



***Hesslandona angustata* (Phosphatocopida, Crustacea) from the Upper Cambrian of western Hunan, South China, with comments on phosphatocopid phylogeny**

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With 9 figures

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Abstract: Although fossils of ‘Orsten’-type preservation from the Cambrian of China represented by Skaracarida and Phosphatocopida were first reported from localities in western Hunan in 2005 (DONG et al. 2005), the species of Phosphatocopida have not been appropriately described and elucidated in terms of evolution so far. Here, we re-describe the phosphatocopid *Hesslandona angustata*, originally described from Swedish ‘Orsten’ limestone, based on new specimens with preserved soft-body details. Two specimens have four pairs of limbs and thus represent head larvae. Based on the previously published material and the present one, comparative morphology investigation of limbs mainly within Phosphatocopida is accomplished. As a main result of the analysis a two-divided mandibular limb stem in younger stages, a plesiomorphic state retained from the stem species of Labrophora, should probably be present in many phosphatocopid taxa, and should be regarded as a synapomorphy of Phosphatocopida and Eucrustacea. The two parts of the limb stem, i. e. a coxa and a basipod, become fused with each other to form an undivided limb stem in later developmental stages of all known euphosphatocopids. Phosphatocopids in an ‘Orsten’ type of preservation have been studied for over 30 years. However the only computer-based phylogenetic analysis of this taxon (MAAS et al. 2003) is now six years old and, therefore, does not include new data brought up in China in the last four years. Accordingly, a new phylogenetic analysis is accomplished herein. Based on the analysis we re-establish the phylogeny of Phosphatocopida and discuss the evolution within this group of crustaceans.

Key words: *Hesslandona angustata*, Phosphatocopida, Crustacea, Orsten, ontogeny, phylogeny, Upper Cambrian, western Hunan, South China.

1. Introduction

Fossils of ‘Orsten’-type preservation were first discovered by MÜLLER (1979, 1982, 1985) who etched ‘Orsten’ calcitic nodules of Cambrian age from southern Sweden. ‘Orsten’ type of preservation is a form of fossil preservation, in which soft-part structures were phosphatized, either by impregnation or by penetration of calcium phosphate (MÜLLER 1979;

MAAS et al. 2006). Mainly cuticle-bearing animals, e.g. arthropods, of small dimensions, usually about 0.1–2 mm in size, are preserved. The imbedded animals are not flattened as, e.g. in the Burgess Shale or Chengjiang lagerstätten (BUTTERFIELD 2003; CHEN 2004), but preserved in three dimensions. Thus, these fossils appear much like living animals. Besides the three-dimensional preservation of soft parts the ‘Orsten’ type of lagerstätten are also known for the

presence of several larval stages belonging to a single species. Consequently, 'Orsten'-type fossils provide a window into the origin, evolution and phylogeny of Arthropoda (MÜLLER 1990; MÜLLER & WALOSZEK 1991; WALOSZEK & MÜLLER 1998; WALOSZEK & MÜLLER 1992, 1998; MAAS et al. 2003; WALOSZEK 2003; HAUG et al. 2009).

Because of the great importance of this type of fossils, many Chinese paleontologists have worked with great perseverance to search for 'Orsten' lagerstätten in Cambrian strata all over China for more than 20 years. At last, DONG et al. (2005) and LIU & DONG (2007) reported well-preserved fossil specimens of the 'Orsten' type of preservation represented by Phosphatocopida and a species of *Skara*, which have been recovered from Middle and Upper Cambrian rocks in Hunan. Subsequently, another example of fossils of the 'Orsten' type of preservation found in China was the report of the epipodite-bearing crown-group crustacean *Yicaris dianensis* from the Lower Cambrian of Yunnan, South China (ZHANG et al. 2007). Accordingly, many Chinese paleontologists have realized that the scientific significance of the discovery of lagerstätten yielding 'Orsten'-type preservation in Hunan and Yunnan could be compared with that of the Chengjiang biota, and that the intensive study of fossils of 'Orsten'-type preservation is vital and inevitable in China.

The main part of the material of the 'Orsten' type of preservation comprises specimens of about 15 species of Phosphatocopida, a taxon identified as the sister group to the crustacean crown group, the Eucrustacea (MAAS et al. 2003). A number of phosphatocopid species are known from other preservational types (see MAAS et al. 2003 and references therein for details). So far, it is MÜLLER who has recovered the greatest numbers of species and individuals of 'Orsten'-type fossils from the 'Orsten' calcitic nodules of Sweden. During the past 30 years, new 'Orsten'-type fossils were continuously discovered in many other regions of the world (MAAS et al. 2006); however, all the new discoveries are sporadically distributed. Hollow shields or isolated shield valves of phosphatocopids have been found in different continents, such as Siberia (MÜLLER et al. 1995) and Europe (MAAS et al. 2003). However, phosphatocopids with soft-body preservation were mainly found in Sweden (MAAS et al. 2003). In addition to the Swedish material, isolated appendages of phosphatocopids were recovered from the Middle Cambrian of Australia (WALOSZEK et al. 1993), and a single

specimen was found in Lower Cambrian rock of England (SIVETER et al. 2001, 2003). Recently, several specimens of phosphatocopids with soft-body preservation have been found in Upper Cambrian borehole samples in Poland (MAAS et al. 2006). Since 2002, many specimens of phosphatocopids with well-preserved soft-body details have been recovered from the Upper Cambrian of Hunan, South China. Of these, only a single unnamed specimen has briefly been described (DONG et al. 2005).

This paper is an in-depth investigation into the phosphatocopids ('Orsten'-type fossils) from the Upper Cambrian of western Hunan, South China. Here we report a species known hitherto only from Sweden, *Hesslandona angustata* MAAS, WALOSZEK & MÜLLER, 2003, two specimens of which display soft-part details, making it feasible for a comparative investigation of the limb morphology of phosphatocopids. Based on a computer-based phylogenetic analysis made already earlier (MAAS et al. 2003), we renew the study and re-establish the phylogeny of Phosphatocopida.

2. Material and methods

The present specimens were recovered from the micrite of the Upper Cambrian Bitiao Formation in Wangcun section, Yongshun County, western Hunan, South China. The co-occurring conodonts indicate the specimen-bearing horizon is within the *Westergaardodina* cf. *calix-Prooneotodus rotundatus* conodont zone (DONG et al. 2004), which is in the Paibian Stage of Furongian Series. The samples were processed by routine etching with 10 % technical acetic acid in plastic pails with a capacity of 10,000 cm³. The cycle of sieving and changing acid required ten to fourteen days. The samples (including duplicate samples) generally needed to be processed in three to four cycles for complete dissolution. During processing, the reaction time and the pH value of the solution were adjusted according to lab temperature (around 20°C in winter and up to 35°C in July and August). All the samples were processed in plastic pails with two layers of screens as recommended by MÜLLER (1985). All the residues were sorted manually under optical microscopes by laboratory assistants.

All the figured specimens are housed in the Geological Museum of Peking University (GMPKU).

3. Systematic paleontology

Crustacea BRÜNNICH, 1772
Phosphatocopida MÜLLER, 1964
Hesslandona MÜLLER, 1964

Type species: *Hesslandona necopina* MÜLLER, 1964.

