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Orders Haplopoda and Onychopoda (Crustacea: Branchiopoda: Cladocera) do not form a monophyletic group: morphological evidence

Отряды Haplopoda и Onychopoda (Crustacea: Branchiopoda: Cladocera) не образуют монофилетическую группу: морфологические доказательства

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КЛЮЧЕВЫЕ СЛОВА: Onychopoda, Haplopoda, сравнительная морфология, особенности размножения, филогения, монофилия, родство.

ABSTRACT. G.O. Sars was the first who united the tribes (now orders) Onychopoda (family Polyphemidae) and Haplopoda (family Leptodoridae) in the taxon (“divisio”) Gymnomera. The later researcher’s view on this taxon was controversial — one of them followed Sars’ hypothesis, others rejected it and offered their own solution regarding the relationship between orders. Generally, the idea of the rejection of the taxon Gymnomera prevailed for about a century until the 1990s when some researchers proposed to restore the taxon Gymnomera, although, without much evidence, as a monophyletic. They based both on morphological and molecular-genetic data which looked rather poor and superficial. The authors of the present paper collected and analyzed a large set of morphological data concerning the external and internal structure, as well as the features of the reproduction and development of the representatives of Haplopoda and Onychopoda, based on the innovative traditional, not cladistic, approaches and methods of evolutionary biology and systematics. It has been clearly shown that although the features of the representatives of the orders seem superficially similar, in fact they are mostly substantially different. All morphological similarities of Haplopoda and Onychopoda are purely adaptive, associated with a predatory lifestyle, and therefore, these orders do not form a monophyletic group. Recently, this conclusion was confirmed by molecular-genetic studies.

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РЕЗЮМЕ. Г.О. Сарс был первым, кто объединил трибы (теперь отряды) Onychopoda (семейство Polyphemidae) и Haplopoda (семейство Leptodoridae) в таксон Gymnomera. Взгляд последующих исследований на этот таксон был противоречивым — одни из них следовали гипотезе Сарса, другие отвергали её и предлагали свои собственные решения относительно взаимоотношения этих отрядов. В целом идея отвержения таксона Gymnomera превалировала примерно в течение столетия до 1990-х годов, когда ряд исследователей предложил восстановить этот таксон, хотя и без большой доказательности, как монофилетический. Они базировались на морфологических и молекулярно-генетических данных, которые выглядели недостаточными и поверхностными. Авторы настоящей статьи собрали и проанализировали большой набор морфологических данных, касающихся внешнего и внутреннего строения, а также особенностей размножения и развития представителей Onychopoda и Haplopoda, базируясь на традиционных, не кладистических, подходах и методах эволюционной биологии и систематики. Было отчетливо показано, что хотя некоторые из их признаков кажутся поверхностно сходными, но в действительности существенно различаются. Все сходства морфологии Onychopoda и Haplopoda являются чисто адаптивными, связанными с хищным образом жизни представителей данных отрядов и, следовательно, эти отряды не могут образовать монофилетическую группу. Недавно это заключение было подтверждено данными молекулярно-генетических исследований.

Introduction

Sars [1865, 1890] was the first who divided the taxon ("subordo") Cladocera in two parts ("divisios") Calyptomera and Gymnomera. The former one included tribes Ctenopoda (families Sididae and Holopedidae) and Anomopoda (families Daphnidae, Bosminidae, Lyncodaphnidae, Lynceidae) and Gymnomera included tribes Onychopoda (family Polyphemidae) and Haplopoda (family Leptodoridae) (Table 1). The representatives of the former divisio were characterized by the presence of a large bivalve shell covering freely moving thorax and abdomen, mandibles with apical prominences, mobile setulated maxillae, and separated thoracic ganglia connected by the longitudinal and transverse commissures. On the contrary, the representatives of the latter division possessed the following diagnostic traits: the absence of bivalve shell covering trunk and thoracic limbs, presence of subcylindrical distinctly articulated limbs with grasping claws, and fused thoracic ganglia apart the anterior one.

Lilljeborg [1901] followed the Sars' classification. According to him, the taxon Gymnomera comprises carnivorous cladocerans without shell covering the thorax, abdomen, and thoracic limbs, having mandibles with denticulated apical ends, small, rudimentary maxillary outgrowths, four-six pairs of articulated thoracic limbs without epipodites, simple digestive gut and fused thoracic ganglia apart of that one of the thoracic limbs of first pair (tl I). As for the morphological differences between Onychopoda and Haplopoda, this author was more concise, referring only to the number, structure, and armament of the thoracic limbs (Table 1).

The above mentioned system was accepted by Calman [1909] (in the R. Lankaster's Treatise on Zoology) with the indication of minimal distinguishing traits: presence or absence of the carapace enclosing body and trunk limbs (Calyptomera – Gymnomera) and presence of either four or six pairs of limbs (Onychopoda – Haplopoda).

Objections to the Sars' [1865] system appeared early. Already P.E. Müller [1868] did not consider Gymnomera a successfully established taxon. He found onychopods and haplopods more closely related, putting them as members of the different subfamilies, Polypheminae and Leptodorinae, in the same family, Polyphemidae.

Wesenberg-Lund [1904, 1952] was of different opinion, suggesting that Polyphemidae and Leptodoridae differ greatly in structure and position of antennules, which are more or less uniform in both sexes in the former group and very different in females and males of the latter one, in armament of swimming antennae, in number and structure of thoracic limbs, in presence (Polyphemidae) and absence (Leptodoridae) of maxillae, structure of abdomen, postabdomen, shell, and posabdominal setae, etc. In addition, Wesenberg-Lund was inclined to consider nauplius of *Leptodora* Lilljeborg, 1861 as an evolutionary innovation caused by life in the pelagic zone of water-bodies. Based on these differences, he rejected the taxon Gymnomera but paradoxically brought *Leptodora* closer to the family Sididae, placing it as a member of the family. This researcher considered *Leptodora* as a "sidid-form" best adapted to the planktonic mode of life, based on superficial similarity in structure of head shape, eye, male antennules, setation of swimming antennae, and presence of six pairs of thoracic limbs. Certainly, he paid more attention to the ecological adaptations of the crustaceans to the planktonic mode of life than to the fundamentals of comparative morphology. Later, Lityński [1916] mostly followed Wesenberg-Lund, combining the subfamilies Leptodorinae and Sidinae in the family Sididae. Surprisingly, to a certain extent, the conclusions of these researchers anticipated the conclusions of modern geneticists! (see "Discussion").

Table 1. Diagnostic features of Haplopoda and Onychopoda designated by Sars [1865] and Lilljeborg [1901] (originally in Latin).

Таблица 1. Диагностические признаки Haplopoda и Onychopoda, указанные Сарсом [Sars, 1865] и Лильеборгом [Lilljeborg, 1901] (первоначально на латинском языке).

Haplopoda	Onychopoda
Sars (1865): Antennules attached laterally, distantly one from another	Antennules attached closely at one prominence
Sars (1865): Mandibles with simple claw-like apical end, maxillae are absent	Mandibles with sharp denticles apically, maxillae rudimentary, immovable
Sars (1865): Six pairs of subcylindrical thoracic limbs	Four pairs of thoracic limbs with claws and apically denticulated maxillary outgrowths (gnathobases) at base.
Lilljeborg (1901): Six pairs of cylindrical thoracic limbs with setae but without exopodites. Only limbs of first pair possess small maxillary outgrowth	Four pairs of thoracic limbs with thick and converged basal parts and claw-like setae apically. Maxillary outgrowths and exopodites are present
Sars (1865): Abdomen long and distinctly segmented, caudal setae are absent	Abdomen usually small, caudal setae sit on caudal outgrowth, which sometimes may be long
Sars (1865): Gut is very short situated in the posterior part of abdomen, whereas the oesophagus is very long	Gut forms expansion in the head

A number of the following research works also opposed the establishment of the taxon Gymnomera, but in the opposite sense. They noted the peculiar features of the morphology and life cycle of *Leptodora* and suggested attributing these crustaceans to a taxon of a higher rank. Thus, Eriksson [1934] rejected the taxon Gymnomera because "The only representative of the Haplopoda, the genus *Leptodora*, is thought to assume a specific place within the Cladocera because of its mixture of primitive and extremely specialized characteristics. Eriksson viewed the segmented, elongated rear body, the structure of the large antenna and the appearance of a metanauplius…as primitive characteristics of the Haplopoda. As these primitive characteristics do not occur in other cladocerans, Eriksson assumed that the genus originated during very ancient times and believed that it must take a very basic position within the Cladocera. According to Eriksson, the Haplopoda has nothing to do with the Onychopoda, in spite of the fact that both show a reduction of the carapace and possess rod-like legs. Eriksson thought that Onychopoda arose from forms in which the postabdomen was bent under the body. Evidence for this is the fact that their entire body is not elongated as in the Haplopoda, but only the small protuberance that bears the sensory hairs in the other cladocerans possessing a post-abdomen folded under the body. The remaining part of the postabdomen is reduced in the Onychopoda" (quoted from Schminke [1981: 628]). As a result, Eriksson separated the taxon Haplopoda from all other Cladocera, which were all assigned to the taxon Eucladocera, without giving both these taxa a taxonomic rank.

Eriksson's [1934] ideas were well accepted by the following researchers, authors of the popular Crustacea and Cladocera manuals [Brooks, 1959; Tasch, 1969; Flössner, 1972; Bowman, Abele, 1982; Schram, 1986; Mordukhai-Boltovskoi, Rivier, 1987], who started to subdivide Cladocera in two suborders — Eucladocera and Haplopoda. Flössner [1972], for example, cited the following features of Haplopoda: body elongated, not compressed laterally, with six pairs of thoracic limbs lacking exopodites; only protopodite of tl I bears small maxillary outgrowth (in fact, according to his Abb. 15, the author depicted not maxillary outgrowth but small proximal seta of protopodite of tl I); shell reduced and serves as a brood pouch; metanauplius hatches from the resting egg.

Mordukhai-Boltovskoi [1968] supported the separation of *Leptodora* as a taxon of high rank: "*Leptodora* undoubtedly deserves separation as a special family and superfamily (Haplopoda) and the similarity with cercopagids is due to convergence resulting from the similar mode of life as a planktonic predator". He also questioned the relation of "Gymnomera" to Cladocera and Branchiopoda in general due to the presence of stenopodous, not foliaceous, thoracic limbs in the representatives of the group and responded positively to this. As will be seen later (see below), some researchers will act more radically regarding the Onychopoda and Haplopoda taxonomic position.

Wingstrand [1978] investigated the spermatogenesis of Branchiopoda and found that *Leptodora* has unique spermatogenesis and spermatozoa which have nothing in common with those of other cladocerans. The same is true for Onychopoda, the spermatozoa of which have no significant features are shared with other Cladocera, including Haplopoda. This study actually shows nothing about the origin of the groups but just underlines their independence.

Starobogatov [1987] was especially radical, abolishing the taxa Branchiopoda and Cladocera by referring the representatives of the former taxon to three different subclasses and those of the latter one to two subclasses of supraclass Crustacea, one included orders Polyphemiformes (=Onychopoda) and Leptodoriformes (= Haplopoda) of the superorder Polyphemiformii, and another one superorder Daphiiformes with all other cladocerans. Later, this classification was correctly characterized as unacceptable [Dumont, Negrea, 2002]. It is worth noting, however, that in this system onychopods and haplopods stand together in one group (tentatively "gymnomeras") separately from other cladocerans ("eucladocerans"). It looked like a kind of return to the idea of "Gymnomera" and, at the same time, created a new taxonomic configuration: "Gymnomera – Eucladocera" instead of "Haplopoda – Eucladocera".

Fryer [1987a, b] retained the taxon Branchiopoda but considered that it constitutes a heterogeneous assemblage of some rather well separated lineages of unclear affinity, which includes eight extant and two extinct orders. In particular, he considered the group Cladocera as having no taxonomic significance (which was subsequently questioned and rejected [see e.g., Martin, Cash-Clark, 1995; Negrea *et al.*, 1999; Korovchinsky, Boikova, 2008] and did not recognize the affinity of Onychopoda and Haplopoda taking into account numerous morphological differences of the representatives of these two groups. It should be stressed that the publications by Fryer [1987a, b] were most detailed enough at that time in the sense of refuting the validity of the group Gymnomera, which was not sufficiently realized by some following researchers.

Negrea *et al.* [1999] provided the cladistic morphological analysis of Branchiopoda using 42 features, sometimes either strange or erroneous, e.g., in Haplopoda: "telson (of males) long and cylindrical, similar to females", "first pairs (of limbs in males) without clasping hook but, occasionally, old males with a curved spine distally", in Onychopoda: "presumed telson more or less short, as in female". Haplopoda, having the most numerous apomorphies among branchiopods, was separated by these authors from Cladocera and treated as a new superorder, Leptodorida. This system was later adopted in the manual by Dumont & Negrea [2002]. A similar manipulation on the separation of Haplopoda from Cladocera, however, on the ground of different features, was carried out by Flössner [2000] who now gave his system (see above Flössner [1972]) a more radical shade.

So, the tradition of rejection of the taxon Gymnomera, after its introduction by Sars [1865] and Lilljeborg [1901], had been practiced by a number of researchers for about a century. In this regard, probably Eriksson [1934] had an especially strong influence, whose idea of separating haplopods from other cladocerans was developed in different ways for a long time.

