalk. The diameter of the eye bulb is approximately 0.07–0.1L1. Eyes protrude markedly beyond the shield margins both laterally (Figs. 2, 3) and on each side of the anterior rostrum (Fig. 5B, C). The eyes are directed frontwards and slightly downwards, their axis diverging slightly (e.g., Fig. 5B, C). Microscopic observations did not reveal any details such as ommatidia or retinal features. The external cuticular layer (cornea?) is likely to have been more decay-resistant, which probably contributed to preserving the spherical shape of the eye bulbs.

The frontal appendage of *Isoxys acutangulus* typically has a serrated outline. It is uniramous, curved and largely pro-

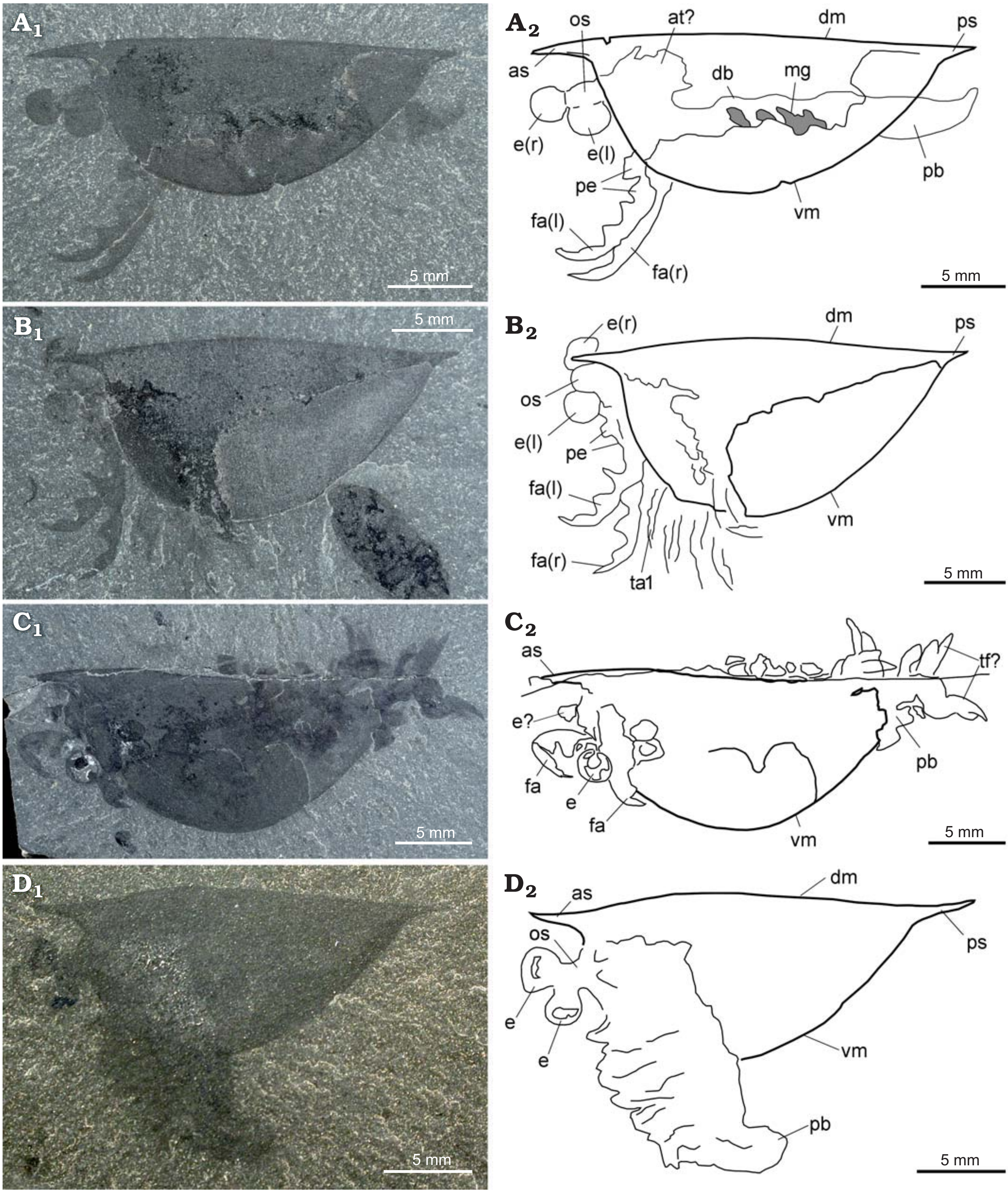


Fig. 3. Bivalved arthropod *Isoxys acutangulus* (Walcott, 1908), Raymond Quarry Shale Member, Burgess Shale Formation, middle Cambrian, near Field, British Columbia, Canada (see Fig. 1), general morphology. **A**. ROM 57898A; A_1, specimen showing large stalked eyes and the pair of raptorial frontal appendages; A_2, line drawing of specimen. **B**. ROM 57914A; B_1, partially decayed specimen with most of body and appendages rotated towards the front; B_2, line drawing of specimen. **C**. ROM 57899A; C_1, specimen with raptorial appendages oriented backwards and possible telson flaps; C_2, line drawing of specimen. **D**. ROM 59871A; D_1, considerably decayed specimen showing forward rotation of body and appendage remains; D_2, line drawing of specimen. All laterally compressed specimens and polarized light. Midgut glands in gray tone.

