Skara hunanensis a new species of Skaracarida (Crustacea) from Upper Cambrian (Furongian) of Hunan, south China*

Liu Jie and Dong Xiping**

(School of Earth and Space Science, Peking University, Beijing 100871, China)

Accepted on January 30, 2007

Abstract The fossils of Orsten-type preservation are as famous as Chengjiang Fauna in the world, but it was not until 2005 that the Orsten-type fossils represented by Skaracarida and Phosphatocopida were first reported to be found in western Hunan, South China. Here, we report the systematic paleontology of all the exquisitely preserved specimens belonging to Skaracarida. They were found at a same horizon of Upper Cambrian (Furongian) in Wangcun section, western Hunan, south China, assigned to a new species *Skara hunanensis* herein. *Skara hunanensis* is characterized by small, soft-integumented, marine forms with slender, annulate body; labrum large and ventrocaudally directed; uniramous antennulae; biramous antennae and mandibulae; maxillas and maxillipeds of the same shape; all postantennular limbs join a short cephalic filter apparatus. The body has two tagmata: a cephalon with five pairs of well developed appendages and a trunk composed of 11 ring-shaped conical segments.

Keywords: *Skara hunanensis*, **Skaracarida, Crustacea, Upper Cambrian, Furongian, Hunan.**

Fossils of Orsten-type preservation were first recovered in 1975 from the Upper Cambrian (Furongian)[1] of southern Sweden by Müller, the Cambrian conodont worker[2,3]. Typical fossils of Orsten-type preservation are dominated by three-dimensionally preserved soft-bodied Arthropods such as Skaracarida and Phosphatocopina. The mode of preservation is quite unusual: the imbedding animals were not flattened as in the Chengjiang Fauna, but they are preserved in three dimensions through secondary phosphatisation. Thus, those fossils look more like the living animals than the fossils of any other type of preservation. After more than twenty years of search for this type of fossils, Orsten-type preserved fossils have been found in China[4,5].

Indeed, the Orsten-type preserved Skaracarids through phosphatisation of cuticles without further diagenetic deformation[6] are quite rare. Before their discovery in Hunan, they had only been recovered from the Upper Cambrian (Furongian)[1] of Sweden[3]. The Skaracarids have also been reported from the Middle Cambrian of Poland[7], but there is only a single fragmentary specimen with a part of trunk. Studies on the *Skara* were firstly presented by Müller[8], and subsequently by Walossek. Müller established the genus *Skara* with the type species *Skara anulata*[9] in 1983. Two years later Müller and Walossek separated a group of small sized specimens at species level after re-examination. These small sized specimens were identified as another species named *Skara minuta*[3]. Here, we describe the third species *Skara hunanensis* of Skaracarida (Crustacean) from the Upper Cambrian (Furongian) of western Hunan, China. Because of their very fine mode of preservation, the small crustaceans reveal morphological details of high phylogenetic interest[10].

1 Geological and taphonomic setting

In South China, the Southeast stratigraphical Region is characterized by flyschoid formation. The Middle and Upper Cambrian are mainly composed of dolostone in the Yangzi stratigraphical Region (Only in the Langyashan subregion, the Middle and Upper Cambrian consist mainly of dolomitic limestone). The upper part of Middle Cambrian through Lowermost Ordovician is mainly made up of limestones in the Danzai-Baojing-Qinyang subregion of Jiangnan stratigraphical region, within which the well-developed and continuously deposited sections have been found in Western Hunan and Northwestern Hunan. Accordingly, Western Hunan and Northwestern Hunan

* Supported by National Natural Science Foundation of China (Grant Nos. 40572003, 40372001), the Laboratory of Paleobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Academia, Sinica (Grant No. 023106), and the Research Fund for Doctoral Program of Higher Education(Grant Nos. 20060001059, 2000000127)

** To whom correspondence should be addressed. E-mail: dongxp@pku.edu.cn

are the ideal areas for studying the Cambrian conodonts of South China. Since 1985, the second author has been studying the Cambrian through lowermost Ordovician conodonts as well as the interesting by-products from processing conodonts such as highly modified sponge spicules and Radiolaria in these areas. In our studied areas, there are mainly five types of lithology from Middle Cambrian Huaqiao Formation to the Lowermost Ordovician Panjiazui Formation as follows:

(1) Dark gray thin-bedded to medium-to thin-bedded laminated argilliferous very fine to fine crystalline limy dolostone. Only algae and protoconodonts almost without any other fossils occuring in this type of lithology.

(2) Alternate layers of dark gray medium-bedded laminated argilliferous dolostone, dark gray medium-bedded calcimicrite and biomicrite. The argilliferous dolostone yields only algae without any other fossils, whereas the limestones yield abundant conodonts as well as some trilobites, brachiopods and small-shelly fossils.