At the same time, at the end of XX century, the trend of returning to the taxon Gymnomera began to be outlined. For instance, Martin & Cash-Clark [1995] suggested the proximity of Onychopoda and Haplopoda, however, without combining them into one taxon, based on the presence of common features among representatives of these taxa, namely reduction of exopodites and ocellus, shell that transformed into the brood pouch, absence of food groove, and presence of stenopoid trunk limbs, predominantly carnivorous mode of life.

Other researchers behaved more decisively, proposing to restore the taxon Gymnomera, although, still without much confidence, as a monophyletic group, which includes Onychopoda and Haplopoda [Olesen, 1998, 2000]. The morphological synapomorphic traits selected for this were few and superficial: stenopodous trunk limbs, the modification of the carapace to a brood pouch, and the coalesced ventral ganglia. These are exactly the same traits which were proposed by Sars [1865] in his first diagnosis of Gymnomera.

That time, the same line of the supporting Gymnomera were developed by some geneticists [Shwenk *et al*., 1998; Taylor *et al*., 1999; Richter *et al*., 2001; Braband *et al*., 2002; Swain, Taylor, 2003; Stenderup *et al*., 2006; DeWaard *et al*., 2006]. All of them came to the conclusion about the monophyletic origin of Gymnomera, though this branch was either supported weekly or supported under certain conditions. In another case, Onychopoda might be paraphyletic, including *Leptodora* in their composition (see Swain, Taylor [2003]; Stenderup *et al*. [2006]).

At the same time, Spears & Abele [2000] did not support the taxon Gymnomera genetically in its traditional sense. Instead, they provided the original taxonomic manipulation by including the new taxon Cyclesthera (with *Cyclestheria hislopi* (Baird, 1859)) in the Cladocera along with the taxon Gymnomera comprising Ctenopoda, Anomopoda, Onychopoda and Haplopoda.

Richter *et al*. [2007] provided the robust combined morphologic-genetic analysis of Branchiopoda. In their morphological cladistic analysis, the taxon Gymnomera is supported as monophyletic but almost all supportive traits are adaptive reflecting a predatory mode of life, thus having no the indicator value. At combined morphologic-genetic approach most of analyses (19 of 20) generally were positive supporting Gymnomera. The analyses using only the molecular data are more controversial because the Gymnomera was only supported by three of 20 analyses.

Further, Olesen [2009] found the monophyly of Gymnomera when provided even more detailed morphological analysis of Branchiopoda including extant taxa. Of 80 traits of Onychopoda and Haplopoda, eight have appeared to be synapomorphic but again six of them are adaptive just reflecting the predatory mode of life while the two others (presence of limbless abdomen and non-articulated furca), seem to be inapplicable because the representatives of Polyphemidae and Podonidae (Onychopoda) practically lack abdomen and in all Cladocera claws (furca) may be attached to postabdomen with or without visible border but this certainly doesn't have any significance because in all cases, they are attached immovably. So, it turns out that Gymnomera actually is not "a very well-supported taxon" as the author thought.

The idea of Gymnomera was also followed by Kotov [2013] who found 15 morphological synapomorphies for Onychopoda and Haplopoda, proving the reliability of their close association. Meanwhile, again, most of the selected traits are of adaptive significance connected directly with the carnivorous mode of life, a few others are obscure ("postabdominal claws are either fused with postabdomen or absent", "size of thoracic limbs abruptly diminished in the rear direction").

Thus, the observation of the recent discussions *pro* and *contra* of the taxon Gymnomera leads to the conclusion that they are based on a poor basis, both morphological and genetic. First of all, rather few morphological traits, both external and internal, have been considered mostly superficially, without involving detailed data on them. Also, the molecular-genetic analyses have appeared insufficient too. Probably for these reasons, the data on the taxon Gymnomera as well as taxa Calyptomera, Eucladocera, etc. have not been included in the recent comprehensive classifications of Crustacea (see Martin, Davis [2001]; Ahyong *et al.* [2011]; Schram, Koenemann [2021]).

At the same time, new, more elaborated data [Korovchinsky, Boikova, 2008, 2017; Korovchinsky, 2015] clearly, though briefly, described the great morphological difference between the representatives of Onychopoda and Haplopoda and definitely testified against their association in one group. Somewhat later, this was supported by the newest well elaborated molecular-genetic data [Xu *et al*., 2021; Van Damme *et al*., 2021].

The aim of the present paper is to summarize the morphological and other data in more detail and provide the comparative morphological analysis of the members of the orders Onychopoda and Haplopoda, in order to assess their mutual phylogenetic relations.

Conceptual grounds

Conceptual grounds of the investigation are based on the innovated traditional, not cladistic, approaches and methods of evolutionary biology and systematics (e.g. Mayr [1969, 1974, 1982]; Rasnitsyn [1996, 2002]), which are believed to treat phylogenetic and taxonomic problems more adequately. In this regard, it is important to point out the insufficiency of the methodology of cladistic analysis (e.g., Mayr [1974]; Ashlock [1979]; Stuessy [1997]; Brower [2018]), in which it is customary to use a small number of arbitrarily selected traits (see e.g., Olesen [1998, 2009]; Negrea *et al.* [1999]; Richter *et al.* [2007]) that seem "synapomorphic" but, contrary, can often be sign of homoplasy of the taxa being compared.

In this regard, the purpose of taxonomy is to identify groups — taxa that are as similar as possible within themselves in terms of the entire set of characters and are most clearly delineated by these characters. One of the most appropriate definitions of a monophyletic taxon may be as follows: "A taxon is monophyletic if the closest common ancestor of all its members is also a member of that taxon in all its characters" [Rasnitsyn, 1983, 2002].

Results — comparatively-morphological analysis

External structures

General body axis. The longitudinal body axis of Haplopoda (*Leptodora*) is almost straight, the head, beginning from its anterior end and the rest of the body are located along the same line. In Onychopoda, on the contrary, the body axis is curved in different degrees, especially strongly in members of the family Podonidae, whose head is frequently located at almost right angle to the trunk (Fig. 1).

Integument. In Haplopoda (*Leptodora*), it is extremely thin and hyaline, whereas in Onychopoda, the integument is comparatively thick and translucent (especially in Cercopagididae), sometimes brightly colored.

Head. In Haplopoda (*Leptodora*), it is large (25–35% of body length) [Boikova, 2005], strongly elongated and slightly narrowing anteriorly (Fig. 1a). Dorsally, it bears a large saddle-shaped neck organ responsible for osmoregulation [Halcrow, 1985; Aladin, 1996]. The head of Onychopoda, especially in Podonidae and Polyphemidae, is comparatively larger (up to 50% or more of body length) [Boikova, 2009], massive, more or less rounded (Fig. 1b–d) bearing dorsally a large rounded (Podonidae) or saddle-shaped (Cercopagididae, Polyphemidae) neck organ [Meurice, 1981; Meurice, Goffinet, 1983].

Antennules. In Haplopoda (*Leptodora*) females, they are small, single-segmented, movable, sit ventro-laterally and bear distally nine aesthetascs and one very small sensory seta which is shorter than aesthetascs (Fig. 2a).

In *Leptodora* males, they are of a specific structure: long (26–30% of body length) with thickened basal part, bearing a group of nine aesthetascs. The elongated part of the antennule bears a long row of 30–70 aesthetascs along the whole anterior margin (Fig. 2e) [Gerschler, 1911; Sebestyén, 1931; Røen, 1994; Korovchinsky, Boikova, 2008].

Antennules of onychopods, Cercopagididae and Polyphemidae females, are small and movable situated on the ventral side of the head beneath the eye, bulbous (*Bythotrephes* Leydig, 1860) or more elongated (*Polyphemus* (O.F. Müller, 1785)) and sit on joint basis. Terminally, they bear five regular aesthetascs in two groups and one shorter sensory seta (*Polyphemus*) or aesthetasc-like structure (*Bythotrephes*) (Fig. 2b, c). In Podonidae, antennules are also small but immovable, with more or less fused basal parts which are also fused with the head surface [Rivier, 1998].

In Cercopagididae and Podonidae males (Mordukhai-Boltovskoi, Rivier, 1987), antennules do not differ from those of females, whereas in males of Polyphemidae, the sensory seta is considerably elongated and thickened (Fig. 2d).

Swimming antennae. In Haplopoda (*Leptodora*), they are long and strong with massive basipodite. Basipodite narrows distally and bears two long branches; the upper branch (exopodite) is four-segmented, and the lower branch (endopodite) is five-segmented. The proximalmost segment of the lower branch is rudimentary and clearly developed only dorsally, while the following segment of the branch articulates with the basipodite ventrally under the rudimentary basal segment. The smallest proximalmost segments of both antennal branches lack setae, while other segments possess a row of two-segmented feathered swimming setae (Fig. 2f, g). The general formula of antennal setae: 0 (7–12) (5–7) (8–11) / 0 (3–7) (6–13) (4–6) (6–8). Thus, the total number of setae can reach 30 and 34 on upper and lower branches, respectively, their number increases in the course of ontogenesis and varies in different populations [Korovchinsky, Boikova, 2008].

Among Onychopoda, the swimming antennae are mostly developed in cercopagidids, the fastest swimmers; they are long with especially strong basipodites. Other members of the order possess moderately developed antennae. Of two antennal branches, the lower (endopodite) is three-segmented and the upper branch (exopodite) is four-segmented. Proximal-most segment of the upper branch is rudimentary and clearly visible only externally; all other segments of both branches are much more developed. The small proximalmost segment of the upper branch lacks setae, while other segments possess two-segmented feathered swimming setae whose number is fixed (Fig. 2h, i). In Cercopagididae, the general formula of antennal setae: 0-1-2-5/1-1-5. Polyphemidae possess similar swimming antennae with fewer setae — seven on each branch (0-1-2-4/1-1-5). The same is true for Podonidae with their comparatively weaker swimming antennae, bearing seven and six setae on their branches (0–1-2-4/1-1-4).

Mouth parts. In Haplopoda (*Leptodora*), they are

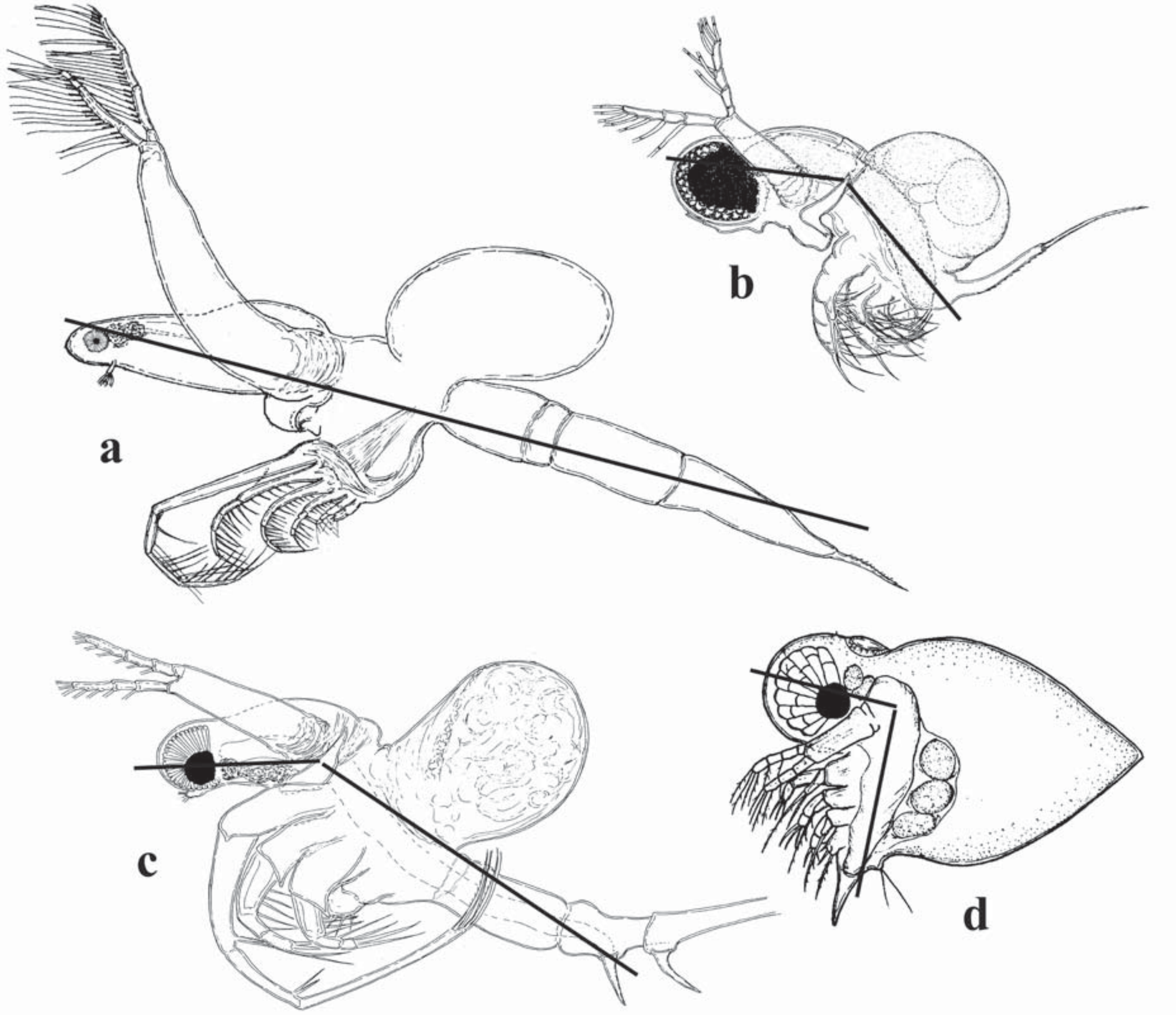

Fig. 1. Main body axis in Haplopoda: *Leptodora* (a) and Onychopoda: *Polyphemus* (Polyphemidae) (b), *Bythotrephes* (Cercopagididae) (c), *Podonevadne* (Podonidae) (d) (orig.).

