N. Jb. Geol. Paläont. Mh. **2002** (7) 385–396 Stuttgart, Juli 2002

Internal anatomy of a new Precambrian dickinsoniid dipleurozoan from northern Russia

Jerzy Dzik, Warszawa, and **Andrey Yu. Ivantsov,** Moscow

With 3 figures

Dzik, J. & Ivantsov, A. Yu. (2002): Internal anatomy of a new Precambrian dickinsoniid dipleurozoan from northern Russia. – N. Jb. geol. Paläont. Mh., **2002**: 385–396; Stuttgart.

Abstract: A new dickinsoniid from a recently discovered fossiliferous horizon within the Mezen Formation at the White Sea shore in Russia shows details of internal anatomy exquisitely preserved in fine sediment. In several specimens, the dorsal segmented unit was specifically deformed under the sudden sediment load. As a result, dense internal organs are reproduced as furrows on the lower bedding surface, whereas those which easily collapsed as oval elevations. This pattern corresponds to the distribution of probable intestinal caeca in *Dickinsonia* and probable gonads in *Yorgia*. A pharyngeal structure is represented by a circular imprint and the intestine by a wide axial furrow.

Zusammenfassung: Die gegenwärtigen Diskussionen über die Art der evolutiven Veränderungen an der Präkambrium-Kambrium-Wende sind stark geprägt durch die Frage, ob die Ediacara-Organismen Metazoen waren oder nicht. Eine neue Dickinsonie aus der Gruppe von *Dickinsonia tenuis* aus einem kürzlich entdeckten fossilführenden Horizont an der Weißmeerküste Russlands ist in feinkörnigem Sediment ausgezeichnet erhalten und bietet die nötige Evidenz für anatomische Details. Bei zahlreichen Exemplaren, die die ursprüngliche hohe Konvexität zeigen, ist die dorsale segmentierte Einheit (der sonst ausschließlich erhaltene Teil der Dickinsonien) auf besondere Weise durch das überdeckende Sediment deformiert. Das führte dazu, dass sich dichte innere Organe als Furchen auf der unteren Schichtseite abprägen, wogegen Teile, die leicht kollabierten, als ovale Erhebungen erhalten sind. Dieses Muster entspricht der Anordnung möglicher Darm-Blindsäcke bei *Dickinsonia costata* und den vermuteten Gonaden bei der verwandten Dipleurozoengattung *Yorgia*. Eine Pharynx-Struktur ist als kreisförmiger Abdruck und der Darm als breite axiale Furche erhalten. Offensichtlich bildete die neue Dickinsonie zusammen mit *Spriggina* und einigen anderen Ediacara-Gattungen eine evolutionäre Einheit. Diese ist durch ein dorsal gelegenes metameres Hydraulik-Skelett, durch seriell angeordnete Gonaden und durch metamere Darmblindsäcke charakterisiert.

0028-3630/02/2002-0385 $ 3.00

Introduction

The origin of the bilaterian segmented metazoans is a controversial issue which is difficult to confront with the paleontological evidence (Seilacher 1989, 1994; Valentine 1992; Narbonne 1998). The main source of information on the oldest known possible bilateral and segmented metazoans is the classic Late Precambrian locality near Ediacara in the Flinders Ranges, Australia. Among them is *Dickinsonia* (Glaessner & Wade 1966; Runnegar 1982; Wade, 1972), known to have had an extremely flat fluid-filled (Seilacher 1989) segmented body unit (normally being the only preserved structure) and possibly additional organs below (Jenkins 1992). A rather crude preservation of the Ediacara fossils is the main cause of the disparity of opinions on affinities of the Ediacarian organisms. Specimens from a recently discovered locality at the White Sea shore, Russia (Grazhdankin & Ivantsov 1996; Ivantsov 1999; Dzik & Ivantsov 1999), preserved in fine sediment, provide much more information on the anatomy of the dickinsoniids.