doi:10.4202/app.2009.0024

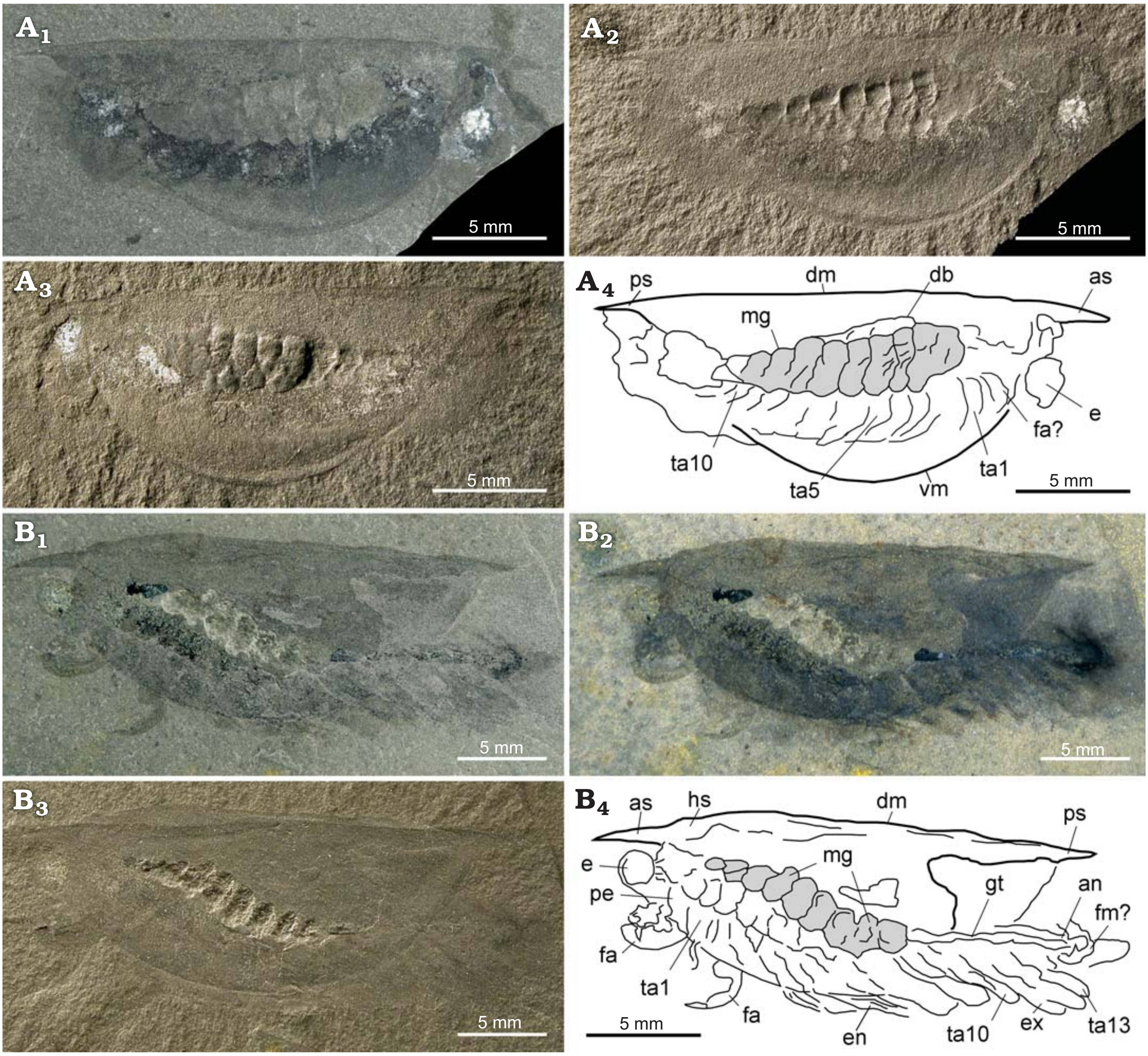


Fig. 4. Bivalved arthropod *Isoxys acutangulus* (Walcott, 1908), Raymond Quarry Shale Member, Burgess Shale Formation, middle Cambrian, near Field, British Columbia, Canada (see Fig. 1). **A**. ROM 57905A, B; A_1, part of specimen alternating midgut glands, possibly due to compaction, and narrow doublure; A_2, specimen under low angle light from top left; A_3, counterpart of specimen under low angle light from top left; A_4, line drawing of specimen. **B**. ROM 57906B; B_1, specimen with raptorial appendage, and 8 sets of midgut glands; B_2, image showing endopod and exopod details; B_3, specimen under low angle light from top left; B_4, line drawing of specimen. All laterally compressed specimens. A_1, B_1, B_2, polarized light; B_2, in water; A_2, A_3, and B_3 dry. Midgut glands in gray tone.

