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Anatomical data on *Novocrania anomala* (Brachiopoda: Craniiformea) support the “brachiopod fold” hypothesis

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ABSTRACT: Brachiopoda is a phylum of marine benthic animals belonging to the Spiralia clade; however, their relationships with other spiralians and the origin of their unusual body plan remain unclear, even with the application of molecular genetics methods.

One of the major ideas on the origin of the brachiopod body plan is the “brachiopod fold” hypothesis, first proposed in 1991, and much developed since then. In its present content it implies that brachiopods derived from metameric ancestor by reduction of the number of metameres, and folding onto the ventral side. Thereby both valves – “dorsal” and “ventral” – turn out to be actually dorsal.

In the present study, we discuss the pros and cons of this hypothesis, and provide some additional data on the anatomy of *Novocrania anomala* adults, which are consistent with the “brachiopod fold” hypothesis. We have found traces of ancient “folding” in the form and co-localisation of lateral mesenteries and metanephridia. We also propose a general scheme of the evolution of the craniiformes’ body plan.

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KEY WORDS: Brachiopoda, morphology, evolution, metanephridia, 3D reconstructions, “brachiopod fold” hypothesis.

Данные по анатомии *Novocrania anomala* (Brachiopoda: Craniiformea) свидетельствуют в пользу «гипотезы складывания» брахиопод

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РЕЗЮМЕ: Брахиоподы — это тип морских бентосных животных, относящийся к кладе Spiralia; однако, их родственные связи с другими представителями этой клады и происхождение их необычного плана строения остаются в некоторых деталях неясным, даже несмотря на применение современных методов молекулярно-генетического анализа.

Одна из основных идей, связанных с происхождение плана строения брахиопод, — это «гипотеза складывания», впервые сформулированная в 1991 году и сильно расширенная с тех пор. В своей современной форме данная гипотеза подразумевает, что брахиоподы произошли от метамерного предка путём олигомеризации и складывания на вентральную сторону — таким образом, что обе створки, «дорсальная» и «вентральная», оказываются на самом деле дорсальными.

В настоящей работе мы обсуждаем достоинства и недостатки упомянутой гипотезы и представляем некоторые данные по морфологии взрослых особей *Novocrania anomala*, согласующиеся с «гипотезой складывания брахиопод». Мы обнаружили следы древнего «складывания» в ориентации и взаимном расположении латеральных мезентериев и метанефридиев. Кроме того, мы предлагаем генерализованную схему эволюции плана строения краниiформных брахиопод.

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КЛЮЧЕВЫЕ СЛОВА: Brachiopoda, морфология, эволюция, метанефридии, 3D-реконструкции, гипотеза «складывания» брахиопод.

Introduction

Brachiopoda is a phylum of marine benthic animals belonging to the Spiralia clade, according to the phylogenetical data (e.g., Halanych *et al*. 1995; Kocot *et al*., 2016; Marlétaz *et al*., 2019). However, the brachiopod body plan stands out among other spiralians, and is difficult to compare with the body plan of any other bilaterian phyla.

The “brachiopod fold” hypothesis (Cohen *et al*., 2003) is one of the oldest and well-designed in terms of the origin of the brachiopods’ unusual body plan and symmetry. Originally (Nielsen, 1991; Cohen *et al*., 2003) it implies that evolution of brachiopods included folding of the anterior-posterior axis onto the ventral side. Gutmann *et al*. (1978) also suggested that brachiopods (as well as other lophophorates) derived from a metameric ancestor. The synthesis of these two hypotheses was presented in several recent studies (Malakhov, Kuzmina, 2006; Temereva, Malakhov, 2011). So, in its modern form, the “brachiopod fold” hypothesis implies that brachiopods derived from annelid-like metameric ancestor by a reduction of the number of metameres and folding onto the ventral side — so that both dorsal and ventral valves of the recent brachiopods are originally dorsal. Although the “brachiopod fold” hypothesis has been supported by data on development and metamorphosis of *Novocrania anomala* (Müller, 1776) (Nielsen, 1991), there are some results interpreted for rejection of this hypothesis (Altenburger *et al*., 2013; Altenburger *et al*., 2017). Thus, the current status of the “brachiopod fold” hypothesis is still uncertain.

