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Partial revision of the genus *Cercopagis* Sars, 1897 (Crustacea: Cladocera: Onychopoda), with the redescription of two species and comments on morphology, taxonomy, reproduction, species richness, zoogeography, and origin

Частичная ревизия рода *Cercopagis* Sars, 1897 (Crustacea: Cladocera: Onychopoda) с переописанием двух видов и комментариями по морфологии, систематике, размножению, видовому обилию, зоогеографии и происхождению

N.M. Korovchinsky
Н.М. Коровчинский

A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences, Leninsky prospect 33, Moscow 119071 Russia.
Институт проблем экологии и эволюции им.А.Н. Северцова РАН, Ленинский проспект, 33, Москва 119071 Россия.
Nikolai Korovchinsky: nmkor@yandex.ru; https://orcid.org/0000-0003-2824-0981

KEY WORDS: *Cercopagis*, taxonomic revision, redescription, morphology, reproduction, species richness, zoogeography, origin.

КЛЮЧЕВЫЕ СЛОВА: *Cercopagis,* систематическая ревизия, переописание, морфология, видовое обилие, зоогеография, размножение, происхождение.

ABSTRACT. A partial revision of the genus *Cercopagis* Sars, 1897 was carried out with a redescription of the type species of the genus *C. socialis* (Grimm, 1877) and the species *C. pengoi* (Ostroumov, 1892). The nearby related genus *Apagis* Sars, 1897 was abolished, since its individuals represent only a temporary stage of the life cycle — females of the first generation hatched from resting eggs. Other species, *C. micronyx* Sars, 1897, *C. longiventris* Mordukhai-Boltovskoi, 1962, *C. spinicaudata* Mordukhai-Boltovskoi, 1962, as well as representatives of the "*Apagis*" forms are described briefly, since only little materials were available for them. There was no material available for the other three species of the genus *Cercopagis*. The partial nature of the revision is due to the fact that the author did not have sufficient material at his disposal, in particular, because the previously extensive collections of zooplankton from the reservoirs of the Ponto-Caspian-Aral basin have not been preserved. The representatives of the genus *Cercopagis* are discussed in the aspects of comparative morphology, taxonomy, peculiarities of sexual reproduction, geographical distribution, species richness, and origin. It is assumed that in recent decades, the species richness of the genus had undergone significant degradation due to large-scale changes in the aquatic ecosystems of the basin, in particular, in connection with the introduction of numerous alien species into the Caspian Sea.

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РЕЗЮМЕ. Проведена частичная ревизия рода *Cercopagis* Sars, 1897 с переописанием типового вида рода *C. socialis* (Grimm, 1877) и вида *C. pengoi* (Ostroumov, 1892). Описанный параллельно с ним близкий род *Apagis* Sars, 1897 был упразднён, поскольку его особи представляют собой лишь временную стадию жизненного цикла — самок первого поколения, вышедших из покоящихся яиц. Другие виды, *C. micronyx* Sars, 1897, *C. longiventris* Mordukhai-Boltovskoi, 1962, *C. spinicaudata* Mordukhai-Boltovskoi, 1962, а также представители форм "*Apagis*" описываются кратко, поскольку по ним имелся только малочисленный материал. По остальным трём видам рода *Cercopagis* материал отсутствовал. Частичный характер ревизии обусловлен тем, что в распоряжение автора не имелось достаточного материала, в частности, в связи с тем, что имевшиеся ранее обширные коллекции зоопланктона из водоёмов Понто-Каспийского-Аральского бассейна не сохранились. Представители рода *Cercopagis* обсуждаются в аспектах сравнительной морфологии, систематики, особенностей полового размножения, географического распространения, видового обилия и происхождения. Предполагается, что в последние десятилетия видовое обилие рода претерпело существенную деградацию в связи с масштабными изменениями экосистем водоемов указанного бассейна, в частности, в связи с вселением в Каспийское море многочисленных видов-вселенцев.