trudes beyond the anteroventral margin of the headshield. It is divided into a possible 2-segmented peduncle-like basal part (Figs. 2B, 3B) followed by a 4-segmented section (Figs. 2B, 3A). This section consists of 3 segments each bearing a stout tooth-like outgrowth and a small terminal subchelated segment. The various positions in which this appendage is preserved (Figs. 2A, B, 3A–C, 4B) indicate that it could flex inwards and fit under the headshield. However, boundaries and possible articulated joints between segments are hardly discernible. The body segment that bore the frontal appendage seems to be adjacent to the ocular segment (e.g., Figs. 2A–C, 3B). However, no boundaries between these segments are visible, suggesting that head segments may be fused. In one specimen (Fig. 3C) the appendage is preserved in an upturned position with the serrated margin directed posteriorly. This unusual orientation probably results from the post-mortem displacement of the decaying body, also apparent in the posterior part of the specimen (last trunk exopods and telson flaps).

The frontal pair of uniramous appendages is followed by a series of 13 pairs of evenly spaced, biramous appendages

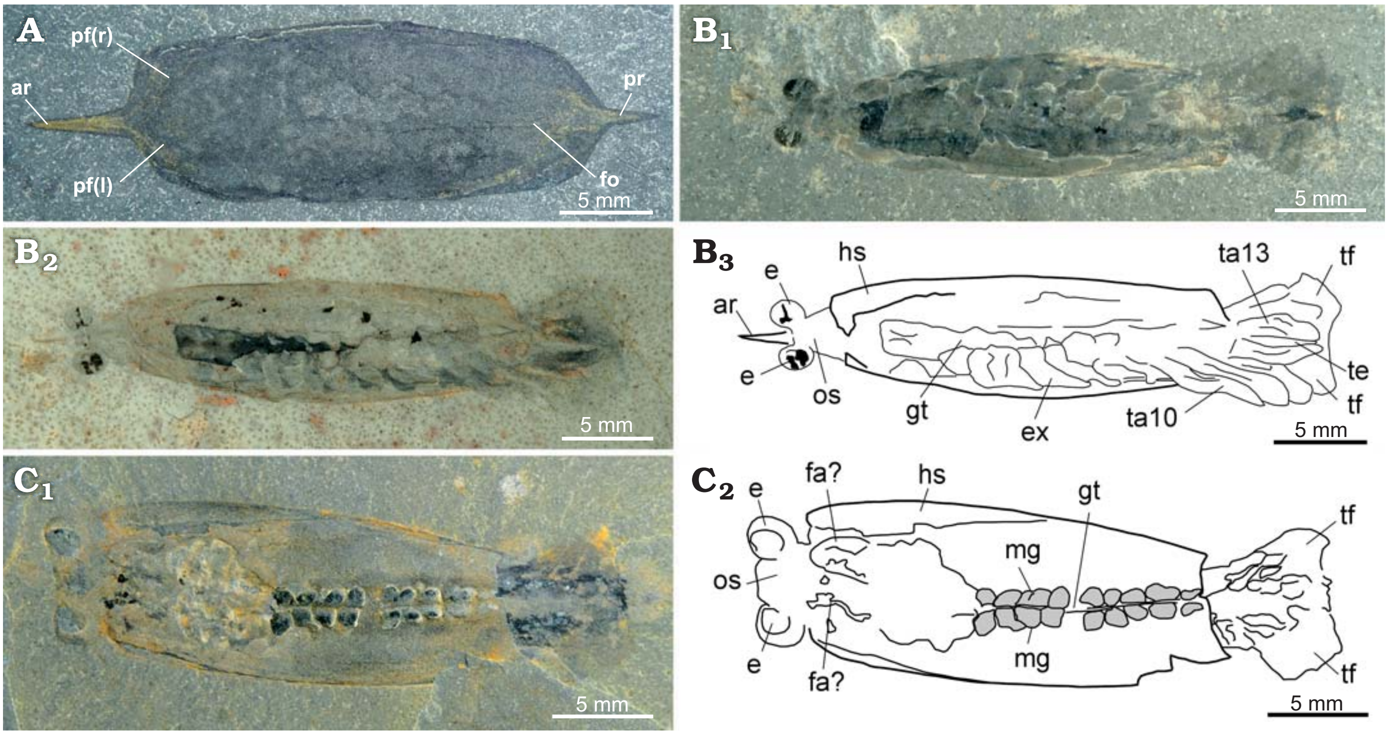


Fig. 5. Bivalved arthropod *Isoxys acutangulus* (Walcott, 1908), Burgess Shale Formation, middle Cambrian, near Field, British Columbia, Canada (see Fig. 1), general morphology. **A**. ROM 57902A, headshield in dorsal view without soft parts, note the different angle of the contact between the pleural folds and the cardinal spines, which allows for the position of the stalked eyes. **B**. ROM 57907A, B; B_1, part of unique specimen from WS locality, with eyes, telson and telson flaps; B_2, counterpart; B_3, line drawing of specimen. **C**. ROM 57904A; C_1, specimen showing paired midgut glands and telson flaps; C_2, line drawing of specimen. All dorsoventrally compressed specimens and photographed under polarized light; B_2, in water. Midgut glands in gray tone.

