Cambrian trilobite *Ovatoryctocara* Tchernysheva, 1962 from Siberia

Elena Naimark, Yuriy Shabanov & Igor Korovnikov



At present the species of the genus *Ovatoryctocara* Tchernysheva, 1962 are important stratigraphic markers of the boundaries between the traditional lower and middle Cambrian strata of Siberia. However, the vague taxonomic concept of the species and the lack of clear illustrations, which might demonstrate intraspecies variability, make the solution of the stratigraphic objective difficult. In regards to these problems, the genus has been revised on the basis of collections from east Siberian sections. Emended diagnoses for *O. ovata* (Tchernysheva, 1960), *O. granulata* (Tchernysheva, 1962), *O. angusta* (Tchernysheva, 1962), including subspecies *O. angusta snegirevae* (Suvorova, 1964), and *O. doliiformis* Korovnikov & Shabanov, 2008 are provided. In addition, the similarity between Siberian representatives of *O. granulata* and the specimens from South China and Greenland is established, based on meraspid morphology. Revision of the species shows that in the River Molodo section, *O. granulata* appears 20–25 cm higher than was previously documented.• Key words: Cambrian, Siberian sections, GSSP Series 2 and 3, *Ovatoryctocara*, intraspecies variability.

NAIMARK, E., SHABANOV, Y. & KOROVNIKOV, I. 2011. Cambrian trilobite *Ovatoryctocara* Tchernysheva, 1962 from Siberia. *Bulletin of Geosciences 86(3)*, 405–422 (7 figures, 1 table). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received December 23, 2010; accepted in revised form July 28, 2011; published online September 19, 2011; issued September 30, 2011.

Elena Naimark, Paleontological Institute RAS, Profsoyuznaya 123, Moscow, Russia; naimark@paleo.ru • Yuriy Shabanov, SNNIIGGiMS, Krasny pr. 67, Russia, Novosibirsk; shabanov36@mail.ru • Igor Korovnikov, Inst.NGiG n.a. A.A.Trofimuk, pr. Acad. Koptuga 3, Novosibirsk, Russia; KorovnikovIV@ipgg.nsc.ru

N. Tchernysheva (1962) established *Ovatoryctocara* as a subgenus of *Oryctocara* Walcott, 1908, with a type species *Oryctocara ovata* Tchernysheva, 1960. She described two other species of this subgenus: *O*. (*Ovatoryctocara*) granulata Tchernysheva, 1962 and *O*. (*Ovatoryctocara*) angusta Tchernysheva, 1962, using material exclusively from several locations in Eastern Siberia, those of the Malaya Kuonamka and Olenek rivers. N. Suvorova (1964) reclassified this group of species and elevated it to generic level by separating it from *Oryctocara geikei* Walcott, 1908. Furthermore she added two new other species to *Oryctocara: O. snegirevae* and *O. majensis*, both from Eastern Siberia.

For a long time scholars had put aside the genus *Ovatoryctocara*, with the exception of H. Wittington (1995), who mentioned it as he had been revising Oryctocephalida from North America. It was only later that a new species *O. doliiformis* Korovnikov & Shabanov, 2008 from Molodo section, was described. Blaker & Peel (1997) merged species *O. granulata* and *Arthricocephalus chauveaui* Bergeron, 1899, as the result of their research of the material from Greenland. At the same time these authors described another species of the genus as *Ovatoryctocara* sp. A. The synonymy list of *Ovatoryctocara* sp. A included Siberian specimens of *O. granulata*, held apart from the

This regrouping was made because *Ovatoryctocara* and *Arthricocephalus* have similar morphology, thus a number of researchers supposed that *Ovaroryctocara* was a close relative to the *Arthicocephalus* (Fletcher 2003, Suvorova 1964, Wittington 1995), while others consider it a direct descendant of the latter (Yuan *et al.* 2001, 2002). *Shergoldiella vincenti* Geyer, 2006, the type and the only species of the genus, is also close to *Ovatoryctocara*. Recently another species "*O. yaxiensis*" Yuan *et al.*, 2009, was supposed, and its type specimens were separated out from the Chinese material on *O. granulata* (Yuan *et al.* 2009). However, this species has never been formally described. Therefore, this name is considered invalid and we put it in quotas.

holotype and paratypes described by Tchernysheva (1962).

Species of *Ovatoryctocara* are found close to the boundary of the traditional Lower and Middle Cambrian of Siberia. That's why the research of this genus has once again been highlighted, and *O. granulata* was considered to be a useful index-species for determining the lower boundary of the Series 3, Stage 5 (Babcock *et al.* 2005; Fletcher 2003, 2007; Geyer 2005). Researchers identified *O. granulata* from a variety of sections in South China (Yuan *et al.* 2002), Greenland (Blaker & Peel 1997) and



Figure 1. The map shows the sections within the Kuonamka Formation, where representatives of the *Ovatoryctocara* have been found. Numbers indicate the follow sections: 1 – Malaya Kuonamka River; 2 – Nekekit River; 3 – Amyday River; 4 – Boroylakh River; 5 – Torkukuy River; 6 – Olenek River; 7 – Molodo River; 8 – Muna River; 9 – Maya River, 10 – Olenek River (Arga-Sala Brook). Dotted line – the boundary of Siberian Platform.

Newfoundland (Fletcher 2003). O. granulata and Oryctocara aff. granulata have been identified by Butov et al. (2003) and Yazmir et al. (1975) from the Altay section (Buryatia). Supplementing this, sections in Siberia geographically enriched the collection of Ovatoryctocara, produced new finds from Muna, Amygay, and Molodo rivers, as well as from previously studied locations. Therefore, the clear understanding of the taxonomic limits of the genus and O. granulata in particular became the key objective of this study. Taxonomic definition would help to identify FAD of O. granulata for various distant locations. In order to solve this problem we need to clarify both intraspecific and growth variability of O. granulata, as well as its taxonomic boundaries within the genus. Otherwise any deviation from the holotype would become the basis for the introduction of the endemic varieties, a case that is highly probable considering the condition of the preservation and long distances between locations. In this case stratigraphic correlation based on a formal species identification may become impossible.

Therefore, this work takes into account the material

from a variety of East Siberian sections and offers taxonomic analysis of the *Ovatoryctocara* representatives and the revision of the genus and species.

Material

This study uses specimens of *Ovatoryctocara* collected from different East Siberian localities, which occur near the proposed GSSP of Series 3 (Fig.1). These localities are Amyday, Muna, Malaya Kuonamka, Molodo, Torkukuy, Maya, and Tokur-Udga rivers. Description of these sections are contained in Bachturov *et al.* (1988) in the following pages: Amyday (p. 20), Muna (p. 12), Malaya Kuonamka (Uylegir-Uyryakh, p. 32), Tokur-Udga (p. 33, and Soloviev 1960), Molodo (p. 19, and Shabanov *et al.* 2008a), Torkukuy (p. 26), and Maya (p. 50). Faunal content of the sections is provided in Savitsky *et al.* 1972. The collections are stored in Novosibirsk: Siberian Institute of Scientific Researches on Geology, Geophysics and Mineral Resources (SNIIGGiMS), Central Siberian Geological Museum (CSGM), St. Petersburg: F. Tchernyshev Central State Geological Museum Museum (CSG), Moscow: Pale-ontological Museum (PIN).

Everywhere the beds containing *Ovatoryctocara* fall within the *Ovatoryctocara* Zone, except in the Molodo section, the distribution in this section is wider going to the Kounamkites Zone. The precise position of the beds is: Muna – points 66/I-z is 90 cm below the base of *Kounamkites* Zone, 66/II-3a – 10 cm below the base of *Kounamkites* Zone; Amyday: points 11/I-4a – shales 4.5 m below *Kounamkites* Zone; Torkukuy – point 17/I-6a the base of the *Ovatoryctocara* Zone, Uylegir-Uyryakh – points 24/6b from the base of the *Ovatoryctocara* Zone, 24/4v – the middle part of the *Ovatoryctocara* Zone.