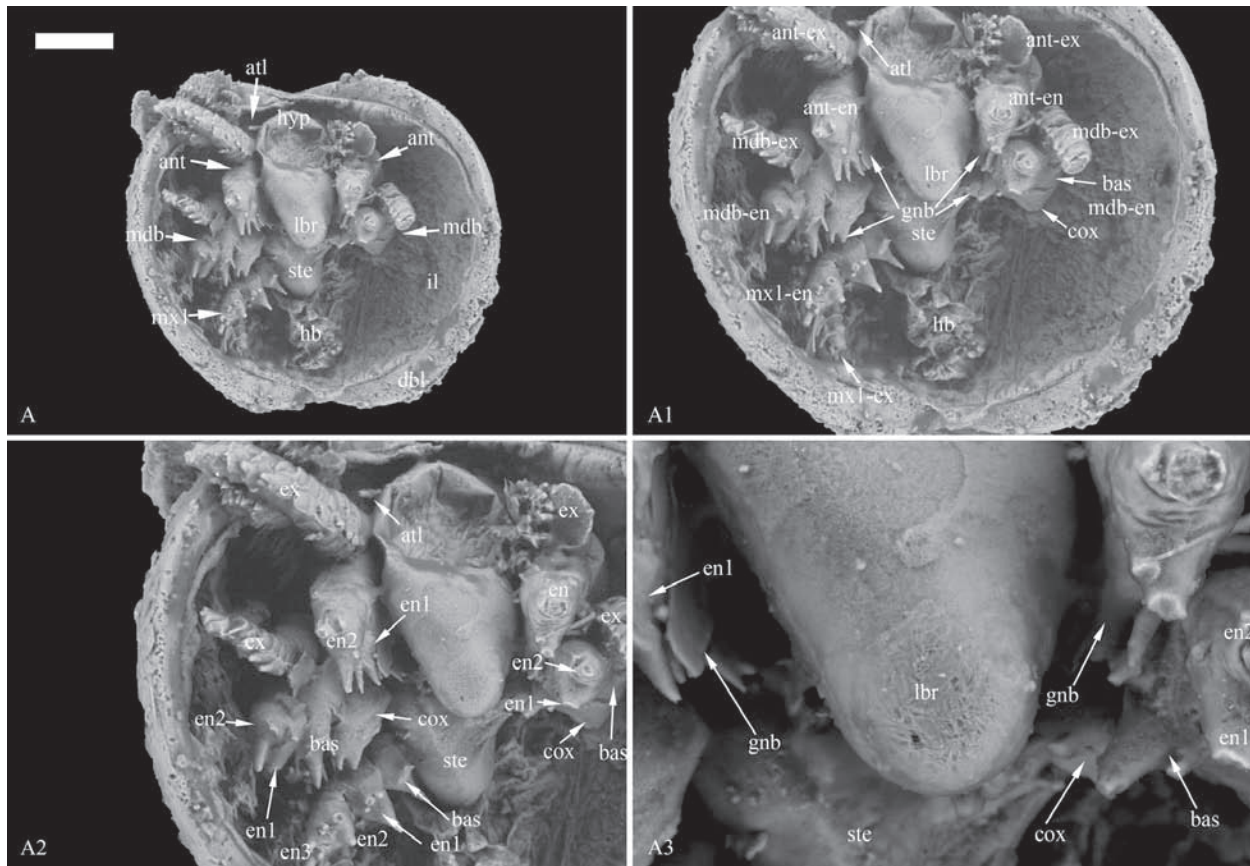


Fig. 1. *Hesslandona angustata*, GMPKU2332, 298 μm long. A: ventral view; A1: close-up of A; A2: close-up of the appendages; A3: close-up of the labrum. Abbreviations: hyp = hypostome, atl = antennulae, ant = antennae, be = basipodal endite, lst = limb stem, dbl = doublure, mdb = mandibles, mx1 = first post-mandibular limbs (maxillulae), lbr = labrum, il = inner lamella, id = interdorsum, me = median eyes, ste = sternum, hb = hind body, en = endopod, en1 = first segment of the endopod, en2 = second segment of the endopod, en3 = third segment of the endopod, ex = exopod, cox = coxa, bas = basipod, gnb = gnathobase. Scale bar: A, 70 μm ; A1, 45 μm ; A2, 36 μm ; A3, 12 μm .

Hesslandona angustata MAAS, WALOSZEK &

MÜLLER, 2003

Figs. 1-6

2003 *Hesslandona angustata* MAAS, WALOSZEK & MÜLLER, p. 89-101, pls. 26-27, text-fig. 39.

Material: 10 specimens, dimensions varying from 204-450 μm in shield length, indicating the presence of more than one ontogenetic stage.

Occurrence: *Westergaardodina* cf. *calix-Prooneotodus rotundatus* conodont zone in Bitiao Formation of Paibian Stage, Furongian Series (conventional Upper Cambrian) from Wangcun section, Yongshun County, western Hunan, South China.

Description: The shield is bivalved. The valves are of equal size and left/right symmetrical. The maximum length of the shield is between the dorsal rim and the midline. The outline of the shield is amplete, i.e. maximum height is located on the antero-posterior midline, but among some individuals it may be slightly anterior to the antero-posterior midline (sub-amplete). The proportion of valve length to height is about 1.60 on average. The outer surface of the valves is smooth, no lobes, no nodes, no grooves or spines or any other ornaments are present. The margins of the valves are smooth without any outgrowths throughout. The interdorsum (Figs. 3A.3, 4B.1, C.1, F.1) is well-developed, straight all through, but rather narrow, accounting for about 1/20 of valve length. Anteriorly and posteriorly the interdorsum simply tapers. A doublure (Figs. 1A, 4B, C, F, 5A, B) is present along the inner margin of the valves, having almost the same width. It is narrowest ventrally and widest

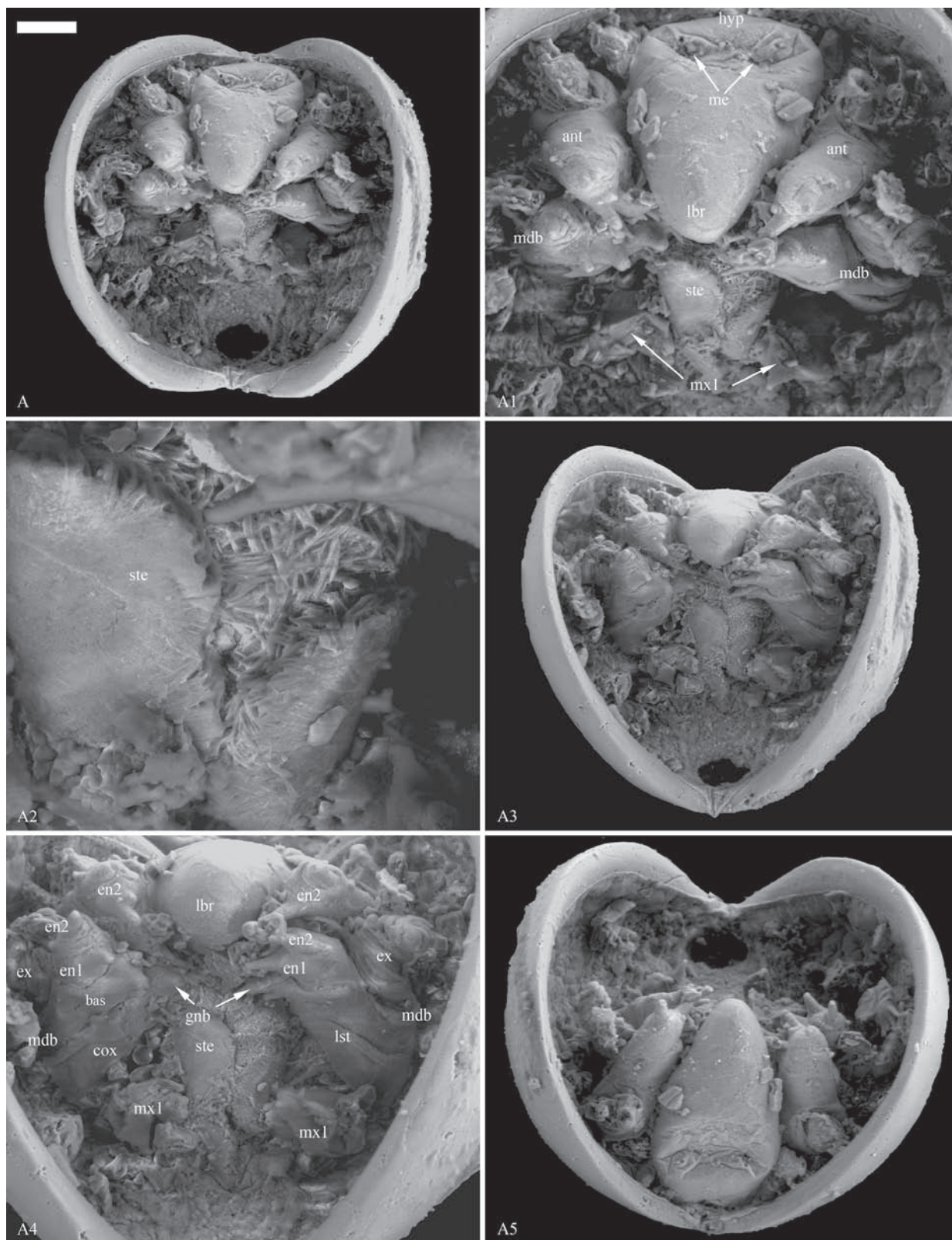


Fig. 2 (Legend see p. 161)

posteriorly, about 1/12 of the maximal valve length. Approximating the dorsal rim, the doublure of both sides becomes rapidly narrower. The doublure is smooth, ornaments or pores or any other structures are absent. The inner lamella (Figs. 1A, 4B, C) extends from the dorso-lateral side of the body and merges into the doublure. The inner lamella is smooth (Fig. 4B); wrinkled (Fig. 1A) or bulged (Fig. 4C) appearance could be observed, which are interpreted as preservational artifact.

The body proper is completely enveloped by the bivalved shield. All segments are fused to the shield in the available stages of *H. angustata* (Figs. 1A, 2A). The anterior part of the body includes the hypostome-labrum complex, of which the most anterior portion is the hypostome. The ventral surface of the hypostome is slightly bulged (Figs. 1A.2, 3A.). Its posterior part is occupied by the median eyes (Fig. 3A). They consist of at least two cups, of which two are located beside each other. Due to poor preservation in this area, it could not be observed whether they are followed by an additional single one posteriorly. The hypostome becomes gradually narrower and higher towards the posterior end where it continues into the labrum. The labrum is proportionally very long compared to the maximal length of the shield (Fig. 5A). Within the antero-lateral edge, at the so-called anterior wings of the hypostome, the first pair of limbs, the antennulae, arises. The second pair of limbs (the antennae) inserts medio- to postero-laterally to the hypostome. The third pair of limbs, the mandibles, arises posteriorly to the hypostome. The mouth is located posterior to the hypostome and covered by the labrum, but it could not be studied. The body proper posterior to the hypostome-labrum complex is, more or less, tubular. The ventral surface of the first three post-antennular segments forms a single plate, the so-called sternum with a pair of elevations, the so-called paragnath humps, located on the mandibular part of the sternum (Fig. 1A.2). Postero-lateral to the sternum, the first pair of post-mandibular limbs (the so-called maxillulae) insert. Other appendages follow successively behind the maxillulae but could not be studied due to poor preservation of the material. The hind body could not be studied either because it is shrunken in the available specimens. Accordingly, a telson or furcal rami and an anus could not be investigated.

Antennulae: The antennulae are uniramous, very short and thin, and weakly annulated (Figs. 1A.2, 3A). Segmentation and setation are unclear.

Antennae: The antennae are biramous and consist of a single limb stem and two rami, the endopod and the exopod.

The limb stem is medially drawn out into a strong gnathobase, which bears an unknown number of setae inserting on the postero-median side. It most likely represents the fusion product of coxa and basipod (MAAS et al. 2003). The endopod is two-divided, inserting medio-distally on the limb stem; the proximal segment bears a few setae inserting on the postero-median side; the terminal segment also bears several setae inserting on the distal and postero-median sides respectively. The exopod is multi-annulated. It consists of less than ten (Fig. 2A.1) or about 12-13 annuli (Fig. 1A.2) in the developmental stages at hand. Each annulus (including the most proximal one) bears a seta inserting on the median side. The number of distal setae is unclear.