characterized by a uniform design (Fig. 6). The endopod is slender, slightly curved and displays no particular features or podomere boundaries. In laterally compressed specimens, it is generally concealed under the exopod (Fig. 2C). Exopods are large, paddle-like and fringed with numerous long setae along their external margins. The size of exopods gradually decreases towards the posterior end of the animal but their overall shape remains unchanged. The exopods are longer than endopods and protrude beyond the ventral margin of the headshield, especially in its posterior half (Fig. 2A, D). The last 4 pairs of appendages have a more oblique position and seem to be lacking long setae. Their paddle-like exopods form, together with the telson flaps, a symmetrical fan-like structure (Fig. 5B, C). In dorsoventrally preserved specimens, exopods are flexed back on each side of the body (Fig. $5B_2$, C_1) and overlap each other slightly. The detailed morphology of the basal part of the biramous appendages could not be observed.

The gut of *Isoxys acutangulus* is thin, cylindrical and runs from the head section to the ventral part of the telson where the anus opens (Fig. 4B). How the gut leads to the mouth opening via, e.g., the esophagus, remains unclear. In numerous specimens (Figs. $2A_3$–A_4, B, 4, 5C), the gut is underlined by lobate to subrectangular, typically 3-dimensional, features preserved in calcium phosphate (apatite). Each of the first 8 segments that bear biramous appendages is provided with one pair of such features that have been convincingly interpreted as serial digestive glands (Butterfield 2002, Vannier and Chen 2002). The glands reach their maximum size in the middle part of the gut. One specimen (Fig. 2A) displays a series of remarkably preserved glands. All are directed upwards and some of them clearly bifurcate into two lobes. So far, no internal features (e.g., tubules, caeca) could be observed, making the relation of the glands with the gut lumen unclear. One specimen (Fig. 4B) shows a diffuse dark area near the anus opening that may result from the squeezing out of fecal material.

Discussion.—*Isoxys acutangulus* differs from all congeneric species by the relatively short cardinal spines of its headshield (see Vannier and Chen 2000) and does not show any lineated or reticulated micro-ornament as seen, for example, in *Isoxys auritus* and *I. curvirostratus*. *Isoxys acutangulus* is so far the species that displays the best preserved soft-bodied features (e.g., visual and digestive organs, full series of appendages). The eyes of *Isoxys acutangulus* are almost identical to those of *I. curvirostratus* (Vannier and Chen 2000: fig. 4), *I. auritus* (e.g., Chen et al. 2002: pl. 11: 3; Hu 2005: pl. 5: 2), *Isoxys* sp. (Vannier et al. 2009: fig. 2k, l), all from the lower Cambrian Maotianshan Shale, as well as *I. communis* and *Isoxys glaessneri* from the lower Cambrian Emu Bay Shale (García-Bellido et al. 2009: pl. 1: 10, 11, pl. 3: 7, 10). The position of the large forward-facing eyes of *Isoxys acutangulus* suggests that panoramic vision or light reception was important for this arthropod. Spherical eyes with a comparable size and overall external morphology are frequent in

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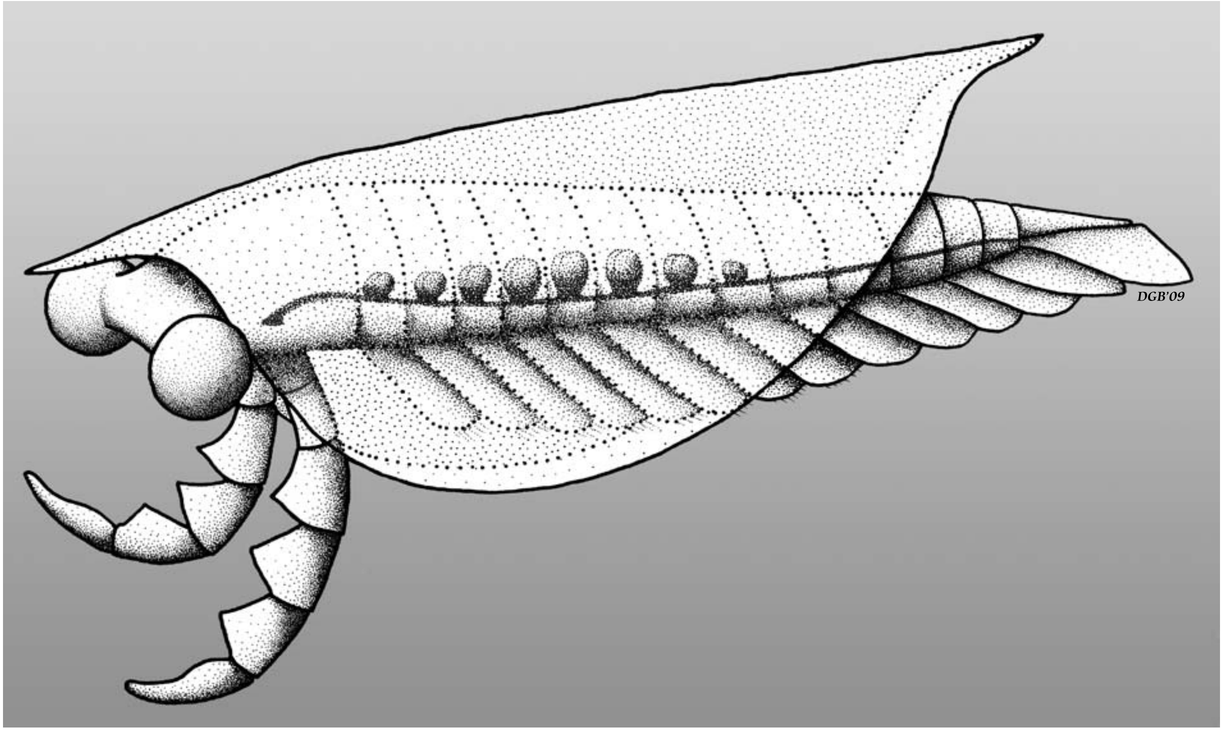