Sections Torkukuy, Maya, and Tokur-Udga contain the type material for *O. angusta, O. majensis*, and *O. granulata*, respectively. We have chosen the typical and adult specimens for the illustrations. Growth variability of *O. granulata* was studied using abundant material from river Amyday, point 11/2-5a. The collection from this point appears to be monospecific, reducing the potential mixing of juveniles from different species. In general, meraspids demonstrate different properties from adults' morphology, and therefore lack species and even genus diagnostic characters. Other horizons from where two-three species were identified, this risk becomes comparatively high.

As a result the diagnoses of four Siberian species were emended: O. ovata, O. angusta, O. granulata, and O. doliiformis, as well as the old and new material has been supported with appropriate illustrations. Ovatoryctocara? majensis which has never been mentioned in modern literature, is also compared with these four species. The taxonomic concept of O. angusta is changed considerably. It is very likely that this species is the most primitive representative of Ovatoryctocara; in the Molodo section it appeared earlier than other four species. O. angusta subdivided to two subspecies O. angusta sbsp. angusta (Tchernysheva, 1962) and O. angusta sbsp. snegirevae (Suvorova, 1964). The former shows significant similarity with both ?O. majensis and Shergoldiella vincenti. A lack of complete exoskeletons or/and pygidia prevents an accurate and more meaningful comparison of O. angusta, ?O. majensis and Shergoldiella.

In the Molodo section the earliest *Ovatoryctocara* representatives belong to *O. angusta snegirevae*. At point 14a, 20–25 cm above the base of *Ovatoryctocara* Zone, the FAD of *O. granulata*, and the species ranges to the middle of the *Kounamkites* Zone. In the middle and upper part of *Ovatoryctocara* Zone (point 18a) two other species appear. *Ovatoryctocara* Zone, while *O. ovata* ranges into the *Kounamkites* Zone together with *O. granulata* and above the latter species.

Elena Naimark et al. • Cambrian trilobite Ovatoryctocara from Siberia

Systematic palaeontology

Family Oryctocephalidae Beecher, 1897 Subfamily Oryctocarinae Hupé, 1953

Genus Ovatoryctocara Tchernysheva, 1962

Type species. – Oryctocara ovata Tchernysheva *in* Kryskov *et al.* (1960), from the *Ovatoryctocara* Zone, Tokur-Udga River, the Anabar Basin, near Malaya Kuonamka, Siberian Platform, Russia.

- 1962 Oryctocara (Ovatoryctocara) Tchernysheva; Tchernysheva, p. 37.
- 1964 Ovatoryctocara (N. Tchernysheva, 1962). Suvorova, p. 242.
- 1972 Oryctocara (Ovatoryctocara) Tchernysheva, 1962. Savitsky et al., p. 76.
- 1976 Oryctocara (Ovatoryctocara) Tchernysheva, 1962. Egorova et al., p. 96.
- 1995 Oryctocara (Ovatoryctocara) Tchernysheva, 1962. Geyer & Palmer, p. 461.
- 1995 Ovatoryctocara Tchernysheva, 1962. Whittington, p. 556.
- 2002 Ovatoryctocara Tchernysheva, 1962. Yuan et al., p. 124 (251).

Diagnosis. – Small oryctocephalid; proparian or gonatoparian facial suture; cranidium wide, glabella subcylindrical or slightly expanded in the middle part or/and in the anterior lobe; S1–S4 are triangular or round pits, S1 and S2 connect with axial furrows by short grooves, S4 weak, transverse glabellar furrows as shallow depressions; preoccipital lobe and lateral glabellar lobes are absent; preocular areas are short but well developed, eye ridges are short; posterolateral projections of fixigenae comparatively long (sag.); palpebral area of fixigenae of narrow or moderate width. The thorax consists of 4–5 segments. Isopygous or macropygous, pygidium consists of 6–12 rings; interpleural furrows are well developed; the border is absent or wire-like thin. The surface may be either granulose or genal caeca or smooth.

Comparison. – Ovatoryctocara differs from *Arthricocephalus* Bergeron, 1899, and *Euarthricocephalus* Ju, 1983, by a combination of glabellar characteristics; well-developed preocular fields (absent in two latter), comparatively narrow palpebral areas (wider in two latter), short eye ridges (longer in two latter) and, S1–S3 less pronounced (well pronounced in two latter). The number of thoracic segments in *Ovatoryctocara* is less than in *Arthricocephalus* and *Euarthricocephalus* (4–5 against 6–8), but number of pygidial rings is increased (7–12 against 4–7).

Oryctocara is diagnosed as having a wider glabella, the presence a preoccipital (or intervening) lobe and a lateral occipital lobes well defined, as well as an opistoparian or gonatoparian facial suture, shorter posterolateral projections of the fixigenae, a wider palpebral area of fixigenae, and a shorter pygidium.

Sandoveria Shergold, 1969 differs by the glabellar shape tapering forward, the linear shape of S1–S4 with the distinct transverse furrows and an occipital ring with a deep occipital furrow. Ovatoryctocara doliiformis has wide posterolateral fixigenae and a comparatively short preocular area similar to Sandoveria. But in Sandoveria the posterolateral projections of the fixigenae are wider and preocular areas of fixigenae are absent. In addition, Sandoveria has a greater number of thoracic segments and decreased number of pygidial rings.

Similar to *Sandoveria*, *Shergoldiella* Geyer, 2005 has more thoracic segments and fewer pygidial rings. The morphology of this monospecific genus bears the greatest similarity to *Ovatoryctocara*, and a detailed comparison is provided in the description of *O. angusta*. G. Geyer (2005), who has summarized the differences of his genus as follows; glabella of similar outline but a more constricted at frontal lobe, a greater adaxial position of the eye lobes and a greater number of thoracic segments. The two former traits occur among *Ovatoryctocara* species, it is only the latter allows the separation of the genus. The taxonomic rank of this morphological feature – a number of thoracic segments – appears to be a determinate. As this feature is not enough reliable, the diagnosis of *Shergoldiella* needs to be revised.

Remarks. – There are three versions of the genus diagnosis. The first one is the original diagnose of Tchernysheva (1962) which was slightly modified by Suvorova (1964). This combined version is based on data from Siberian occurrences. The second set of diagnostic attributes by Whittington (1995) emphasized those features valuable for separation of *Oryctocara* and *Ovatoryctocara*. The third diagnosis by Yuan *et al.* (2002) and reflects a wider diversity of Oryctocarinae Hupe, 1953, known from the South China localities. Therefore these differences, both in base material and research objectives, resulted in very few similarities of these three sets of diagnostic features. Only three features appear to be shared between all three versions (Table 1).

The common features are the proparian facial suture (the distinction between *Oryctocara* with gonatoparian suture and *Metarthricocephalus* with opistoparian suture) and a lack of a pygidial border (the distinction from *Arthricocephalus*). Also the authors agreed on the enlarged size of a pygidium. Authors' opinions concerning the genal spine do not agree, though all authors included this character in a generic diagnosis. According to Tchernysheva and Suvorova the genal spine is present, Chinese and British authors postulated its definite absence. Probably, researchers differed in understanding the terms of a spine condition.

Five additional coincidences occur in Russian and Chinese diagnoses (Table 1). The narrow palpebral area of a fixigenae seems to be the most reliable character. The direction of the palpebral lobes (Fletcher 2003 notes the angle between the eye ridges and palpebral lobes, as 40°) is reliant on the width of the palpebral area, thus the character is derived. Tchernysheva & Suvorova indicated that the cephalon as wider than the thorax with a comparatively wide cranidial border furrow. They used these features to separate the new genus (subgenus) from *Oryctocara geikei*. The same features allow differing *Ovatoryctocara* from *Arthricocephalus* and *Metarthricocephalus*.

Fletcher added to his diagnosis one more important character feature, that is the width of preocular fields. This feature helps to distinguish cranidia *Arthricocephalus* and *Euarthricocephalus* from *Ovatoryctocara*. But it is worth noting that this feature changes during ontogenetic development and looks different in immature and mature specimens. In juveniles the preocular fields are underdeveloped and are extremely short, the eye ridges almost merge with anterior margin of a cranidium. That is why immature cranidia approach the appearance of *Oryctocara*, *Sandoveria*, and *Arthricocephalus*.