Mandibles: The mandibles are somewhat similar to the antennae. They arise laterally to the sternum and consist, in later developmental stages, of a single limb stem and two rami, the endopod and the exopod (Fig. 2A.4, left mandible). The limb stem is most likely the fusion product of coxa and basipod (MAAS et al. 2003). It is medially drawn out into a strong gnathobase, which bears setae along its median edge. Their number and exact position cannot be determined. In younger stages, the mandibular limb stem consists of separate coxa and basipod (Fig. 1A). In one of our specimens, right and left mandibles seem to be asymmetrical (Fig. 2A.4), i.e. coxa and basipod of the left mandible have been fused to form an undivided limb stem while the coxa and basipod of the right one are still separated. Endopod and exopod are very similar to those of the antennae apart of being slightly smaller. The endopod is two-divided; the proximal segment bears several setae, which insert medially; the terminal segment also bears several setae, which are medially directed. The exopod is multi-annulated as that of the antenna. Since only the basal part of the mandibular exopod is preserved in the specimens at hand, no data on the number of annuli and setation can be given.

First post-mandibular limbs (maxillulae): The first pair of post-mandibular limbs insert postero-laterally to the sternum. These limbs, the maxillulae in crustacean terminology, consist of a basipod, an endopod and a multi-annulated exopod (Fig. 1A.2). The proximal endite is unclear from the material examined. The endopod is three-divided. The exopod consists of about 5 annuli. Each annulus including the most proximal one bears one seta medially. The number of terminal setae is unknown. Details of successive limbs could not be determined due to the poor preservation of the remaining body part in the material at hand.

Fig. 2. *Hesslandona angustata*, GMPKU2333, 224 µm long. A: ventral view; A1: close-up of the cephalic part; A2: close-up of the sternum; A3: postero-ventral view; A4: close-up of A3, displaying the asymmetrical development of left and right mandibles. The right mandibular coxa and basipod are still separate, whereas those of the left are already fused to form an undivided limb stem; A5: antero-ventral view. For abbreviations refer to Fig. 1. Scale bar: A, 38 µm; A1, 21 µm; A2, 5 µm; A3, 36 µm; A4, 23 µm; A5, 31 µm.

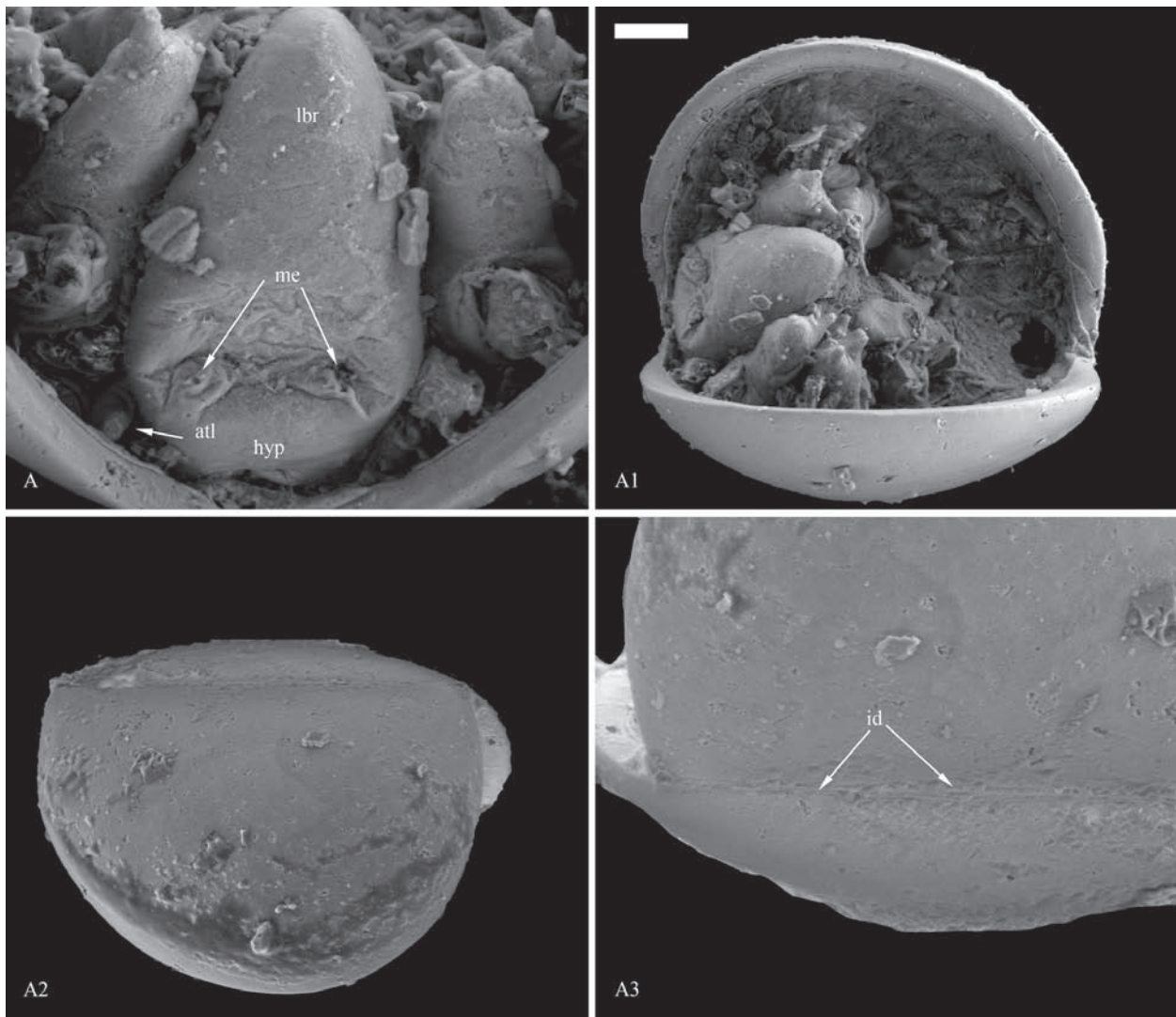


Fig. 3. *Hesslandona angustata*, the same specimen in Fig. 2. A: close-up of the hypostome-labrum complex; A1, latero-ventral view; A2, latero-dorsal view; A3, close-up of the interdorsum, showing there is no thickening at the end of the interdorsum. Scale bar: A, 17 μm ; A1, 36 μm ; A2, 37 μm ; A3, 23 μm .

Comparison: *Hesslandona angustata* and *H. suecica* MAAS, WALOSZEK & MÜLLER, 2003 are similar to each other in valve outline and valve morphology (MAAS et al. 2003). They both possess smooth valves, which are amplete (or sub-amplete), with no lobes, no nodes or spines. The characteristic interdorsum, an elongated plate located dorsally between the two valves, is smooth throughout in *H. angustata*, while the anterior end of the interdorsum of *H. suecica* is drawn out into a dome-like thickening (or in other words, a dome-like short spine), whereas the posterior end is drawn out into a short spine, which is oriented towards postero-dorsal. *H. angustata* is unique for its relatively narrow interdorsum compared with the interdorsum of *H. suecica* and that of *H. necopina*. Accordingly,

valve morphology of *H. angustata* appears to be rather simple compared to valve morphology with dorsal spines or various valve lobes as present in many phosphatocopids, such as species of *Vestrogothia* MÜLLER, 1964 and *Waldoria* GRÜNDEL, 1980. The specimens presented herein accord well with those of *H. angustata* from Sweden except for their smaller dimensions, and thus they are considered conspecific but most likely represent much younger ontogenetic stages. The dimensions of the specimens of *H. angustata* from Sweden range from 330 μm to 700 μm , and the smallest specimen is a larva with four pairs of fully developed limbs, representing a head larva (MAAS et al. 2003). In contrast to that, specimens of *H. angustata* from South China are much smaller, mostly with dimensions less