Рис. 1. Главная ось тела Haplopoda: *Leptodora* (a) и Onychopoda: *Polyphemus* (Polyphemidae) (b), *Bythotrephes* (Cercopagididae) (c), *Podonevadne* (Podonidae) (d) (ориг.).

represented by upper and lower lips and mandibles. The upper lip (labrum) is comparatively short and broad, looks like a thick plate inflated externally, having a spade-like, broad distal margin and two papillae on the inner surface. Under the labrum there is a large three-lobed lower lip with a large median lobe and two smaller lateral lobes. Lower lip is a unique structure first described by Wagner [1868]. Each lateral lobe possesses a large anterior palpus-like outgrowth and either one or two rows of flattened, lanceolate prominences along the external margin. Mandibles styliform, large with massive, widened proximal part and long saber-like distal part. The latter one is armed distally with three large denticles, the proximalmost of which is thinner and longer than the others and bent apically. Maxillules (mx I) in their usual form are absent, being specifically transformed into the lateral lobes of the lower lip (see below). Maxillae (mx II) are absent [Korovchinsky, Boikova, 2008]. The pores of maxillary glands open laterally at the anterior part of the thorax, dorsally to the bases of the trunk limbs of the first pair [Olesen *et al*., 2003].

The mouth parts of Onychopoda consist of the upper lip, mandibles, and maxillules (mx I). The upper lip is well developed, broad and massive, covering the mandibles and the mouth on the ventral side. In *Bythotrephes,* it bears massive proboscis-like ventral outgrowth [Martin, Cash-Clark, 1995]. Mandibles are bilobed, with a toothed, blade-like posterior lobe and small anterior lobe (“mandibular process”) armored with a cluster of long prominences. The posterior lobe is strongly sclerotized and divided into two tooth-shaped parts. Podonidae show the same mandibular structure. However, their mandibular process is elaborated variously [Rivier, 1998], whereas the mandibles of Polyphemidae possess a more complex apical structure [Bu-

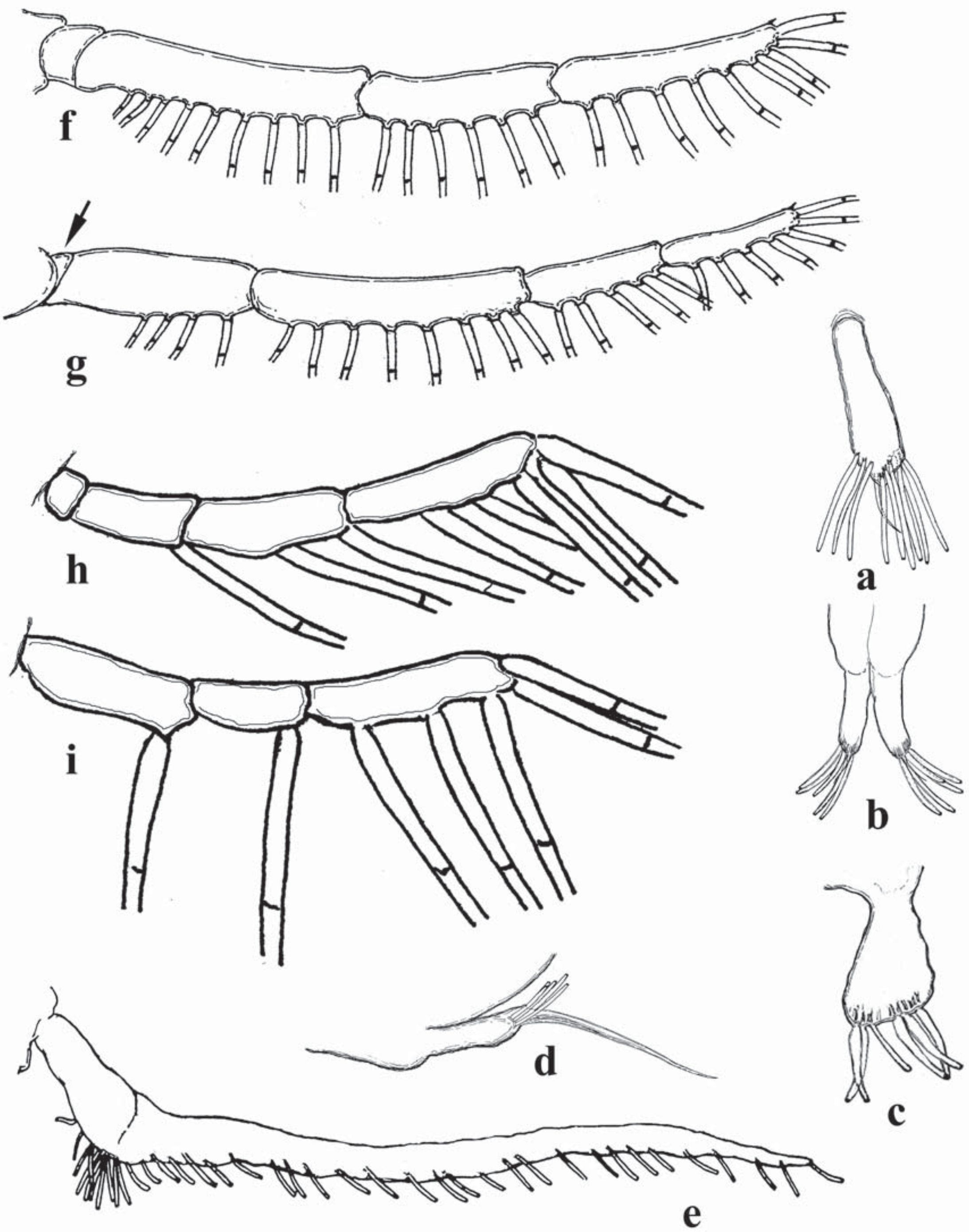

Fig. 2. Antennules of females (a–c) and males (d, e) and branches of swimming antennae (exopodite (f, h) and endopodite (g, i)) of Haplopoda: *Leptodora* (a, f, g) (rudimental proximal segment of endopodite is arrowed) and Onychopoda: *Polyphemus* (Polypemidae) (b, d), *Bythotrephes* (Cercopagididae) (c, h, i) (setules on antennal setae are not shown) (after Korovchinsky *et al*., [2021]).

Рис. 2. Антеннулы самок (a–c) и самцов (d, e) и ветви плавательных антенн (экзоподит (f, h) и эндоподит (g, i)) Haplopoda: *Leptodora* (a, f, g) (рудиментарный проксимальный членик эндоподита отмечен стрелкой) и Onychopoda: *Polyphemus* (Polypemidae) (b, d), *Bythotrephes* (Cercopagididae) (c, h, i) (сетулы на антеннальных щетинках не показаны) (по: Korovchinsky *et al*., 2021).

torina, 1995b; Rivier, 1998]. Maxillules (mx I) are present in all Onychopoda, looking like two small cylindrical structures with short central seta situated posterior to the mandibles (*Bythotrephes*). Maxillae (mx II) are absent; pores of maxillary glands are situated near the bases of tl I laterally at the trunk (*Cercopagis* Sars, 1897, *Bythotrephes*) [Olesen *et al*., 2003].

C*arapace*. In Haplopoda (*Leptodora*), it does not cover the thoracic limbs. In adult females, it is seen as a large bag-like structure attached to the posterior-dorsal margin of the thorax, and situated over the dorsal side of the abdomen. It consists of two valves, the ventral edges of which overlap one another. As a result, a cavity is formed, which serves as an open brood pouch. In *Leptodora* males, the carapace looks like a small plate-like prominence.

In Onychopoda, the carapace does not cover the thoracic limbs, as well as in haplopods. In adult females, it creates a closed space over the dorsal side of the thorax (chitinous brood chamber) (terminology by Rivier [1998: 41]) not connected with the outer environment. Gamogenetic females possess sexual openings, two ones in Polyphemidae and one in Cercopagididae and Podonidae [Rivier, 1998]. Externally, the chitinous chamber of females of Polyphemidae and Cercopagididae looks like a bag situated on the back side of the thorax which increases its size significantly with grows of embryos. In Podonidae, the shape of the chitinous chamber is variable, but its size is rather stable and increases slightly with the growth of embryos. In these crustaceans, it performs the hydrostatic function as well.

In males of Polyphemidae and Cercopagididae, the carapace is reduced up to the postero-dorsal outgrowth and reminiscent of that of juvenile females. In Podonidae males, it forms a chitinous chamber similar to that of females, which also performs the hydrostatic function.

Thoracic limbs. In Haplopoda (*Leptodora*), six pairs of strongly chitinized, stenopodous grasping limbs are situated along the massive muscular ventral part of the thorax and directed antero-ventrally. The food groove is absent, but so called "catch basket" formed by the thoracic limbs is present. All limbs are single-branched, limbs tl I – tl V are four-segmented having complex setae armament along their inner side. Tl VI is two-segmented. Setae of the limbs are also strongly chitinized, sit on an elevated basis, and most of them lack setules, having instead denticles of a different shape. The limbs of the first pair (tl I) are especially long and strong (29–57% of body length) with very long basal segments; they are always pointing forward. There is a rudimental outgrowth, gnathobase ("processus maxillaris"), on the ventral side of the thotax near basis of tl I, bearing one long and one short seta and a tiny prominence between them (Fig. 3b) [Korovchinsky, Boikova, 2008].

In Haplopoda (*Leptodora*) males, the structure of thoracic limbs mostly as in females, except for the presence of the clasping organ on tl I, which has a unique structure. This organ is composed of a large bud-like outgrowth covered by tiny spinules on the inner, proximalmost part of the distal fourth segment, and a group of two-six larger denticles on the apical end of the previous, third segment (Fig. 3e). The former one is movable, can protrude and retract, being supplied with a muscle.

Onychopoda possess four pairs of strongly chitinized, stenopodous limbs which are densely situated along the muscular ventral side of the thorax and directed either ventrally, antero-ventrally or anteriorly; those of tl I are especially long and strong, which is more pronounced in Cercopagididae. In Onychopoda, limbs of all pairs possess two-segmented protopodites. Limbs of Polyphemidae and Podonidae have endopodites and small exopodites or at least the rudiment of the latter with one-six feathered setae, whereas in Cercopagididae the exopodite is absent. In all onychopods, the epipodites are absent. Protopodites, covered with a comparatively softer cuticle, are inconspicuously delimited into two parts (segments), coxa and basis.The endopodites of three anterior pairs are composed of two or three well developed segments and those ones of the fourth pair are single-segmented. Terminally, the inner side of protopodite, namely its distal segment, of all limbs (Cercopagididae, Polyphemidae) or only those of tl I – tl III (Podonidae) bears a small outgrowth, sometimes rudimental, "gnathobasic" process (the nature and homology of this structure will be discussed below), armed with some denticles and/or spinules (Fig. 3a).

The male's clasping organ of onychopods is situated on the distal segment of tl I either proximally (Cercopagididae) or terminally (Polyphemidae, Podonidae). In the former case, the distal segment of tl I is slightly swollen proximally and bears on its inner side a small strongly chitinized movable hook with denticles on its inner side; a field of tiny prominences is situated near it (Fig. 3c). In the latter case, the endopodite is armed apically with a hook of different size and shape (Fig. 3d).

Abdomen. In Haplopoda (*Leptodora*), it is long, flexible and composed of three segments, the second of which is the shortest, while the first and third ones are of almost equal size (Fig. 4b). The abdominal integument is thin, subtly chitinized and lacks tiny spinules as in the case of most other body parts.

In Onychopoda, the abdomen is developed to varying degrees in different families. In Cercopagididae, it is long, especially in some species of *Cercopagis*, in which it lacks segmentation, whereas in *Bythotrephes* it is inconspicuously delimited in two segments, short proximal and longer distal, with prominent fold in the middle dorsal side (Fig. 4a). But in fact, it is three-segmented (to be discussed below). In Polyphemidae and Podonidae, the abdomen is reduced up to a very small area behind the last pair of limbs, and in males it is indicated by the presence of copulatory appendages of different shape.