(3) Dark gray medium-bedded biomicrosparite, yielding extremely abundant conodonts as well as a number of trilobites, brachiopods and phosphatocopine bradoricopids, etc.

(4) Gray thick-bedded calcirudite. Trilobites have been found occasionally in the gravel and matrix. No conodont samples have been collected in this type of lithology.

(5) Dark gray medium-to thick-bedded micrite intercalated with dark gray medium-bedded laminated dolomitic calcisiltite, bearing organic matter and scattered pyrite. Burrow and bioturbation may be found. The sedimentary structure such as nodular structure and ptygmatic structure both formed by differential compaction is common in the field. The micrite yields abundant conodonts, as well as trilobites, brachiopods, small-shelly fossils, sponge spicules and radiolarians, etc.

So far, we have processed more than 8000 kg of limestone. The lifelike, three-dimensional fossils of typical Orsten-type preservation represented by Skaracarida, Phosphatocopida and unnamed larvae were recovered from the micrite of Type (5) in Wangcun section. The occurring horizon is 241 m higher than the bottom of Furongian Series[4], and within the conodont *Proconodontus* zone[5].

The micrite represents a deeper water setting along the marginal areas of the Cambrian sea (Yangtze Platform). Although the micrite in Hunan superficially looks like the Upper Cambrian (Furongian)[1] Orsten in Sweden[2,11], i.e. the nodules of bituminous limestone, in terms of dark colour and stinking smell, the facies of the Upper Cambrian (Furongian)[1] Orsten in Sweden is shallow water[11]. The experimental taphonomy of the soft parts of the marine animals as well as marine embryos and larvae[12—14] indicates that the soft parts of the marine animals and marine embryos preserved by early diagenetic impregnation and encrustation with calcium phosphate have taken place in reducing condition and the activity of anaerobic bacteria seems to have played a major role. Accordingly, the deeper water facies characterized by the micrite in Hunan may represent a stronger reducing condition than the facies of the Upper Cambrian (Furongian)[1] Orsten in Sweden.

2 Material and method

The samples were processed by routine etching with 10% technical acetic acid in plastic pail, 10000 cm^3 in volume. The cycle of sieving and changing acid is seven to ten days. The samples (including duplicate samples) generally need to be processed with three to four cycles, till they have been all dissolved. During the processing, the reaction time and the pH value of the solution are adjusted according to the lab temperature (around 20℃ in winter and up to 35℃ in July and August). All the samples for the soft-integumented fossils are processed in the plastic pails with two-layer screens recommended by Müller[11]. The residues are dried naturally by sunshine and wind rather than by heating machine such as oven to prevent the artifact of color alteration due to organic metamorphism[15]. Heavy-liquid techniques as well as interfacial and magnetic separation were avoided, because the delicate soft-integumented fossils would not have survived such a rough procedure[16]. All the dried residues are picked up by hands of lab assistants under optical stereo-microscopes.

3 Systematic paleontology

All the figured specimens of the present paper are deposited in Geological Museum of Peking University, China, GMPKU 2202, GMPKU 2206—

2207.

Class Crustacea, Brünnnich, 1772

Order Skaracarida Müller et Walossek, 1985

Family Skaraidae Müller et Walossek, 1985

Genus *Skara* Müller, 1983

Type species *Skara anulata* Müller, 1983

Skara hunanensis Dong sp. nov. (Figs. 1—5)

Skara sp. Dong et al., 2005 (in Chinese), p. 1231, Fig.4; Fig.5 (a), (b)

Skara sp. Dong et al., 2005 (in English), p. 1355, Fig.4; Fig.5 (a), (b)

Etymology—Named for its provenance in the Chinese province of Hunan.

Diagnosis—The body has two tagmata: a cephalon with appendages, and a trunk composed of 11 ring-shaped and conical segments and telson. The head shield is small and does not overhang the body. The forehead extends from the shield terminating in a tubular dorsofrontal process. The labrum is prominent, nose-shaped and posteroventrally directed.

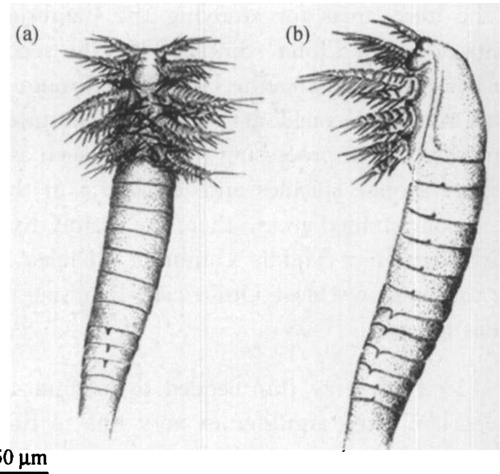

Fig. 1. Reconstruction of *Skara hunanensis*. (a) Ventral view; (b) lateral view.