Fig. 6. Reconstruction of the bivalved arthropod *Isoxys acutangulus* (Walcott, 1908), swimming in the water column. Note that the position of the mouth and the attachments of the appendages to the body are conjectural. Not to scale.

Recent crustaceans (e.g., krill, Fig. 8; compare with Fig. 5B, C). However, the lack of information concerning the visual/optical properties of the eyes does not allow inferring how effectively they may have perceived images and how they could have estimated distances.

A single specimen of *Isoxys* from the lower Cambrian of China (Hu 2005; Hu et al. 2007; Vannier et al. 2009) has a prominent frontal appendage that resembles that of *I. acutangulus*. However, its outline is straight and its inner margin, instead of being coarsely serrated as in *I. acutangulus*, bears a series of tiny spines. This small-sized specimen is likely to belong to the juvenile stage of possibly *I. auritus* (Vannier et al. 2009). One specimen of *I. volucris* from the lower Cambrian of north Greenland has also been described as having a pair of uniramous frontal appendages, yet these bear a pair of long, thin spines per podomere, when preserved (Stein et al. 2008: figs. 1, 2).

The series of 13 biramous trunk appendages bearing large flap-like setose exopods seems to be a recurrent feature now recognized in both lower and middle Cambrian *Isoxys* species. However, some differences may occur in the pattern and density of these marginal setae. For example, *Isoxys* sp. from the lower Cambrian of China (Vannier et al. 2009) has well-defined, stiff, radiating primary setae along the margins of its exopods that may not have exact counterparts in *Isoxys acutangulus*. A comparable serial pattern of digestive glands is recognized in *I. acutangulus*, *I. curvirostratus*, and *Isoxys* sp. from the Maotianshan Shale of China, and also *I. communis* from the Emu Bay Shale of Australia (García-Bellido et al. 2009: pl. 2: 4–6).

Stratigraphic and geographic range.—Kicking Horse Shale Member to Emerald Lake Oncolite Member, Burgess Shale Formation and Waputik Member, Stephen Formation, Stage 5, Series 3, Cambrian (Fig. 1B); Fossil Ridge, Mount Stephen and Stanley Glacier, British Columbia, Canada (Fig. 1A).

Isoxys longissimus Simonetta and Delle Cave, 1975

Fig. 7.

1975 *Isoxys longissimus* sp. nov.; Simonetta and Delle Cave 1975: 6–7, pl. 5: 7, pl. 54: 3 A, B.

1991 *Isoxys longissimus* Simonetta and Delle Cave, 1975; Delle Cave and Simonetta 1991: fig. 20G.

Type material: Simonetta and Delle Cave (1975: 6) designated USNM 189170 as the holotype of *Isoxys longissimus*. This specimen (Fig. 7A) is represented by its part and counterpart and comes most probably from Walcott's "35k" locality, which corresponds to the Phyllopod Bed on Fossil Ridge (Fig. 1).

Material.—One laterally compressed specimen showing remains of soft-bodied features (ROM 57908; Fig. 7E), and four headshields (ROM 57909, 57910, 57911, 57919; Figs. 7B–D, F), also laterally compressed. ROM 57910, 57911 were recovered from the Raymond Quarry Shale Member (Fig. 1B), at layer +10.4 m and from the "*Tuzoia* layer", about 3 m below the top of this member, respectively. ROM 57908 and ROM 57909 are both from the same horizon within the Emerald Lake Oncolite Member, more precisely the bed known as the "Upper *Ehmaniella* layer" of the Collins Quarry (UE; Fig. 1B). The three localities where *Isoxys longissimus* was collected lie adjacent to the contact between the Burgess Shale Formation and the escarpment of the Ca-