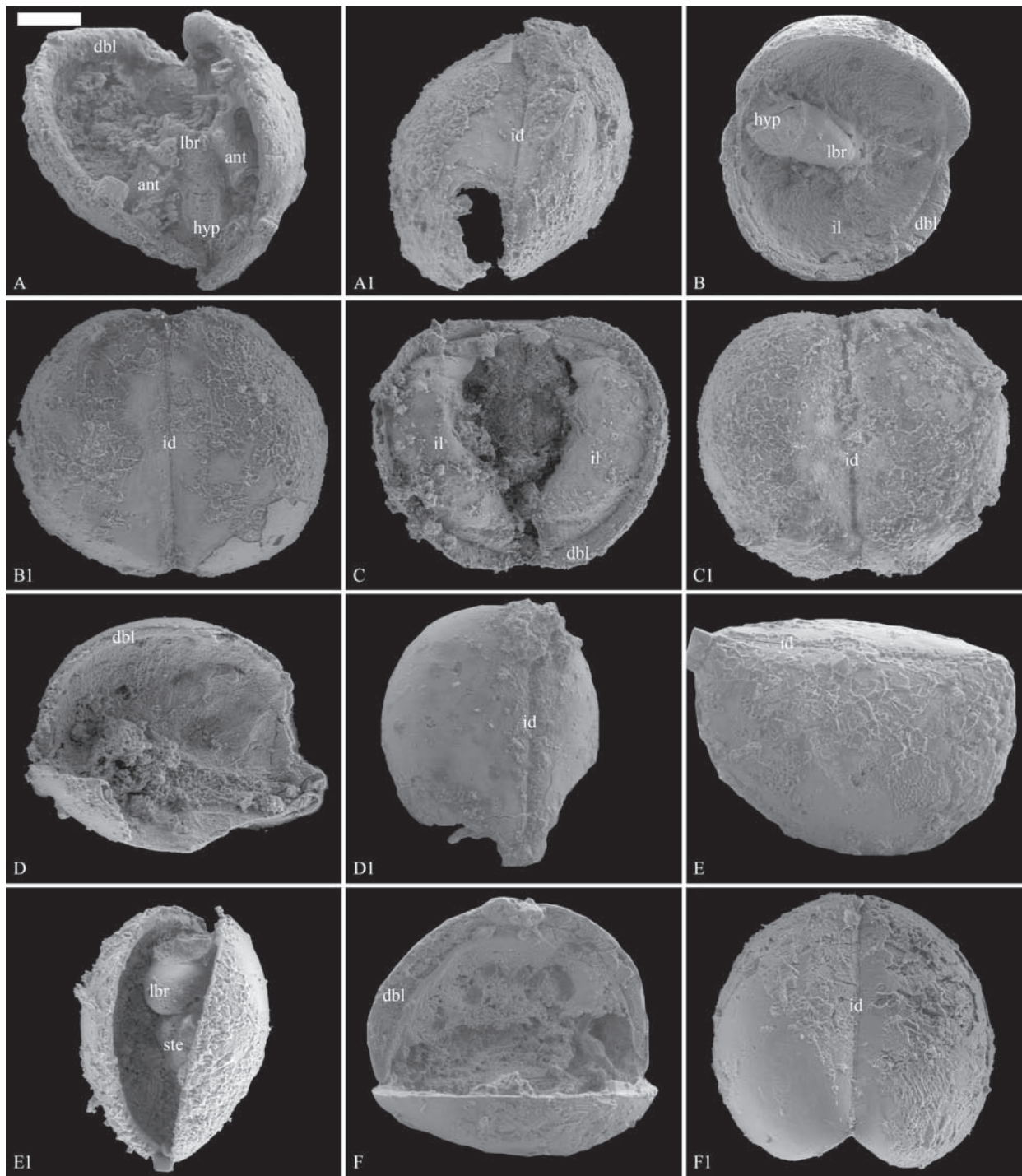


Fig. 4. *Hesslandona angustata*. A-A1: GMPKU2334, 268 μm long. A: anterior view, with partly-preserved soft-body; A1: dorsal view. B-B1: GMPKU2335, 363 μm long. B: ventral view with only hypostome-labrum complex of soft-part morphology preserved; B1: dorsal view. C-C1: GMPKU2336, 405 μm long. C: ventral view; C1: dorsal view. Note the extremely narrow interdorsum. D-D1: GMPKU2337, 392 μm long. D: ventral view of isolated shield; D1: dorsal view. E-E1: GMPKU2338, 371 μm long. E: almost lateral view; E1: latero-ventral view, with partly-preserved hypostome-labrum complex and sternum. F-F1: GMPKU2342, 368 μm long. F: lateral view, isolated shield; F1: dorsal view. For abbreviations refer to Fig. 1. Scale bar: A, 64 μm ; A1, 72 μm ; B, 97 μm ; B1, 85 μm ; C, 102 μm ; C1, 98 μm ; D, 83 μm ; D1, 93 μm ; E, 72 μm ; E1, 90 μm ; F, 89 μm ; F1, 85 μm .

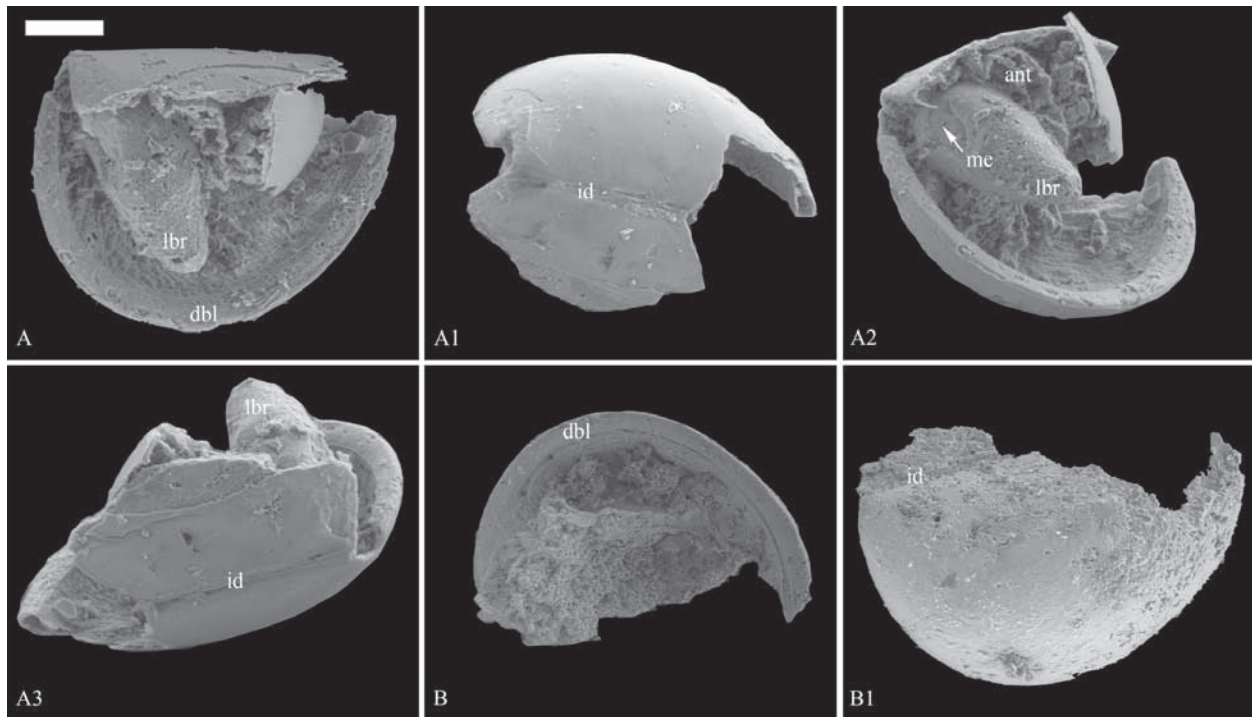


Fig. 5. *Hesslandona angustata*. A-A3: GMPKU2339, 204 μm long, shield strongly damaged and parts missing. A: lateral view. Labrum proportionally about half as long as the shield; A1: dorsal view; A2: anterior view; A3: dorsal view. B-B1: GMPKU2341, 450 μm long, fragmentary specimen, only part of left valve preserved. B: lateral view of inner surface of valve; B1: lateral view of outer surface. For abbreviations refer to Fig. 1. Scale bar: A, 46 μm ; A1, 51 μm ; A2, 49 μm ; A3, 43 μm ; B, 103 μm ; B1, 88 μm .

than 300 μm but with a still functional fourth pair of limbs, hence, also representing head-larvae, and with the mandibular coxa and basipod still separate, representing the first and the second ontogenetic stages.

Ontogeny: The overall shield outline and the soft body of *H. angustata* studied are reconstructed (Fig. 6A-C). Four pairs of limbs (or in other words, the so-called head larvae) characterize the first growth stage of phosphatocopids (MAAS et al. 2003). This first growth stage of *H. angustata* is represented by one individual of 224 μm with four pairs of limbs (Fig. 2A). The other specimen of about 298 μm (Fig. 1A) possesses a mandibular limb stem that consists of separate coxa and basipod, a character that is the primary condition for these appendages in Labrophora and the primary condition for early larvae of the phosphatocopid *Vestrogothia spinata* MÜLLER, 1964 (MAAS et al. 2003) and *Klausmuelleria salopensis* SIVETER, WALOSZEK & WILLIAMS, 2003 (SIVETER et al. 2003). Therefore, the 298 μm sized specimen (Fig. 1A), together with two smaller specimens, GMPKU2334 of about 268 μm in length (Fig. 4A) and GMPKU2339 of about 204 μm in length (Fig. 5A), should represent the first growth stage, and with regard to the other equally small specimen of 224 μm of *H. angustata* (Fig. 2A), we tentatively assign it to the second growth

stage, because its already fused left mandibular coxa and basipod evidently indicate a more advanced ontogenetic level. The discrepancy in size might be explainable by, e.g., individual polymorphism (one specimen might have lived one million years before the other), sexual dimorphism or one of the specimens actually belongs to another species. The latter is, however, not evident by possible morphological differences of the specimens. We therefore treat them, most parsimoniously, as conspecific. The coxa and basipod of its right mandible are still separated whereas those of its left mandible are already fused. This asymmetrical development of the left and right mandibles probably represents a developmental link bridging the first and the third ontogenetic stages. Due to lack of distinct pairs of preserved limbs in other available specimens, they could only be assigned to specific growth stages based on their shield dimensions. As indicated by MAAS et al. (2003), their material of 330 μm to about 700 μm long specimens may represent about 4 different growth stages. The largest specimens of our material (Fig. 5B, 450 μm long) probably belong to the second growth stage found by MAAS et al. (2003, cf. their fig. 40). Our specimens of around 400 μm in size (e.g. Fig. 4B-E) should belong to the first stage found by MAAS et al. (2003), while our smaller specimens would add two more and earlier ontogenetic stages to the re-