Comparison of the diagnoses elicits the characteristic features distinguishing Ovatoryctocara representatives from other Oryctocarinae. According to the emended diagnosis above, the generic assignment of Oryctocara snegirevae Suvorova, 1964 and O. majensis Suvorova, 1964 should be revised. Only the cranidia of these species are known and have been described, though Oryctocara snegirevae is supplemented with the meraspid pygidia description. Both species lack glabellar lobes L1, the occipital furrow not deepened medially and without lateral occipital lobes which is typical for Ovatoryctocara, and they bear 4 round glabellar pits, of which S1-S3 join with axial furrows. The features mentioned allows us to ascribe the species to Ovatoryctocara. Oryctocara's features are a gonatoparian facial suture, and a transverse S1, which is more expressed than S2-S4. Here the gonatoparian suture is considered transitional between opistoparian and proparian, and therefore may be included into generic diagnosis of Ovatoryctocara. In Oryctocara snegirevae and O. majensis the transverse S1 is not expressed as distinctly as in Oryctocara geikei, and here such a manifestation of S1 is also included into the generic diagnosis. The only craniduim and no pygidia are known for Oryctocara majensis, thus there is no possibility to define the variability of the diagnostic features. However the morphology is closest to Ovatoryctocara than to other genera. Here the generic assignment is left open.

Thus, the diversity of *Ovatoryctocara* comprises eight species: *O. ovata*, *O. granulata*, *O. angusta*, *O. snegirevae*,

Table 1. The diagnostic characters of the genus Ovatoryctocara Tchernysheva, 1962 pointed out by different authors. Shared features are shown in bo	old.
---	------

Tchernysheva (1962), Suvorova (1964)	Yuan et al. (2002)	Whittington (1995), Fletcher (2003)
cranidium wide and exceeds the width of a thorax	ζ.	
S1–S4 with weak transverse furrows, S1 close to axial furrows	S1–S4 just inside axial furrows, S1–S3 are more or less connected by transverse furrows	
posterolateral projections both long and wide, almost equi-wide to the distal ends , with genal spine	posterolateral limb broad, genal spine absent	genal angle rounded and lacking a spine
posterior marginal furrow wide		
palpebral lobes short oblique and incurvate	palpebral lobes short, situated anteriorly	
anterior border wirelike convex	anterior border very short, wirelike convex	
4 thoracic segments	4 –5 thoracic segments	4 thoracic segments
axial width in a pygidium is near one-fourth of a pygidial		
pleural furrows wide, somehow oblique	pleural furrows deep, interpleural furrows distinct	
thoracic pleurae with acuminate ends	pleurae with rounded terminal ends	
pygidium with subserrate margin	border absent	border absent
pygidium is longer than cephalon	isopygous	pygidium long
glabella subcylindrical	glabella long, subcylindrical or slightly expanded forwardly	anterior glabellar lobe comparatively wide (wider than in <i>Arthricocephalus</i>)
fixed cheeks narrow between palpebral lobes	fixed cheeks very narrow between palpebral lobes	
pygidium with 9-12 rings	pygidium with 7-12 rings and a terminal piece	10– 12 segments
proparian facial suture	proparian facial suture	proparian facial suture
	occipital furrow deep, laterally isolating from axial furrows and shallower medially	
	axis narrower than pleural lobe	
	granulate sculpture	sculpture absent except a network of fine ridges; granulate sculpture may present
	lateral glabellar lobes absent	preoccipital lobe and lateral glabellar lobes absent
		eye ridge passes posteriorly at the angle of appr. 40 degrees from anterior glabellar lobe
		preocular genal region short but exists

O. doliiformis, "O. yaxiensis" and *?Ovatoryctocara majensis.* In addition the form *Ovatoryctocara* sp. A described from North Greenland locations should be taken into consideration.

Ovatoryctocara ovata (Tchernysheva, 1960) Figure 2A–G

- 1960 Oryctocara ovata Tchernysheva, 1960 in Kryskov et al., p. 220, pl. 51, figs 4–6.
- 1962 Oryctocara (Ovatoryctocara) ovata Tchernysheva, 1960; Tchernysheva, p. 37, pl. 4, figs 1–4.
- 1972 Oryctocara (Ovatoryctocara) ovata Tchernysheva, 1960. – Savitsky et al., p. 76, pl. 16, figs 6–9.
- 1976 Oryctocara (Ovatoryctocara) ovata Tchernysheva, 1960. – Egorova et al., p. 96, pl. 46, figs 15, 16, pl. 48, fig. 17.
- 1964 Ovatoryctocara ovata (N. Tchernysheva, 1960). Suvorova, p. 244, pl. 27, fig. 17.

- 2008 Ovatoryctocara ovata (N. Tchern., 1960). Korovnikov & Shabanov, p. 86, pl. 2, fig. 12, pl. 4, figs 9, 14, pl. 5, fig. 15, pl. 6, figs 10, 12.
- 2008 Ovatoryctocara granulata (N. Tchern., 1962). Shabanov et al., pl. 3, fig. 12.
- 2008 Ovatoryctocara granulata (N. Tchern., 1962). Korovnikov & Shabanov, pl. 2, fig. 12.

Holotype. – Exoskeleton, No. 2-4/9180, CSM, St. Petersburg, East Siberia, Malaya Kuonamka River, lowermost Amagian; Tchernysheva (1960), pl. 51, fig. 4.

Material. – Numerous complete exoskeletons, cranidia and pygidia from rivers Malaya Kuonamka, Amyday (point 11/1-4a), Muna, Nekekit, Molodo.

Diagnosis. – Glabella subcylindrical or widening to anterior margin, with four round pits, S1, S2 often connected with axial furrows; preocular area well developed and comparatively wide, posterolateral projections of fixigenae

long (trans.), exceed the widest measure of a thorax. Pygidium is round-triangular shape, nearly half of the shield length, axis consists of 10–12 rings. Surface smooth, or with faint genal caeca.

Comparison. – The species are readily recognizable among other *Ovatoryctocara* species by its triangular-shaped, non-granulated pygidium and by the smooth cephalon. The granulated surface characterizes two other species (or three if *O. yaxiensis* appears to be valid) and, therefore, separates them from the nongranulated species. *O. angusta* also has a non-granulated surface, but differs by comparatively short and narrow posterolateral projections of fixigenae. Besides, in *O. ovata* the glabella is usually expanded in its anterior part; its preocular areas are wider, while in *O. angusta* the glabella is expanded in its middle, its preocular areas are reduced in width.

Occurrence. – Malay Kuonamka, Amyday, Muna, Olenek, and Nekekt rivers, *Ovatoryctocara* Zone, Molodo River, *Ovatoryctocara*, and *Kounamkites* zones.

Ovatoryctocara angusta (Tchernysheva, 1962) Figures 3A–G, 4A–F

1962 Oryctocara (Ovatoryctocara) angusta N. Tchernysheva, 1962; Tchernysheva, p. 39, pl. 4, figs 9–12.

Holotype. – The cranidium, St. Petersburg, CSM, No. 43/8194, East Siberia, Malaya Kuonamka River, the lowermost Amagian, *Ovatoryctocara* Zone, Tchernysheva (1962), pl. 4, fig. 12.

Material. - See the descriptions of subspecies.

Diagnosis. – Glabella subcylindrical, slightly expanded in the middle part and slightly convergent to the anterior margin. S1 is developed better than S2–S4, and expressed in more or less transverse direction, bending rearward. Preocular areas well developed, eye ridges start at S4 or slightly anterior; palpebral lobes directed obliquely and comparatively long. Posterolateral projections of fixigenae are short and narrow, and lack the genal spine. Surface smooth, though some specimens may have irregular asperity due to preservation (Fig. 3B, D, F). *Comparison.* – The narrow and short posterolateral projections of the fixigenae and shortened preocular areas separate *O. angusta* from *O. ovata*. The glabella of *O. angusta* tends to be more constricted in the anterior part, and bears a more pronounced S1 bend rearward. Unlike *O. granulata*, *O. doliiformis*, "*O. yaxiensis*", *Ovatoryctocara* sp. A, this species does not have the granulation.