In the present study, we discuss this hypothesis in the context of modern views on the brachiopod evolution and development, including those rejecting the “brachiopod fold” hypothesis. We also provide some new data on the morphology of the adults of *N. anomala*, which is consistent with the “brachiopod fold” hypothesis. Closest attention was paid to morphology, function, and co-localisation of the mesenteries in the perivisceral coelom.

Material and methods

Material collection

In September 1980, adults of *N. anomala* were collected at the Tofiño Seamount in the west part of the Mediterranean Sea (35º33′00″N; 3º46′36″ W) at a depth of 100 m. The specimens were fixed in 4% formalin and stored in 70% ethanol.

In October 2022, about 30 adults of *N. anomala* were also collected by dredging from a rocky substrate near the Espegrend Marine Biological Station, the University of Bergen, North Sea (60º 20′14″N 51º 1′42″E), at a depth of 40 m. Specimens were fixed with 2,5% glutaraldehyde in 0.05M cacodylate buffer and then stored in 0.05M cacodylate buffer. These specimens were photographed with Leica M165C (Leica Microsystems, Wetzlar, Germany) stereomicroscope equipped with a Leica DFC420 digital camera. Some specimens were postfixed in 1% OsO_4 with the same buffer.

Histology

Specimens were rinsed in distilled water; decalcinated in 7% nitric acid; dehydrated in a series of ethanol, butanol, and xylene; and embedded in Paraplast Regular (Sigma). Sagittal and cross histological sections (7 µm thick) were obtained with a Leica RM 2125 microtome (Leica Microsystems, Wetzlar, Germany). The sections were stained with Caracci haematoxylin and then examined and photographed with a Zeiss Axioplan2 microscope (Carl Zeiss AG, Jena, Germany) equipped with an AxioCam HRm camera, and with an Olympus VS-120-S slide microscope (Olympus Corporation, Tokyo, Japan). 3D reconstructions of the body cavity, including mesenteries and metanephridia, were made using Imaris ver. 7.1.1. software (Bitplane, Zürich, Switzerland) with preliminary stack processing with Amira ver. 5.2.2. (Thermo Fisher Scientific, Waltham, MA, U.S.), PTGui ver. 8.3.7. (New House Internet Services, Rotterdam, the Netherlands), and IrfanView ver. 4.51 (Irfan Škiljan).

Terminology used

All terms used herein have been used in previous studies of brachiopods. The names of coelomic chambers, as well as the names of mesenteries, follow the names used by Blochmann (1892), Hyman (1959), and James (1997). The names of digestive system parts are used as in James (1997) and Robinson (2014). The term “brachiopod fold” hypothesis is used after Cohen *et al*. (2003).

Results

General morphology

The body of *N. anomala* is enclosed with shell of two valves, traditionally named “dorsal” and “ventral”, and consists of three general parts (Fig. 1A): lophophore with tentacles in the anterior part of mantle cavity, trunk in the posterior part, and mantle, which underlays both valves and encircles the mantle cavity. The digestive system (Figs 1, 2) consists of pharynx, oesophagus, stomach, pylorus, and intestine. The coelomic system (Figs 1, 2) consists of lophophore sinuses, perioesophageal coelom, surrounding the pharynx and anterior portion of the oesophagus, broad perivisceral coelom and separate chambers containing brachial protractors (frontal chambers) and posterior adductors (posterior adductor chambers). Perivisceral coelomic cavity continues into mantle, where it forms mantle sinuses (Fig. 1A).

Specialties in the organisation of the perivisceral coelom

The perivisceral coelom of *N. anomala* is the widest compartment of the coelomic system. It surrounds most of the digestive tract (Figs 1, 2), anterior adductors and oblique muscles (Fig. 2), a pair of metanephridia (Figs 2, 3) and gametogenic tissues (Fig. 3).

The perivisceral coelom contains mesenteries, splitting it into several parts. However, all the parts of the perivisceral coelom are only partially divided, as they interconnect each other; none of the mesenteries present a complete border between different chambers of the coelom.

There is an almost complete dorso-ventral mesentery, dividing the perivisceral coelomic cavity into left and right parts (Fig. 2). It breaks up only in the rearmost part of the body, where the intestine forms a prominent loop (Fig. 2).