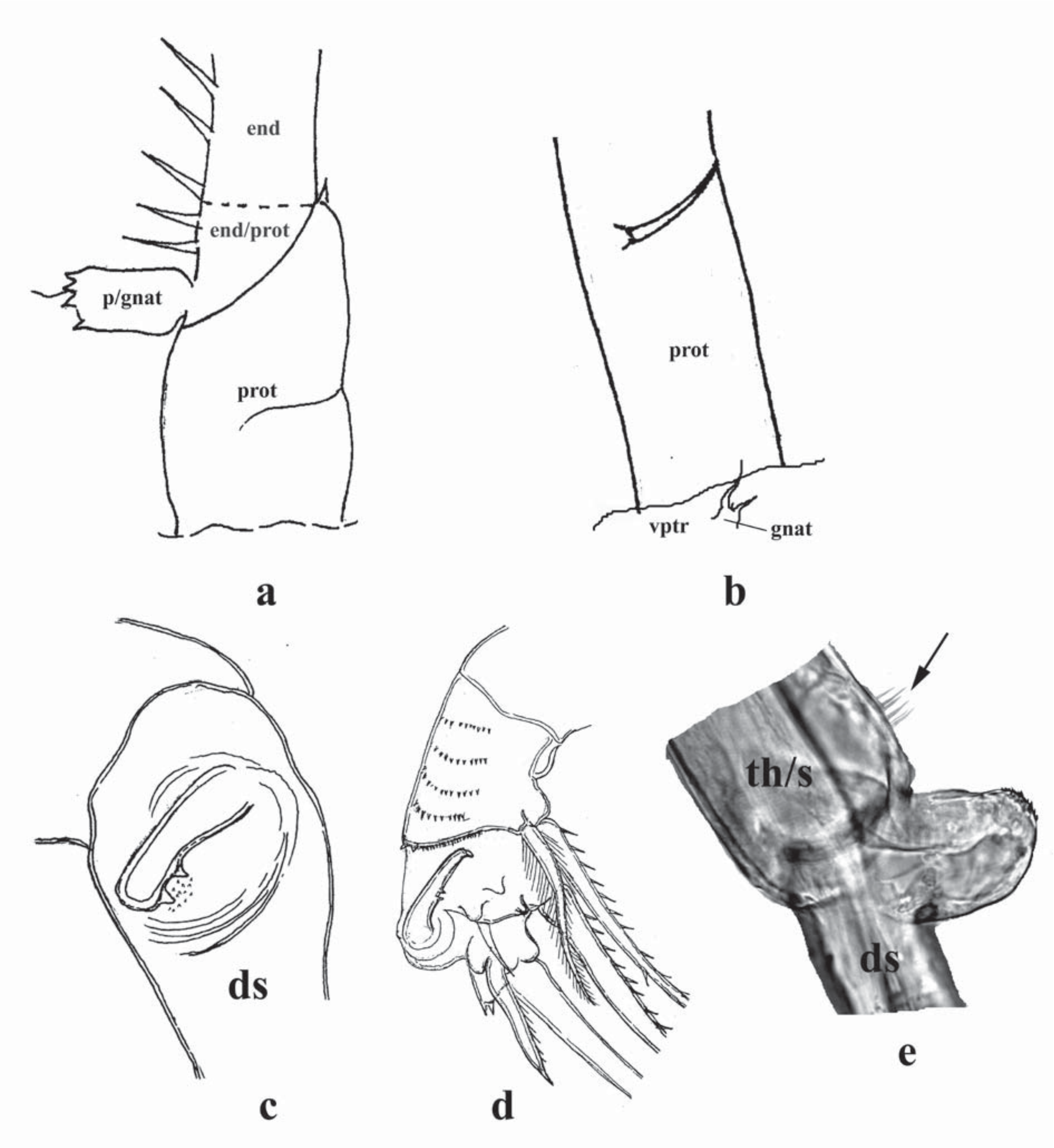

Fig. 3. Schemes of structure of basal part of thoracic limbs: Onychopoda (*Bythotrephes*) (Cercopagididae) (a) and Haplopoda (*Leptodora*) (b) (end — endopodite, end/prot — area of fusion of endopodite and protopodite, gnat — gnathobase, p/gnat — pseudognathobase, prot — protopodite, vptr — ventral part of thorax). Clasping organs of Onychopoda males: *Bythotrephes* (Cercopagididae) (c), *Polyphemus* (Polyphemidae) (d) and Haplopoda: *Leptodora* (e) (ds — distal segment of tl I, th/s — third segment of tl I (a group of small prominences of third segment is arrowed) (a, c, d — after Korovchinsky *et al.*, 2021; b — orig., e — after Korovchinsky, Boikova, 2008).

Рис. 3. Схемы структуры базальной части торакальных конечностей: Onychopoda (*Bythotrephes*) (Cercopagididae) (a) и Haplopoda (*Leptodora*) (b) (end — эндоподит, end/prot — область слияния эндородита и протоподита, gnat — гнатобаза, p/gnat — псевдогнатобаза, prot — протоподит, vptr — вентральная часть торакса). Хватательные органы самцов Onychopoda: *Bythotrephes* (Cercopagididae) (c), *Polyphemus* (Polyphemidae) (d) и Haplopoda: *Leptodora* (e) (ds — дистальный членик tl I, th/s — третий членик tl I (группа мелких выростов третьего членика указана стрелкой) (a, c, d — по: Korovchinsky *et al.*, 2021; b — ориг., e — по: Korovchinsky, Boikova, 2008).

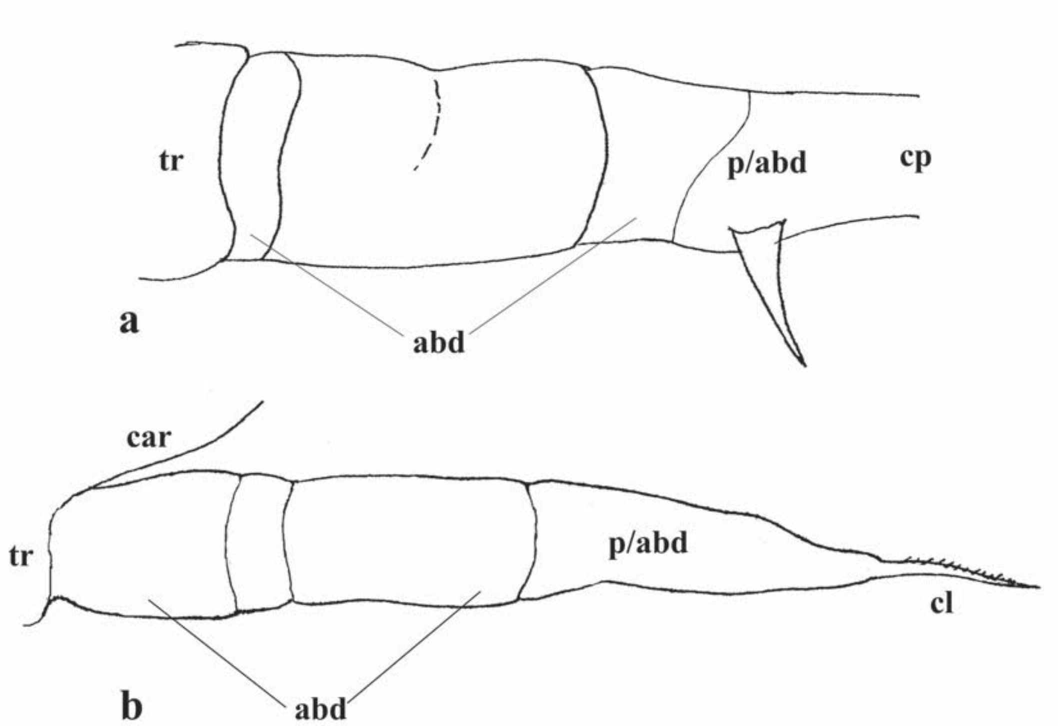

Fig. 4. Schemes of structure of abdomen and postabdomen of Onychopoda (*Bythotrephes*) (Cercopagididae) (a) and Haplopoda (*Leptodora*) (b) (abd — abdomen, car — carapace, cl — postabdominal claw, cp — caudal process, p/abd — postabdomen, tr — thorax) (a — after Korovchinsky, 2015; b — orig.).

Рис. 4. Схемы структуры абдомена и постабдомена Onychopoda (*Bythotrephes*) (Cercopagididae) (a) и Haplopoda (*Leptodora*) (b) (abd — абдомен, car — раковинка, cl — коготок постабдомена, cp — каудальный вырост, p/abd — постабдомен, tr — торакс) (a — по: Korovchinsky, 2015; b — ориг.).

Postabdomen. In Haplopoda (*Leptodora*), it is straight, comparatively long, and possesses strongly chitinized integument covered by numerous spinules. Two very small, two-segmented and setulated postabdominal setae are situated in the antero-dorsal position. Postabdomen terminates in a pair of postabdominal claws with an anal opening between them (Fig. 4b). The claws are long and almost straight with the dorsal row of 10–29 denticles and numerous groups and combs of spinules all over their surface.

The postabdomen of Onychopoda, is comparatively small and strongly transformed. In Polyphemidae, the postabdominal claws are absent, the anal opening opens between the anal lobes of postabdomen, from which the massive, long caudal process with two long postabdominal setae covered by tiny denticled extends dorsally. The representatives of the family Cercopagididae, characteristically, possess long, sometimes very long, caudal process, bearing one-two additional pairs of claws similar to those of the postabdomen, formed as a result of incomplete molting, and two tiny sensory setae apically. In Podonidae, the postabdomen is short with two pairs of distal claws of different shape and size; postabdominal setae sit on the reduced caudal process. The anal opening opens between claws.

The above presented data are briefly summarized in Table 2.

Table 2. Comparison of external morphological structures of Haplopoda and Onychopoda (females and males).
Таблица 2. Сравнение строения внешних морфологических структур Haplopoda и Onychopoda (самки и самцы).

Morphological features	Haplopoda	Onychopoda
Longitudinal body axis	Almost straight	Curved, sometimes the head and the trunk are almost at right angle to each other (Podonidae)
Body shape, integument	Elongated, integument is extremely thin and hyaline	In Polyphemidae and Podonidae not elongated, in Cercopagididae the posterior body part (abdomen and caudal process) is elongated; integument is comparatively thick, translucent, may be colored.

Table 2 (continued).
Таблица 2 (продолжение).

Morphological features	Haplopoda	Onychopoda
Head	Elongated, slightly narrowing anteriorly	Large, massive, rounded anteriorly
Antennules (females)	Small, movable, sit distantly ventro-laterally, with nine aesthetascs and small regular sensory seta	Small, movable or immovable, sit ventrally on a common basis, with five aesthetascs and small transformed or regular sensory seta
Antennules (males)	Long, with a row of numerous aesthetascs sitting along the whole anterior margin	As in females, only in Polyphemidae the sensory seta is enlarged
Swimming antennae	Long and strong; exopodite four-segmented, endopodite five-segmented; swimming setae numerous, their number is not constant	Moderately developed; exopodite four-segmented, endopodite three-segmented; swimming setae are comparatively few, their number is constant
Mouth parts	Upper lip (labrum) is well developed as well as lower three-lobed lip; mandibles are long and thin, with rudimentary maxillary process; maxillules (mx I) are transformed into the lateral lobes of the lower lip; maxillae (mx II) are absent	Upper lip (labrum) is well developed; lower lip is absent; mandibles are comparatively massive with different apical structure and maxillary process developed in different degree; regular maxillules (mx I) are present, maxillae (mx II) are absent
Carapace	Strongly transformed, its large anterior part is fused with the dorsal side of thorax, while the posterior part attached to the dorso-posterior end of thorax is free, in females it forms bag-like open brood pouch	Reduced, without lateral valves, forms closed chitinous brood chamber on the dorsal side of the thorax. In Podonidae, this chamber also performs the hydrostatic function.
Thoracic limbs	Six pairs; tl I – tl V — single-branched, four-segmented, tl VI — two-segmented; exopodites and epipodites are absent; the remnant of gnathobase is situated near the base of tl I	Four pairs; tl I – tl III — single- or two-branched (exopodites either present or absent), endopodites two- or three-segmented, tl IV — two- or three-segmented; protopodyte two-segmented with a pseudognathobase.
Male clasping organ	Bud-like structure on the inner side of proximal part of the distal segment of tl I and small denticles on the distal end of the preceding segment	Hook either on the inner proximal side (Cercopagididae) or on the apical end (Polyphemidae, Podonidae) of the distal segment of tl I
Abdomen	Long, distinctly three-segmented	Long, inconspicuously three-segmented (Cercopagididae) or strongly reduced (Polyphemidae, Podonidae)
Postabdomen	Large, cylinder-shaped, with large terminal claws and small setulated postabdominal setae	Reduced, with claws of different size and long caudal process with one-two pairs of similar claws and tiny apical setae (Cercopagididae); without claws with large caudal prominence with long setae (Polyphemidae); with/without claws and small setae on a small prominence (Podonidae)
Copulatory appendages of males	Absent	Present

Internal structures

Eye. In Haplopoda (*Leptodora*), it is comparatively small (13–15% of head length) [Boikova, 2005] but with numerous ommatidia (~500 according to Wolken & Gallik [1965] and Nilsson *et al.* [1983]) and small central pigment spot. Ocellus (naupliar eye) is usually absent [Elofsson, 1966], being present only in specimens of the first generation hatched from resting eggs [Sars, 1874]. The morphological characteristics of the eye of *Leptodora* strongly differ from those of other cladocerans: the optical structure of *Leptodora'*s eye closely resembles that of some pelagic marine amphipods family Hyperiidae; the microvillar pattern of the rhabdom of these cladocerans is unique within crustaceans being of a non-layered orthogonal pattern [Nilsson *et al*., 1983].