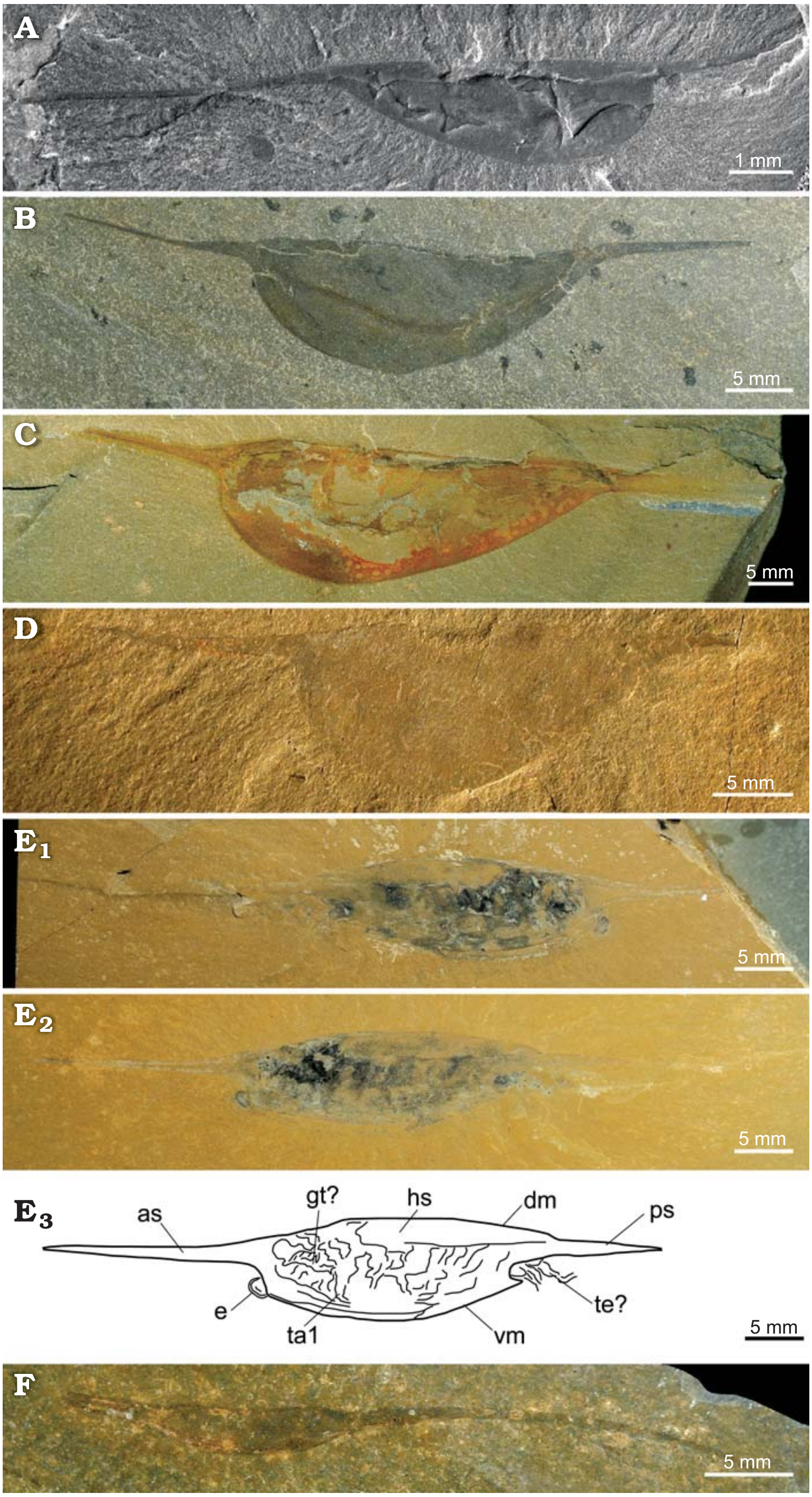

Fig. 7. Bivalved arthropod *Isoxys longissimus* Simonetta and Delle Cave 1975. Burgess Shale Formation, middle Cambrian, near Field, British Columbia, Canada (see Fig. 1), general morphology. **A**. USNM 18170, holotype. **B**. ROM 57910A. *C*. ROM 57911A. **D**. ROM 57909A. **E**. ROM 57908A, B; E_1, part of slightly oblique specimen with soft-body preservation, including large eye, telson and some possible exopods; E_2, counterpart; E_3, line drawing of specimen. **F**. ROM 57919A. All laterally compressed specimens. A, low angle light from top left; B–F, polarized light.

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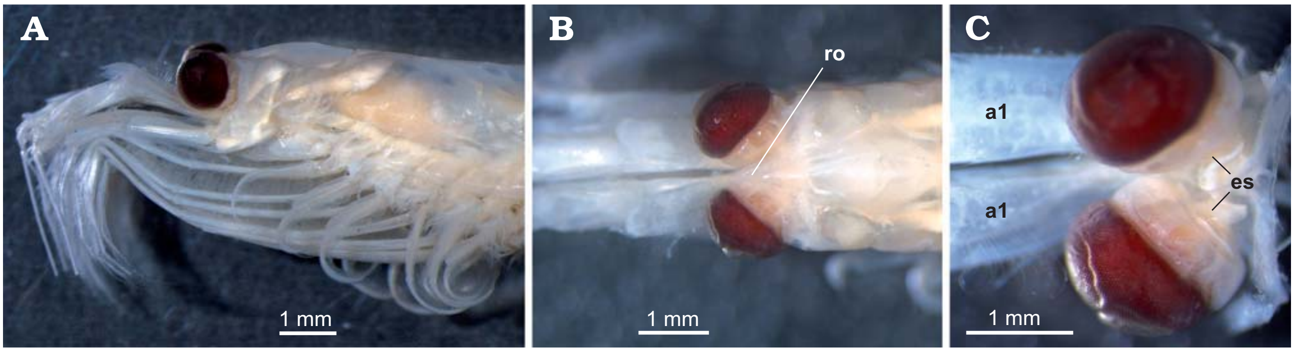