There is one pair of ileoparietal mesenteries, which are thin bands of coelothelium and connective tissue extending between the pylorus and the lateral body walls (Figs 2, 3). Ileoparietal mesenteries are located obliquely in respect to the body frontal plane: they attach to the pylorus dorsally and approach body walls ventrally and ahead of the attachment to the pylorus. They divide the perivisceral coelom into two “metameres”: the large anterior and small posterior. It must be mentioned that each ileoparietal mesentery consists of two parts (Fig. 3), we call them “main” part (ventral, lateral-oriented, metanephridia-bearing) and “dorsal” part (located dorsally of the main part, posterior-oriented, bearing gametogenic tissue). Only the main parts of the ileoparietal mesenteries are shown in 3D reconstructions (Fig. 2), and only the main parts are referred further in the text as simply ileoparietal mesenteries.

The ileoparietal mesenteries bear large funnels of one pair of metanephridia (Fig. 3A). The proximal part of each metanephridium, including the entire funnel, is located along the ileoparietal mesentery and opens into the perivisceral coelom posteriorly, facing the dorsal body wall. The funnels are merged with ileoparietal mesenteries. The funnel forms prominent

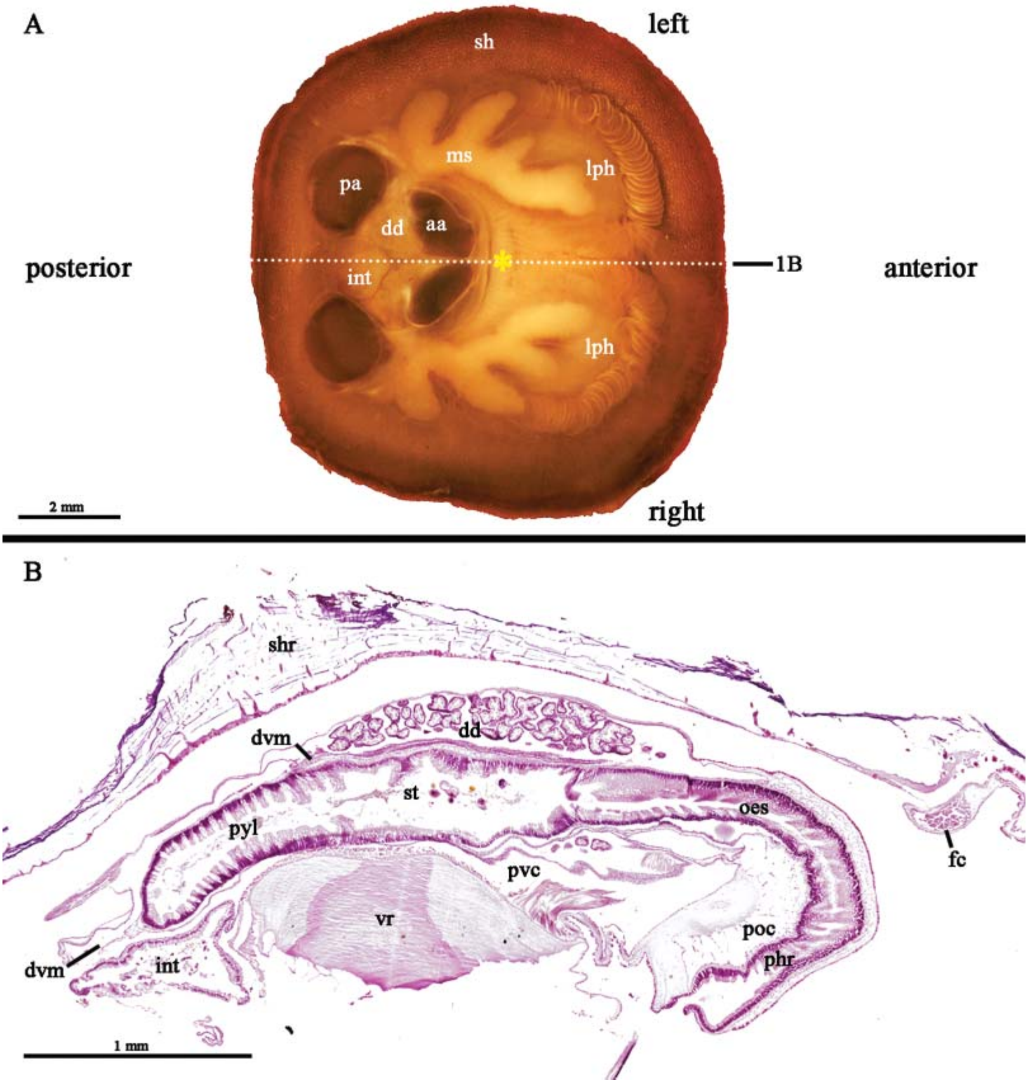

Fig. 1. General anatomy of *Novocrania anomala*. A — the total body viewed from the ventral side (vental valve is removed). Dotted line marks the plane of the sagittal section 1B. Yellow asterisk points the lophophore base and mouth (not visible); B — sagittal section of the entire body.