Ovatoryctocara angusta and ?O. majensis are similar in several ways. They can be distinguished by the glabella, which is more constricted in its anterior in the latter species. This shape predetermines the position of the pairs of glabellar pits situated along exsagittal lines; in O. angusta the pairs of pits are arranged in more or less parallel lines, and in ?O. majensis in convergent lines. The pygidia of both species are unknown. The lack of pygidia makes it difficult to distinguish Shergoldiella vincenti (Fig. 3H) from O. angusta and ?O. majensis. All three species are characterized by a convergent anterior part of the glabella, more or less expressed through the rearward bending of the transverse S1, and by the round glabellar pits. The original description of Shergoldiella indicates three main differences that are; a narrowing anterior glabellar lobe, short preocular areas, and an increased number of thoracic segments. The two former features are common with both O. angusta and ?O. majensis. The similarity between ?O. majensis and S. vincenti appears to be even more dramatic. The shape of S4 with the deep embayment of axial furrows seems to be the only diagnostic feature in a cranidium for S. vincenti. Geyer (2005) did not include this feature into generic diagnosis as it is probably species-specific. Therefore, due to the lack of the pygidia of O. angusta or ?O. majensis, Shergoldiella and Ovatoryctocara cannot be decidedly separated. There is a continuous morphological transition from S. vincenti to O. ovata progressing through ?O. majensis and O. angusta.

It is just as likely that the transient species, ?O. majensis, could be included in Ovatoryctocara, as in Shergoldiella, and here we leave the matter somewhat unresolved, placing it in Ovatoryctocara.

Remarks. – The description of *Ovatoryctocara angusta* was based on four cranidia, while no pygidia were found. The original diagnosis (Tchernysheva 1962, p. 39) mainly referred to the holotype. It indicates narrow (sag.) posterolateral projections of fixigenae, bending up and with rounded distal angles, oblique eye ridges, anteriorly placed

Figure 2. *Ovatoryctocara ovata* (Tchernysheva, 1960) from different East Siberian sections. • A – complete exoskeleton, CSG Museum coll. 401-E, river Tokur-Udzha, rephotographed by Tchernysheva (1962), pl. 5, fig. 1, 10.1 mm. • B – cranidium, SNIIGGiMS 66/I-z#1, Muna River, 1.5 mm. • C – cranidium, SNIIGGiMS 24/4v#1, Olenek (Uylegir-Uyryakh), 3 mm. • D – cranidium, SNIIGGiMS 66/I-z#2, Muna River, 5.3 mm. • E – SNIIGGiMS 66/I-z#3, Muna River, pygidium, 3.1 mm. • F – cranidium, Novosibirsk CSGM 980/54, Molodo River, point 06/14, 5.1 mm (the same as Korovnikov & Shabanov 2008, pl. 4, fig. 9). • G – pygidium, SNIIGGiMS, 24/4v#2, Malaya Kuonamka (Uylegir-Uyryakh), 6.6 mm.

В C D Е F G

Elena Naimark et al. • Cambrian trilobite Ovatoryctocara from Siberia

long palpebral lobes, an expanded L1 glabellar lobe, and a smooth surface of the shield. That diagnosis separated the new species from the type species O. ovata. Other adult paratype specimens do not fit the diagnosis completely. Specifically, the distance between tips of L1 may be narrower than that of L2 or L3, also the posterior margin of the cranidium is sometimes straight and not bending up. The direction of the posterior margin most probably reflects the preservation of a convexity of the cranidium. In addition, there is variation in the length of the palpebral lobe. Unfortunately, the type collection in the CSM in St. Petersburg could not be found; thus we were not able to reinvestigate them. However, there is a collection from the Torkukuy locality situated very close to the Malaya Kuonamka section used for this study. The bed 17/1-1-6a in Torkukuy contains numerous specimens of O. angusta, which fit both the species description and the images of type specimens.

Ovatoryctocara angusta shows considerable similarity with O. snegirevae. The correct identification of these forms is only possible in a sample large enough to estimate the variability. Extreme forms of O. angusta and O. snegirevae seem quite identical. Accordingly, we have assigned O. snegirevae as a subspecies. Therefore, O. angusta is subdivided into the two subspecies: O. angusta angusta and O. angusta snegirevae. ?O. majensis is morphologically more similar to O. angusta angusta.

Ovatoryctocara angusta angusta (Tchernysheva, 1962) Figure 3A–F

1962 Oryctocara (Ovatoryctocara) angusta N. Tchernysheva, 1962; Tchernysheva, p. 39, pl. 4, figs 9–12.

Holotype. – Cranidium, Novosibirsk, SNIIGGiMS No. 17/1-1-6a#1, Torkukuy River, point 17/1-1-6a, *Ovatoryc*-*tocara* Zone, Fig. 3A.

Material. – Nearly twenty cranidia of good preservation from Torkukuy River, two juvenile pygidia.

Diagnosis. – Glabella with the tendency to narrow in its anterior part, posterolateral projections of fixed cheeks comparatively long (tr.), posterior marginal furrow without triangular widening at the distal ends.

Comparison. – The *O. angusta angusta* differs from the other subspecies by the more convergent anterior part of the glabella as opposed to the parallel sided glabella in *O. angusta snegirevae*. The former one has longer (tr.) fixigenae and the rear margin is more or less straight, whereas the latter has shorter posterolateral projections sometimes bending slightly up. The posterior furrow in

the cranidia of *O. angusta angusta* is uniform, whereas the posterior margin in *O. angusta snegirevae* has triangular incurvation at two-thirds the length of the fixigenae.

Remarks. – The differences between the two species appear as averaged morphological trends and may be detected only in a large number of specimens. Two pygidia existed in the collection are too small (less than 1 mm, Fig. 3C) for any meaningful comparison or for the judgement about species-specific features.

Occurrence. – Malaya Kuonamka and Torkukuy rivers, the lower part of *Ovatoryctocara* Zone.

Ovatoryctocara angusta snegirevae (Suvorova, 1964) Figure 4A–F

- 1964 *Oryctocara snegirevae* Suvorova, p. 236, pl. 27, figs 1, 9–15.
- 2008a Ovatoryctocara granulata (N. Tchern., 1962). Shabanov et al., pl. 2, figs 2, 3.
- 2008 Ovatoryctocara granulata (N. Tchern., 1962). Korovnikov & Shabanov, pl. 1, figs 2, 3.

Holotype. – Cranidium, Moscow, PIN No. 1788/56, Malaya Kuonamka River, lowermost Middle Cambrian (without precise position), Suvorova (1964), pl. 27, fig. 1.

Material. – Six cranidia from the collections N1778 and 709 from Maya River (Suvorova 1964, p. 6), 2 cranidia from Malaya Kuonamka, 2 cranidia from Molodo River.

Diagnosis. – Posterolateral projections of fixed cheeks shorter and bent slightly upward, posterior margin of a cranidium bears triangular incurvation in its distal part, glabella more or less subcylindrical.

Comparison. – The comparison was discussed above, within *O. angusta angusta*. The cranidium of this subspecies bears greater similarity to *O. ovata* because of its subcylindical shape of a glabella, but it differs due to its shorter posterolateral parts of fixigena, the fixigenae are narrower between palpebral lobes, and the transverse furrow S1 is more expressed. This species differs from *O. granulata* in having a nongranulated surface and shorter posterolateral parts of fixigena. *O. granulata* sometimes shows either a more or a less developed transverse S1, and the granulation may be blurred out due to insufficient preservation (Fig. 5H). Therefore the two species can be distinguished by the length of posterolateral projections of fixigenae, and the length of palpebral lobes (they are longer and more oblique in *O. angusta snegirevae*).

Elena Naimark et al. • Cambrian trilobite Ovatoryctocara from Siberia



Figure 3. Ovatoryctocara angusta angusta (Tchernysheva, 1962) from different East Siberian sections (A–F) and close species (G, H). • A – cranidium (holotype), SNIIGGiMS 17/I-6a#1, Torkukuy River, 2.7 mm. • B – SNIIGGiMS 17/I-6a#2, Torkukuy River, 2.8 mm. • C – pygidium, SNIIGGiMS 17/I-6a#3, Torkukuy River, 0.9 mm. • D – SNIIGGiMS 17/I-6a#4, Torkukuy River, 1.3 mm. • E – SNIIGGiMS 17/I-6a#5, Torkukuy River, 1.7 mm. • F – SNIIGGiMS 17/I-6a#6, Torkukuy River, 2.5 mm. • G – ?Ovatoryctocara majensis (Suvorova, 1964), cranidium (holotype), Moscow, PIN N1766/41 (Suvorova 1964, pl. 27, fig. 16), Maya River (Innikan), 3 mm. • H – Shergoldiella vincenti Geyer, 2005, part of the holotype complete exoskeleton, scale bar 1 mm (from Geyer 2005, fig. 3D).