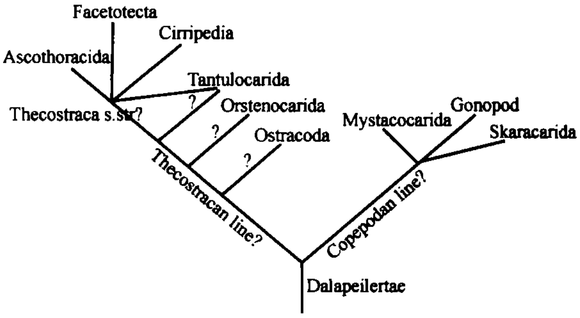

Fig. 2. Assumed phylogeny of the Maxillopoda, including Skaracarida and some other Orsten fossils. Question marks emphasize uncertainties (Modified after Müller et Walossek, 1998)

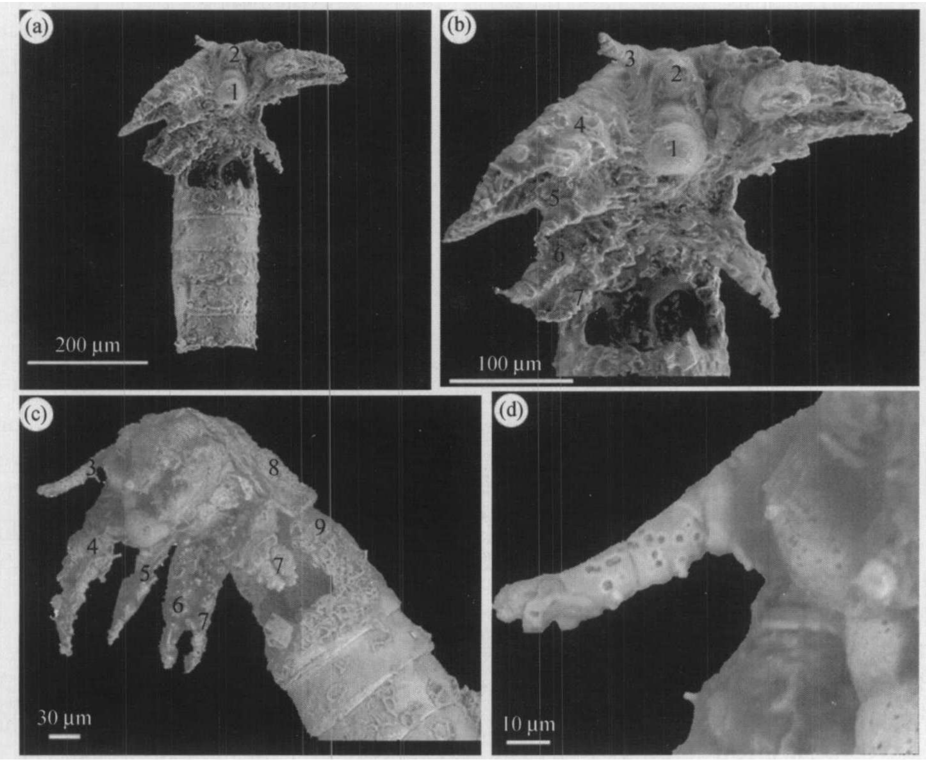

Fig. 3. ESEM of *Skara hunanensis* (specimen No. GMPKU2206) (1. labrum; 2. forehead; 3. antennula; 4. antenna; 5. mandibula; 6. maxillula; 7. maxilla; 8. shield; 9. trunk segment 1). (a) Ventral view of the anterior portion with well-preserved appendages; (b) enlarged view of the appendages and labrum; (c) lateral view of the anterior portion; (d) oblique lateral view of the antennula.