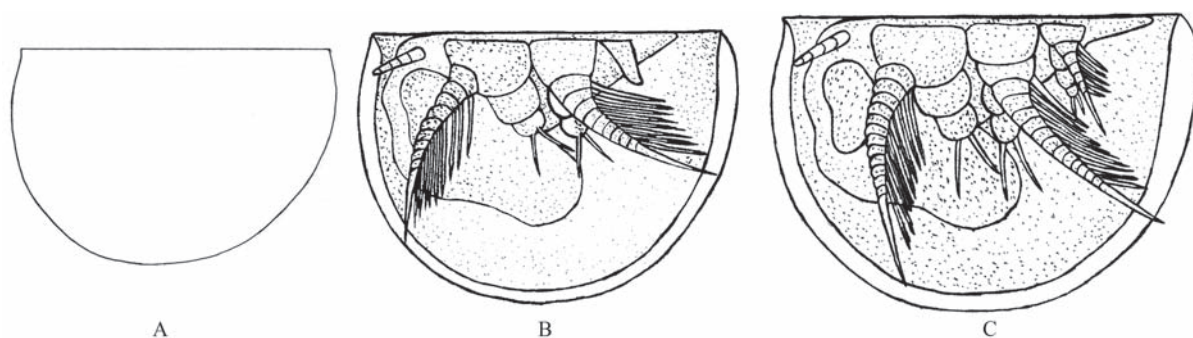


Fig. 6. Reconstructions of *Hesslandona angustata*, not to scale. A: general outer surface of shield, lateral view; B: GMPKU2333, displaying the soft-body, the maxillulae are not so well-preserved; C: GMPKU2332, displaying the soft-body, lateral view.

construction of the ontogeny of *H. angustata* made by MAAS et al. (2003). Therefore, at least six ontogenetic stages of *H. angustata* are recognized so far, the first and the second stages from South China, the third and fourth from South China and Sweden and the fifth and sixth stages from Sweden (MAAS et al. 2003). The first ontogenetic stage is characterized by the separated mandibular coxa and basipod, both left and right mandibular limb stems equally developed. The second ontogenetic stage exhibited fusion of the mandibular coxa and basipod from a single side of the mandible on, for example, from the left mandible on in our material (Fig. A4). Since the third ontogenetic stage, the mandibular coxa and basipod, both left and right, have entirely been fused to form undivided limb stems.

3. Comparative morphology of phosphatocopid limbs

Comparative morphology of phosphatocopid limbs has been discussed in detail by many authors (e.g. SIVETER et al. 2003; MAAS et al. 2003; MAAS & WALOSZEK 2005). Here, our material has brought up new information. The new material of *H. angustata* studied is well preserved and the specimens exhibit, at least, the first three pairs of limbs, which makes a comparative study of limbs of species within Labrophora possible. Antennulae and post-mandibular limbs are less well-preserved, so they are not included in this discussion.

3.1 Antennal and mandibular morphology

With regard to the specimens of *H. angustata* from South China, though in their youngest ontogenetic stages (Figs. 1A, 2A), the antennae are already of the same design as those of other species in larger stages from Sweden, made up of an undivided limb stem

since the beginning which might be the fusion product of coxa and basipod (MAAS et al. 2003), a two-divided endopod and a multi-annulated exopod. As documented in much detail, the early evolution of Crustacea is characterized by a movable endite, the proximal endite, appearing medio-proximally at least on the second post-antennular appendage (the mandible) and also on other post-antennular appendages including the antenna later on during crustacean evolution (WALOSZEK & MÜLLER 1990; WALOSZEK 1999; STEIN et al. 2008). The proximal endite can also be observed as gradually appearing along the limb series during larval development of the so-called stem-lineage derivatives of Labrophora (see HAUG et al. 2009 for details). According to MAAS et al. (2003), a coxa, as an autapomorphy of Labrophora, evolved from the proximal endite of the antenna and mandible (see also WALOSZEK & MÜLLER 1990; WALOSZEK 1993). Thus, the antennae and mandibles of the Labrophora have a two-divided limb stem. Eucrustacea retained this character as a plesiomorphic state (Maas et al. 2003). Within Phosphatocopida, the Euphosphatocopida is characterized by an undivided limb stem in the antenna from the very beginning of their ontogeny onwards (MAAS et al. 2003). The Lower Cambrian *Klausmuel-leria salopensis* (SIVETER et al. 2001, 2003), from which we only know a very early larval stage, is the only phosphatocopid species, in which the antennal limb stem is plesiomorphically two-divided, at least in early larval development (SIVETER et al. 2003). Whether the two portions would get fused with each other in older stages is unclear. Fusion of coxa and basipod occurs very rarely in Eucrustacea. The plesiomorphic state of separated elements is the main case,

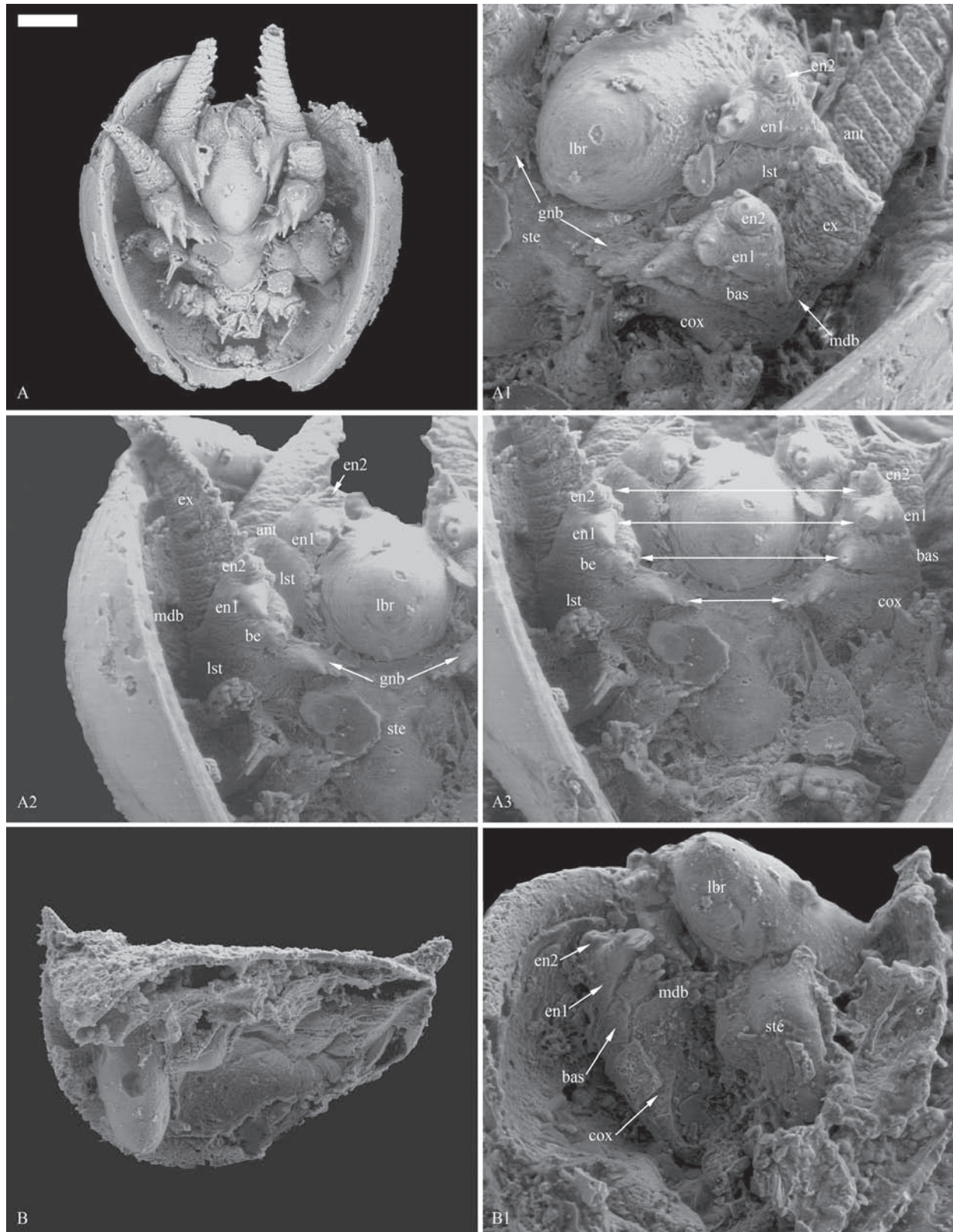


Fig. 7 (Legend see p. 167)

which also holds true for the Cambrian entomostracans *Rehbachella kinnekullensis* (WALOSZEK 1993) and *Yicaris dianensis* (ZHANG et al. 2007). As an example coxa and basipod of the antenna become autapomorphically fused with each other in older stages of the extant malacostracan taxon Euphausiacea (MAAS & WALOSZEK 2001).

The mandibles of *H. angustata* are more or less similar to the antennae. They consist of an undivided limb stem in later stages (Fig. 2A.4, left mandible) plus a two-divided endopod and a multi-annulated exopod. The limb stem is the fusion product of coxa and basipod, and separation of coxa and basipod is exemplified by a 298 µm small specimen of our material (Fig. 1A) and the right mandible of a 224 µm specimen (Fig. 2A.4). However, different conditions exist within Phosphatocopida. In *K. salopensis*, the mandibles have a two-divided limb stem, consisting of a coxa and a basipod. According to MAAS et al. (2003), in later stages of euphosphatocopids, the mandibular limb stems are undivided. The fusion of a separate coxa and basipod could be demonstrated for *V. spinata* (MAAS et al. 2003; MAAS & WALOSZEK 2005), in which the mandibles have a two-divided limb stem in younger stages. WALOSZEK et al. (2007, their fig. 2D) illustrated an early larva of *H. suecica* with a two-divided mandibular limb stem. As we could demonstrate now also for *H. angustata* the mandibular limb stem is also two-divided in young larvae, consisting of a coxa and a basipod (Fig. 1A.2) and is undivided in later stages (Fig. 2A.4).