The locality

The new White Sea locality with Ediacaran fossils is located in the Winter Coast cliff 4-5 km south of Zimnie Gory lighthouse, Arkhangelsk District, NW Russia (Ivantsov 1999; Sokolov 1997). The fossils occur at the base of a 10 cm thick sandstone bed within the Yorga Beds of the Mezen Formation which extends for at least 200 m without any significant change in thickness in the exposure. The fossil assemblage is dominated by large specimens of *Yorgia* (Ivantsov 1999; Dzik & Ivantsov 1999) and two kinds of *Swartpuntia*-like feathery organisms. Along with the new dickinsoniid a tongue-like undescribed organisms (possibly related to *Ovatoscutum*) and very rare *Kimberella* occur there as well. About 3 m below, another fossiliferous horizon at the base of lenticular sand bodies yielded *Dickinsonia costata* and another dickinsoniid with extremely elongated body ("*D. lissa*"), together with numerous *Kimberella, Parvancorina*, and *Tribrachidium* (Grazhdankin & Ivantsov 1996; Fedonkin &

WAGGONER 1997). The strata belong to the Redkino stage of the Vendian with radiometrically determined age of 555 Ma (FEDONKIN 1987; MARTIN et al. 2000).

Description and anatomical interpretation

Internal anatomical structures of the dickinsoniids other than the quilt have been known to date only in the type species of the genus *Dickinsonia, D. costata*, which seems to be present also in the White Sea fossil assemblages (SOKOLOV 1997). The new Russian dickinsoniid is similar to the Australian dickinsoniids of the *D. tenuis* group with very dense 'quilt' segmentation.

The new dickinsoniid is relatively small (up to about 7 cm in length) with an ovoid contour of the body; its width/length ratio mean being approximately 2/3 in juveniles but decreasing to about 1/2 in adults. Altogether 31 specimens have been collected from the upper horizon at Zimnie Gory. All represent negative imprints on the lower bedding plane of the sandstone. Its surface is fine-grained, with an elephant-skin pattern indicative of cyanobacterian mats (GEHLING 1999), partially pyritised. No positive relief fossils, common in case of the associated *Yorgia* (DZIK & IVANTSOV 1999), have been found. Most of the imprints are preserved in the same way as the *Dickinsonia* specimens at Ediacara (WADE 1968; GEHLING 1991), that is with uniformly flat surface (SCHOPF & BAUMILLER 1998) of the depression (Fig. 1 A). These probably represent dorsal units ('quilts') isolated from the rest of the body which was more prone to decomposition (DZIK 2000). Unlike associated *Yorgia* and *Dickinsonia*, the precisely replicated 'quilt' units of the new dickinsoniid (Fig. 1 A) do not show any signs of collapse under sediment load. This may mean that the chambers were relatively thick walled or even completely filled with tissue, rather than being fluid-filled.

The dickinsoniids had no cuticular structures which, if present, would be preserved in the Zimnie Gory fossils. However, the segmented unit was rich in organic matter as a rather thick pyrite crust develops over it in some specimens (Fig. 1 B). The original convexity of the body was significant and the dickinsoniids were not as flat as their dorsal 'quilts' might suggest. The observed depth of impression of the 28 mm wide specimen shows that its original height was at least 5 mm, and similar height is documented for another, 22 mm wide, specimen.

Ten of the specimens in the collection show a more or less concave surface and a recurrent pattern of additional structures imprinted over the quilt segmentation. This apparently resulted from differential taphonomic behaviour of soft tissue organs. Organs which are reproduced as linear furrows that run obliquely to segmentation did not collapse so easily under the sediment pressure as the surrounding areas. Instead, the 'quilt' located above them was folded. This is well exemplified by specimens 5065 and 5069 (Fig. 2 C-D, G-H) with a wide central furrow and narrow, laterally arched furrows over the body imprint. The furrows are gently sloped and terminate bluntly (Fig. 2 A). This makes them unlike the admesially sharp radial folds in the Australian *Chondroplon* which also lack distinction between the medial and lateral furrows (WADE 1971; HOFMANN 1988). *Chondroplon* is known from a single strongly deformed specimen and it probably is an asymmetric dipleurozoan related to *Yorgia* and the unnamed White Sea animal referred to as *Andiva* by FEDONKIN (1998: fig. 12), thus rather distantly related to the organisms discussed here. In case of elevated