In Onychopoda, rounded anterior part of the head is mostly filled by large compound eye. Ocellus (naupliar eye) is always absent [Elofsson, 1966; Rivier, 1998]. In *Bythotrephes,* the eye contains numerous ommatidia (~300 or >200 according to Miltz [1899] and Martin & Cash-Clark [1995], respectively) and have large pigment spot which occupies about one-third or at most a half of the eye's volume (see also Ekman [1904]) whereas in *Cercopagis* this spot is considerably smaller. In *Polyphemus,* the eye (diameter ~36% of head length) [Boikova, 2009] contains 130–160 ommatidia and its internal structure is complex being represented by four different types of rhabdom; even externally it deviates from that of other cladocerans being divided into parts of completely different appearance [Odselius, Nilsson, 1983]. According to these authors, the presence of a layered rhabdom and distal pigment cells of *Polyphemus*' eye have previously been reported only in the Malacostraca.

Digestive system. The digestive system of Haplopoda (*Leptodora*), is highly specific being represented by very long, thin oesophagus, which stretches up to the third abdominal segment where it passes into much wider middle gut, posterior gut is very short.

In Onyhopoda, the gut is of ordinary structure, possessing well developed middle and posterior guts. In *Cercopagis* species with shortened abdomen, the gut forms a loop whereas in those with long abdomen, the gut is straight. The anterior part of the middle gut possesses paired dilated areas which are homologous to the *hepatic caeca* of the Daphniidae [Rivier, 1998].

Circulatory system. The heart of Haplopoda (*Leptodora*), is enormously large and occupies almost the whole thoracic region. It possesses the complex muscular system and large aorta with the internal valve [Weismann, 1874]. There is also a special organ (appendage organ) situated on the distal part of the proximal segment of tl I and serving to enhance the blood circulation in these especially long thoracic limbs [Gershler, 1911; Rivier, 1998; Korovchinsky, Boikova, 2008].

In Onychopoda, the heart is comparatively small, sack-like. In Cercopagididae, it also possesses a short aorta.

Nervous system. The uniqueness of the nervous system of Haplopoda (*Leptodora*) lies in the presence of the specific optic fibres, the elongated circumoesophageal connectives and the short ventral nerve cord without separate ganglia in the thoracic part. The thoracic ganglia are fused into a single mass. The innervation of the unique "lateral lobes" of the "lower lip" of *Leptodora* indicates a correspondence between these lobes and the maxillules [Olesen *et al*., 2003; Kirsch, Richter, 2007].

In Onychopoda and Haplopoda, the protocerebrum is especially developed. In Cercopagididae, it is as massive as deutocerebrum. In Podonidae, these two ganglia are brought together, forming a single spherical nerve node [Van den Bosch de Aguilar, 1971]. The thoracic ganglia of Onychopoda, although highly concentrated, but, despite this, left and right ganglia are clearly separated, not completely fused longitudinally [Claus, 1877; Olesen *et al*., 2003].

Excretory system. The maxillary glands of Haplopoda (*Leptodora*) is of unique structure, they possess the end sac and one small coil of the efferent duct, but from that point the efferent duct is uncoiled and rather large. In Onychopoda, for example in Polyphemidae, these glands are compact, a rather long efferent ductis strongly coiled [Cannon, Manton, 1927, quoted by Martin, 1992]. The openings of the maxillary glands in haplopods and onychopods have the same location: they open dorsally to the base of the limbs of first pair (tl I).

Reproductive system. In Haplopoda (*Leptodora*) females, long, tube-like ovaries are located in the abdominal region, occupying ventro-lateral position with respect to the gut (Fig. 5a). The left ovary is located mainly in the first abdominal segment, and the right one — in the second and third abdominal segments. At the same time, the germaria of both ovaries are located nearby, in the junction of the first and second abdominal segments, where both oviducts begin (Fig. 5a). Thus, in the left ovary pushed forward, the germarium is located at its posterior end, like in anomopods and most of onychopods, and in the right ovary pushed back, the germarium is located at its anterior end, like in ctenopods, but in both cases they are situated near the oviduct [Weismann, 1874]. The oviducts open on the dorsal side of abdomen at the very beginning of its third segment.

Males of Haplopoda (*Leptodora*) have an unpaired testis, the structure of which is unique not only for cladocerans, but also for branchiopods in general (Fig. 5b). It is located ventrally with respect to the gut and consists of two relatively short lateral lobes located in the posterior part of the first abdominal segment and a wide unpaired isthmus connecting them, located in the second abdominal segment. Two seminal ducts depart from the testis, opening with two gonopores on the ventral side of the trunk at the very beginning of the third abdominal segment [Weismann, 1874]. The sper-

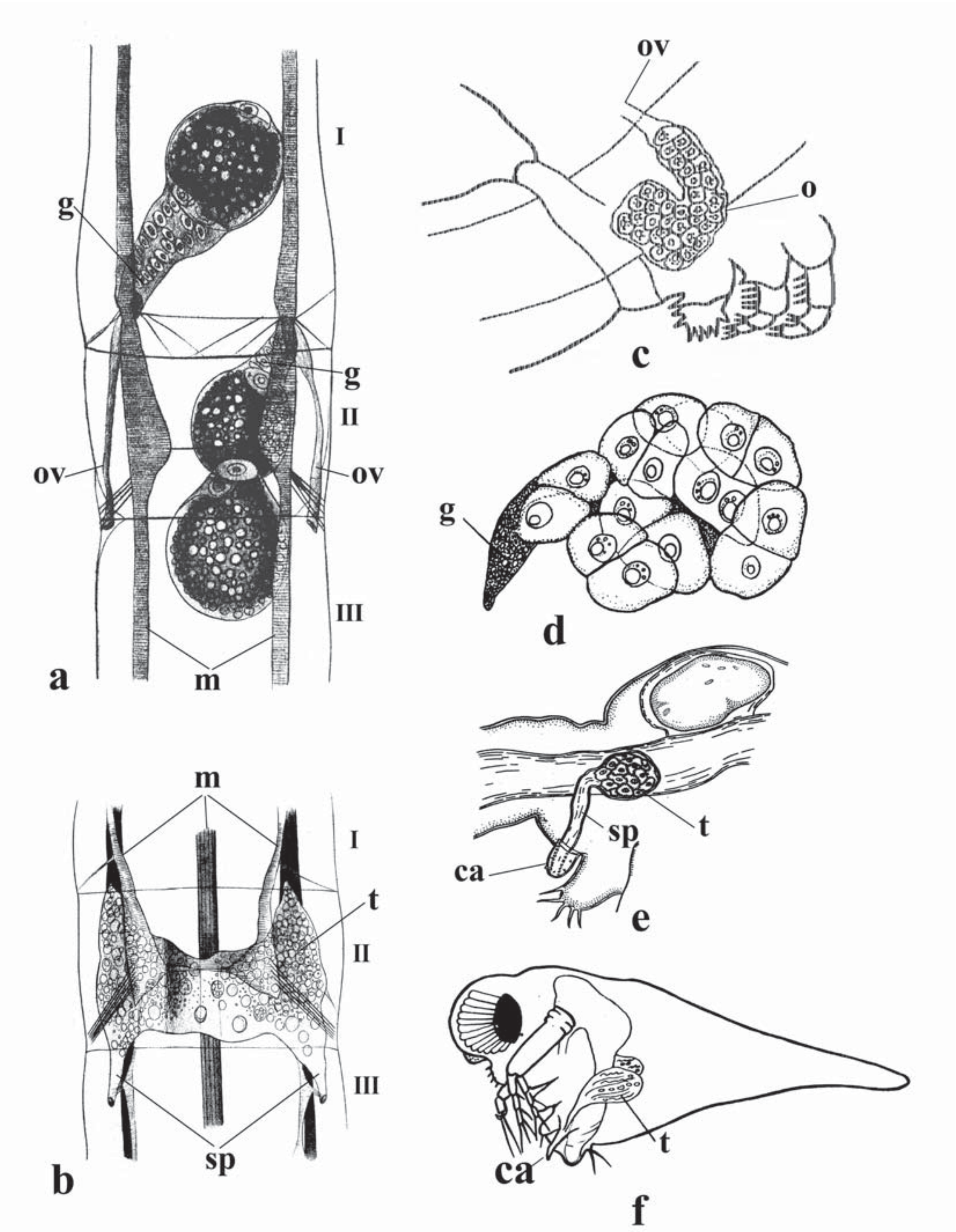

Fig. 5. Reproductive system of Hapolopoda (*Leptodora*), females (a) and males (b) and Onychopoda, females (c — *Cercopagis* (Cercopagididae); d — *Evadne* (Podonidae)) and males (e — *Bythotrephes* (Cercopagididae), f — *Evadne* (Podonidae)) (ca — copulatory appendage, g — germarium, m — muscles, o — ovary, ov — oviduct, sp — spermaduct, t — testis) (a, b — after Weismann, 1874; c, d, f — after Mordukhai-Boltovskoi, Rivier, 1987; e — after Rivier, 1974).

Рис. 5. Органы размножения Hapolopoda (*Leptodora*), самок (a) и самцов (b) и Onychopoda, самок (c — *Cercopagis* (Cercopagididae); d — *Evadne* (Podonidae)) и самцов (e — *Bythotrephes* (Cercopagididae), f — *Evadne* (Podonidae)) (ca — копулятивные придатки, g — гермариум, m — мускулы, o — яичник, ov — яйцеводы, sp — семепроводы, t — семенник) (a, b — по: Weismann, 1874; c, d, f — по: Mordukhai-Boltovskoi, Rivier, 1987; e — по: Rivier, 1974).

matozoa of Haplopoda are moderately large and filled with densely packed sacs of smooth endoplasmic reticulum. Their structure has nothing in common with those of other Cladocera [Wingstrànd, 1978].

In Onychopoda females, the ovaries are located in the thoracic region, on the sides of the gut. In the adult females, they have an irregular-rounded shape [Mordukhai-Boltovskoi, Rivier, 1987; Rivier, 1998] (Fig.

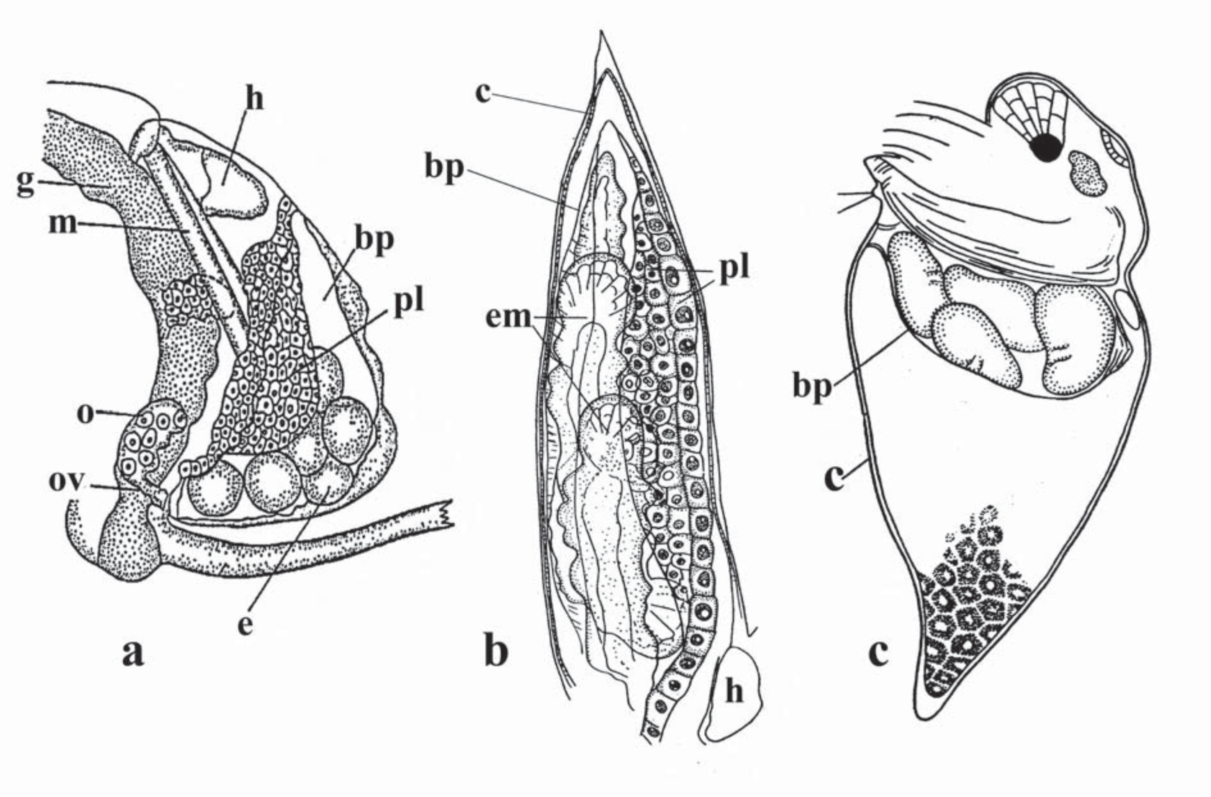

Fig. 6. Structure of the female reproductive system of Onychopoda: *Polyphemus* (Polyphemidae) (a), *Cercopagis* (Cercopagididae) (b), and *Evadne* (Podonidae) (c) (bp — brood pouch, c — transformed carapace, em — embryos, g — gut, h — heart, m — muscle, o — ovary, ov — oviduct, pl — "placenta") (a — after Butorina, 1968; b — after Rivier, 1969; c — after Rivier, 1968).