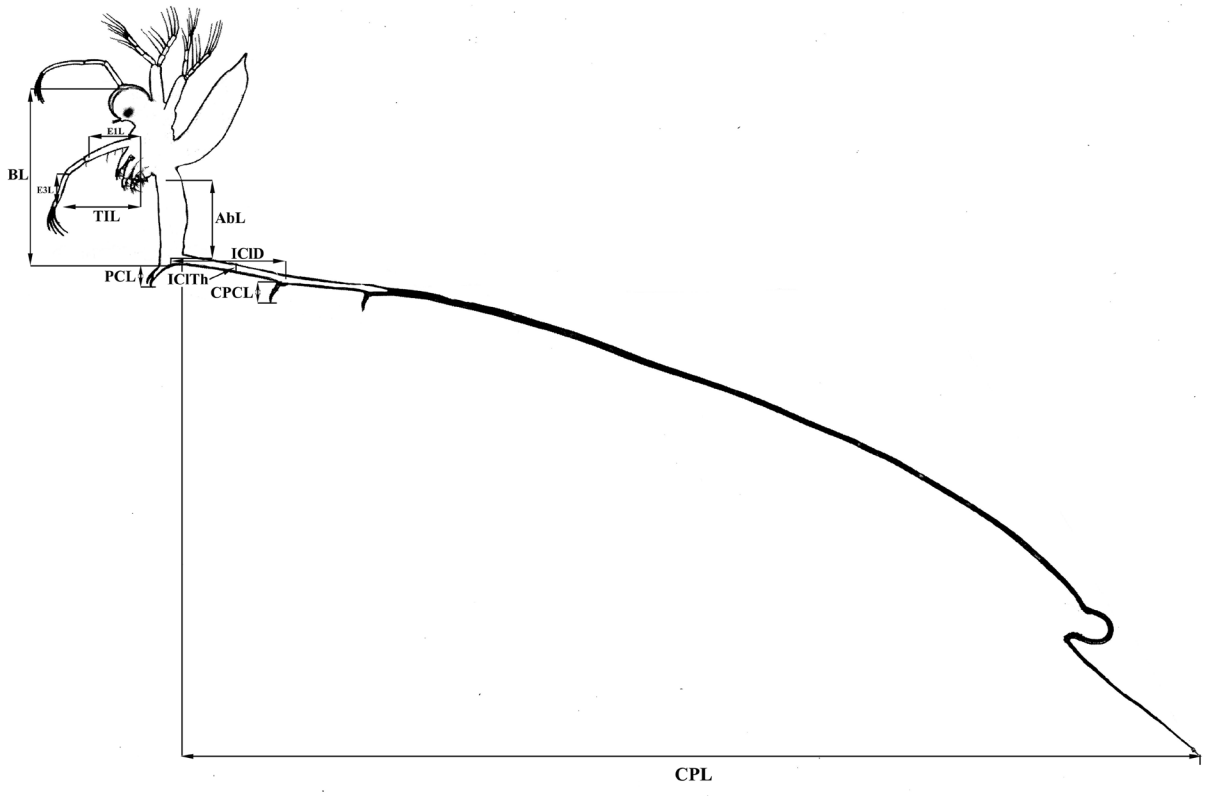

Fig. 1. Scheme of body and body parts measurements of *Cercopagis* adult specimens: AbL — abdomen length, BL — body length, CPCL — caudal process' claws length, CPL — postabdomen' claws length, E1L — length of first segment of tl I, E3L — length of third segment of tl I, ICID — length of caudal process between two anterior pairs of claws, ICITh — thickness of caudal process between two anterior pairs of claws. The figure of *Cercopagis* has been derived from Grigorovich *et al*. [2000].

Рис. 1. Схема измерений тела и его частей взрослых особей *Cercopagis*: AbL — длина абдомена, BL — длина тела, CPCL — длина когтей каудального выроста, CPL — длина когтей постабдомена, E1L — длина первого членика первой пары торакальных конечностей, E3L — длина третьего членика тех же конечностей, ICID — длина участка каудального выроста между двумя передними парами когтей, ICITh — толщина каудального выроста между двумя передними парами когтей. Рисунок *Cercopagis* заимствован из Grigorovich *et al*. [2000].