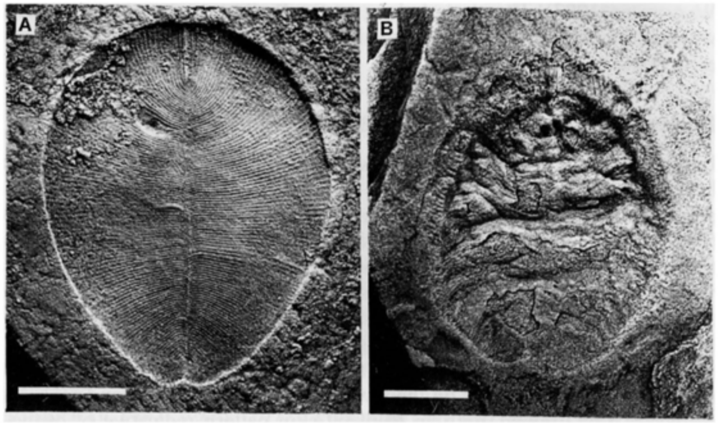

Fig. 1. Extreme modes of preservation of a new dickinsoniid of the *D. tenuis* species group on the bedding surface with *Yorgia* within the Yorga Beds of the Mezen Formation at Zimnie Gory, Arkhangelsk District, northern Russia. Both represent depressions on the lower surface of the sandstone bed. A: Typically preserved flat specimen 5063, earlier identified as *Dickinsonia* cf. *tenuis* (SOKOLOV 1997), probably representing an isolated dorsal 'quilt'. B: Strongly concave specimen 5060 with its dorsal surface covered with an early diagenetic pyritic crust which was subsequently crushed by the sediment compaction. Bar scale equals 1 cm.

oval fields in specimens 5067 and 5062 (Fig. 2A-B, E-F) the soft organs cavities had collapsed before the sediment cementation had been completed and the sediment filled the void from above. The prominence of the imprints indicates that the organs were orginally rather voluminous.

At least in two specimens, the anterior end of the medial furrow is covered by a large oval imprint (Fig. 2A-B), which resembles similar structures interpreted as oral organs in *Dickinsonia costata* (Jenkins 1992). This is supported by the presence of a sediment fill in the corresponding area in specimen 5069 (Fig. 2G-H) that suggests the structure was open to the outside environment. Its similarity to the attachment discs of the frond-like Ediacarian fossils (Jenkins & Gehling 1977; Narbonne et al. 1997) is notable, but it may have been a contractible proboscis or a muscular oesophagus, the medial furrow reproducing then the intestine.

The oblique lateral furrows meet the posterior part of inferred intestine. Similarly arranged, but sediment-filled tubular structures were reported in *Dickinsonia costata* and interpreted as intestinal caeca (Glaessner & Wade 1966; Dzik 2000). The Russian material supports this interpretation, as the distribution of these tubular structures closely resembles that of intestinal caeca in arthropods and nemerteans. There is a clear correspondence between the body shape and the distribution of furrows which, despite irregular bifurcation, rather uniformly cover the whole central surface (Fig. 2G-H). The new dickinsoniid is thus different from *D. costata* in having less numerous caeca with more persistent bifurcations, emerging only from the posterior region of the probable intestine.

Fig. 2. Specimens of the new Russian dickinsoniid from Zimnie Gory showing imprints of internal organs. Photographs and interpretative drawings indicating the course of oblique furrows and oval elevations for each of the specimens are given. **A-B:** Specimen 5067 with well represented oval elevations resulting from collapse of soft tissue organs and immigration of sediment from above; note also a circular field behind the medial segment of the dorsal chambered unit surrounding the tip of the wide axial furrow. **C-D:** Specimen 5065 with wide central and narrow arched furrows in the anterior part of the body resulting from collapse of the dorsal regions of the soft body over more resistant, presumably sediment-filled internal organs. **E-F:** Specimen 5062 showing anterior segment of the dorsal metameric unit and medial ridge separating its chambers along the midline, interpreted as medial septum, bifurcating narrow furrows and oval elevations. **G-H:** Specimen 5069 with unusually elaborated pattern of branching of lateral furrows and sediment-filled circular field at the anterior and of the body. Bar scale equals 1 cm.