Fig. 8. Recent crustacean *Euphausia superba* Dana, 1852 (krill) from Gerlache Strait, Antarctica. **A**. Left lateral view. **B**. Dorsal view. **C**. Detail of stalked eyes after removing head shield. All light micrographs.

thedral Limestone Formation, on the west slope of Fossil Ridge, between Wapta Mountain and Mt. Field, in Yoho National Park (Fig. 1B; locs. 1b, 1c, 1e).

Emended diagnosis.—Headshield with elongated, hemielliptical lateral outline tapering posteriorly and extremely long cardinal spines; anterior one ca. 0.75L1 with thick basal part almost parallel to dorsal margin extending into a much thinner distal section directed slightly upwards; posterior one at least as long as L1, straight or slightly curved downwards. Angle between anterior spine axis and anterior margins between 75° and 90°; angle between posterior spine axis and posterior margin between 30° and 45°. L1:H ca. 3. Anterior part of dorsal margin slightly convex. Spherical eyes present, protruding beyond the anteroventral margin of the headshield. Homonomous series of more than 10 trunk appendages. Telson protruding beyond the posteroventral margin of headshield.

Description.—*Isoxys longissimus* has extremely long cardinal spines and an unusually high L1:H ratio approaching 3. L2 reaches 105 mm in the holotype (Simonetta and Delle Cave 1975: 6; Fig. 7A), and ranges from 40 to 60.5 mm in the ROM specimens. The posterior spine of the holotype is more than three times the length of the anterior spine, and exceeds L1. A close inspection of the specimens shows that the tips of the cardinal spines are often buried under the matrix (e.g., anterior spine of holotype), making their measurement difficult without careful preparation. Although always very high (ca. 3), the L1:H shows significant variations due to the effect of the orientation of the specimens to bedding and to the frequent wrinkling and folding of the headshields. Hmax lies at 0.5L (amplete outline, Fig. 7B) or slightly anterior to it (preplete outline, Fig. 7C, D). Each cardinal spine has a relatively strong basal part that extends into a long foil-like projection. The anterior spine is slightly curved upwards, the posterior one straight or tilted slightly downwards. The dorsal margin is convex with maximum convexity in the anterior half of headshield (Fig. 7B, C). The angle between the anterior spine axis and the anterior margin is between 75° and 90°, that between the posterior spine and the dorsoventral margin between 30° and 45°. No micro-ornament is visible on the external surface of the headshield. The soft anatomy of *Isoxys longissimus* is known from a single specimen (Fig. 7E). A rounded feature in front of the headshield and under the anterior spine is interpreted as an eye. The succeeding (possibly 10 to 15) segments bear a series of appendages but no details of their fine structure is revealed. The posteriormost appendages are shorter and stick out of the shield. The body ends into a small pointed telson-like feature. Ill-defined black areas may suggest the presence of digestive features such as midgut glands.

Discussion.—*Isoxys longissimus* is unique among *Isoxys* by its extremely long cardinal spines and elongated shape. Comparable exoskeletal features occur in *I. paradoxus* from the lower Cambrian Chengjiang biota, which has unusually long spines (Hou et al. 2004) although shorter and stouter than those of *I. longissimus*. *Isoxys curvirostratus* also from the lower Cambrian of China (Vannier and Chen 2000) has a slightly recurved anterior spine that recalls that of *Isoxys*

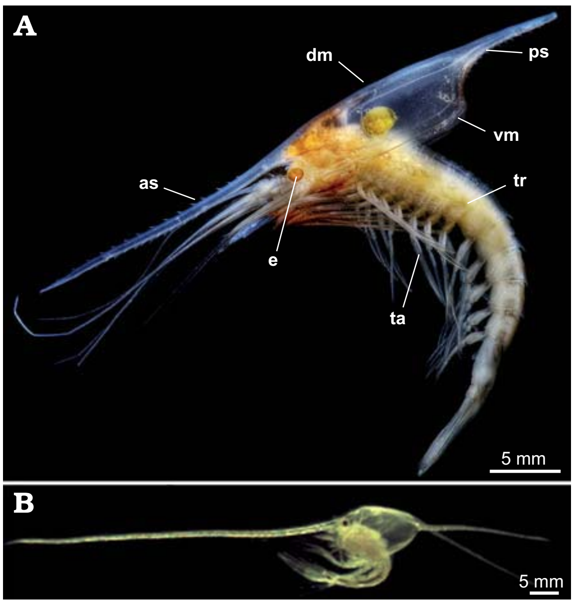

Fig. 9. Spiny shields in Recent crustaceans. **A**. Gnathophausia zoea Willemoes-Suhm 1873 (Malacostraca, Lophogastrida). **B**. Porcellanid larva (Decapoda). A from http://en.wikipedia.org/wiki/Crustacean; B from www.zooplankton-online.net/gallery.html (courtesy of W.S. Johnson, Goucher College); both used with permission of the copyright holders.