Several examples from the fossil record demonstrate now that a mandible with a two-divided limb stem at least in younger stages among Phosphatocopida is a rather widespread plesiomorphy retained from the ground pattern of the Labrophora. Examples have been reported from South China, e.g. *H. angu-*

stata (this paper), *Hesslandona* sp. sensu DONG et al. 2005 (Fig. 7A, A.1), *H. necopina* (Fig. 7B, B.1), and from Sweden, e.g. *V. spinata* (MAAS et al. 2003; MAAS & WALOSZEK 2005) and *H. suecica* (WALOSZEK et al. 2007). The mandibles of *Hesslandona* sp. sensu DONG et al. 2005 (Fig. 7A-A.3) should be paid special attention to. Its left and right mandibles are asymmetrical: coxa and basipod of the left mandible are separate, while coxa and basipod of the right one are fused to form an undivided limb stem, the remaining part of the basipod, the basipodal endite, is wedge-shaped and is located between the endopod and the coxa (Fig. 7A.2, be). This asymmetrical condition is somewhat similar to that exhibited by one specimen of *H. angustata*, of which the left and right mandibles are also asymmetrically developed (Fig. 2A.4). The characteristic basipodal endite (cf. Fig. 7A.2, be), as the remaining enditic part of the basipod after fusion of the basipodal and coxal bodies, is known from many species from Sweden (MAAS et al. 2003), e.g. in *H. suecica*, *H. unisulcata*, *H. ventrospinata*, *V. spinata*, and from South China, in *Hesslandona* sp. sensu DONG et al. 2005 (Fig. 7A.2). With the new data brought up, we cannot exclude that in the aforementioned four species, from which we do not know the youngest stages, e.g. *H. ventrospinata*, the mandibular limb stem might also have been two-divided in young stages.

3.2 Phylogeny within Phosphatocopida

Within Phosphatocopida, *K. salopensis* is the sister taxon to the remaining phosphatocopids, the Euphosphatocopida (SIVETER et al. 2003; MAAS et al. 2003). It is not clear whether *K. salopensis* may belong to the Dabashanellidae, a taxon of a few Lower Cambrian univalved species of Phosphatocopida mainly from

Fig. 7. Phosphatocopids recovered from the Upper Cambrian Bitiao Formation in Wangcun section, western Hunan, South China, from the same horizon as that of *H. angustata* in this paper. A-A3: *Hesslandona* sp. sensu DONG et al., 2005, GMPKU2201, 382 µm long. A is the Fig. 2 in DONG et al. (2005), whereas A1-A3 are new images. A: ventral view, six pairs of limbs imply that it should be included at least in the third growth stage; A1: close-up of the left mandible, showing the limb stem consisting of separate coxa and basipod; A2: close-up of the right mandible, showing that the coxa and the basipod is being fused to form a single undivided limb stem, and the basipodal endite is the remaining proximal part of the basipod; A3: close-up of the mandibles, making a comparison between the right and the left mandible. B-B1: *Hesslandona necopina*, GMPKU2347, 378 µm long. B: lateral view, with a labrum half as long as the dorsal rim; B1: close-up of the right mandible, showing that the limb stem is still two-divided consisting of a coxa and a basipod, and the endopod is also two-divided. For abbreviations, please refer to Fig. 1. Scale bar: A, 68 µm; A1, 26 µm; A2, 34 µm, A3, 35 µm; B, 57 µm; B1, 35 µm.

China, but from which only shields or isolated valves are known (HOU et al. 2001; MAAS et al. 2003). Within Euphosphatocopida, the taxon *Vestrogothia* belongs to Vestrogothiidae (KOZUR 1974), whereas the taxon *Hesslandona* belongs to Hesslandonidae MÜLLER, 1964 (MAAS & WALOSZEK 2005). Phylogenetic analysis carried out here confirmed the position of *H. necopina* deeply within the Hesslandonidae, while *H. angustata* – based on the plesiomorphically two-divided mandibular limb stem in early larvae and its rather simple valve structures – is a fairly early offshoot within Euphosphatocopida. *Hesslandona* sp. sensu DONG et al. 2005 may most probably belong to or share close relationship with *H. angustata* or *H. suecica* due to its similar valve morphology. However, its final assignment to any specific species will surely provide us with more helpful information on the evolution of phosphatocopid appendages.

4. Phosphatocopida phylogeny

A computer-based phylogenetic analysis of Phosphatocopida was made only by MAAS et al. (2003) thus far. According to their analysis, as hypothesized by WALOSZEK & MÜLLER (1992, 1998), WALOSZEK & MÜLLER (1998) and WALOSZEK (2003), Phosphatocopida is resolved as the sister group of Eucrustacea (MAAS et al. 2003; MAAS & WALOSZEK 2005). The two taxa share a number of features that are interpreted as synapomorphies resp. autapomorphies of the stem-species of Labrophora (SIVETER et al. 2003). Among these synapomorphies, a significant character is the labrum. The anterior ventral surface of the head of euarthropods is a sclerotised plate, the hypostome, from which margins the antennulae and antennae and their musculature insert (MAAS et al. 2003; WALOSZEK et al. 2007). In Labrophora the posterior part of the hypostome is drawn out into a slightly cone-shaped structure with a blunt end, the labrum, which obviously contains sensilla and glands to check the food and add slime to the food (MAAS et al. 2003).

The sister-taxon relationship of Phosphatocopida and Eucrustacea is accepted more and more widely (e.g. SIVETER et al. 2003; ZHANG et al. 2007). However, the evolutionary relationships within Phosphatocopida are not settled yet. Since the analysis of MAAS et al. (2003) is now 6 years old and does not consider new evidence brought up in China recently, especially the new data presented herein, we adopted the character list and data matrix from MAAS et al. (2003) and

amended it accordingly and made another computer-based phylogenetic analysis of Phosphatocopida.

Sixteen phosphatocopid species are adopted as in-groups, in which fourteen have been described in detail by MAAS et al. (2003). *Cyclotron lapworthi* (GROOM, 1902) is a phosphatocopid known from several isolated valves and shields from the Upper Cambrian of England (WILLIAMS et al. 1994). *Klausmuelleria salopensis* is a phosphatocopid known only by a young univalved larva from the Lower Cambrian of England (SIVETER et al. 2003). *Oelandocaris oelandica* MÜLLER, 1983 is used as a representative of stem-lineage derivatives of Labrophora. The so-called proximal endite, an autapomorphy of Crustacea, occurred only on the third limb of *O. oelandica*, determining the most basal position of this species within the phylogeny of Crustacea (STEIN et al. 2005, 2008; HAUG et al. 2009). The maxillopod *Bredocaris admirabilis* Müller, 1983 is adopted as a representative of Eucrustacea (MÜLLER & WALOSZEK 1988). *Agnostus pisiformis* (LINNAEUS, 1757), described in detail by MÜLLER & WALOSZEK (1987), is used as the out-group. *A. pisiformis* is a euarthropod of unclear affinities. It has traditionally been assigned to Trilobita, but it seems to have closer relationships with Crustacea. The three anterior head limbs of *A. pisiformis* are specialized and differ from the succeeding ones, a character assumed for the ground pattern of Crustacea (WALOSZEK & MÜLLER 1990; STEIN et al. 2005). The limb stem of *A. pisiformis* comprises only a basipod, phylogenetically prior to the development of a separate proximal endite (WALOSZEK & MÜLLER 1990) in the ground pattern of Crustacea (MAAS et al. 2003; HAUG et al. 2009). *K. salopensis* is here coded as a univalved species, as originally described by SIVETER et al. (2003), because we do not know whether it would become bivalved in later stages. If it remained univalved, this means, applying the parsimony principle, that the Phosphatocopida should be univalved (plesiomorphic state) whereas Euphosphatocopida are bivalved (autapomorphy). Dabashanellidae plesiomorphically retained a univalved shield (HOU et al. 2001; MAAS et al. 2003). The revised character list and data matrix are provided in the appendix to this article. The character list includes mainly valve-related characters but also some soft-part features. Unfortunately there is not sufficient information on soft-part morphology of Phosphatocopida to base an analysis only on those. The data matrix is analyzed using PAUP4.0beta10. The branch-and-bound algorithm is employed, resulting in five

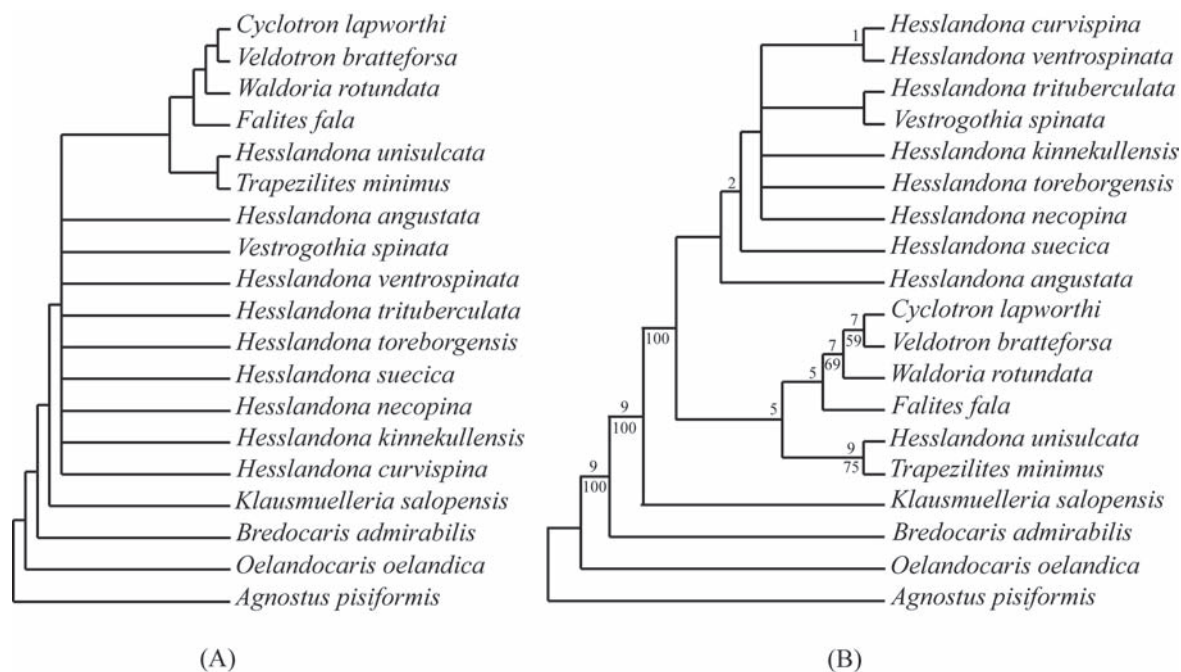


Fig. 8. Cladograms of (A) strict consensus tree and (B) 50% majority rule consensus tree of five equal shortest trees resulted from PAUP. Numbers adjacent to nodes in (B) represent their respective support values: the upper value is the Bremer Support and the lower value is the Bootstrap Support.

equally long trees (tree length = 163, CI = 0.7117, RI = 0.7552). The strict consensus tree and the 50% majority rule consensus tree are computed (Fig. 8A, B). Fig. 8B also illustrates the results of bootstrap analyses based on 10000 replicates (using heuristic search and all groups compatible with the 50% majority rule consensus tree were recognized) and the Bremer Support values (using branch-and-bound search), respectively. The phylogeny of Phosphatocopida (Fig. 9) is re-established on the basis of the 50% majority rule tree (Fig. 8B).