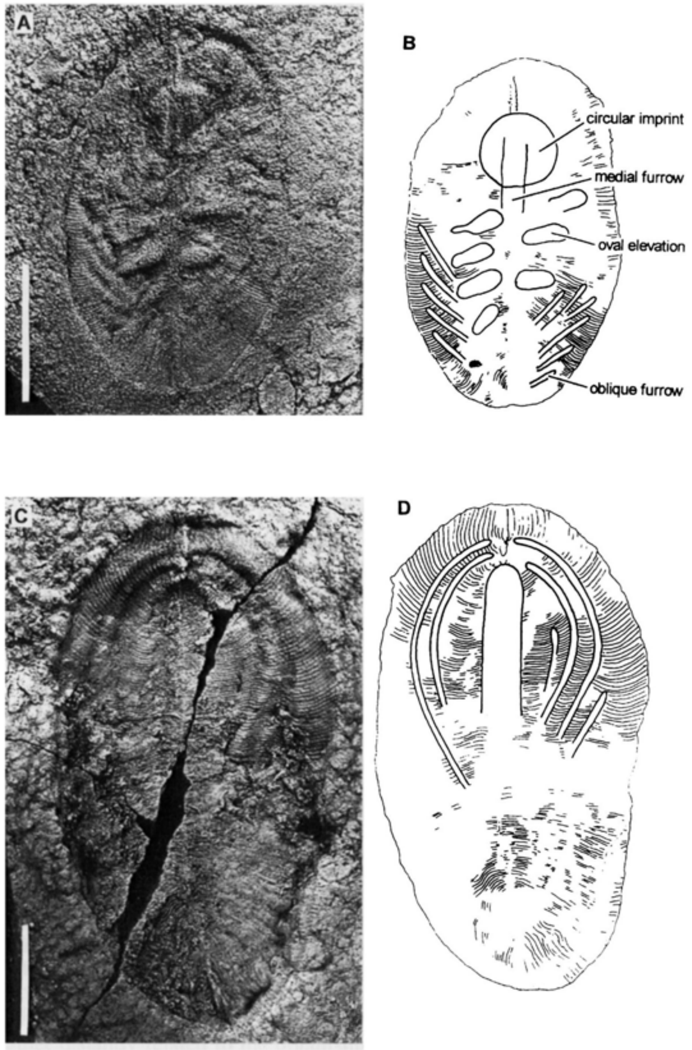

Fig. 2 (Legend see p. 389)