Abbreviations: aa — anterior adductor; dd — digestive diverticula; dvm — dorso-ventral mesentery; fc — frontal coelomic chambers (containing brachial protractors); int — intestine; lph — lophophore; ms — mantle sinus; oes — oesophagus; phr — pharynx; poc — perioesophageal coelom; pvc — perivisceral coelom; pyl — pylorus; sh — shell (dorsal valve); shr — shell remainder (organic components of the dorsal valve); st — stomach; vr — ventral ridge of connective tissue.

Рис. 1. Общая анатомия *Novocrania anomala*. A — общий вид с вентральной стороны (вентральная створка удалена). Пунктирная линия отмечает плоскость сагиттального среза 1B. Жёлтый астериск указывает на основание лофофора и рот (не виден). B — сагиттальный срез через всё тело.

Обозначения: aa — передний аддуктор; dd — пищеварительные отростки; dvm — дорсо-вентральный мезентерий; fc — фронтальные целомические камеры (содержат протракторы лофофора); int — задняя кишка; lph — лофофор; ms — мантийный синус; oes — пищевод; phr — глотка; poc — периэзофагеальный целом; pvc — перивисцеральный целом; pyl — средняя кишка; sh — раковина (дорсальная створка); shr — остатки раковины (органический компонент дорсальной створки); st — желудок; vr — вентральный гребень соединительной ткани.

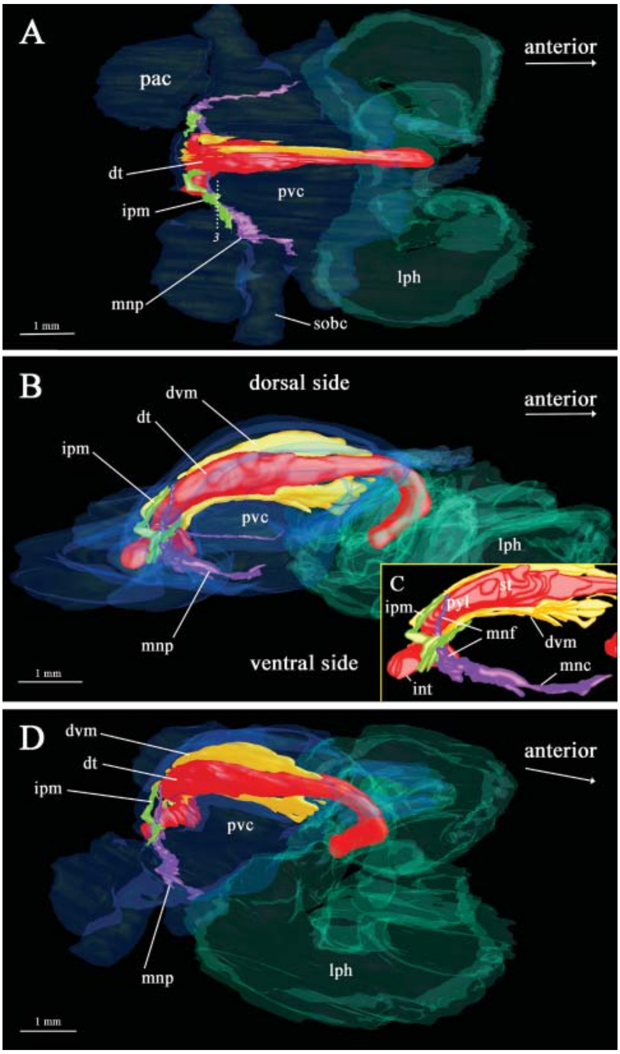

Fig. 2. Three dimensional reconstructions of the body of *Novocrania anomala*. The co-localisation of ileoparietal mesenteries and metanephridia in the perivisceral coelom is reconstructed. A — dorsal view. Dotted line indicates the plane of the cross section in Fig. 3; B — lateral (right) view; C — posterior portion of the trunk with the ileoparietal mesentery, right metanephridium, and intestine; D — latero-anterial view from the right side.