In our analysis, different from the result given by MAAS et al. (2003), the Hesslandonidae, a monophylum in MAAS et al. (2003) comprising all species of *Hesslandona* plus *Trapezilites minimus*, is not supported as being monophyletic. The former taxon Vestrogothiidae comprising *Vestrogothia* and *Falites* (MÜLLER 1964) is, as in the former analysis (MAAS et al. 2003), not supported.

Phosphatocopida is divided into two sub-units, univalved *K. salopensis* and bivalved Euphospatocopida (= Phosphatocopina *sensu* MÜLLER 1964), compatible with the previous study (MAAS et al. 2003; SIVETER et al. 2003). According to SIVETER et al.

(2003), Euphospatocopida was characterized as a group embracing taxa bearing two-divided endopods of antennae and mandibles, different from *K. salopensis* bearing three-divided endopods of antennae and mandibles. *K. salopensis* may be a representative of the univalved Dabashanellida, and according to the parsimony principle, a univalved shield will become a plesiomorphic state of Phosphatocopida (box 1 in Fig. 9) retained from the ground pattern of Crustacea, whereas a bivalved shield represents an autapomorphy of Euphospatocopida (box 2 in Fig. 9) instead.

As to summarize the results of our analysis, the Euphospatocopida can be distinguished in two distinct taxa, Taxon A and Taxon B.

The most important character of Taxon A (box 3 in Fig. 9) is the presence of one large lobe L1 on the valves, retained as such in the stem species of *T. minimus* plus *H. unisulcata* (box 4 in Fig. 9). The other taxa are characterized by a higher number of lobes. Three lobes L1–L3 occur in *Falites fala* and might represent the ground-pattern condition of a taxon comprising this and other species (box 5 in Fig. 9). Five lobes L1–L5 characterize *Waldoria rotundata*. Among some individuals of *W. rotundata* the fifth

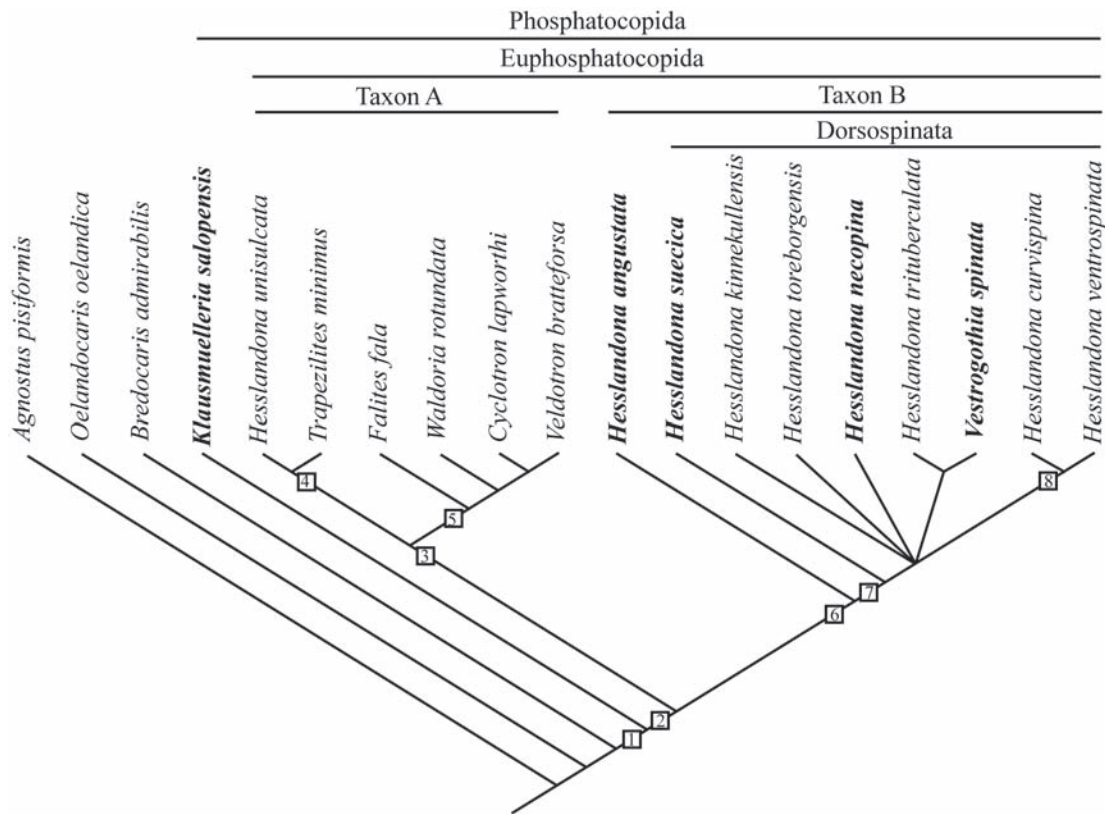


Fig. 9. Phylogeny of Phosphatocopida, based on Fig. 8 (B). For detailed interpretation on each character box and each taxon, please refer to the discussion in the text. Five taxa are typed in boldface, representing those which have retained a two-divided mandibular limb stem in younger stages as a plesiomorphy from the ancestral Labrophoran stem species.

lobe extends into a long spine during ontogeny. *C. lapworthi* and *Veldotron bratteforsa* possess the greatest numbers of lobes, L1–L6, most likely a synapomorphy of these taxa. On the other hand, Taxon A is distinct for the (plesiomorphic) lack of dorsal spines. The ends of the interdorsum of *H. unisulcata* and *T. minimus* are drawn out into hump-like thickenings, and the ends of the dorsal furrow of *F. fala* are extended into triangular plates, but the other three species possess no ornaments at the ends of their interdorsa.

Taxon B is (box 6 in Fig. 9) characterized by its simple valves, with no lobes, no spines and no ornaments, exemplified by *Hesslandona angustata*. In the sister taxon to *H. angustata*, dorsal spines occurred independently, which characterizes the taxon Dorsospinata (box 7 in Fig. 9). Dorsospinata is characterized by anterior and posterior spines occurring at the same time on both ends of the interdorsum (box 7 in Fig. 9). Accordingly, dorsal spines originated only

once during the phylogeny of Phosphatocopida. Consequently, the species composition of Dorsospinata established by MAAS et al. (2003), originally characterized as a group to encompass all the species which possess an interdorsum with dorsal spines (including *H. angustata* at the same time, but excluding *V. spinata*, which has a posterior dorsal spine but no distinct interdorsum), is not supported herein. We, therefore, emend the taxon as encompassing all species with distinct dorsal spines (excluding *H. angustata*, but including *V. spinata*; box 7 in Fig. 9). Within Dorsospinata (MAAS et al., 2003), *H. ventrospinata* possesses six lobes L1–L6, while *H. curvispina* and *H. trituberculata* both possess three large lobes L1–L3. Phylogenetic analysis resulted in the assumption of an autapomorphic appearance of at least 3 lobes within Dorsospinata (MAAS et al., 2003). Lobes within Taxon A have, consequently, to be interpreted as a convergence. The analysis herein shows lower Bremer Support and Bootstrap Support within

the Dorsospinata (above box 7 in Fig. 9). Taxa of Dorsospinata still need further study to clarify in-group relationships.

The two distinct taxa within Euphosphatocopida are (1) characterized by different numbers of lobes and valves lacking dorsal spines and (2) valves originally with no lobes and spines, which most likely represents the plesiomorphic condition. According to our analysis, lobes originated convergently three times, i.e. in Taxon A and within Dorsospinata in *H. trituberculata* and the stem species of *H. curvispina* and *H. ventrospinata* (box 8 in Fig. 9) respectively.

The re-established phylogeny also results in a non-monophyletic taxon *Hesslandona*, which was interpreted as a monophylum in the earlier analysis (MAAS et al. 2003). Another interesting difference between the first analysis and the current one is that *H. unisulcata* is interpreted here as the sister group of *T. minimus* based on some similar valve characters, e.g. valves with a big lobe L1 and without dorsal spines but with hump-like thickenings at the ends of the interdorsa, while in the analysis of MAAS et al. (2003) *T. minimus* is the sister species of all *Hesslandona* species, of which *H. unisulcata* was the sister species to all others. That means that the lobe characters are assigned differently in the new analysis compared to the first one. HINZ-SCHALLREUTER (1993) proposed that Falitidae MÜLLER, 1964 should combine three species which are *H. unisulcata*, *T. minimus* and *F. fala* without giving detailed arguments. However, our analysis does not support Falitidae in this combination. Another result of our analysis is that *Vestrogothia* originated from within *Hesslandona* species. According to the new analysis, the interdorsum originated once in the ground pattern of Euphosphatocopida (box 2 in Fig. 9), while the analysis of MAAS et al. (2003) suggested the initial development of a dorsal furrow first, represented by species of *Vestrogothia* and *Falites*, that gave rise to the interdorsum in the ground pattern of the taxon Hesslandonina. This taxon is not supported herein. Another convergence we have to face is that a dorsal furrow occurs in *F. fala* and, independently, in the taxon *Vestrogothia*.