Introduction

The genus *Cercopagis* Sars, 1897, together with a nearby genus *Bythotrephes* Leydig, 1860, relates to the family Cercopagidae, which was erected by Mordukhai-Boltovskoi [1968a] (later the corrected name Cercopagididae for the family was provided by Martin & Cash-Clark [1995]). The nearest families are Polyphemidae Baird, 1845 and Podonidae Mordukhai-Boltovskoi, 1968, which altogether comprises the cladoceran order Onychopoda Sars, 1865.

The first person who collected and described the representatives of the genus *Cercopagis*, was Russian researcher Dr. Oscar Grimm [1877], one of the first investigators of the Caspian Sea aquatic fauna, who published the brief and partly incorrect description of "*Bythotrephes socialis* Grimm" (later *Cercopagis socialis* (Grimm, 1877)). These crustaceans live, according to the author's opinion, in large numbers at great depths. Then he added obviously fantastic assumptions about the lifestyle of the unusual animals he collected: "They are characterized by the fact that they have a tail 11 times longer than the length of the body (1 mm), curved near their free end in the form of a high arc, bearing spinules at its base; they cling to each other in this arc and thus unite in large colonies, which obviously represent a certain benefit for them".

This was followed by Mrs. Neonilla Pengo [1880] who described "*Bythotrephes* sp." from the Sea of Azov. Actually, this was the first detailed description of the representatives of the genus *Cercopagis,* supplied with good illustrations, including those of mandibles and thoracic limbs. Ostroumov [1892] noted the differences of these specimens from the previous ones found in the Caspian Sea and attributed them to a new species "*Bythotrephes Pengoi*", providing it with a brief differential diagnosis.

G.O. Sars [1897] made a real breakthrough in the taxonomy of the genus, presenting an extensive study on the species diversity of the genus. He investigated "a number of samples belonging to the collection of Dr. Grimm, and another sample taken in 1895 by Dr. Andrusov" in the Caspian Sea. He attributed the marine species of "*Bythotrephes*" to a new genus *Cercopagis* Sars, 1897 with six species, five of which were new to science (*C. robusta* Sars, 1897, *C. micronyx* Sars, 1897, *C. prolongata* Sars, 1897, *C. tenera* Sars, 1897, *C. anonyx* Sars, 1897), another one, already known (*C. socialis*) was redescribed in detail with the inclusion both external and internal structures. Besides, a new genus, *Apagis* Sars,

1897, was erected with one species, *A. cylindrata* Sars, 1897. However, Sars was clearly unaware of the previous data presented by Pengo [1880] and Ostroumov [1892].

In his next investigation, Sars [1902] continued the study of species richness of the Caspian *Cercopagis* and *Apagis.* In this respect, he described new species *C. neonilae* Sars, 1902 and *C. gracillima* Sars, 1902, along with *Apagis cylindrata* Sars, 1902 and *A. longicaudata* Sars, 1902. Under the name *C. neonilae,* Sars described individuals similar, in his opinion, to those studied by N. Pengo [1880] from the Sea of Azov but left by her without a species name.

Commenting on the Sars' data, some authors noted the unreliability of the distinctive species features [Sovinsky, 1902], and further great closeness and even identity of the species *C. pengoi*, *C. tenera*, and *C. neonilae* [Zernov, 1903; Meissner, 1908], which was also noted in a number of subsequent publications (see below). Zernov [1903] also described the features of the gamogenetic female of the former species.

At this point, the first stage of the study of the genus *Cercopagis* ended, and there was a big break of about 60 years, during which it was possible to note the appearance of only one work by Valkanov [1951], where the males of *C. pengoi* were described for the first time.