Abbreviations: dt — digestive tract; dvm — dorso-ventral mesentery; int — intestine; ipm — ileoparietal mesentery (main part); lph — lophophore; mnc — metanephridium canal; mnf — metanephridium funnel; mnp — metanephridium; pac — posterior adductor chamber; pvc — perivisceral coelom; pyl — pylorus; sobc — superior oblique muscle chamber; st — stomach.

Рис. 2. Трёхмерные реконструкции тела *Novocrania anomala*. Реконструирована колокализация илеопариетальных мезентериев и метанефридиев в туловищном целоме. A — вид с дорсальной стороны. Пунктирная линия на рис. 2A указывают на плоскость поперечного среза на рис. 3; B — вид с латеральной (правой) стороны; C — участок туловища с илеопариетальным мезентерием, правым метанефридием и кишечником; D — вид спереди справа (вполоборота).

Обозначения: dt — пищеварительный тракт; dvm — дорсо-вентральный мезентерий; int — задняя кишка; ipm — илеопариетальный мезентерий; lph — лофофор; mnc — канал метанефридия; mnf — воронка метанефридия; mnp — метанефридий; pac — камера заднего аддуктора; pvc — перивисцеральный целом; pyl — средняя кишка; sobc — камера верхней косой мышцы; st — желудок.

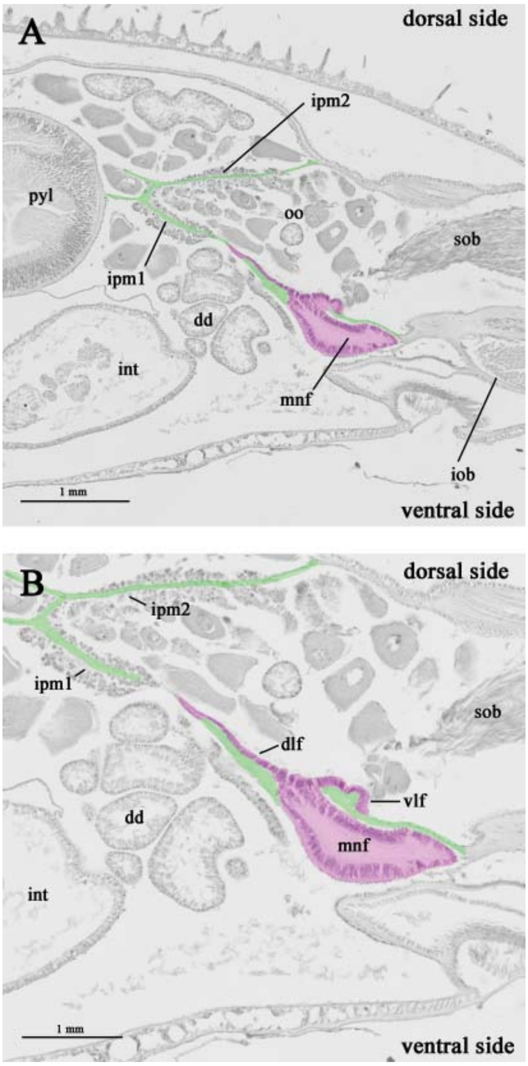

Fig. 3. Co-localisation of ileoparietal mesenteries and metanephridia in *Novocrania anomala*. Histological cross sections in the region of the left metanephridium. A — cross section of the metanephridium funnel; B — magnified portion of the previous cross section, demonstrating lips of the metanephridium funnel.

Abbreviations: dd — digestive diverticula; dlf — dorsal lip of the metanephridium funnel; int — intestine; iob — inferior oblique muscle; ipm1 — main (metanephidium-bearing) part of the ileoparietal mesentery; ipm2 — dorsal part of the ileoparietal mesentery (with gametogenic tissue); lph — lophophore; mnc — metanephridim canal; mnf — metanephridium funnel; oo — growing oocytes; pyl — pylorus; sob — superior oblique muscle; vlf — ventral lip of the metanephridium funnel. Ileoparietal mesentery is highlighted in green, and different parts of metanephidium in purple.

Рис. 3. Ко-локализация илеопариетальных мезентериев и метанефридиев у *Novocrania anomala*. Гистологические поперечные срезы в области метанефридия. A — поперечный срез через воронку метанефридия; B — увеличенная часть предыдущего поперечного среза, демонстрирующая губы воронки метанефридия.