Рис. 6. Структура репродуктивной системы самок Onychopoda: *Polyphemus* (Polyphemidae) (a), *Cercopagis* (Cercopagididae) (b) и *Evadne* (Podonidae) (c) (bp — выводковая камера, c — видоизменённая раковинка, em — эмбрионы, g — кишка, h — сердце, m — мускул, o — яичник, ov — яйцевод, pl — "плацента") (a — по: Butorina, 1968; b — по: Rivier, 1969; c — по: Rivier, 1968).

5c). The germarium is usually clearly distinguishable in the ovary. In *Bythotrephes* (Cercopagididae), it is located closer to the posterior end of the ovary, the oviduct begins from it [Rossi, 1980], in *Evadne* Lovén, 1836 (Podonidae), on the contrary, the germarium is located at the anterior end of ovary [Egloff *et al*., 1997] (Fig. 5d). The structure of the germarium of adult females is the same as that of *Daphnia* O.F. Müller, 1776 (Anomopoda): germ cells are located on the periphery, in the center there are somatic cells, the functional significance of which is unknown [Rossi, 1980]. The oviducts open on the dorsal side of thorax into the brood pouch (Fig. 5c).

The brood pouch of Polyphemidae females is a closed cavity between the carapace and the dorsal side of the trunk (chitinous brood chamber — see above) (Fig. 6a). Its structure was described by Weismann [1877].

The brood pouch of Cercopagididae and Podonidae is a special structure located inside the closed chitinous brood chamber [Mordukhai- Boltovskoi, Rivier, 1987; Rivier, 1998].The eggs proceed directly to it from the oviducts (Fig. 6b, c). This is a unique organ that looks like a thin-walled bag, the volume of which increases significantly with the growth of embryos. A narrow canal proceeds from the brood pouch to the chitinous chamber. Through it, the fully developed "embryos" pass under the carapace chitin before going outside. At gamogenesis, the canal forms an opening to the environment, performing the role of the genital opening. The posterior wall of the internal brood pouch of cercopagidids is tightly attached to the hypoderm of carapace (Fig. 6b) whereas in Podonidae, it is clearly separated from it (Fig. 6c).

In mature males of Onychopoda, the testes are compact, rounded or oval [Mordukhai-Boltovskoi, Rivier, 1987; Rivier, 1998] (Fig. 5e). The large testes of Podonidae protrude into the chitinous chamber (Fig. 5f). In all Onychopoda, the seminal ducts open with gonopores at the end of the copulatory organs located on the abdomen immediately behind the last pair of thoracic limbs (Fig. 5e, f). Onychopoda have very specific gigantic spermatozoa with a smooth surface, marginal vesicles, and a dense cytoplasm filled with complicated tubular and filamentous structures. No of these significant and unique features are shared with other Cladocera, including Haplopoda [Wingstrand, 1978].

The above presented data are briefly summarized in Table 3.

Table 3. Comparison of structure of internal organs and reproductive peculiarities of Haplopoda and Onychopoda (females and males).
Таблица 3. Сравнение строения внутренних органов и репродуктивных особенностей Haplopoda и Onychopoda (самки и самцы).

Internal organs/ reproductive peculiarities	Haplopoda	Onychopoda
Eye, ocellus	Comparatively small, with ~500 ommatidia; microvillar structure of the rhabdom is unique within crustaceans being of a non-layered orthogonal pattern; ocellus present only in specimens hatched from resting eggs.	Large, with ~130–300 ommatidia; its internal structure is complex being represented by four different types of rhabdom which is layered, distal pigment cells are present; ocellus is absent.
Digestive system	Oesophagus is very long, thin, stretches up to the third abdominal segment where it passes into the wider middle gut, posterior gut is very short.	Oesophagus is of ordinary structure, possessing well developed middle and posterior guts; sometimes the gut forms a loop
Circulatory system	Large heart with complex muscular system, large aorta and the internal valve occupies almost the whole thoracic region; a special appendage organ is present on tl I.	Heart is comparatively small, sack-like
Nervous system	There are specific optic fibres, the elongated circumoesophageal connectives and a short ventral nerve cord without ganglia in the thoracic part, which are fused	Protocerebrum is as massive as deutocerebrum, these two ganglia may be brought together, forming a single spherical nerve node; thoracic ganglia are not completely fused.
Reproductive system (females)	Paired ovaries are situated in the abdominal region. Brood pouch is of open type.	Paired, more or less globular ovaries are situated in the thoracic region. The space between the carapace and the dorsal side of trunk forms a closed chitinous brood chamber. Cercopagididae and Podonidae have a special internal brood pouch inside the chitinous chamber.
Reproductive system (males)	Unpaired testis of unique shape and structure located in the abdomen ventrally with respect to the gut	Paired elongated, rounded or oval testes located in the thoracic region laterally with respect to the gut
Subitaneous eggs	Large, with large amount of especially coarse-grained yolk and without fat vacuoles	Small, poor in yolk and without fat vacuoles.
Resting eggs	Large, practically do not differ in size and structure of yolk from those of the subitaneous eggs	Large, with large amount of large-grained yolk; greatly differ in size and appearance from subitaneous eggs. Eggs of *Bythotrephes* (Cercopagididae) with fat vacuoles
Spermatozoa	Unique spermatozoa, moderately large and filled with the densely packed sacs of a smooth endoplasmic reticulum.	Very specific gigantic spermatozoa with a smooth surface, marginal vesicles, and a dense cytoplasm filled with the complicated tubular and filamentous structures.
Development of subitaneous eggs	Pseudo-direct, it is carried out due to the yolk accumulated in the egg.	Pseudo-direct, it is carried out due to the nutrient substance secreted by the special glands of females.
Development of resting eggs	Indirect, with three free-living larvae	Direct

Reproductive peculiarities

Development of subitaneous (*parthenogenetic*) *eggs*. In Haplopoda (*Leptodora*), these eggs are large (up to 400 µm) [Gershler, 1911; Boikova, 2005], without fatty vacuoles but with large amounts of large-grained yolk, which is not known in other Cladocera [Makrushin, 1991; Dumont, Negrea, 2002]. The development of the eggs occurs solely due to the nutrients accumulated by the eggs during the period of trophoplasmic growth.The development of these eggs is pseudo-direct (terminology by Fritsch *et al*. [2013]). The hatching from the egg membranes occurs long before the developed "embryos" leave the brood pouch of the female [Olesen *et al*., 2003; Boikova, 2008]. The embryo-like larva, which morphologically corresponds to the metanauplius, hatches from the egg (see below). In some time, this larva molts and becomes similar to the postlarval stage, but continues to develop in the brood pouch. After entering the external environment, it molts and turns into a juvenile.

The subitaneous eggs of Onychopoda are very small (from 50–80 to about 120 µm), contain little yolk and develop mainly at the expense of the nutritive medium, secreted by a special gland of female, named "Nährboden" [Weismann, 1877) or "placenta" [Goulden, 1968; Rivier, 1998] (Fig. 6a). In *Polyphemus*, this gland is a strip of cells between the intestine and cuticular floor of the brood pouch. The functioning of this gland was described by Patt [1947]. In gamogenetic females, this gland is small and does not show secretory activity.

In *Bythotrephes* (Cercopagididae), the "placenta" function is performed by large glandular cells of the anterior wall of the brood pouch. In Podonidae, the walls of the brood pouch consist of homogeneous glandular cells that perform the function of the "placenta".The walls of the brood pouch of gamogenetic females of podonids consist of larger, granular-rich cells which participate in the formation of the outer shell of the resting eggs [Mordukhai-Boltovskoi, Rivier, 1987; Rivier, 1998]. In *Polyphemus*, the outer shell of the resting eggs is probably formed by the secret of glandular cells of massive oviducts [Weismann, 1877].

The development of the subitaneous eggs of Onychopoda is poorly studied, but judging from the observations of *Polyphemus* development [Olesen, 2003; Olesen *et al*., 2003] it is also pseudo-direct, as in the development of the subitaneous eggs of Haplopoda [Olesen, 2003; Boikova, 2012].

Development of resting eggs. The resting eggs of Haplopoda are very similar in size and yolk composition to their subitaneous eggs [Makrushin, 1985], but have indirect development, which is accompanied by the appearance of three free-living lecithrophic larvae (two metanaupliuses, and transitional larvae) [Sars, 1874; Warren, 1901; Sebestyén, 1949]. The life span of the first larva is only about one-two hours (Warren, 1901). Free-living larvae of *Leptodora* differ from the embryo-like larvae of the parthenogenetic cycle only by the presence of mandibular palps and an ocellus. The mandibular pulps gradually degenerate, but the ocellus remains throughout the whole life of the specimen of the first generation [Sars, 1874].

The resting eggs of Onychopoda are much larger (200–660 µm) [Riviere, 1998] than their subitaneous eggs and rich in coarse-grained homogeneous yolk; the resting eggs of *Bythotrephes* (Cercopagididae) have fat vacuoles [Makrushin, 1985]. The development of these eggs is direct: a fully developed crustacean hatched from the egg, molts and turns into a juvenile [Onbe, 1974, 1978; Butorina, 1998; Rivier, 1998].

Discussion

General considerations

It was noted above that there were some attempts to represent Cladocera as an unnatural group having no taxonomic significance [Starobogatov, 1986; Fryer, 1987a, b; Negrea *et al*., 1999; Flössner, 2000; Dumont, Negrea, 2002]. But further this was not confirmed by a number of morphological and molecular-genetic investigations [Hebert, Taylor, 1997; Schwenk *et al*., 1998; Olesen, 1998, 2009; Taylor *et al*., 1999; Martin, Davis, 2001; Richter *et al*., 2007; Korovchinsky, Boikova, 2008; Kotov, 2013; Schwentner *et al*., 2018; Van Damme *et al*., 2021]. Thus, it was found that Cladocera is a well substantiated taxon whose members have widely diverged morphologically, genetically, and ecologically.

As for Haplopoda and Onychopoda, we have to state that by the beginning of the XXI century, many years after their original description, these supposedly well-known taxa had appeared not to be studied satisfactorily in basic morphological and taxonomic respects. Actually, the knowledge of their morphology and the level of its comprehension, at least in the minds of a wide range of zoologists, remained largely at the level of the 19th – first half of the 20th century. Thus, the best illustrated description of *Leptodora,* despite few errors, was presented by Sars [1861(1993)], Weismann [1874] and Lilljeborg [1901], whose data has been updated and corrected to some extant by the following researchers (e.g., Scourfield [1896, 1905]; Sebestyén [1931]). More recent morphological data on *Leptodora*, concerned predominantly either only particular traits (e.g., thoracic limbs) [Olesen *et al*., 2001] or the ontogeny of the crustacean [Sebestyén, 1949; Olesen *et al*., 2003].

The same was true for onychopods, of which the representatives of the genus *Polyphemus* (Polyphemidae) [Butorina, 1969, 1995a, b; Rivier, 1998] and family Podonidae [Mordukhai-Boltovskoi, 1967, 1968, 1978; Rivier, 1998] were studied morphologically in many details but not in comparatively morphological aspect. Weismann [1877] and then Martin and Cash-

Clark [1995] presented the excellent morphological description of *Bythotrephes* (Cercopagididae), however, the latter authors either missed or underestimated some important peculiarities, e.g., those of the structure of thoracic limbs, abdomen-postabdomen, etc. Other representatives of the family Cercopagididae were described at a lower level (see Rivier [1998]).

Despite the relative poverty of the available morphological data on Haplopoda and Onychopoda, it would undoubtedly be sufficient to analyze the relationship of these groups. Unfortunately, no one has presented a comprehensive comparative morphological analysis of these crustaceans but rather focused on a few selected traits like segmented thoracic limbs, presence of shell transformed into brood pouch, etc. And even these few features were analyzed superficially, which led to contradictory conclusions. For instance, the readily used synapomorphic statements of Gymnomera: "the modification of the carapace to a smaller, dorsal brood pouch, attached dorsally to the trunk", "the stenopodous, four-segmented trunk limbs", "presence of eye with numerous ommatidia" (e.g., Olesen [2009]; Kotov [2013]) neither do not reflect the essence of the issue, nor correctly estimate the complexity of the structures, very different, in fact, in members of the two orders.

The failure and inconsistency of recent research on the relationship of Haplopoda and Onychopoda is based on the inconsistency of cladistic methodology which uses only a few subjectively selected traits ("synapomorphies") in its analysis (see e.g., Olesen [1998, 2000, 2009]; Richter *et al*. [2007]). Actually, the set of traits in these analyses is very close to that used by Sars [1865] and Lilljeborg [1901] more than a century ago. In reality, organisms evolve as complete systems and therefore they must be analyzed in full or at least in relation to a large set of morphological features.