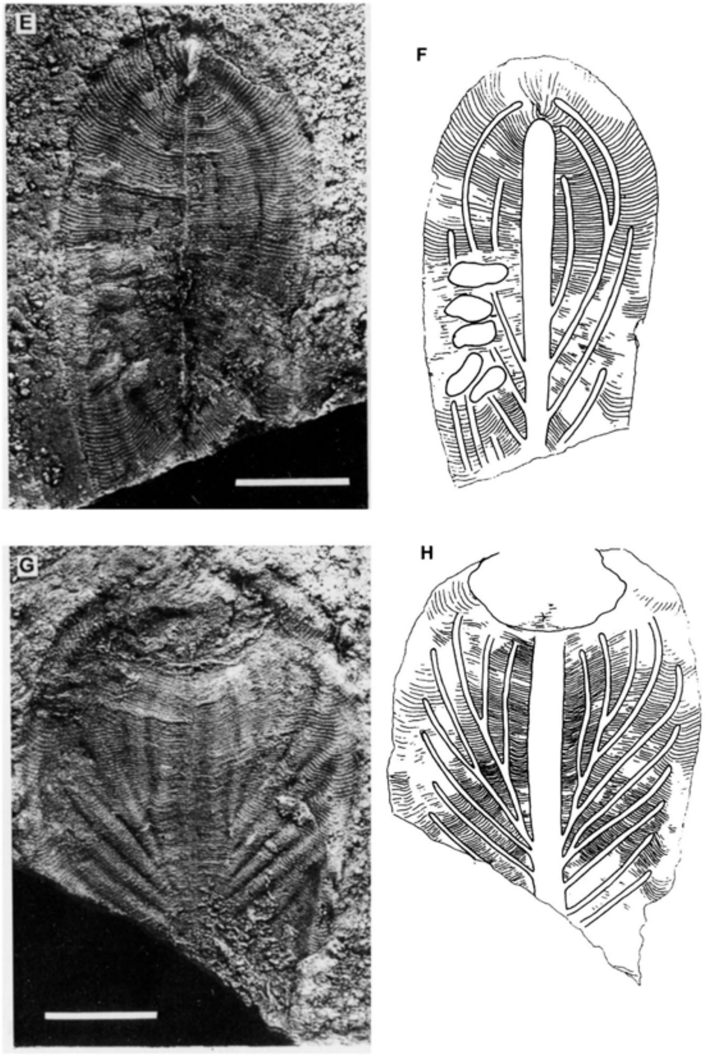

Fig. 2 (Legend see p. 389)

The oval bodies topographically correspond to similarly preserved intersegmental organs in *Yorgia*, interpreted as gonads (Dzik & Ivantsov 1999). In specimens of size similar to that of the new dickinsoniid, they are preserved in the same way as the oval organs, that is in positive relief (Ivantsov 1999). In the new form, approximately every sixth septum had an oval organ. Their axes are parallel to the quilt segments, as shown by specimens 5067 and 5062 (Fig. 2A-B, E-F). This points to some connection between the septa of the dorsal unit and the oval bodies. There is no significant disturbance in the distribution of the dorsal unit segments or oblique furrows near the oval organs. The original structures were thus not inserted in between the quilt segments or the structures which are reproduced as furrows, but were apparently located at another level. Some of them are slightly displaced from their original position, being then out of the linear arrangement of the others. The oval organs apparently had some freedom in rotation which suggests that they were attached to the septa only by a narrow mesenterium.

The body grew by adding segments posteriorly, similar to *Dickinsonia costata* (Runnegar 1982), from 18 segments at 5 mm length to 105 segments at 33 mm. The largest, incomplete specimen in the collection was at least 75 mm long. The anterior-most segments of the quilt did not change in shape during ontogeny: it is virtually of the same length in specimens of very different size. The absence of oval organs in the anterior part and greater number in the larger specimen 5062 suggests that they developed only after reaching a certain size and then were added posteriorly together with the 'quilt' units.

Conclusion

The new Russian dickinsoniid had thus a strongly convex and voluminous body, being composed of several layers of internal organs. The dorsally located metameric muscular quilt had oval organs (gonads?) attached to some of its septa on the lower surface in central and posterior parts of

Fig. 3. Restoration of preserved organs of the new Russian dickinsoniid shown from the venter, based on analogy with *Dickinsonia* and *Yorgia*, and tentative identification of the circular imprint as pharyngeal structures, wide axial furrow as an imprint of the intestine, oblique lateral furrows as caeca, oval elevations as possible gonads.