Обозначения: dd — пищеварительные отростки; dlf — досальная губа воронки метанефридия; int — задняя кишка; iob — нижняя косая мышца; ipm1 — основная часть илеопариетального мезентерия (несущая метанефридий); ipm2 — дорсальная часть илеопариетального мезентерия (с гаметогенной тканью); mnc — канал метанефридия; mnf — воронка метанефридия; oo — созревающие ооциты; pyl — средняя кишка; sob — верхняя косая мышца; vlf — вентральная губа воронки метанефридия. Илеопариетальный мезентерий выделен зелёным цветом, различные части метанефридия — фиолетовым.

dorsal and ventral lips, which extend along the mesentery (Fig. 2, 3B). A narrow distal canal of each metanephridium extends anteriorly and laterally along the ventral side of the body wall, and opens into the mantle cavity by a nephropore aside of the superior and inferior oblique muscles.

Discussion

Lateral mesenteries in other brachiopods

The presence of lateral mesenteries, bearing metanephridia funnels, is well-known for brachiopods of all subphyla (Hyman, 1959; Gutmann *et al*., 1978; James, 1997; Malakhov, Kuzmina, 2006). In lingulids and rhynchonelliforms, there are gastroparietal (anterior) and ileoparietal (posterior) lateral mesenteries, while *N. anomala* possesses only ileoparietal ones. It should be also noted that in rhynchonelliform *Hemithiris psittacea*, in each mesentery, its left and right halves merge with each other on the dorsal side of the digestive tract. Hereby, each mesentery may be regarded as single dissepiment – one gastroparietal and one ileoparietal (Malakhov, Kuzmina, 2006). According to our results, no such connection is found in *N. anomala*; thus, we consider left and right ileoparietal bands as separate mesenteries.

The "brachiopod fold" hypothesis: history of changes and challenges

The origin of the brachiopod body plan is not precisely defined. As this group of animals is broadly present in fossils, palaeontological studies could shed light on this topic; however, palaeontological findings frequently turn out to be inconsistent and incomplete in point of soft body evolution, as the soft body is usually poorly preserved in fossils. It can be argued that brachiopods (and other lophophorates) are related to annelids and molluscs (including halkieriids), as well as to extinct groups of halwaxiids and tommotiids (Holmer *et al*., 2002, 2008, 2011; Cohen *et al*., 2003; Balthasar, 2004, Conway Morris, Caron, 2007; Skovsted *et al*., 2009), and probably to the hyoliths (Moysiuk *et al*., 2017; Sun *et al*., 2018; see also discussion in Liu *et al*., 2020). However, palaeontological methods are most likely insufficient for the reconstruction of the specific way of the brachiopod evolution (Gutmann *et al*., 1978). Thus, comparative anatomy and embryology might help to unravel the evolution of the brachiopod body plan.

To date, the best-designed hypothesis on the origin of the brachiopod body plan is the "brachiopod fold" hypothesis. Its history begins with the paper by Gutmann *et al*. (1978), in which it was supposed that brachiopods could evolve from metameric ancestors by the reducing of the number of metameres. Although Gutmann *et al*. (1978) presumably interpreted the body axes of lingulids in the wrong way and did not give much significance to a possible folding event, this work nevertheless is of significant historical importance.

The further development to the "brachiopod fold" hypothesis occurred through the study of the development in *N. anomala* larvae (Nielsen, 1991). It was discovered that in the beginning of metamorphosis the larvae undergo folding onto the ventral side. During development, valves of the juvenile shell are secreted by larval dorsal mantle epithelium; therefore, both valves are originally dorsal: dorsal anterior (= "dorsal") and dorsal posterior (= "ventral"). This observation allows to suggest that a similar process might be found in development of other species of brachiopods (Nielsen, 1991; Kuzmina *et al*., 2019), and also that it reflects some similar process that could occur in the evolution of brachiopods.

Morphology and metamorphosis of larvae of *N. anomala* differ greatly from that in rhynchonelliform brachiopods (Santagata, 2015). It raises the question: can we find any marks of evolutionary folding of brachiopods in the development of recent rhynchonelliforms? Recent data on the development of *Coptothyris grayi* have been interpreted as supporting the "brachiopod fold" hypothesis (Kuzmina *et al*., 2019). In the larvae of *C. grayi*, coelomic pouches and setal bundles develop in the oblique position in respect to the larval anterior-posterior axis, but not along the anterior-posterior axis as it is in the larvae of *N. anomala*. This stage of development of *C. grayi* may be compared with the larva of *N. anomala* in a semi-folded condition (Kuzmina *et al*., 2019).