Remarks. – The conception of the species was based on a few cranidia and also several meraspid cranidia and pygidia were described as paratypes. Rock samples in the type collection of *O. snegirevae* contain numerous specimens of *Cheiruroides* and frequent meraspid cranidia and pygidia. N. Suvorova ascribed the juveniles to *O. snegirevae*, but they are too small and frequent to be referred to as such without some doubt. That is why we did not include some of Tchernysheva's immature cranidia to the synonymy list.

Two specimens, identified as *O. granulata* from the base of the *Ovatoryctocara* Zone, layer 4a (Shabanov *et al.* 2008a, pl. 2, figs 2, 3, here Fig. 4E) demonstrate more similarity with *O. angusta snegirevae*. These two cranidia were assigned to *O. granulata* because of faint granulation. This was thought to be a form of the normal granulation, but effaced via preservation. Except very faint granulation all other features fit the diagnosis of *O. angusta snegirevae*.

One specimen (Fig. 4F) represents the cast of small complete exoskeleton, which shows 6 thoracic segments. If this specimen is the example of normal adult tagmata subdivision, then Ovatoryctocara representatives may bear more the 4–5 thoracic segments and this feature should be excluded from the generic diagnosis.

Occurrence. – Maya River, Amayday horizon, Molodo River, Zone *Ovatoryctocara* (point 4a, 14a), Malaya Kuonamka River, *Ovatoryctocara* Zone (point III-24/6b) (Fig. 4E, F).

Ovatoryctocara doliiformis Korovnikov & Shabanov, 2008

Figure 5C-G

- 2008 *Ovatoryctocara* sp.; Shabanov *et al.*, pl. 6, figs 1–3, pl. 8, figs 3, 4.
- 2008 Ovatoryctocara doliiformis Korovnikov & Shabanov; Korovnikov & Shabanov, p. 87, pl. 5, figs 1–3, pl. 7, figs 3, 4.
- 2008 Ovatoryctocara granulate (N. Tchern., 1962). Korovnikov & Shabanov, pl. 7, figs 5–7.
- 2008a Ovatoryctocara granulata (N. Tchern., 1962). Shabanov et al., pl. 8, figs 5, 7, 8.

Holotype. – Cranidium, Novosibirsk, CSGM, No. 980/90, East Siberia, Molodo River, *Ovatoryctocara* Zone, Korovnikov & Shabanov (2008), pl. 7, fig. 4. *Material.* – Several cranidia and pygidia (one with thoracic segments), two casts of near complete exoskeletons questionably assigned to the species. All came from Molodo section, the upper stratum of the *Ovatoryctocara* Zone, beds 20, 20a, 8 (Shabanov *et al.* 2008a).

Diagnosis. – Glabella expanded in the middle part, very short preocular areas, comparatively wide (sag.) and short (tr.) posterolateral projections of fixigenae, consequently palpebral lobes oblique and shifted forward; straight or bending upward posterior margin of a cranidium. Pygidium with very thin margin. Coarsely granulated surface of the exoskeleton.

Comparison. – Ovatoryctocara doliiformis differs from *O. ovata* and *O. angusta* by the granulation of their exoskeleton. In cases when the granulation is effaced as a result of preservation, the difference manifests in short and wide (sag.) posterolateral projections of fixigenae, and in preocular fields of fixigenae that are much shorter than in the two smooth species. The pygidium of *O. doliiformis* is granulated and shorter (6–8 rings) in comparison with *O. ovata*.

Much more difficulties are encountered when distinguishing O. doliiformis from O. granulata and "O. yaxiensis". All three species exhibit the granulation on their cranidia, pygidia, and thorax. Ovatoryctocara doliiformis has the glabella expanded in its middle, and a more pronounced transverse S1, S2 and especially S3. The granulation in O. doliiformis is coarser than in O. granulata. However, these attributes appear as an average morphological design and not necessary a standard of each O. doliiformis specimen. More reliable attributes for making the distinction include posterolateral projections of fixigenae, very short preocular areas of fixigenae, and a thin border on the pygidial margin. Posterolateral projections are shorter and also wider (sag.). The shape of the fixigenae makes the palpebral lobes shift upward therefore they occupy a more anterior position, and preocular fields of fixigenae contracted in comparison with O. granulata.

It should be emphasized that juvenile cranidia of *O. granulata* demonstrate many characters similar to *O. doliiformis* (see below in the discussion of *O. granulata*). No reliable feature could be indicated to separate *O. granulata* meraspids from *O. doliiformis*. A pygidium

Figure 4. *Ovatoryctocara angusta snegirevae* (Suvorova, 1964) from different East Siberian sections. • A – cranidium (paratype), Moscow, PIN N1178/105 (Suvorova 1964, pl. 27, fig. 15), Olenek River (Arga-Sala), 2.8 mm. • B – cranidium (holotype), Moscow, PIN N1178/56 (Suvorova 1964, pl. 27, fig. 1), Olenek River (Arga-Sala), 2.8 mm. • B – cranidium (holotype), Moscow, PIN N1178/56 (Suvorova 1964, pl. 27, fig. 1), Olenek River (Arga-Sala), 3 mm. • C – cranidium (paratype), Moscow, PIN N1178/63 (Suvorova 1964, pl. 27, fig. 13), Olenek River (Arga-Sala), 1.4 mm. D – pygidium, Moscow, PIN N1178/38a, 0.8 mm. • F – cast of complete exoskeleton (inverted image), SNIIGGiMS, Molodo River, sample 14a, 5 mm. • E – cranidium, Molodo River, 4a (the same as *O. granulata* in Korovnikov & Shabanov 2008, pl. 1, fig. 2), 3.1 mm. • G – the cast of the cranidium, SNIIGGiMS, 24/6b, Malaya Kuonamka (Uylegir-Uyryakh), 2 mm.

Elena Naimark et al. • Cambrian trilobite Ovatoryctocara from Siberia



of *O. doliiformis* is a more confident way to identify the species. Even very small pygidia bear the wire-like border (Fig. 5G) and they usually have indistinct (smoothed) segmentation on the postaxial field behind the terminal piece or/and gentle embayment of the margin on the pygidial rear. The granulation of small pygidia is slightly coarser than those in pygidia of *O. granulata*.

Remarks. – This species resembles *Euarthricocephalus* Ju, 1983, but differs strikingly with a narrow palpebral area of fixigenae, it lacks the pronounced transverse S1 and lateral lobes L1, its short genal spines are absent, and the thorax has less segments. Therefore the similarity is superficial only. This species can be considered as transient between *Euarthricocephalus* and *Ovatoryctocara*.

Ovatoryctocara doliiformis also shares some common characters with *Sandoveria*, but again the resemblance is quite superficial (Fig. 5H). Though *Sandoveria* has granulated shields and wide (sag.) posterolateral projections, other features are different. These are the width of fixigenae, the shape of a glabella, the shape of occipital ring and S1, the number of axial rings both in the thorax and the pygidium. As the representative of *Sandoveria* was found in the Siberian Platform (Fig. 5H), we presumably suspect the presence of *Sandoveria* in the Molodo section as well. One pygidium from the Molodo section shows a good resemblance to the *Sandoveria* specimen, especially its balb-like posteroaxial terminal piece (*Ovatorycrocara* sp. in Shabanov *et al.* 2008a, pl. 8, fig. 10, Korovnikov & Shabanov 2008, pl. 7, fig. 10).

As there is a deficiency of material on the species, its concept is more or less amorphous and allows the inclusion of some questionable samples. There are the casts of two complete shields of very bad preservation (here Fig. 5A, B) and among them are two cranidia, assigned earlier to *O. granulata* (Korovnikov & Shabanov 2008, pl. 7, figs 5, 6). The casts have the specific shape of posterolateral fixigenae and pygidial border, but lack the widening in the middle part of the glabella. Here we assign the difference to very bad preservation of the casts. Two cranidia mentioned above may be referred either to *O. granulata* or to *O. do-liiformis*: their posterolateral fixigenae is a little too wide to be "granulata", and their glabella is slightly too slim to be "doliiformis".