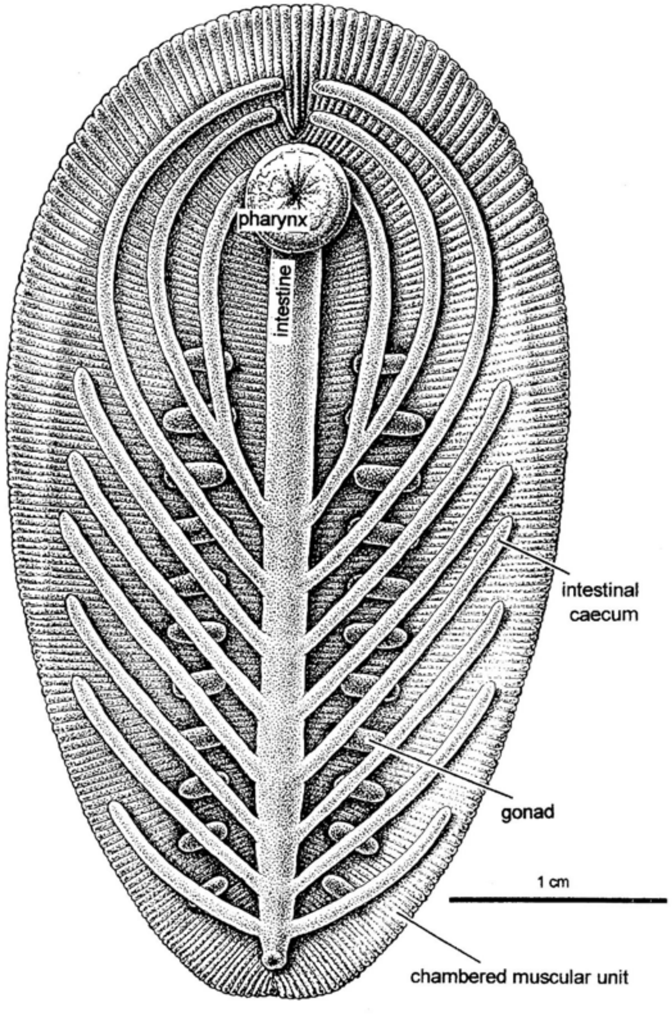

Fig. 3 (Legend see p. 392)

the body. A wide straight intestine terminated anteriorly with a voluminous, possibly evertible pharynx and was armed with numerous caeca in its posterior part, running anteriorly and bifurcating there (Fig. 3). Caeca originated only from the posterior part of the intestine, were bifurcating anteriorly and curved admesially. Their number is much smaller than chambers of densely segmented dorsal quilt.

Dorsally located metameric muscular body chambers, probably of a coelomic nature and hydraulic skeletal function, serially arranged dense organs probably representing gonads, and metameric intestinal caeca seem to characterize also several other Ediacaran organisms which can be grouped into the class Dipleurozoa (Dzik & Ivantsov 1999). With the new evidence on the external morphology and internal organisation of the dipleurozoans, their allegedly annelid or arthropod nature (Glaessner & Wade 1966; Wade 1968) is no longer tenable. Zoological affinities of the dipleurozoans remain obscure. A co-occurrence of dorsally located muscular possibly coelomic chambers, straight intestine with caeca and metameric gonads may be a plesiomorphic set of characters inherited by so distant Recent phyla as the Nemertini and Chordates (Bjerring 1984; Dzik 1995, 2000).

Acknowledgement

We thank Tomasz K. Baumiller, Adolf Seilacher, and Ben Waggoner for commenting on the manuscript. James G. Gehling and Richard F. J. Jenkins introduced one of us (JD) to their collections of the Ediacarian dipleurozoans. The research was supported by the Polish Committee of Scientific Research (grant No. 6 PO4D 071 19; JD) and the Russian Foundation of Basic Research (99-05-64547; AI).

References

Bjerring, H. C. (1984): Major anatomical steps toward craniotedness: A heterodox view based largely on embryological data. – J. Vertebrate Paleont., **4**: 17-29.

Dzik, J. (1995): *Yunnanozoon* and the ancestry of chordates. – Acta Palaeont. Polon., **40**: 341-360.

– (2000): The origin of the mineral skeleton in chordates. – Evolutionary Biol., **31**: 105-154.

Dzik, J. & Ivantsov, A. Y. (1999): An asymmetric segmented organism from the Vendian of Russia and the status of the Dipleurozoa. – Historical Biol., **13**: 255-268.