longissimus. Resemblances with *Isoxys volucris* from the lower Cambrian Buen Formation of Greenland (Williams et al. 1996) should be also noted. The dorsal outline of the headshield of *I. volucris* forms a small cusp-like projection behind the basal part of the anterior cardinal spine. This feature also occurs in some specimens of *Isoxys longissimus* (e.g., Fig. 7C). The two species are armed with the same type of slender, probably very fragile spines that occur in no other congeneric species.

Examples of long cardinal spines are known in Recent pelagic crustaceans such as *Gnathophausia* (Lophogastrida; Fig. 9A), the planktotrophic larvae of some malacostracans (Fig. 9B), and halocypridid ostracods (Vannier and Chen 2000). Their exoskeletons show a remarkable development of shield spines that are indeed very similar to the cardinal spines of *Isoxys longissimus* (compare Figs. 7 and 9). This example of exoskeletal convergence between Cambrian and Recent marine arthropods is probably the expression of comparable morphological adaptations to the pelagic lifestyle (Vannier and Chen 2000; Vannier et al. 2009).

Stratigraphic and geographic range.—Raymond Quarry Shale Member to Emerald Lake Oncolite Member, Burgess Shale Formation, Stage 5, Series 3, Cambrian (Fig. 1B); Fossil Ridge, British Columbia, Canada (Fig. 1A).

Conclusions

The specimens from the Burgess Shale bring new essential information that leads to a better understanding of the anatomy and lifestyle of *Isoxys*. The previous tentative reconstructions of the animal were based on a limited amount of evidence from incomplete specimens (Vannier and Chen 2000) and major uncertainties remained concerning the head appendages. The frontal appendages of *Isoxys* were known to occur in a single, probably juvenile specimen from the lower Cambrian of China (Hu 2005; Hu et al. 2007), which shows major differences from those of *Isoxys acutangulus* (Vannier et al. 2009). The presence of frontal, prehensile appendages and spherical eyes indicates that *Isoxys* was a visual predator of possibly small prey living in the water column or near the water-sediment interface. The paddle-like design of its multiple exopods, in addition to its tail fan, demonstrates the swimming and steering capabilities of *Isoxys*. *Isoxys acutangulus* from the Burgess Shale displays a series of midgut glands interpreted as digestive organs that are consistent with predation and intermittent feeding (Butterfield 2002; Vannier and Chen 2002). *Isoxys* appears to be one of the rare animals of the Burgess Shale fauna clearly adapted to living off-bottom, although its exact habitat and dynamics within the water column need to be clarified (Vannier et al. 2009). The frontal appendage of *Isoxys* shows some similarities to the "great appendage" of numerous Cambrian arthropods such as *Leanchoilia*, *Alalcomenaeus*, *Yohoia*, and *Jianfengia*. However, the possible relationship of *Isoxys* with this group of arthropods requires support from detailed phylogenetic analyses. Two "great appendage" arthropods from the lower Cambrian of China, namely *Occacaris* and *Forfexicaris*, have a headshield comparable with that of *Isoxys* —i.e., with large lateral folds covering most of the animal's body. The three of them are likely to have been non-benthic predators and may belong to the same clade within the "great appendage" arthropod group.

Acknowledgements

The authors thank Jean-Bernard Caron (ROM) and Parks Canada for access to the Burgess Shale collections of ROM. We are grateful to Doug Erwin (USNM-SI) for the information regarding the type specimens of both species treated here, and to Xing-Ling Zhang (USNM-SI) for the picture of the holotype of *Isoxys longissimus.* Thanks are due to Greg Edgecombe and Geoff Boxshall (both Natural History Museum, London, UK) for providing useful reviews that helped improve the manuscript. Funding was provided by the Spanish Ministry of Education and Science (to DCGB; Postdoctoral Grant EX2002-0632 and Project CGL 2006-12245BTE) and by the Agence Nationale de la Recherche (ANR; to JV, ORECO project BLAN06-3-136294). The 17 seasons of fieldwork that yielded the *Isoxys* specimens in this study could not have been completed without the support of Parks Canada in the Western Region in Calgary, and by the officers of Yoho National Park. D.C.'s financial support for the fieldwork came from Energy, Mines and Resources awards 175/4/81 and 179/4/82, NSERC grant A8427, Canadian Parks Service contracts in 1982 and from 1988 to 1997, and National Geographic grants 4310-90, 4532-92, 5242-94, 5952-97, 6283-98, 6499-99, and 6788-00. The 1996 field season was supported by the Helen McCrimmon Fund of the Royal Ontario Museum Foundation.

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