Occurrence. – East Siberia, Molodo River, the upper strata of *Ovatoryctocara* Zone.

Ovatorycrocara granulata (Tchernysheva, 1962) Figures 6A–H, 7A–K

1962 Oryctocara (Ovatoryctocara) granulata; Tchernysheva, p. 40, pl. 5, figs 6–8.

- 1972 Oryctocara (Ovatoryctocara) granulata N. Tchernysheva, 1962. – Savitskiy et al., p. 77, pl. 16, fig. 10.
- 1976 Oryctocara (Ovatoryctocara) granulata N. Tchernysheva, 1962. – Egorova et al., p. 96, pl. 43, figs 15–17.
- 1997 Ovatoryctocara sp. A.; Blaker & Peel, pp. 114, 115, figs 65, 66, 67 (5).
- 2002 Ovatoryctocara sp.; Yuan et al., pl. 31, fig. 8.
- 2002 Ovatoryctocara granulate Tchernysheva, 1962. Yuan et al., p. 125 (252), pl. 31, figs 10–13.
- 2003 Ovatoryctocara granulata Tchernysheva, 1962. Fletcher, p. 98, fig. 2C–F.
- 2005 Ovatoryctocara granulata Tchernysheva, 1962. Geyer, pp. 85, 86, fig. 2 (1-3).
- 2008a Ovatoryctocara granulata (N. Tchernysheva, 1962).
 Shabanov et al., pl. 2, fig. 1, pl. 8, figs 1, 2, 5(?), 6–9, pl. 10, figs 8, 9.
- 2008 Ovatoryctocara granulata (N. Tchern., 1962). Korovnikov & Shabanov, pp. 85, 86, pl. 7, figs 1, 2, 5 (?), 7–9, pl. 9, figs 8, 9.
- ?2009 Ovatoryctocara yaxiensis Yuan, 2009; Yuan et al.,
 p. 216, fig. 4a–e. (= Ovatoryctocara granulata Yuan et al., 2002, pl. 31, figs 11, 12).

Holotype. – Cranidium, St. Petersburg, SGM No. 46/8194 (coll. 401-E), East Siberia, Olenek River, lowermost Amgaian Stage, Tchernysheva (1962), pl. 5, fig. 7.

Material. – Numerous specimens from Molodo and Muna rivers, abundant material from Amyday River.

Diagnosis. – Small oryctocephalid with granulated sculpture. Glabella subcylindrical or slightly expanded medially; S1 situate close to axial furrow or connect with it; S2 are shifted somehow further from axial furrows, but connected with them by thin grooves; S3 may or may not connect with the axial furrows while very week S4 adjacent to axial furrow; transverse furrows straight, expressed as shallow depressions in the glabellar relief. Preocular fields developed, though narrow, posterolateral projections of fixigenae are of middle width both sagitally and transversely, palpebral areas of fixigenae comparatively narrow or moderate in size, palpebral lobes directed parallel or obliquely to glabella, posterolateral projections straight or bend rearward. Pygidial axis consists of 7–9 rings, pleuras lack border.

Comparison. – Most difficulties arise from the comparison between *O. doliiformis*. As mentioned above, adult specimens of *O. doliiformis* characterized by wider (tr.) posterolateral projections of fixigenae and shorter preocular parts of the frontal limb. Probably two species can be distinguished by the size of granulation, but this feature largely depends on preservation. Immature cranidia of *O. doliiformis*



Figure 5. Ovatorycrocara doliiformis Korovnikov & Shabanov, 2008 (A–G) and Sandoveria sp. (H). • A – O. ?doliiformis, near complete cast of the exoskeleton, SNIIGGiMS, Molodo River, point 8, 3.75 mm. • B – O. ?doliiformis, near complete cast of the exoskeleton, SNIIGGiMS, Molodo River, point 20, 4 mm. • C – cranidium, SNIIGGiMS, Molodo River, point 8 (the same as Ovatoryctocara sp. in Shabanov et al. 2008a, pl. 8, fig. 3), 2 mm.
• D – cranidium, CSGM No. 980/85 (the same as O. granulata in Korovnikov & Shabanov 2008, pl. 7, fig. 6), Molodo River, point 8, 1.8 mm.
• E – cranidium, SNIIGGiMS, Molodo River, point 20a, 1.6 mm. • F – cranidium, SNIIGGiMS, Molodo River, point 8, 1.7 mm. • G – pygidium, SNIIGGiMS, Molodo River, point 20a, 1 mm. • H – Sandoveria sp., complete exoskeleton, SNIIGGiMS, from Molodo River, limestone scree, 9 mm.

are unknown, but immature cranidia of *O. granulata* have comparatively wide posterolateral fixigenae and eye ridges are situated very close to the anterior margin. As these two features seem to be the main differences between *O. granulata* and *O. doliiformis*, the identification of species based on immature cranidia is questionable. Therefore, identification of juveniles of these two species is possible via analysing pygidia until data on juvenile specimens of *O. doliiformis* becomes available.

Remarks. - Some specimens among Chinese material of O. granulata were isolated to the separate species. This species got the formal name O. yaxiensis Yuan, 2009 but was never formally described. This species was diagnosed by the following main features (Yuan 2009, p. 213): "glabella club-shaped, slightly expanded medially, with four pairs of lateral furrows, of which S1–S3 are triangular pits, S4 is shallow, connecting with axial furrow; shorter palpebral lobe situated a little anterior to the midway of facial suture across the fixigenae, longer posterolateral area (exsag.); semielliptical pygidium consisting of seven axial rings with a terminal piece and with eight pairs of marginal tips giving a sawtooth-like shape of the lateral margins in dorsal view". The diagnostic characters, mentioned in the original description fall within the diagnosis of O. granulata. Among the main differential features, is the number of axial rings in a pygidium (precise number is 8) and the chevron-shaped glabellar S1–S3. But the former characteristic is still O. granulata's feature, albeit with wider limits (6-9 rings), and the latter is a subject of intraspecies variability (see for comparison Fig. 6C, D: O. granulata with chevron-shaped S2-S3) and is somewhat dependant on its preservation. The second matter that should be mention is the immature morphology of "O. yaxiensis" type specimens (Yuan et al. 2002, pl. 31, figs 10, 12), and it is quite difficult to extrapolate the development of morphology in "O. yaxiensis". Juveniles of O. granulata do not have their species-specific characters, consequently any identification of immature specimens of different species would be doubtful. Therefore there are no reliable character states to separate these two species. Probably with the acquisition of new adult specimens of "O. yaxiensis", the definition of this species will improve.

Some samples from Chinese material, shown on Yuan *et al.* 2002, pl. 29, figs 4, 5 (the same as in Yuan *et al.* 2001b, pl. 1, fig. 5), probably correspond to another species. It differs in a more pronounced glabellar S3, S4 transverse furrows, and smoothed rings on the axis. These traits never appear in *O. granulata* either immature and mature forms. Two mentioned specimens have more pronounced longitudinal glabellar grooves between S1–S3, although the feature occurred in *O. granulata*, although not as deep. The information about two specimens illustrated under the generic name *Ovatoryctocara* sp. (Yuan

et al. 2002, pl. 31, figs 7, 9) is too poor and details could not be deciphered. Therefore it seems to be impossible to determine both the species and genus level of these specimens.

The two illustrated specimens - a cranidium and pygidium - known from Newfoundland (Fletcher 2003), represent O. granulata (Geyer 2005, pp. 85, 86). The cranidium has an anterior margin slightly bent forward, developed preocular fields, S1-S3 as round pits, eye ridges starting at the level S4, S1 and S2 connecting to axial furrows with short thin grooves, and bears short palpebral lobes. The convex shape of the cranidium reflects its preservation in limestone. Most specimens from river Amyday have convex cranidia with their posterolateral projections of fixed cheeks covered by matrix or broken. The convexity of the Newfoundland pygidium is similar to that one from Amyday, shown on Fig. 6B. The convexity of the "granulata" pygidium differs from those of "ovata" pygidium (compare with Fig. 2F, both preserved in limestone).