Somewhat later, more detailed morphological investigations of Haplopoda (*Leptodora*) and Onychopoda (*Bythotrephes*) were provided, which made it possible to evaluate the structures and their evolutionary transformation in more detail (see Boikova [2008]; Korovchinsky, Boikova [2008, 2017]; Korovchinsky [2015]).

Overview of particular external and internal morphological structures

Haplopoda and Onychopoda differ from the vast majority of other cladocerans in the predatory mode of life — catching and holding of moving prey (the only other cladoceran predator, *Anchistropus* Sars, 1862 (Chydoridae), feeds on sedentary hydra [Van Damme, Dumont, 2007]. The large eye, long and strong swimming antennae, modified mandibles, sclerotized stenopodous trunk limbs forming a "catch basket", reduced carapace and other morphological features of these crustaceans are fully adapted to this lifestyle.

At the same time, the representatives of these two orders solve the problem of this adaptability in its own way. For example, in all of them, the trunk limbs are directed forward to the front edge of the head, which is needed to capture and manipulate prey. But in haplopods, this is achieved as a result of specific growth of the postero-ventral part of thorax, which takes place during the molt, completing embryogenesis (Boikova, 2008), and in onychopodes — bending the head section down, which occurs during the embryonic period [Olesen, 2003].

Head and eye. The head shape of Haplopoda and Onychopoda is quite different, but in the representatives of both orders, the eye occupies an extremely forward position, which suggests the important role of vision for detecting and catching prey. However, Herzig and Auer [1990] suggested that in *Leptodora* the prey's "searching mode is nonvisual and tactile" because in the experiment, their representatives did not react to dead and motionless food objects. But it seems doubtful that the highly developed visual organs of these crustaceans are not used in prey search. The fact that predatory crustaceans react only to movable prey, not to dead ones, only indicates that they are specifically adapted to such a consumption mode. Polyphemidae and Cercopagididae also catch only colored, moving prey using visual clues [Rivier, 1998]. It should be noted that potential prey of these invertebrate predators use akinesis as a means of defensive behavior [Smirnov, 1977].

There are differences in the composition of eye pigments in haplopods and onychopods. In the embryo-like larva of *Polyphemus* (Onychopoda), the pigment biliverdin, very rare among crustaceans, was found, which gives the rudiment of the eye of *Polyphemus* a green color [Green, 1965]. The rudiment of the eye of *Leptodora* (Haplopoda) and other Cladocera (Ctenopoda and Anomopoda) are red in colour [Kotov, Boikova, 1998, 2001; Boikova, 2008].

The facts presented above, indicating that the eyes of haplopods and onychopods have a completely different structure, prove that they originated in representatives of each order independently.

Antennules. In Haplopoda females, the ventro-lateral position of antennules on the head and presence of nine aesthetascs are similar to what is observed in most other Cladocera. In Onychopoda, antennules are situated very closely to each other beneath the eye; the number of their aesthetascs is diminished by up to five (a sign of oligomerization). It should be noted that at the early embryonic stage they are located on the head laterally, but then gradually move to the ventral side, their bases fuse together and with the head of the crustacean [Olesen, 2003].

In *Leptodora* males, antennules are unique (see above), completely differing not only from those of *Leptodora* females but also from all other Cladocera, including Onychopoda males. In the latter, they mostly do not differ from those of females apart of *Polyphemus*, in which the sensory seta is elongated and thickened. All this probably testifies to different modes of searching for gamogenetic females and differences in the copulation process in Haplopoda and Onychopoda.

In the adult *Leptodora* males, the antennules are long, incurved, pointed structures with numerous aesthetascs along their anterior margin. In neonate males, they are short, triangular, with nine aesthetascs distally. But then there is a gradual elongation of the antennae and the appearance of new aesthetascs along their anterior margin [Sebestyén, 1931].

Swimming antennae. Among all the Cladocera, Haplopoda possess the largest number of segments and setae on the branches of swimming antennae, which reminds the antennae of the extinct Jurassic *Leptodorasida* Kotov, 2007 (order Cryptopoda) [Kotov, 2007], which have four-segmented antennal branches armed with numerous setae. The representatives of Onychopoda and a number of Anomopoda families have a four-segmented upper antennal branch, while the lower branch is predominantly three-segmented. All other Cladocera have two- or three-segmented branches. Thus, the presence of four- and five-segmented branches in *Leptodora* is aunique and most probably a primitive feature [Eriksson, 1934], not secondary as was suggested by Olesen [1998: 529] who counted only four segments on both antennae of adult leptodoras. He suggested, based on the Sars [1874] figure, that if "larvae of *Leptodora* have only 4 and 3 segments in the antennal rami", then this should prove that "the extra segment in one of the rami [of adults] could have been achieved secondarily". But this is incorrect because the earliest *Leptodora* larva depicted by Warren [1901] already had four-segmented antennal branches.

In different cladoceran lineages, the process of oligomerization in evolution of some of their structures are usually predominates, in particular, in segmentation of the swimming antennae [Smirnov, 1969; Korovchinsky, 2004; Korovchinsky *et al*., 2021]. As a rule, in such a process, just the proximal segments of the branches are diminished, lose their setae and disappear (e.g., in Sididae and Bosminidae). In *L. kindtii* (Focke, 1844), the proximal segments of both branches are small and reduced, which indicates that the process of oligomerization is going the same way.

Compared to *Leptodora*, the antennal segmentation and branches' armament of Onychopoda looks evolutionary more advanced (more oligomerized), taking into consideration the diminished number of antennal segments and swimming setae.

Mouth parts. In general, the structure of the mouth parts of Haplopoda is unique and complex; however, it is possible to find some features in common with Onychopoda. Thus, its labrum is similar to that of *Bythotrephes* (see Martin, Cash-Clark [1995]), though in the latter it is bilobed, having large ventral prominence (in *Cercopagis* the latter is absent). Besides, there are clear similarities in the mandibles of the two groups. Both are heavily sclerotized appendages obviously adapted for biting; however, in *Leptodora* they are more delicate, long, and styliform, possibly intended for smaller and softer prey. Distally, in both groups, they have three prominences, namely three denticles in *L. kindtii* and two denticles (one of them rudimentary) and a mandibular process in *Bythotrephes*. The mandibular process of the latter occupies the same position as the proximalmost denticle on the mandibles of *Leptodora*, which differs conspicuously from that of *Bythotrephes*, being slender. This probably means that the proximalmost mandibular denticle of *Leptodora* may represent a rudiment of a mandibular process which was described previously by Lilljeborg [1901] under the name "processus maxillaris". The use of the latter term is misleading due to its synonymy with the term "gnathobase" [Kotov, 1996], which is applicable rather to the whole distal part of the mandibles of Branchiopoda [Manton, 1977], not just to one of its prominence [Korovchinsky, Boikova, 2008].

The lower lip of *Leptodora* is a unique structure in Cladocera. In many Crustacea, there is a labium which consists of a pair of paragnats, but they are absent in most Cladocera including Onychopoda. It may be suggested that in *L. kindtii* these structures were transformed into the median lobe of the lower lip. But the study of the embryogenesis of *Leptodora* showed [Olesen *et al*., 2003; Boikova, 2008] that the latter is formed by an elevated sternal region under the labrum. At the same time, the lateral lobes of the lower lip are formed by the transformed maxillules (maxillae I). This fact is also proved by the study of embryonic development [Olesen *et al*., 2003; Boikova, 2008] and innervation of the lower lip [Kirsch, Richter, 2007]. At the same time, Onychopoda possess well developed maxillules (maxillae I) of ordinary structure which are situated behind the mandibles [Rivier, 1998].

Carapace. The similarity in the structure of the carapace of Haplopoda and Onychopoda consists only in the fact that it does not cover the thoracic limbs laterally. The carapace of *Leptodora* is an unusually organized structure, having arisen from the posterior part of the thorax, while in all other Cladocera it is derived from the maxillary area of the head [Fryer, 1996; Kotov 1996]. To explain the displacement of the *Leptodora* carapace, Fryer [1996] suggested that it had migrated to the posterior part of the thorax due to the elongation and rotation of the latter during the evolutionary transformation. As a result, "the abdomen articulates with the morphologically dorsal surface of the thorax, and the carapace lies physically remote from the head but is still attached in a morphologically antero-dorsal position". However, recent embryological studies [Olesen *et al*., 2003; Boikova, 2008] do not support this hypothesis. It has been interpreted, in accordance with previous investigations (see P.E. Müller [1868]; Samter [1895]), that the carapace, arising initially from the posterior area of the head, then moves posteriorly and gradually merges with the dorsal side of the thorax, so that only its posterior part remains free. This means that the latter, forming the open brood pouch, is only homologous to the posterior part of the carapace of other Cladocera [Olesen *et al*., 2003; Boikova, 2008; Korovchinsky, Boikova, 2008]. In newborn crustaceans, the carapace is seen as a short outgrowth of the posterior edge of the thorax. In growing males, it does not undergo noticeable changes in the future, but in females it gradually lengthens until the time of formation of the brood pouch.

It should be noted that in *Leptodora,* the anterior part of the carapace, fused with the dorsal area of the thorax, covers the area occupied by the heart. Such a phenomenon may be seen in other Cladocera (see, for instance, numerous figures by Sars [1861 (1993)] and Mordukhai-Boltovskoi & Rivier [1987]), with the difference that the heart of these crustaceans is much smaller than in *Leptodora* and, correspondingly, only the anteriormost part of the carapace turns out to be merged with the thorax.

In Onychopoda, the carapace has been evolutionary transformed in a different way: in females it forms a dorsal, entirely closed chitinous chamber. In Cercopagididae and Podonidae, it turned out to be even more complicated, since it has a special internal brood pouch inside [Mordukhai-Boltovskoi, Rivier, 1987; Rivier, 1998] (see above). The origin of the latter is unclear. Fryer [1996] suggested that it could arise as a result of the formation of the carapace fold and the fusion of its inner layer with the dorsal integument of the thorax. Pedogenesis, long known in Podonidae, is obviously related to this structure. The embryo-like larvae of these crustaceans, developing inside the mother's body, already carry eggs in their brood pouches (see below). Recently, pedogenesis was also discovered in Cercopagididae, in one of the populations of *Bythotrephes brevimanus* Lillieborg, 1901 [Korovchinsky, 2018]. Unlike females, Podonidae males have two well-identified juvenile stages [Sinev, Degtyareva, 2018].

In the representatives of both orders, the carapace structure is unique in its own way, but in Onychopoda, it is undoubtedly morphologically more elaborated, having gone through a more complex path of evolutionary transformation.

Thoracic limbs. The evolutionary transformation of *Leptodora*'s limbs has been traced by Olesen *et al.* [2001, 2003] who used various methods such as SEM, Hoechst fluorescent stain and expression of the *Distalless* gene.They showed that the elongated limb buds of tl I – tl V of early embryos (embryo-like larva) consist of five "portions" (a term by Olesen *et al.* [2001]). At the same time, in the adult leptodoras, these limbs comprise four segments: a long proximal segment and three smaller distal ones.These authors suggest that the three distal portions of limb buds of embryos would become three short distal segments of the trunk limbs of adults, whereas "the two proximal portions will fuse to a single segment" [Olesen *et al*., 2001: 872]. The question arises, how the so-called "maxillary process" of the tl I turned out to be attached to the ventral side of the thorax, close to the bases of the limbs (Fig. 3b), but not connected to them [Sebestyén, 1931]. Korovchinsky and Boikova [2008] suggested that disconnection of the gnathobase from tl I and its location on the ventral side of the thorax may be explained by the fusion of the proximal segment of the limb's protopodite (coxa) with the ventral side of thorax, which is strongly developed and obviously requires the additional material for its formation. Therefore, the large basal segment of tl I of *Leptodora* has not been formed by the fusion of two proximal limb portions of embryos, as was suggested by Olesen *et al*. [2001, 2003], but developed from the single, strongly enlarged, second (2nd) proximal portion of the embryonic limb (morphologically this part corresponds to distal segment of protopodite — basis). In Olesen's *et al*. [2001, 2003] drawings of embryos, the "maxillary process" is seen as located separately from the leg at its base, which may be an artifact of the fixation of the material for SEM, since in photographs of living embryos it is clearly located on a short proximal portion of the embryonic limb (see Boikova [2008: fig. 7E]). Four segments of the adult tl I correspond to four distal limb portions of the embryo. Probably the formation of other limbs follows the same pattern. However, their transformation seems more radical because no signs of gnathobases may be found [Korovchinsky, Boikova, 2008].

Unlike Haplopoda, Onychopoda has four pairs of stenopoid trunk limbs, tl I – tl III with two-segmented protopodite and two- three-segmented endopodite. In Polyphemidae and Podonidae, they also carry exopodites which are absent in Cercopagididae.

The peculiarity of the thoracic limbs of *Bythotrephes* and probably other Onychopoda lies in the fact that the inner side of their endopodital proximal segment has grown in a proximal direction and occupied a distal part of the protopodite together with its"gnathobasic" process (probably this is true for tl IV as well) (Fig. 3a). Possibly this has occurred for morpho-functional reasons, given a chance for the "gnathobasic" processes to be more developed and for endopodital setae to be more numerous and distributed more proximally along the limbs (protopodites themselves lack setae) [Korovchinsky, 2015].