The beginning of a new stage was marked by the publication of a short note by Mordukhai-Boltovskoi [1962] in which the author gives very brief diagnoses of a new species of *Cercopagis* (*C. longiventris* sp.n., *C. spinicaudata* sp.n.) and *Apagis ossiani* sp.n. found in the material collected in the Caspian Sea. Soon after this, the former new species was described in more details together with *Apagis beklemishevi* sp.n. [Mordukhai-Boltovskoi,1964]. Here, an idea was expressed, agreeing with the opinion of some previous authors (see above), that species *C. pengoi*, *C. gracillima*, and *C. neonilae* may possibly be combined.

In the same year, the identification book by Manuilova [1964] was published which contained descriptions of eight species of *Cercopagis* and two species of *Apagis.* All data were presented according to Sars [1897, 1902]. This information clearly lagged behind the current dynamics of the genus research because in his following overview of the Ponto-Caspian Polyphemidae Mordukhai-Boltovskoi [1965] already enumerated nine and four species of the above two genera, respectively. Besides the taxonomy, the latter author presented the scheme of the evolutionary transformation of their representatives, which, however, might have only historical interest because in it, along with real species, the ontogenetic forms with a specific appearance are considered under the name *Apagis* (see further).

This was followed by a description of the gamogenetic forms (both gamogenetic females with resting eggs and males) of some species (*C. pengoi*, *C. socialis*, *C. micronyx*, *C. anonyx*, *C. spinicaudata*). In the latter species, only one juvenile male was found in the Middle Caspian Sea, while in the common and numerous *C. prolongata* the gamogenetic forms have not been found at all [Mordukhai-Boltovskoi, 1967; Mordukhai-Boltovskoi, Rivier, 1971]. The authors concluded that males of the genus *Cercopagis* in the Caspian Sea are very rare, bisexual reproduction is practically absent, and parthenogenesis absolutely prevails.

At that time, the publication of the faunistic atlases of the Caspian Sea, Black Sea together with the Sea of Azov, and Aral Sea was also initiated, where the representatives of the genus *Cercopagis* have also been described [Mordukhai-Boltovskoi, 1968b, 1969, 1974]. The species richness of the genus in the Caspian Sea was especially high (ten species) while from the Aral Sea a new subspecies *C. pengoi aralensis* Mordukhai-Boltovskoi, 1974 was described.

The data of the subsequently published identification books [Mordukhai-Boltovskoi, Rivier, 1987; Rivier, 1998] did not contain new discoveries; they were and remain only useful compilations summarizing information on the Onychopoda obtained over more than a century.

Starting from the 1950s, the representatives of onychopods, including those of *Cercopagis*, together with other invertebrates and vertebrates began to be recorded in reservoirs and other water bodies belonging to rivers flowing into the Black Sea, Sea of Azov, and Caspian Sea [Mordukhai-Boltovskoi, 1960, 1979]. Later on, a special interest in *Cercopagis* (and some other onychopods) arose after the discovery of their occurrence in new habitats where they had never been found before — in the Baltic Sea, and then in the Great American Lakes [Ojaveer, Lumberg, 1995; Panov *et al*., 1996; McIsaak, Grigorovich, 1999].

The high morphological variability of the representatives of the genus found beyond the native range has raised questions, active discussion and the need to conduct some research on this issue. In particular, it was assumed and then proved that the form "*Apagis ossiani*" represents only a special ontogenetic stage, namely, the specimens of the first generation emerged in the spring from resting eggs, sharply differing in their morphological features [Simm, Ojaveer, 1999, 2006; Macarewicz *et al*., 2001]. It was also suggested that, in addition to the *C. pengoi*, other species of the genus have invaded the Baltic Sea [Aladin *et al*., 1999], which was not confirmed afterward [Gorokhova *et al*., 2000; Simm, Ojaveer, 2006].

At the same time, in the last decades, taxonomic studies of the particular groups of the planktonic cladocerans of the Caspian Sea have not been provided. Only the regular research works on zooplankton without details, drawings and descriptions were published (e.g., Troshina *et al*. [2012]; Osmanov *et al.* [2015]; Bagheri, Sabcara [2019]), which makes it impossible to reliably assess the taxonomic status of the forms under consideration.