In 2003, the "brachiopod fold" hypothesis acquired detailed justification from numerous ontogenetic and palaeontological evidences on different brachiopods' subtaxa (Cohen *et al*., 2003).

In several later studies (Malakhov, Kuzmina, 2006; Temereva, Malakhov, 2011), the "brachiopod fold" hypothesis was expanded (with special attention to the oligomerisation processes); a similar conception was also offered for the evolution of phoronids (Cohen *et al*., 2003; Temereva, Malakhov, 2011; Guo *et al*., 2022).

Recently, the "brachiopod fold" hypothesis has been refuted by studies of gene expression in ontogenesis. Modern study of *N. anomala* metamorphosis does not confirm the secretion of both adult valves by larval dorsal epithelium; in particular, it was suggested that vental valve is homologous to the pedicle of rhynchonelliform brachiopods (Altenburger *et al*., 2013). Therefore, new results contradict Nielsen's observations (Altenburger *et al*., 2013). However, we doubt if these accurate ontogenetic findings could be used to refute the "brachiopod fold" hypothesis, as the secretion of the ventral valve starts two weeks after settling, while the folding event is supposed to be during metamorphosis.

Besides, it was found that the gene expression pattern in *N. anomala* larval development (Martín-Durán *et al*., 2016) does not correspond to the "brachiopod fold" hypothesis (Altenburger *et al*., 2017). Specifically, the authors revealed that anterior markers (*six3/6*, *NK2.1*, *gsc*, *otx*, *foxC*, *foxF*) are expressed anteriorly, while posterior markers (*cdx*, *evx*) are expressed posteriorly in pre-metamorphic larvae. It is important to mention that this study (Martín-Durán *et al*., 2016) does not concern metamorphic animals or juveniles. This data (Martín-Durán *et al*., 2016, Altenburger *et al*., 2017) just implies that anterior-posterior axis in larvae is actually straight as it is in most animal phyla, and does not contradict the "brachiopod fold" hypothesis, the main point of which is axis folding in post-metamorphic animals specifically. It does not support the "brachiopod fold" hypothesis either. A similarly designed study on juvenile stages of *N. anomala* could probably resolve this controversy.

The palaeontological studies, which had first agreed with the hypothesis (Holmer et al., 2002), recently brought several arguments against it (Holmer *et al*., 2008; Murdock *et al*., 2014; Zhang *et al*., 2014). However, we would like to emphasise that all these studies are more *non-consistent* with the "brachiopod fold" hypothesis rather than completely refuting it.

How is the anatomy of *N. anomala* adults consistent with the "brachiopod fold" hypothesis?

The 3D reconstruction of the anatomy of mature specimens of *N. anomala* allowed us to reveal some morphological features, which can be interpreted as arguments for the "brachiopod fold" hypothesis.

The first argument is the presence and location of ileoparietal mesenteries. According to some studies (Gutmann *et al*., 1978; Malakhov, Kuzmina, 2006; Temereva, Malakhov, 2011), ileoparietal (as well as gastroparietal, absent in *N. anomala*) mesenteries can be regarded as derivatives of dissepiments between the body metameres of oligomerous brachiopod ancestor (Fig. 2). The metameric nature of lateral mesenteries is proved by their function: lateral mesenteries bear metanephridia funnels like dissepiments of typical metameric lophotrochozoans such as annelids (Malakhov, Kuzmina, 2006; Temereva, Malakhov, 2011). According to our data, in *N. anomala* adults, ileoparietal mesenteries extend between the gut and the body wall and are located at the oblique angle in respect of the gut. We consider the oblique orientation of dissepiments as one of the arguments for the "brachiopod fold" hypothesis.

The second argument is the co-localisation of ileoparietal mesenteries and metanephridia. It is very important to pay attention to the shape and location of the *N. anomala* metanephridia. The specific feature of metanephridia is that their proximal parts (funnels) are attached to the ileoparietal mesenteries (i.e., in the posterior portion of the perivisceral coelom), while their distal parts (nephropores) open anteriorly in the region of the inferior oblique muscle, not far from the lophophore base. The "anterior-directed" pattern in metanephridia orientation in *N. anomala* is easy to detect because of the presence of the long metanephridial canal. However, in other brachiopods, which have a short metanephridial canal, the "anterior-directed" pattern of metanephridia orientation can be observed as well (James, 1997; Malakhov, Kuzmina, 2006), though it is not so obvious as in the case of *N. anomala*. On the contrary, in typical metameric animals (like annelids), the funnels of metanephridia are located in the anterior metamere, whereas the canals extend into the posterior metamere (Schmidt-Rhaesa, 2007).