The specimens from Altay, which had been identified as Ovatoryctocara aff. granulata (Yazmir et al. 1975, pl. 31, figs 8, 9), probably belong to another species. Though descriptions are lacking in this paper and the images are very small and indistinct, but it is possible that the specimens on his fig. 8 maybe referred to Sandoveria or Euarthricocephalus, and that one on his fig. 9 - to Arthricocephalus or to some new species of Ovatoryctocara. More recent report of *Ovatoryctocara* from Altay can be found in the description of fossils from Buryatia (Butov et al. 2003). There are two specimens, referred to Oryctocara granulata (pl. 42, figs 4, 5) and one specimen with a supposed affinity to O. granulata (pl. 43, fig. 3). The latter one (Oryctocara aff. granulata) is most probably ascribed to Arthricocephalus chauveaui, while the former two (Oryctocara granulata) belong to Euarthricocephalus or Metarthricocephalus. This material needs to be reviewed, because the species indicate taxonomic similarity with South China and Nevada.

Variability. – While analyzing the material from different locations we have determined the following limits of both adult and ontogenetic (growth variability) intraspecies variability.

There are cranidial features that vary among adult representatives of the species: Posterior margin of a cranidium is straight (Fig. 6A, E, G, F, H) or curved rearward (Fig. 6D, H); posterior border furrow is uniformly wide or slightly widens at two-thirds of its length (Fig. 6D, H). A glabella is more or less subcylindrical (Fig. 6G) or expands medially (Fig. 6A, C, D, H) or anteriorly (Fig. 6E, F). The anterior margin is slightly convex (Fig. 6A, C, E, G, H) or may be straight with the faint hint of concavity (Fig. 6D, F); which depends on the original convexity of the glabella.

Elena Naimark et al. • Cambrian trilobite Ovatoryctocara from Siberia



Figure 6. *Ovatorycrocara granulata* (Tchernysheva, 1962) from different East Siberian sections. • A – cranidium (paratype Tchernysheva 1962, pl. 5, figs 6–8), St. Petersburg, CSG Museum coll. 401-E, Tokur-Udzha River, 2.8 mm. • B – pygidium, SNIIGGiMS, Muna River, 66/II-3a#1, 3 mm. • C – cranidium, SNIIGGiMS, Amyday River, 11/2-5a#1, 2.2 mm. • D – cranidium, SNIIGGiMS, Amyday River, 11/2-5a#2, 2.9 mm. • E – cranidium, SNIIGGiMS, Amyday River, 11/2-5a#3, 2 mm. • F – cranidium, SNIIGGiMS, Molodo River, bed 27 (the upper point with this species), *Kounamkites* Zone, 3.1 mm. • G – cranidium, SNIIGGiMS, Molodo River, bed 14a (the lower point with this species), 2.3 mm. • H – cranidium (shows different preservation of the left and right projections of fixigenae), SNIIGGiMS, Molodo River, bed 18a, 2.5 mm.

The more convex the glabellar anterior the straighter or concave the glabellar margin becomes when flattened. The length of posterolateral projections of fixigenae ranges from long (Fig. 6D, F) to moderate (Fig. 6A, E, G), but their width stays more or less uniform.

The width of palpebral areas of fixigenae also changes insignificantly. The position of palpebral lobes shifts from almost parallel to glabellar sides (Fig. 6D) to oblique (Fig. 6C). Genal spine is well expressed (Fig. 6C, D) or absent (Fig. 6A, E). The longitudinal grooves connecting S1–S3 deepen differently (compare Fig. 6D and H). The granulation may depend on the preservation; for example, the granulation on the left and right posterolateral projections of the specimen on the Fig. 6H looks different due to the preservation. Even poor preservation keeps the relicts of granulation.

The variation in pygidial characters occurs in the number of axial rings and the shape of the pygidium. The number of axial rings is usually 6–7, but sometimes increases up to 9 and in small pygidia up to 11; those in small pygidia are difficult to calculate precisely, because there are unreleased thoracic rings in the anterior part and underdeveloped rings in the rear part. The vital shape of a pygidium is fairly convex, therefore flattened pygidia may vary due to preservational distortion; however it never becomes very wide in the anterior part. Interpleural furrows are always visible but may have slightly different depth. Also the relative width of the axis ranges from narrow (0.25 of a pygidial width) to moderate (0.36) values (probably the wider axis' result from postmortal flattening and therefore widening).

Ontogentic changes creates significant difficulties for identifying the species. Very abundant material available from Amyday River contains both numerous adult and immature specimens (Fig. 7A). Only the species *O. granulata* was found in this sample, therefore there is very little risk of mixing juveniles of different species. This limited risk is important as juveniles often do not bear species-specific characters until certain size, and thus may be easily define erroneously.

Cranidia of juveniles (up to 1 mm long) has an arthricocephalid appearance (Fig. 7F–H). The similarity consists in expanded anteriorly and typical transverse segmentation of the glabellar shape, position of the palbebral lobes and eye ridges shifted forward. The main difference that allows the separation of *Ovatoryctocara* meraspid cranidia is in the narrow palpebral areas of fixigenae.

The cranidia of some larger size (1–1.3 mm) resemble both *Arthricocephalus* and *O. doliiformis* (Fig. 7I–K). They share S1–S3 positioned close to the axial furrows and very short underdeveloped preocular areas, and a well-expressed anterior wire-like border.

The number of axial rings in a transitory pygidium

changes as the growth advances. Both incipient and unreleased thoracic rings are discernable in a transitory pygidium (Fig. 7B). There is no information concerning the scenario of the addition and releasing of segments in *Ovatoryctocara* representatives. Thus the counting of rings in *Ovatoryctocara* juveniles appears meaningless.

When comparing immature specimens of the same size from different regions, the similarity becomes evident. Figure 7C–K demonstrates meraspid cranidia and pygidia of more or less the same size from Siberia, China, and Newfoundland. The earliest cranidia, as mentioned above, have an arthricocephalid appearance with transverse S1–S4, and lacking preocular fields, present comparatively wide palpebral areas of fixigenae, as well as oblique and long palpebral lobes. The difference in these earliest meraspids consists in the expression of transverse S1–S4, the form of the granulation, besides, the posterolateral projections in the cranidium from China (Fig. 7G) seems wider (sag.).

The larger cranidia bear S1–S3 connecting with axial furrows, the width of palpebral areas of fixigenae become smaller, and palpebral lobe itself becomes shorter, posterolateral projections of fixigenae become relatively narrower. The cranidia from Newfoundland and Siberia look the same (Fig. 7J, K), and the Chinese specimen (Fig. 7J) differs in displaying hints of longitudinal grooves, a slightly longer groove between S3 and an axial furrow, and the relief of the transverse S1–S3 is distinct in comparison with the two other specimens. We couldn't infer on the base of our data if these differences fall within the limits of the intraspecies variability.

Occurrence. – East Siberia, Nekekit, M. Kuonamka, Olenek, Amyday, and Muna rivers, Ovatoryctocara Zone, Molodo River, Ovatoryctocara and lower Kounamkites zones, South China, Kaili Formation, late Duyunian, Ovatoryctocara granulata-Bathynotus holopygus Zone, Greenland, Henson Glatcher Formation, upper Olenellus Zone, Newfoundland, Easter Cove of Branch, Branch Cove Marl member, top of the Cephalopyge notabilis Zone.

Acknowledgements

Russian Foundation of Fundamental Researches and President Program for Supporting of Scientific Schools are acknowledged for financial support of this work (grants RFFR-09-04-00294 and SS-65493.2010.4). We are profoundly grateful to Ivan Gogin from St. Petersburg, VSEGEI, for searching the required collections and taking the photographs in F. Tchernyshev Central State Geological Museum, St.Petersburg. Reviews by Frederick A. Sundberg and Gerd Geyer considerably improved the manuscript, and we are thankful to them for this work.