Meanwhile, the aquatic biota of the Caspian Sea has dramatically changed during this time, especially after the invasion of the ctenophore *Mnemyopsis leidyi* A. Agassiz, 1865 [Shiganova, 2010; Shiganova *et al.,* 2023]. As a result, the proportion of the native representatives has sharply decreased. In particular, the species richness of the genus *Cercopagis* appears to have declined sharply, which will be discussed in more detail below. At the same time, the alien copepods of the genus *Acartia* Dana, 1846, have certainly become predominant and among the

cladocerans, the representatives of Podonidae turned out to be the most prominent (e.g., Kurochkina *et al*. [2023]; Shiganova *et al*. [2023]).

The aim of the present work is to revise, at least partially, the genus *Cercopagis*, clarify its taxonomic status and the status of its constituent species, as well as to provide a more detailed description of some of them. It also seems important to estimate, at least approximately, the current species richness of the genus in the Caspian Sea — in the area of its highest diversity in the past.

ABBREVIATIONS. Morphology: ad — adult parthenogenetic females, AbL — length of abdomen, as — anterior setae, BL — body length (HL+ TrL+AbL + PL), CPCL — length of claws of caudal process, CPL — length of caudal process, E1L, E2L, E3L — length of first, second, and third segments of endopodite of thoracic limbs of first pair, gam — gamogenetic females, HL — head length, ICD — distance between claws (interclaw distance), ICTh — thickness of caudal process between claws (interclaw thickness), is — inner setae, juv — juvenile females, mx I — maxillules, os — outer setae, PCL — length of postabdominal claws, PL — length of postabdomen, PrL — length of protopodite of thoracic limbs of first pair, psg — pseudognathobase, T1L — length of the thoracic limbs of first pair (PrL+E1L+E2L+E3L), tl I…tl IV — thoracic limbs of first… fourth pairs, TrL — trunk length.

MUSEUMS AND PERSONAL COLLECTIONS. SMNH — Swedish Museum of Natural History (Stockholm, Sweden), NMK — author's collection, ZIN — Zoological Institute (St.-Petersburg, Russia).

Material and methods

The author had to use rather limited material in his research. Unfortunately, the extensive collection of zooplankton from the Caspian Sea that Prof. Ph.D. Mordukhai-Boltovskoi and Dr. I.K. Rivier had at their disposal, working at the Institute of Biology of Inland Waters (Borok, Yaroslavl District) in the 1960–1970s, have not been preserved, although Dr. L.F. Litvinchuk [2002] had the opportunity to use these materials rather recently. Only the relatively little material in the group from this collection from the Sea of Azov, Caspian Sea, and Aral Sea has been found in the Zoological Institute (St.-Petersburg, Russia); frequently it was only represented by a few type specimens of some species. Some additional materials were kindly provided by staff of the Caspian Research Institute (CaspNIRH) and a number of colleagues, as indicated in more detail below.

Data on the localities of material of each species will be given in the sections devoted to their descriptions. The morphometric measurements of specimens were provided according to the original scheme presented in Figure 1. The reliability of the difference in values was calculated according to the Student's t-criterion.

For SEM examination, specimens were subject to critical point drying (Leica EM CPD 300, Germany) and coated with gold-palladium (S150A Sputter Coater (Edwards, UK)). The preparations were examined with a TESCAN MIRA 3 LMH microscope at the Institute of Ecology and Evolution. Mandibles were prepared without dehydration.