The second peculiarity is that the "gnathobasic" process in *Bythotrephes* and other onychopods arises from the distal segment of protopodite (basis) (Fig. 3a), not from the proximal one (coxa), which is characteristic for true gnathobase (about the characteristic of the latter structures see Manton [1977] and Kotov [2013]). In other words, they are the derivatives of the second, not of the first, inner endite of the thoracic limb and, for this reason, they are not homologues to the gnathobases of other cladocerans (and other branchiopods in general) and should be called pseudognathobases. In turn, the tl IV of onychopods is represented mostly by the protopodite; only its distal setulated part externally and apically is of endopodital origin. This feature makes the members of the order Onychopoda having pseudognathobases instead of gnatobases on the thoracic limbs, unique among Cladocera and the whole class Branchiopoda [Korovchinsky, 2015].

Thus, it is quite evident that the thoracic limbs of Haplopoda and Onychopoda, being stenopodous in the representatives of both orders, have passed a different path of evolutionary transformation. Those of Haplopoda (*Leptodora*) lost the proximal segment of protopodite, which has fused with the ventral overgrown part of the thorax, together with its gnathobase. On the other hand, some Onychopoda retained exopodites but, at the same time, other parts of limbs have appeared to be specifically transformed.

The clasping organs of males of haplopods and onychopods have different structures (see above). In the former ones, the functioning of the specific male's clasping organs is probably connected with the bending of two distal segments of their tl I. In Onychopoda males, on the contrary, the capture of the females is carried out by hooks of different structure and location situated on the distal segment of tl I.

Abdomen and postabdomen. The abdomen of Haplopoda (*Leptodora*) is large, occupying not less than one third of body length, and very flexible. Their abdomen and postabdomen are straightened and coupled together to form a quite impressive and functionally effective structure which is used for maintaining body balance, during swimming, prey catching, and cleaning of the "catch basket" and swimming antennae [Kuzitchkin, 1975; Kashin, Rudyakov, 1978; Browman *et al*., 1989; Herzig, Auer, 1990].

At the same time, the vast majority of cladocerans have a short abdomen. The only exceptions are some Anomopoda (Ilyocryptidae and some Chydoridae), which have a relatively large, non-segmented abdomen, as well as onychopods of the Cercopagididae family with a long and segmented abdomen. A study of the embryogenesis of the *Leptodora* showed that the formation of its abdomen is associated with the growth zone located in front of the rudiment of the postabdomen [Boikova, 2008]. It is interesting to note that the postabdomen of *Leptodora* reminds postabdomen of the late nauplius of Spinicaudata (see e.g., Olesen, Grygier [2003]).

The postabdomen of *Leptodora* is highly modified, cylinder-shaped, bears two very small postabdominal setae and a pair of large terminal claws. Weismann [1874] was the first to describe tiny postabdominal setae of *L. kindtii* as two-segmented, setulated, and functionally-active sensory appendages, similar to those in other Cladocera. However, in the latter, they are mostly long and quite conspicuous. In *L. kindtii,* the small size of the postabdominal setae is probably related to loss of their hydrostatic function while their sensory function has been retained.

Some authors [Martin, 1992; Olesen *et al*., 2003] contrasted the postabdomen (telson) of *L. kindtii* to that of most other Branchiopoda (Spinicaudata, Ctenopoda, Anomopoda) because its terminal claws lack articulation with postabdomen. According to Rivier [1998], the representatives of Onychopoda also possess no articulated terminal claws, while Korovchinsky [2015, 2018] recorded the articulated or not articulated connection of claws with the postabdomen in *Bythotrephes* (Cercopagididae). Obviously, the sign of articulation of claws with postabdomen has no importance.

It was shown that the postabdominal claws of all Cladocera and most other Branchiopoda, are homologous, originating not from the furcal rami themselves but from the setae of the furca [Kotov, 2006, 2013]. In living embryo-like larvae of *Leptodora*, it is clearly visible that the postabdominal claws are situated in deep pockets formed at the end of the furcal rami (see Boikova [2008: fig. 6c]).

Among onychopods, there are representatives with both a very short non-segmented abdomen (Polyphemidae, Podonidae) and a long segmented one (Cercopagididae). In the latter family, the abdominal segmentation is usually disguised by folds and wrinkling of its thin, soft cuticle, which readily appears in preserved specimens. The transverse line between the narrow anterior part of the abdomen and its larger following part is almost permanently visible and may be regarded as a remnant border separating two segments. The larger following part of the abdomen, often having a conspicuous dorsal fold, obviously plays an active functional role, favoring the movements of the posterior body part with a long caudal process. This part of the abdomen is abruptly separated from the smaller "postabdomen". The latter is often visible as composed of two parts separated by a transverse curved line, representing a border from which the molted old integument of postabdomen and caudal process is shifted backwards. Judging from this, it seems that just the posterior part of the mentioned "postabdomen", bearing claws and an anal opening between them, is a postabdomen in its true sense, while the anterior part of the structure situated closer to the abdomen represents in fact the transformed third segment of the latter, structurally and functionally joined with the postabdomen (Fig. 4a). Thus, it may be concluded that, morphologically, *Bythotrephes* has a three-segmented abdomen, but its posterior segment has proved to be transformed and morpho-functionally joined with the postabdomen [Korovchinsky, 2015].

The postabdomen of Polyphemidae and Cercopagididae are not similar to postabdomen of other Cladocera, including Haplopoda (*Leptodora*). Its main function is to stabilize the position of the crustacean body in the water, because in the representatives of the two former families, it forms a comparatively short and massive (Polyphemidae) or very long (Cercopagididae) caudal process dorsally, which in the first case, terminates in two long postabdominal setae, and in the second case in two minute rudimentary ones. The long postabdominal setae of polyphemids have no sensillae, being covered only with tiny denticles. According to Rivier [1998: 36], they perform the tactile function, and according to Butorina [1995a], they take part in stabilizing the body position of the crustacean.

In Cercopagididae, the formation of a long and massive caudal process required a lot of body mass material which was probably taken in the process of evolutionary transformation from the postabdomen and the last segment of the abdomen, which has proved to be morpho-functionally joined. The minute rudimentary postabdominal setae occur on the terminus of the caudal process and probably fulfill a sensory function. The presence of these setae and their common attachment to one basis probably testify more precisely the involvement of "postabdominal" dorsum (dorsal part of postabdomen with the basis of postabdominal setae + dorsal part of last segment of abdomen), not postabdominal setae basis only as it was suggested earlier (see Olesen [1998]; Dumont, Negrea [2002]), in the formation of the caudal process. This suggestion explains the comparatively small size of the posteriormost body segments (last segment of abdomen + postabdomen) under consideration [Korovchinsky, 2015].

In Podonidae, the chitinous chamber formed by the carapace performs a hydrostatic function; the postabdomen of these crustaceans and its appendages are often reduced. It bears a pair of claws (sometimes they are absent) and two short setulated setae sitting on a small basis.

Internal structures

The representatives of Haplopoda demonstrate a unique disposition of the internal trunk organs. Whereas in most cladocerans, including Onychopoda, the ovaries and testes are located in the thoracic region, in haplopods they are situated in the abdomen. There the left ovary is located mainly in the first abdominal segment, the right ovary — in the third abdominal segment (see above). Haplopoda males have an unusual unpaired testis, also located in the abdomen (see above). The digestive system of the crustaceans of this order is also of an unusual structure, consisting of a very long and thin oesophagus, which stretches to the third abdominal segment, where it passes into the middle intestine. Probably this unusual arrangement of the internal organs of haplopoda is due to the presence of the enormously large heart occupying almost the whole thoracic region.

Unlike haplopods, onychopods have the location of reproduction organs usual for cladocerans (in the thoracic region) and the usual structure of the digestive system (see above).

Besides the unique digestive and circulatory systems, haplopods are distinguished by the specific and advanced nervous system with its specific optic fibres, the elongated circumoesophageal connectives, and merging of the ganglia of the thoracic regions, as well as by the structure of the excretory system.

If haplopods seem to be more evolutionary advanced in relation to the above mentioned organs, then the reproduction system of onychopods is more elaborated, being represented by closed brood pouches, including the unique internal one in Cercopagididae and Podonidae, and nourishing organs ("placenta"). Besides this, the Onychopoda males possess copulatory appendages lacking in Haplopoda. Also, Onychopoda, along with other Cladocera, lost the larva stage in their life cycle.

Development of eggs

The development of subitaneous eggs in both Haplopoda and Onychopoda is pseudo-direct. In both cases, an embryo-like larva hatches from the egg (stage 3 of *Leptodora* [Olesen *et al*., 2003; Boikova, 2008] and intermediate embryo of *Polyphemus* [Olesen, 2003]), which morphologically corresponds to the late metanauplius. After molting, the embryo-like larva becomes similar to the juvenile stage (stage 4 of *Leptodora* [Olesen *et al*., 1999; Boikova, 2008]; late embryo of *Polyphemus* [Olesen *et al*., 2003]); at the same time, it differs from the latter by the underdevelopment of a number of morphological structures and the lag of functionality [Boikova, 2012]. In Podonidae and some Cercopagididae, the embryo-like larvae of this stage become sexually mature and carry eggs in their brood pouches (neoteny) (see above). The embryo-like larvae of *Leptodora* are very similar to the free-living larvae of its gamogenetic cycle (metanauplius and transitional larva (the term was proposed by Sebestyén [1949]) and differ from them only in the absence of mandibular palps and an eye. Mandibular pulps gradually degenerate, but the ocellus remains throughout the life of the crustaceans of the first generation [Sars, 1874].

As was noted above, the development of the resting egg of Haplopoda and Onychopoda differs. Haplopods have a unique for the cladocerans indirect development from the resting eggs, which is accompanied by the appearance of three free-living lecithrophic larvae (two metanaupliuses and a transitional larva) [Sars, 1874; Warren, 1901; Sebestyén, 1949]. However, they are quite different from the larvae of other brachiopods in the absence of a naupliar feeding apparatus ("masticatory spines" on the protopod of the second antennae) and presence of a large amount of yolk. The mandibular palps of the larvae of *Leptodora* are unsegmented and have only apical setae [Olesen, 2003]. They do not participate in the food gathering, as in other Brachiopoda. Sars [1874] suggested that they act as stabilizers of the body position during swimming. A number of authors [Olesen, 2003; Fritsch *et al*., 2013] consider the indirect development of *Leptodora* secondary, but recognize that the only argument for this is the parsimony argument.

The development of the resting eggs of Onychopoda is direct, as well as other Cladocera. A fully developed crustacean hatches from the egg, molts and turns into a juvenile [Onbe, 1974, 1978; Butorina, 1998; Rivier, 1998).

On the non-monophyly of Gymnomera

It is clearly seen from above described external and internal features of Haplopoda and Onychopoda, their reproductive traits, that although some of them seem superficially similar, in fact they are mostly substantially different (Tables 2, 3). All their morphological similarities are purely adaptive, associated with a predatory lifestyle of the representatives of the orders.

For this reason, the usually used synapomorphies of Gymnomera such as e.g., "eye with numerous ommatidia", "modification of the carapace to a smaller, dorsal brood pouch", "stenopodous trunk limbs", etc. [Sars, 1865; Lilljeborg, 1901; Olesen, 1998, 2000, 2009; Richter *et al*., 2007; Kotov, 2013] just don't make sense because each of these structures in the representatives of each order in fact is very specific obviously having independent origin from different ancestors [Korovchinsky, 2015; Korovchinsky, Boikova, 2017]. Recently, this has been confirmed by molecular-genetic studies [Xu *et al*., 2021; Van Damme *et al*., 2021]. In particular, the latter authors attributed Haplopoda and Onychopoda to different distant branches of Cladocera, postulating the proximity of the former to the order Ctenopoda, and the latter to the order Anomopoda.

Thus, Van Damme *et al*. [2021] do not support the hypothesis of the existence of the taxon Gymnomera and, to a certain extent, and at a new level, reproduced the hypothesis of the evolutionary proximity of Haplopoda and Ctenopoda, which was first put forward by Wesenberg-Lund [1904, 1952] and Lityński [1916] although too radical. Thus, the former author considered *Leptodora* only a genus of the Sididae family, and the another one referred them to two subfamilies, Leptodorinae and Sidinae, of the same Sididae family. That time no one supported their hypotheses, but now it is being partly confirmed by the latest molecular-genetic research studies.

Researchers who have recently tried to prove the reality of the taxon Gymnomera have relied on modern methodology — cladistic analysis and molecular-genetic data, which have been used to clarify Cladocera phylogeny since the 1990s. While the researchers hoped for the perfection of the approaches used, the analysis of the material was carried out purely formally, without understanding of its actual peculiarities. At that time, genetic methods were not yet sufficiently developed, and morphological features were not adequately evaluated as well, which could not be a reliable basis for the applied cladistic analysis.

So, if a monophyletic taxon is defined as a taxon, whose nearest common ancestor of all its members is also a member of that taxon in all its characters [Rasnitsyn, 1983, 2002], this cannot be applied to the taxon Gymnomera that united orders Haplopoda and Onychopoda, the representatives of which are very different in many of their characteristics described above.

Compliance with ethical standards

CONFLICT OF INTERESTS: The authors declare that they have no conflicts of interests.

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