Based on the data obtained and previous studies in the frame of the "brachiopod fold" hypothesis (Nielsen, 1991; Cohen *et al*., 2003), we propose the generalised scheme of the craniiformean body plan evolution (Fig. 4).

Conclusions

In this study, some features of the anatomy of *N. anomala* adults have been revealed by the use of the method of 3D reconstructions. We have discovered an "anterior-directed" pattern of metanephridia orientation. These feature, as well as the oblique orientation of the ileoparietal mesenteries (=dissepiments), is considered to be in the frame of the "brachiopod fold" hypothesis (Fig. 4), which nowadays is the best developed idea about the evolutionary formation of the brachiopod body plan. Our study does not claim to be any sort of final solution to the problem of an unusual brachiopod body plan origin, and we would be grateful for any criticism on our work or any alternative interpretation of discussed specific features in *N. anomala* and brachiopods altogether.

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Author contribution statement

FP partially designed the study, prepared 3D reconstructions and figures, and wrote the text. ET partially designed the study, prepared histological sections, and contributed to the writing of the text. All authors read and approved the text.

CONFLICT OF INTERESTS

The authors declare that they have no competing interests.

Data availability statement

The data sets analysed within this study are available from the authors upon request.

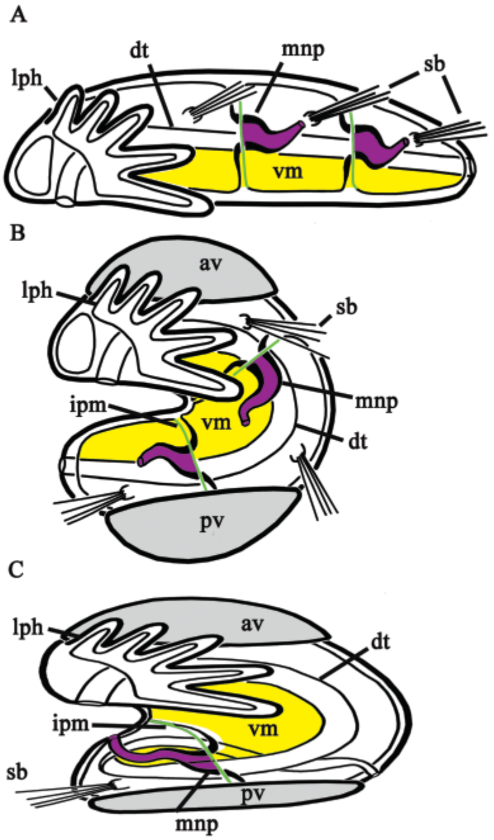

Fig. 4. Hypothetical reconstruction of the body plan evolution in craniiformeans. Modified after Temereva, Malakhov, 2011. A — hypothetical oligomeric ancestor of the brachiopods; B — intermediate stage while "folding" onto the ventral side; C — craniiformean-like brachiopod, completely "folded" onto the ventral side and having a reduced number of semi-detached metameres.

Abbreviations: av — anterior (dorsal) valve; dt — digestive tract; ipm — ileoparietal mesentery; lph — lophophore; mnp — metanephridium; pv — posterior (ventral) valve; sb — setal bundle; vm — ventral mesentery.

Рис. 4. Гипотетическая реконструкция эволюции плана строения краниiформных брахиопод. A — гипотетический олигомерный предок брахиопод; B — промежуточная стадия в процессе «складывания» на вентральную сторону; C — брахиопода, близкая краниiформной, полностью «сложенная» на вентральную сторону и обладающая сниженным количеством полуотделённых сегментов.

Обозначения: av — передняя (дорсальная) створка; dt — digestive tract; ipm — илеопариетальный мезентерий; lph — лофофор; mnp — метанефридий; pv — задняя (вентральная) створка; sb — пучок щетинок; vm — вентральный мезентерий.

Ethics statement

The field sampling did not involve endangered or protected species. The use of brachiopods in the laboratory does not raise any ethical issues.

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