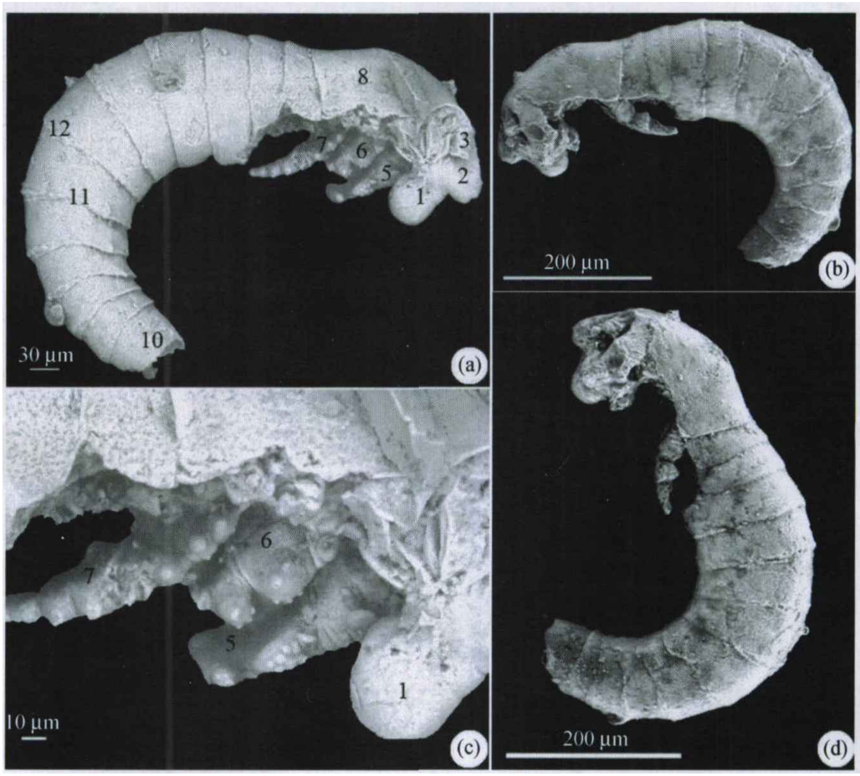

Fig. 4. *Skara hunanensis* (specimen No. GMPKU2202) (1. labrum; 2. forehead; 3. antennula; 5. mandibula; 6. maxillula; 7. maxilla; 8. shield; 10. telson; 11. attachment point; 12. arthrodial membrance). (a) Lateral view of the whole specimen, cephalic shield, prominent labrum and almost complete trunk; (b) and (d) another side of (a); (c) slightly oblique view of anterior portion, showing the details of the same specimen.

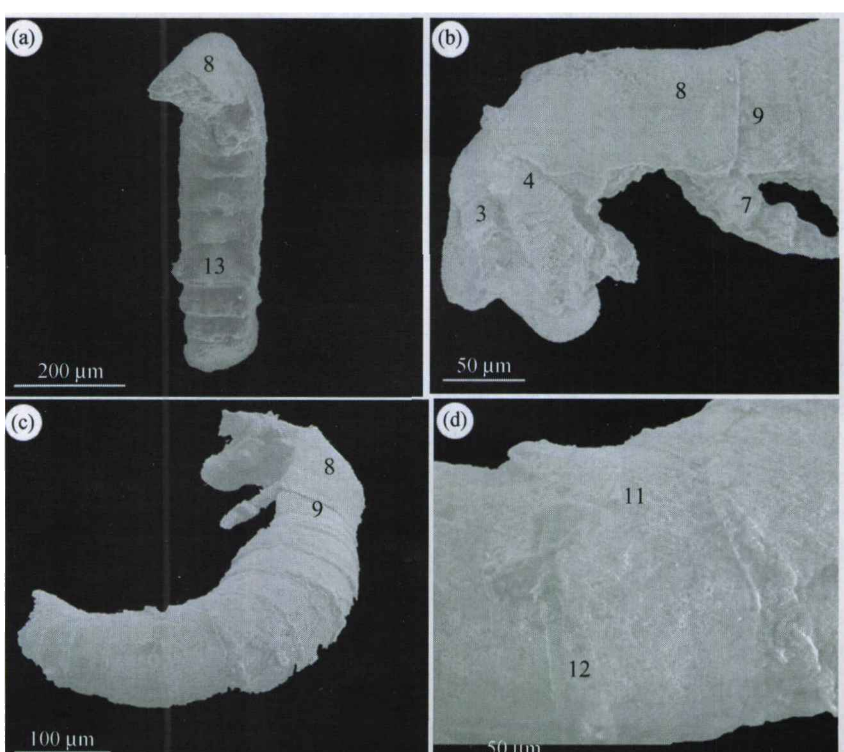

Fig. 5. ESEM photographs of some specimens in the material. (3. antennula; 4. antenna; 7. maxilla; 8. shield; 9. trunk segment 1; 11. attachment point; 12. arthrodial membrance; 13. spine). (a) Ventral view of the whole specimen; specimen No. GMPKU2207; (b) lateral view of the anterior portion; specimen No. GMPKU2202; (c) dorsolateral view of the whole specimen; specimen No. GMP-KU2202; (d) enlarged detail of (a), dorsolateral view of the segments 6—8.

Comparison—*Skara hunanensis* differs from the other two species strongly in size. Furthermore, they possess a large number of minute morphological differences which are regarded as distinct specific characteristics rather than simply expressing individual variability. All the major diagnostic features which permit the assignation of even fragments to one or the other two species are summarized in Table 1.