Figure 7. Juvenile specimens of *Ovatorycrocara granulata* (Tchernysheva, 1962) from different regions. • A – mass material from river Amyday (11/2-5a) represents the only species including immature specimens, this piece is near 2.5 cm. • B – transitory pygidium of an early meraspis with 9 axial rings and 6 pleural segments, interpleural furrows weak, upper arrow indicates the unreleased thoracic segment, the arrow below shows developing segments at the rear, Amyday River, 0.7 mm. • C, F, I – specimens from Greenland, Henson Glatcher Form, in Blaker & Peel (1997), fig. 66 (1, 3, 2, respectively); C – pygidium, near 1 mm, F – cranidium, near 0.8 mm, I – cranidium, near 1 mm. • D, G, J – specimens from the lower part of Kaili Form, in Yuan *et al.* (2002), pl. 31, figs 13, 8, 10, respectively; D – pygidium, near 1.6 mm, G – cranidium, near 1 mm, J – 1.6 mm. • E, H, K – specimens from Amyday River; E – pygidium, 0.85 mm, H – cranidium, 0.7 mm, K – cranidium, 1.3 mm.

References

- BABCOCK, L.E., PENG, S., GEYER, G. & SHERGOLD, J.H. 2005. Changing perspectives on Cambrian chronostratigraphy and progress toward subdivision of the Cambrian System. *Geosciences Journal* 9, 101–106. DOI 10.1007/BF02910572
- BACHTUROV, C.F., EVTYSHENKO, V.M. & PERELADOV, V.S. 1988. *Kuonamskaya* bituminous sparry limestone formation (Kuonamskaya bituminoznaya karbonatno-slantsevaya formatsya). 156 pp. Nauka, Novosibirsk. [in Russian]
- BLAKER, M.R. & PEEL, J.S. 1997. Lower Cambrian trilobites from North Greenland. Meddelelser om Grønland. *Geo*science 35, 1–145.
- BUTOV, Y.P., KORDE, K.B., DOLMATOV, K.A., OSADCHAYA, D.V., NEBERIKUTINA, L.N., ORLOVA, E.F., MININA, O.R., VERTLUZHSKIKH, L.I. & CHULKOVA, A.P. 2003. Atlas on Paleozoic fossil flora and fauna of the Republic Buriytia. 171 pp. Buriytsky Scientific Centre of Siberian Academy of Science Publishing House, Ulan-Ude. [in Russian]
- EGOROVA, L.I., SHABANOV, Y.Y., ROZANOV, A.Y., SAVITSKY, V.E., TCHERNYSHEVA, N.E & SHISHKIN, B.B. 1976. Elansk and Kuonamsk facies stratotypes in the lower boundary of the Siberian Middle Cambrian. *Trudy Sibiriskogo nauchno issleddovatel'skogo Instituta Geologii, Geofiziki i Mineral'nogo* Syr'ya 211, 1–167. [in Russian]
- FLETCHER, T.P. 2003. Ovatoryctocara granulata: the key to a global Cambrian stage boundary and the correlation of the olenellid, redlichiid and paradoxidid realms. Special Papers in Palaeontology 70, 73–102.
- FLETCHER, T.P. 2007. The base of Cambrian Series 3: the global significance of key oryctocephalid trilobite ranges in the Kaili Formation of South China. *Memoir of the Association of Australasian Palaeontologists 33*, 29–33.
- GEYER, G. 2005. The base of a revised Middle Cambrian: are suitable concepts for a series boundary in reach? *Geosciences Journal* 9(2), 81–99. DOI 10.1007/BF02910571
- GEYER, G. 2006. First African oryctocephalid trilobites from the Lower–Middle Cambrian boundary interval. *Paleoworld* 15(3–4), 348–359. DOI 10.1016/j.palwor.2006.10.004
- KOROVNIKOV, I.V. & SHABANOV, Y.Y. 2008. Trilobites from boundary rocks of Lower-Middle stratotype section on Molodo River (East of the Siberian Platform). Cambrian sections of the Siberian Platform – candidates for stratotypes of subdivisions of the International Stratigraphical scheme (Stratigraphy and Palaeontology), 71–104. Materials for 13th International Field Conference of the Cambrian Stage Subdivision Working Group. SB RAN, Novosibirsk. [in Russian]
- KRYSKOV, L.N., LAZARENKO, N.P., OGIENKO, L.V. & TCHER-NYSHEVA, N.E. 1960. New early Palaeozoic trilobites of Eastern Siberia and Kazakhstan, 211–255. *In MARKOVSKY*, B.P. (ed.) *New species of prehistoric plants and invertebrates of the* USSR, Vol. 2. VSEGEI, Moscow. [in Russian]
- SAVITSKY, V.E., EVTUSHENKO, V.M., EGOROVA, L.I., KONTO-ROVITCH, A.E. & SHABANOV, Y.Y. 1972. Cambrian of the Siberian Platform (the Yudoma-Olenek type section. Kuonamka complex). *Trudy Sibiriskogo nauchno-issledovatel'skogo*

Instituta Geologii, Geofiziki i Mineral'nogo Syr'ya 130, 1–199. [in Russian]

- SHABANOV, Y.Y., KOROVNIKOV, I.V., PERELADOV, V.S. & FEFELOV, A.F. 2008a. Excursion 1a. The traditional Lower-Middle Cambrian boundary in the Kuonamka Formation of the Molodo River section (the southeastern slope of the Olenek Uplift of the Siberian Platform) proposed as a candidate for GSSP of the lower boundary of the Middle Cambrian and its basal (Molodian) stage, defined by the FAD of Ovatoryctocara granulata, 8–59. The Cambrian System of the Siberian Platform. Part 2: North-East of the Siberian Platform. XIII. International Field Conference Cambrian Stage subdivision Working Group. PIN RAS, Moscow & Novosibirsk.
- SHABANOV, Y.Y., KOROVNIKOV, I.V., PERELADOV, V.S., PAK, K.L. & FEFELOV, A.F. 2008b. Kuonamka Formation on Molodo River – a candidate for global stratotype of the lower boundary of the Middle Cambrian (East of the Siberian Platform). Cambrian sections of the Siberian Platform – candidates for stratotypes of subdivisions of the International Stratigraphical scheme (Stratigraphy and Palaeontology), 59–70. *Materials for 13th International Field Conference of the Cambrian Stage Subdivision Working Group.* SB RAN, Novosibirsk.
- SHERGOLD, J.H. 1969. Oryctocephalidae (Trilobita: Middle Cambrian) of Australia. Bulletin of Bureau of Mineral Resources, Geology and Geophysics 104, 1–66.
- SUVOROVA, N.P. 1964. Corynexochoid trilobites and their evolutionary history. *Trudy Paleontologicheskogo Instituta 103*, 1–319. [in Russian]
- TCHERNYSHEVA, N.E. 1962. Cambrian trilobites of the family Oryctocephalidae, 3–64. In SHVEDOV, N.A. (ed.) Trudy nauchnoissledovatel'skii geologii Institut Arktiki (NIIGA) 127. 188 pp. Leningrad. [in Russian]
- WALCOTT, C.D. 1908. Cambrian Geology and Paleontology. 2. Cambrian trilobites. *Smithsonian Miscellaneous Collections* 53, 13–52.
- WHITTINGTON, H.B. 1995. Oryctocephalid trilobites from the Cambrian of North America. *Palaeontology* 38(3), 543–562.
- YAZMIR, M.M., DOLMATOV, B.A. & YAZMIR, I.K. 1975. Atlas on Paleozoic and Mesozoic flora and fauna of Buryatskaya ASSR. 184 pp. Nedra, Moscow. [in Russian]
- YUAN, J.L., ZHAO, Y.L. & LI, Y. 2001a. Notes on the classification and phylogeny of oryctocephalids (Trilobita: Arthropoda). Acta Palaeontologica Sinica 40 (Supplement), 214–226. [in English with Chinese abstract]
- YUAN, J. L., ZHAO, Y.L. & LI, Y. 2001b. Notes of Oryctocephalid trilobites. Acta Palaeontologica Sinica 40 (Supplement), 143–156.
- YUAN, J.L., ZHAO, Y.L., LI, Y. & HUANG, Y.Z. 2002. Trilobite fauna of the Kaili Formation (uppermost Lower Cambrianlower Middle Cambrian) from southeastern Guizhou, South China. 422 pp. Shanghai Science and Technology Press, Shanghai. [in Chinese with English summary]
- YUAN, J.L., ZHAO, Y.L., PENG, J., ZHU, X. & LIN, J.P. 2009. Cambrian trilobite Ovatoryctocara granulata Tchernysheva, 1962 and its biostratigraphic significance. Progress in Natural Science 19(2), 213–221. DOI 10.1016/j.pnsc.2008.08.002