Fedonkin, M. A. (1987): Non-skeletal fauna of the Vendian and its place in the evolution of Metazoa. – Trudy Paleont. Inst. AN SSSR, **226**: 1-178. [In Russian]
– (1998): Metameric features in the Vendian metazoans. – Ital. J. Zool., **65**: 11-17.
Fedonkin, M. A. & Waggoner, B. M. (1997): The Late Precambrian fossil *Kimberella* is a mollusc-like bilaterian organism. – Nature, **388**: 868-871.
Gehling, J. G. (1991): The case for Ediacaran fossil roots to the metazoan tree. – Mem. Geol. Soc. India, **20**: 181-124.
– (1999): Microbial mats in terminal Proterozoic siliciclastics: Ediacaran death masks. – Palaios, **14**: 40-57.
Glaessner, M. F. & Wade, M. (1966): The late Precambrian fossils from Ediacara, South Australia. – Palaeontology, **9**: 599-628.
Grazhdankin, D. V. & Ivantsov, A. Yu. (1996): Reconstruction of biotopes of ancient Metazoa of the Late Vendian White Sea biota. – Paleont. J. **30**: 676-680.
Hofmann, H. J. (1988): An alternative interpretation of the Ediacaran (Precambrian) chondrophore *Chondroplon* Wade. – Alcheringa **12**: 315-318.
Ivantsov, A. Yu. (1999): A new dickinsoniid from the Upper Vendian of the White Sea Winter Coast (Russia, Arkhangelsk district). – Paleont. J., **33**: 211-222.
Jenkins, R. F. J. (1992): Functional and ecological aspects of Ediacaran assemblages. Origin and Early Evolution of the Metazoa (Lipps, J. H. & Signor, P. W. Eds.): 131-176. New York (Plenum Press).
Jenkins, R. F. J. & Gehling, J. G. (1977): A review of the frond-like fossils of the Ediacara assemblage. – Rec. South Austral. Mus., **17**: 347-359.
Martin, M. W., Grazhdankin, D. V., Bowring, S. A., Evans, D. A. D., Fedonkin, M. A., & Kirschvink, J. L. (2000): Age of Neoproterozoic bilatarian body and trace fossils, White Sea, Russia: Implications for metazoan evolution. – Science **288**: 841-845.
Narbonne, G. M. (1998): The Ediacaran biota: a terminal Neoproterozoic experiment in the evolution of life. – GSA Today, **8**: 1-6.
Narbonne, G. M., Saylor, B. Z. & Grotzinger, J. P. (1997): The youngest Ediacarian fossils from Southwestern Africa. – J. Paleont., **71**: 953-967.
Runnegar, B. (1982): Oxygen requirements, biology and phylogenetic significance of the late Precambrian worm *Dickinsonia*, and the evolution of the burrowing habit. – Alcheringa, **6**: 223-239.
Schopf, K. M. & Baumiller, T. K. (1998): A biomechanical approach to Ediacaran hypothesis: how to weed the Garden of Ediacara. – Lethaia, **31**: 89-97.
Seilacher, A. (1989): Vendozoa: Organismic construction in the Proterozoic biosphere. – Lethaia, **22**: 229-239.
– (1994): Early multicellular life: Late Proterozoic fossils and the Cambrian explosion. Early Life on Earth (Bengtson, S., Ed.): 389-400. New York (Nobel Symposium No. 84. Columbia University Press).
Sokolov, B. S. (1997): Ocherki Stanovlenia Venda. 154 pp. Moscow (KMK Scientific Press Ltd.).
Valentine, J. (1992): *Dickinsonia* as a polypoid organism. – Paleobiology, **18**: 378-382.

Wade, M. (1968): Preservation of soft-bodied animals in Precambrian sandstones at Ediacara, south Australia. – Lethaia, **1**: 238-267.
– (1971): Bilateral Precambrian chondrophores from the Ediacara fauna. – Proc. Royal Soc. Victoria, **84**: 183-188.
– (1972): *Dickinsonia*: polychaete worms from the late Precambrian Ediacara fauna, South Australia. – Mem. Queensland Mus., **16**: 171-190.

Received: December 22, 2000.
Revised manuscript accepted by the Tübingen editors: March 30, 2001.

Addresses of the authors:

Jerzy Dzik, Instytut Paleobiologii PAN, Twarda 51/55, PL-00-818 Warszawa, Poland.
Andrey Yu. Ivantsov, Paleontological Institute of the RAS, Profsojuznaja 123, Moskwa 117647, Russia.