Table 1. Major morphological differences between *Skara anulata*, *Skara minuta* and *Skara hunanensis*[1]. Measurements in μm. (For *Skara anulata* and *Skara minuta*, modified after Müller et Walossek, 1985)

	Skara minuta					*Skara anulata*					*Skara hunanensis*				
Range of total length	490—970					1060—1360					600—1000?				
Shield(l/h/w)	135/60/90—190/85/135					250/80/145					165/85/125				
Pore below frontal organ	No					Yes					No				
Labrum: profile	Concave					Straight					Obviously concave				
Origin	Recessed					Slightly bulged					Bulged				
Lateral bulges	Distinct, rounded					Absent					Not very distinct, elliptical				
Agl with 'walled area	No					Yes					No				
Limbs: mandibular coxa	Grinding plate					2 masticatory spines					2 masticatory spines				
Endopodal podomeres	Width > length, tapering					Length > width, little tapering					Width > length, little tapering				
Postmandibular exopods	Rounded margins					Concave median margin					Rounded margins				
	a Ⅱ	md	mx1	mx2	mxp	a Ⅱ	md	mx1	mx2	mxp	a Ⅱ	md	mx1	mx2	mxp
Endites on coxa	1	1	3	* 4	2?	1	1	3	3	2?	1	1		4	
Setae on coxa (a Ⅱ, md)	3 + 4	gn + 1?				2 + 4	2				gn + 2				
Proximal endite (ml-mxp)			7	3 + 4	?			3	1	?					
Median endite (mx1-mxp)			6	3	?			1	1	?					
Distal endite (mx1-mxp)			5	6	?			2	2	1			5		
Setae on basipod	4	9	4	4	2	2	5	3	3	1		8	5		
S on end: proximal podomere	2	4	3	3	2	1	3	2	2	1				3	
Median podomere	2	3	3	3	2	2	2	2	2	1				3	
Distal podomere	2 + 2	2 + 2	5	4	4	1 + 2	1 + 2	4	3	3				4	
Setae on exopods	14	12	9	8	8	14	12	8 + 1	7 + 1	6					
Relation en/ex	en < 1/2ex	en > ex		en = ex		en = 1/2ex			ex < en		en < 1/2ex			en = ex	
Trunk:	Spindle-shaped, compact					Conical, slender					Little spindle-shaped, compact				
Segments: length decrease	o40-20/o60-30					80-60					55-30				
Width change of segments	Increase and decrease					Only decrease					Increase and decrease				
Range of membranous area	ts2 + anterior part of ts3					Only half of ts 2					ts2				
ts7-ts9: distance betw. sp	50/40/40					40/30/20					55/45/40				

1) The following abbreviations are used: a Ⅱ, antenna; agl, antennal gland; en, endopod; ex, exopod; gn, gnathobase; md, mandibula; mx1, maxillula; mx2, maxilla; mxp, maxilliped; s, seta; ts, trunk segment.

The slender *Skara anulata* Müller 1983 is 1.2 mm long and the *Skara minuta* Müller et Walossek 1985 is only 0.7 mm long. However, the length of *Skara hunanensis* is about 0.85 mm long between *Skara anulata* and *Skara minuta*. In addition to the difference in size and proportions of different features, the feeding aids of *Skara hunanensis* particularly serve as a feature to distinguish the species: the largest species has the longest limbs and fewest but strongest setae than the other species. Another one of the prominent differences of *Skara hunanensis* is: as the length decreases successively, the width first increases slightly from one segment to three or four and then tapers towards the end, which results in a little spindle-shaped habit of the trunk. While the width of the trunk segments of *Skara minuta* increases from one segment to six then tapers towards the end and *Skara anulata* slightly tapers only. The head shield of *Skara hunanensis* is small and does not overhang the body. The forehead extends from the shield terminating in a tubular dorsofrontal process. The labrum is very prominent, nose-shaped and posteroventrally directed.

Material—Four specimens

Holotype—Geological Museum of Peking University, Beijing, China: GMPKU2202, illustrated in Fig. 4(a—d).

Occurrence—Upper Cambrian in Wangcun section, Yongshun County, western Hunan, South China.

3.1 Description of the cephalon

3.1.1 Shield The soft shield comprises about 1/5 of the body length and covers only the five limb-bearing cephalic segments. The cross section approximates to an inverted U-shape. The shield lacks any ornamentation and its lateral rim fades anteriorly into the forehead; an anterior margin is absent. The rim starts above the antennae. It curves sharply ventrally to the maxillae. The caudal rim of the shield looks straight. Because of the sharp ventrocaudal corners and the straight caudal rim, the shield looks caudally truncated. The height of the shield is almost as long as wide. In contrast to *Skara anulata*, it is more arched and much shorter, causing the postantennular limbs to be nearer to each other. Fringes at the dorsocaudal rims of the shield and tergite are not developed. Below the caudal corners of the shield, the lateral cuticle turns directly into the shafts of the adjacent limbs. A pliable arthrodial membrane connects the shield and tergite. On the surface of the shield several shallow grooves can be seen. The grooves probably represent scars of musculature which attached underneath and ran towards limbs and labrum.