Our analysis includes five species that have plesiomorphically retained a two-divided mandibular limb stem at least in the beginning of their ontogeny. Their scattered positions within the phylogenetic tree imply that the fusion of mandibular coxa and basipod did occur early in phosphatocopid evolution.

According to our observation, the phosphatocopids recovered from South China are all characterized by

smooth valves, i.e. lacking lobes, nodes or any other ornaments. Dorsal outgrowths occur, either being short humps or distinct long spines. Interestingly, none of the species from Taxon A has been recovered from South China yet.

5. Conclusions

We described *Hesslandona angustata* recovered from the Upper Cambrian Bitiao Formation in western Hunan, South China. Two specimens developed with four pairs of limbs represent phosphatocopid head larvae. We thus established the first and second ontogenetic stages of *H. angustata*. Together with another four later stages found by MAAS et al. (2003), six successive ontogenetic stages of *H. angustata* are established. The comparative investigation on comparative morphology of limbs among *H. angustata* and other species of Phosphatocopida indicates that the antennal design of euphosphatocopids is unchanged since the beginning, and a two-divided mandibular limb stem in younger stages, as a plesiomorphic state from the ground pattern of Labrophora and a synapomorphy shared by Phosphatocopida and Eucrustacea, should probably be well retained in many if not all phosphatocopid taxa, and that the two separate parts (coxa and a basipod) would get fused with each other to form an undivided limb stem in all known euphosphatocopid adults in different instars of different species respectively. According to the computer-based phylogenetic analysis of Phosphatocopida made herein, the taxon *Hesslandona* is non-monophyletic, whereas *Vestrogothia* is closely related to some *Hesslandona* species. The sister group of *Klausmuelleria salopensis*, the Euphosphatocopida, consists of Taxon A characterized by the presence of valve lobes, and Taxon B that can only be characterized by plesiomorphic character conditions. Its status has to be confirmed by future investigations. In any case *H. angustata* is an early offshoot of euphosphatocopids due to its plesiomorphically simple valve morphology. Dorsal spines originated only once in Dorsospinata (MAAS et al. 2003), while valve lobes originated independently three times. Another convergence is the independent reduction of the interdorsum to a furrow within Taxon A and Taxon B. The convergences and other deviations from the earlier analysis by MAAS et al. (2003) might also be related to a high plasticity among valve characters that, e.g., occurs in ostracods, a eucrustacean taxon with a bivalved shield (HORNE, pers. comm. 2009). However, the present study again

demonstrates the value of three-dimensionally preserved fossil specimens for phylogenetic analyses and discussion of the early evolution of taxa, in this case the Phosphatocopida. Although there are no sufficient data on the crucial dabashanellid phosphatocopid taxa to reveal character evolution within the first step of phosphatocopid evolution, the present study is another step to contribute significantly to the evolutionary role of the eucrustacean sister group.

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Appendix

Character list

- 1 dorsal hinge line of the shield: not applicable (0); short, dorsal area curved (1); long, dorsal area straight (2);
- 2 location of the maximum length of the shield: ventral to the midline or on the midline (1); on the dorsal rim (2); between the dorsal rim and the midline (3);
- 3 location of the maximum height of the valves: not applicable (0); anterior to the antero-posterior midline (pre-plete) (1); on the antero-posterior midline (am-plete) (2); posterior to the antero-posterior midline (post-plete) (3);
- 4 free margin of the valves curves back dorsally: not applicable (0); more anteriorly (1); more posteriorly (2); anteriorly and posteriorly more or less equal (3);
- 5 anterior margin of the valves: not applicable (0); rather straight (1); curved (2);
- 6 median/ventral margin of the valves: not applicable (0); rather straight (1); curved (2);
- 7 posterior margin of the valves: not applicable (0); straight (1); curved (2);
- 8 valves leave a gap: not applicable (0); no, close tightly (1); yes (2);
- 9 lobe L1: absent (0); present (1);
- 10 lobe L2: absent (0); present (1);
- 11 lobe L3: absent (0); present (1);
- 12 lobe L4: absent (0); present (1);
- 13 lobe L5: absent (0); present (1);
- 14 lobe L6: absent (0); present (1);
- 15 location of the valve spines: absent (0); centrally (1); antero-centrally (2); postero-centrally (3);
- 16 direction of the valve spines: absent (0); lateral (1); postero-lateral (2);

Character list cont.

- 17 outgrowths of the right shield margin: not present (0); present, short triangular outgrowth (1); present, distinct spine (2);
- 18 outgrowths of the left shield margin: not present (0); present, short triangular outgrowth (1); present, distinct spine (3);
- 19 groove at the outer rim of the shield: absent (0); present (1);
- 20 shield and its dorsal area: not applicable (0); all-embracing and univalved, without any hinge structures (1); all-embracing and bivalved, with a dorsal furrow (2); all-embracing and bivalved, with an interdorsum (3);
- 21 width of the interdorsum: not applicable (0); between 1/14 and 1/25 of the length of the valve (1); less than 1/25 of the length of the valve (2); more than 1/12 of the length of the valve (3);
- 22 interdorsum in cross-section: not applicable (0); flat (1); convex (2);
- 23 ornamentation on the median part of the interdorsum: not applicable (1); absent (2); present (3);
- 24 shape of the anterior dorsal ornaments of the dorsal rim: not applicable (0); absent (1); a triangular plate (2); hump-like thickening (3); dome-like thickening (4); short spine (shorter than or equal to one ninth the length of the valves) (5); long spine (longer than one eighth the length of the valves) (6);
- 25 direction of the anterior cardinal spine: not applicable (0); directed dorsally (1); directed antero-dorsally (2); directed anteriorly (3);
- 26 shape of the posterior ornaments of the dorsal rim: not applicable (0); absent (1); a triangular plate (2); hump-like thickening (3); dome-like thickening (4); short spine (shorter than or equal to one ninth the length of the valve) (5); long spine (longer than one sixth the length of the valves) (6);
- 27 direction of the posterior cardinal spine: not applicable (0); directed dorsally (1); directed postero-dorsally (2); directed posteriorly (3); directed postero-ventrally (4);
- 28 outgrowths on the anterior spine: not applicable (0); not present (1); present (2);
- 29 outgrowths on the posterior cardinal spine: not applicable (0); not present (1); present (2);
- 30 doublure: absent (0); present (1);
- 31 location of the minimum width of the doublure: not applicable (0); anteriorly (1); ventrally (2); posteriorly (3); anteriorly and posteriorly equally narrow (4); anteriorly and ventrally equally narrow (5);
- 32 location of the maximum width of the doublure: not applicable (0); anteriorly (1); medially (2); posteriorly (3); postero-ventrally (4); antero-ventrally (5);
- 33 maximum width of the doublure relative to the length of the valves: not applicable (0); less than or equal to 1/10 the length of the valves (1); between one sixth and one ninth the length of the valves (2); more than one fifth the length of the valves (3);
- 34 pits on the doublure: not applicable (0); not present (1); present (2);
- 35 small outgrowth structures on the doublure: not applicable (0); not present (1); conical, dome-like (2); bottle-like (3);
- 36 pores on the doublure: not applicable (0); absent (1); present (2);
- 37 parallel lines on the doublure: not applicable (0); absent (1); present (2);
- 38 segments of the body fused to the shield: 2 (0), 3 (1), 4(2), 5 (3), 6 (4), 7 (5), 8 (6), 9 (7), 10 or more than 10 (8);
- 39 length of the antennulae to the head: equal to or less than 1/4 (0), more than 1/4 (1);
- 40 segments of the antennulae; equal to or less than 14 (0); more than 14 (1);
- 41 limb stem of the antennae in younger stages: basipod only (0), proximal endite + basipod (1), coxa + basipod (2), coxa and basipod fused (3);
- 42 limb stem of the antennae in older stages: basipod only (0), proximal endite + basipod (1), coxa + basipod (2), coxa and basipod fused (3);
- 43 segments of endopod of the antennae: more than 7 (0), 7 (1), 6 (2), 5 (3), 4 (4), 3 (5), 2 (6), 1 (7);
- 44 limb stem of the mandibles in younger stages: basipod only (0), proximal endite + basipod (1), coxa + basipod (2), coxa and basipod fused (3);
- 45 limb stem of the mandibles in older stages: basipod only (0), proximal endite + basipod (1), coxa + basipod (2), coxa and basipod fused (3);
- 46 segments of endopod of the mandibles: more than 7 (0), 7 (1), 6 (2), 5 (3), 4 (4), 3 (5), 2 (6), 1 (7);
- 47 the design of the post-mandibular limbs: all the same, only different in size (0), at least on pair is different from the others (1);
- 48 limb stem of the first post-mandibular limbs in younger stages: basipod only (0), proximal endite + basipod (1), coxa + basipod (2), coxa and basipod fused (3);
- 49 limb stem of the first post-mandibular limbs in older stages: basipod only (0), proximal endite + basipod (1), coxa + basipod (2), coxa and basipod fused (3);
- 50 segments of endopod of the first post-mandibular limbs: more than 7 (0), 7 (1), 6 (2), 5 (3), 4 (4), 3 (5), 2 (6), 1 (7);
- 51 limb stem of the second post-mandibular limbs in younger stages: basipod only (0), proximal endite + basipod (1), coxa + basipod (2), coxa and basipod fused (3);