3.1.2 Forehead and labrum The forehead extends from the shield by about 1/5 to 1/4 of the shield length and is not distinctly separated from the shield. The frontoteminal process or organ is completely preserved in several specimens. It is assumed that the ventrally jointed, tubular organ could be moved up and down to some extent[3]. Posteroventrally the forehead broadens to a nose-shaped labrum. The latter comprises about 1/3 of the head length. Its base is laterally bulged, being bordered by shallow transverse furrows. Shallow depressions on the surface in front of the rounded posterior end of the labrum indicate the position of interior muscles which could move the labrum abaxially. There are some folds behind the furrows. The distal end of the nose-shaped labrum is broadly rounded, slightly depressed at the tip and overhanging the mouth region. Behind the recessed origin bordered by shallow transverse furrows, the side of the labrum is slightly or even not bulged.

3.2 Description of the appendages

Skara hunanensis has five pairs of well preserved cephalic appendages and maybe one pair of maxillipeds based on the specimens found in Sweden. As an exception of the antennulae, the limbs are attached beneath the shield rims, with the protopods being more or less ventrally directed. In most cases the distal portions of the setae have been omitted. Sometimes the setae on endites, basipods and endopodal podomeres are all broken off, only leaving the origins of them. Thus, they are drawn with their origins or with their proximal portions.

3.2.1 Antennula The uniramouse antennulae inserted in front of the starting point of the shield rims are the smallest appendages. They are almost cylindrical and composed of more than eight podomeres. The outer surface of the proximal portion is well sclerotized and shows a division into several short ringlets. The distal portion is composed of four tubular podomeres. The distal podomeres two, three and four bear one or two thin setae each on their median margins, and the distal segment two has another one on the outer surface. The distal podomere carries medially two thin setae, laterally a thin seta and terminally two strong ones.

3.2.2 Antennae and mandibulae These two pairs are the most prominent limbs. They have the same basic design. Their long exopods served as the main locomotory organs. The biramous antennae inserted below the starting point of the shield rims. The bases of the antennae reach the lateral sides of the labrum origin. They are slightly preoral. The outer surface of the antenna is well sclerotized, bearing a scale at its base and some nicked folds distally of it. The exopod inserts on the sloping diatolateral surface of the basipod which imports a slightly lateral orientation to the ramus. The exopod is composed of some ring-shaped podomeres. Each distal ones bear one rigid, postermedially directed seta. The protopod and endopod have some setae towards the mouth area. The three endopodal podomeres remarkably in size. The endopods reach less than half way up to the exopods. The width of the podomeres seems to be longer than its length.

The mandibula is inserted behind the posterolateral folds of labrum and looks quite similar to the antennae. The coxa has a slightly oblique gnathobase (shovel-like endite) which points posteromedially flanking the rounded distal end of the labrum. The coxa bears about three endites(or big folds). The elongate coxal endite has two pilose masticatory spines, one thick proximal and a less strong distal one. The basipodal endite is protruding and bears at least five setae. The width of the succeeding proximal podomeres is longer than the length and medially elongated into a setose process. The setae on basipod and endopodal podomere are broken off only leaving the origins of them.

3.2.3 Postmandibular appendages Apart from a successive size decrease, and related to this some minor differences in shape and armature with setae, the maxilles have the same design. As in antennae and mandibulae, the protopods are oval-shaped in cross section. In accordance with an oral orientation, they are successively more axially positioned. Some setae on endites, basipods and endopodal podomeres are all broken off, only leaving the origins of them. The shafts are medially soft and finely wrinkled. Due to their bulging endites, the coxa is medially enlarged and peg-like. The two maxillas bear three setose endites.

As illustrated in Fig. 3(b), the anterior and posterior sides of the protopods are differently designed. Anteriorly, the coax is uniform, but its distal margin runs on the posterior side medially down to the proximal endite. This separates the well sclerotized proximal portion with one endite from the distal one with the remaining two distally directed endites and the latter portion being soft and wrinkled. This part of the coxa probably functioned as a joint for the whole distal limb portion. The basipod is slightly divided by a shallow furrow into two portions and arises from the sloping back of the coxa: a median one towards the endopod, and an outer portion carrying the exopod.

The endopod is tube-shaped, having the same shape as the mandibula. It is composed of three podomeres. The three endopodal podomeres decrease sharply in size. The width of two proximal podomeres of the tri-segmented endopod is longer than length. All the endites are posteromedially elongated into a pilose spine. Medially they are also armed with a cluster of setae around. The terminal podomere bears three to four distally directed setae apically. In front of it, pilose setae curve towards the mouth and form a sieve from proximal to distal.

The exopods are uniform, rounded and leaf-like, and their median margins are almost straight. A seta develops in the maxilles. From lateral to terminal position the exopods bear more than four strong setae. The sizes of endopods are equal to the exopods.

All the major differences in shape and setation between the limbs are listed in Table 1, in comparison with *Skara anulata* and *Skara minuta*. Some of the exites are broken off (smooth surface of fracture with sharp-edged borders).

3.3 Description of the trunk

The slender trunk is composed of 11 ring-shaped segments and a telson. The telsons of all specimens are posteriorly broken off. There are some holes in the specimens which are caused by breakage, indicated by the sharp-edged margin. The uncovered cylindrical steinkern (sk) within the cavity appeared (Fig. 3(a); Fig. 4(b)). Some holes are filled with rough phosphatic matter which blur details.

3.3.1 Segment The first trunk segment carries a pliable tergite. The following segments are ring-shaped and almost circular in cross section. The segments are jointed each other by lateral attachment points, with the articulations being covered by pliable arthrodial membranes. The anterior six segments is about 55 μm long whereas from the 7th to 11th the length decreases successively to 30 μm. Again the diameter, which is 140 μm in the anterior three segments, decreases successively to 100 μm in segment 11. While the length decreases successively, the width and length both first increase slightly from segments one to three or four and then taper towards the end. This results in a little spindle-shaped habit of the trunk.

There is a hole in the anterior trunk of each specimen. It is maybe the pliable membranous area which is hard to be preserved. The ventral side of the presumed membranous area expands from the rims of shield to a small anterior part of segment three. Therefore, the entire ventral cuticle of segment two is pliable. This recession may provide space for the appendages when the trunk was ventrally curved. The trunk segments are not separated into tergites and sternites. The lateral attachment points divide the arthrodial membranes into distal and ventral portions, which probably indicate a former boundary between the two sclerites[5]. The cuticle close to the attachment points is very pliable, and in some cases muscle scars can be observed there.

It is presumed that the ventrocaudal rims of segments are adorned with a row of tiny fringes, because a piece of such fringes was preserved on a specimen. The fringes are composed of subordinate fibres. The ventrocaudal rims of segments seven to eleven are slightly and backwardly extended. The ventrocaudal rims of segments seven to nine bear three tooth-shaped, slightly lifted and posteriorly directed spines (Fig. 5(a)). In accordance with the successive size decrease of the segments, the spines become smaller too. The distance between the lateral spines and the shorter median one also decreases.

4 Discussion

Skara is a primitive soft-integument crustacean, which was mainly found in the dark limestone of southern Sweden. Two species of the genus have been described previously, *Skara anulata* Müller 1983 and *Skara minuta* Müller et Walossek 1985. The specimens herein recovered from Hunan are referred to as genus *Skara* on the basis of the following characters: small, soft-integumented, marine forms with slender, annulate body. The body has two tagmata: a cephalon with five pairs of well developed appendages; small dorsal shield of about 1/5 to 1/4 of the total length; forehead with moveable, rod-shaped frontoterminal process; eye absent; labrum large and ventrocaudally directed; uniramous antennulae, shorter than the succeeding limbs; biramous antennae and mandibulae, with one coxal endite and multisegmented exopods; maxillas and maxillipeds of the same shape, their exopods being paddle-shaped; all postantennular limbs join a short cephalic filter apparatus and a trunk composed of 11 ring-shaped conical segments.

Therefore, the specimens from Hunan are closely comparable to the earliest specimens known from Upper Cambrian (Furongian)[1] Orsten *Skara* in Sweden. The specimens studied here are similar in most characters to *Skara minuta* Müller et Walossek 1985, but have many differences. The slender *Skara anulata* Müller 1983 is 1.2 mm long and the *Skara minuta* Müller et Walossek 1985 is only 0.7 mm long. However, the length of *Skara hunanensis* is about 0.85 mm between *Skara anulata* and *Skara minuta*. In addition to the difference in size and proportions of different features, the feeding aids of *Skara hunanensis* particularly serve as a feature to distinguish the species: the largest species has the longest limbs and fewest but strongest setae than the other species. Another one of the prominent differences of *Skara hunanensis* is, as the length decreases successively, the width first increases slightly from segments one to three or four and then tapers towards the end. This results in a little spindle-shaped habit of the trunk. The width of the trunk segments of *Skara minuta* increases from one to six and then tapers towards the end and *Skara anulata* slightly tapers only. *Skara hunanensis* is also characterized by the following features: The head shield is small and does not overhang the body. The forehead extends from the shield terminating in a tubular dorsofrontal process. The labrum is very prominent, nose-shaped and posteroventrally directed. We think *Skara hunanensis* is the sister group of the *Skara minuta* Müller et Walossek 1985 found in Sweden, and belongs to the same genus. They are assigned to a new species *Skara hunanensis* herein. The Hunan species has exquisitely preserved limbs and trunks (tripartite endopods), thus enhancing the ground pattern character set[17,18] of the Skaracarida (autapomorphy, and plesiomorphic within the group).

No larvae are known for all species of Skaracarida. It is possible that these animals changed to a life at or near the bottom after a series of pelagic larval stages[17]. In such cases, larvae were not preserved, most likely due to life in a different regime.

5 Conclusions

The morphology of the Hunan material provides evidence for the occurrence of *Skara* and thereby three-dimensionally preserved Crustacea, including Eucrustacea[19] in the continent of Gangwana in the late Cambrian.

Skara hunanensis has exquisitely preserved limbs and trunks (tripartite endopods), thus enhancing and reinforcing the ground pattern character set of the Skaracarida (autapomorphy, and plesiomorphic within the group). These remarkable fossils found in Hunan not only complete the portfolio of spectacular fossil preservation for China, but also open a window to the evolution and development of Arthropods. Therefore, their discovery is as important as the discovery of the Chengjiang Fauna for the knowledge of the early evolution of the Arthropoda, particularly the

Crustacea.

Acknowledgements We thank Guo Wei for field assistance, Philip Donoghue, Dieter Walossek and Liu Zheng for discussion, Wu Feixiang for technical help.

References

1 Maas A, Braun A, Dong XP, et al. The "Orsten"—More than a Cambrian Konservat-Lagerstätte yielding exceptional preservation, Palaeoworld, 2006, 15: 266—282

2 Müller KJ. Phosphatocopine ostracodes with preserved appendages from the Upper Cambrian of Sweden. Lethaia, 1979, 12(1): 1—27

3 Müller KJ and Walossek D. Skaracarida a new order of Crustacea from the Upper Cambrian of Vätergötland, Sweden. Fossils & Strata, 1985, 17: 1—65

4 Dong XP, Donoghue PCJ, Liu Z, et al. The fossils of Orsten-type preservation from Middle and Upper Cambrian in Hunan, China. Chinese Science Bulletin, 2005, 50(12): 1228—1233

5 Dong XP, Bergstrom SM and Repetski JE. Conodont biostratigraphy of the Middle Cambrian through Lowermost Ordovician in Hunan, South china. Acta Geologica Sinica, 2004, 78 (6): 1185—1206

6 Butterfield NJ. Exceptional fossil preservation and the Cambrian Explosion. Integrative and Comparative Biology, 2003, 43: 166—177

7 Walossek D and Szaniawski H. *Cambrocaris baltica* n. gen. n. sp., a possible stem-lineage crustacean from the Upper Cambrian of Poland. Lethaia, 1991, 24(4): 363—378

8 Müller K J. Arthropods with phosphatized soft parts from the Upper Cambrian "Orsten" of Sweden. II. International Symp. Cambrian System; U. S. Dept. Int. Geol. Surv., 1981: Open-File Report 81—743, 147—151

9 Müller KJ. Crustacea with preserved soft parts from the Upper Cambrian of Sweden. Lethaia, 1982, 16: 93—109

10 Waloszek D. The "Orsten" window—a three-dimensionally preserved Upper Cambrian meiofauna and its contribution to our understanding of the evolution of Arthropoda. Paleontological Research, 2003, 7(1): 71—88

11 Müller KJ. Exceptional preservation in calcareous nodules. Philosophical Transactions of the Royal Society of London B, 1985, 311: 67—73

12 Briggs DEG. Experimental taphonomy. Palaios, 1996, 10: 539—550

13 Briggs DEG and Kear AJ. Fossilization of soft tissue in the laboratory. Science, 1993, 259: 1439—1442

14 Briggs DEG and Wilby PR. The role of the calcium carbonate-calcium phosphate switch in the mineralization of soft-bodied fossils. Journal of the Geological Society, London, 1996, 153: 665—668

15 Epstein AG, Epstein JB and Harris LD. Conodont color alteration—An index to organic metamorphism, U. S. Geological Survey (Professional paper), 1977, 995: 1—27

16 Müller KJ and Hinz I. Upper Cambrian conodonts from Sweden. Fossil and Strata, 1991, 28: 1—153

17 Walossek D and Müller KJ. Cambrian "Orsten"-type arthropods and the phylogeny of Crustacea. In: Arthropod Relationships (ed. Fortey RR and Thomas RH), London: Chapman and Hall, 1997, 139—153

18 Walossek D and Müller KJ. Early arthropod phylogeny in the light of the Cambrian "Orsten" Fossils. In: Arthropod Fossils and Phylogeny (ed. Edgecombe G), New York: Columbia University Press, 1998, 185—231

19 Walossek D. On the Cambrian diversity of Crustacea. In: Proceedings of the 4th International Crustacean Congress. Leiden, Netherlands, 1999, 3—27