Descriptions

Class Branchiopoda Latreille, 1817
Superorder Cladocera Latreille, 1829
Order Onychopoda Sars, 1865
Family Cercopagididae Mordukhai-Boltovskoi, 1966, emend. Martin et Cash-Clark, 1995
Genus *Cercopagis* Sars, 1897

Sars, 1897: 4–5, 23–24 (genera *Cercopagis, Apagis*), 1902: 34, 37–38 (genera *Cercopagis, Apagis*:); Sovinsky, 1902: 371–373, 376 (genera *Cercopagis, Apagis*); Manuilova, 1964: 294, 300 (genera *Cercopagis, Apagis*); Mordukhai-Boltovskoi, 1968b: 128–129, 138–139 (genera *Cercopagis, Apagis*), 1969: 19–20, 1974: 133; Mordukhai-Boltovskoi, Rivier, 1987: 153 (genus *Cercopagis,* subgenera *Cercopagis, Apagis*); Rivier, 1998: 173–174 (genus *Cercopagis,* subgenera *Cercopagis, Apagis*); Korovchinsky *et al*., 2021: 471–472.

The pigment spot occupies a relatively small part of the large eye. The upper lip (labrum) has no ventral outgrowth. The antennules are small, with 5 aesthetasks and a short sensitive seta which is as long as aesthetasks. Both branches of swimming antennae bear 7 setae. The thoracic limbs of the first pair (tl I) are especially long, with a relatively small number of setae; there are no setae on the middle segment of their endopodite. The brood chamber is of a different shape, often elongated and pointed at the end. The abdomen is long, often almost equal in length to the rest of the body, sometimes surpasses it, without traces of segmentation. Postabdomen is short, bearing a very long caudal process that is four–seven times longer than the rest of the body and has a large loop-like bend with two groups of denticles near its end. There are one–three pairs of claws of different size on the postabdomen and caudal process, which may be either relatively large or small and even rudimentary.

The type species is *Cercopagis socialis* (Grimm, 1877).

REMARKS. Initially, Sars [1897] described two close genera, *Cercopagis* and *Apagis*. Representatives of the latter one differ in the presence of a comparatively short and straight caudal process, having no posterior bend. The significant variability of this trait caused the lowering of the rank of the taxon *Apagis* to the subgenus level [Mordukhai-Boltovskoi, Rivier, 1987; Rivier, 1998]. Subsequently, it was found that the individuals of the taxon *C.* (*Apagis*) *ossiani* Mordukhai-Boltovskoi, 1968 represent in fact only the individuals of the first generation of the species *C. pengoi* (Ostroumov, 1892) released from the resting eggs [Simm, Ojaveer, 1999, 2006; Macarewicz *et al*., 2001]. Accordingly, and by analogy with the individuals of the first generation of the genus *Bythotrephes*, it can be concluded that the representatives of other "species" of *Apagis* represent, in fact, only individuals of the first generation of other species of the genus *Cercopagis*, the species correspondence of which has yet to be established. In this regard, the taxon *Apagis* and its "species" are excluded from the taxonomic composition of the family Cercopagididae.

Mordukhai-Boltovskoi & Rivier [1987] and Rivier [1998] considered *Cercopagis pengoi* as the type species of the genus which is not correct.

Cercopagis socialis (Grimm, 1877)
Figs 2–4

Grimm, 1877: 18, Tab. IX, Fig. 9 (*Bythotrephes*); Sars, 1897: 5–16, Pl. I, figs 1–14, 1902: 35; Sovinsky, 1902: 373; Manuilova, 1964: 295–296, fig. 162; Mordukhai-Boltovskoi, 1967: 115, figs 5–9, 1968b: 135, fig. 144; Mordukhai-Boltovskoi, Rivier, 1987: 154–156, fig. 96; Rivier, 1998: 177–178, figs 227–232; Korovchinsky *et al*., 2021: 477–478, fig. 148, 1–4.

Data on body and body parts measurements of the representatives of the species are presented in Table 1.

MATERIAL EXAMINED: Caspian Sea, numerous specimens, females: 1) ZIN, bottle No. 6964a with two labels: old one "*Bythotrephes socialis* Grimm, Caspian Sea, St. 107, 0°26′ E; 40°57′ N, 4.VII. 76 g, 75–80 sazh., Grimm" and new one: "*Cercopagis socialis* Grimm +

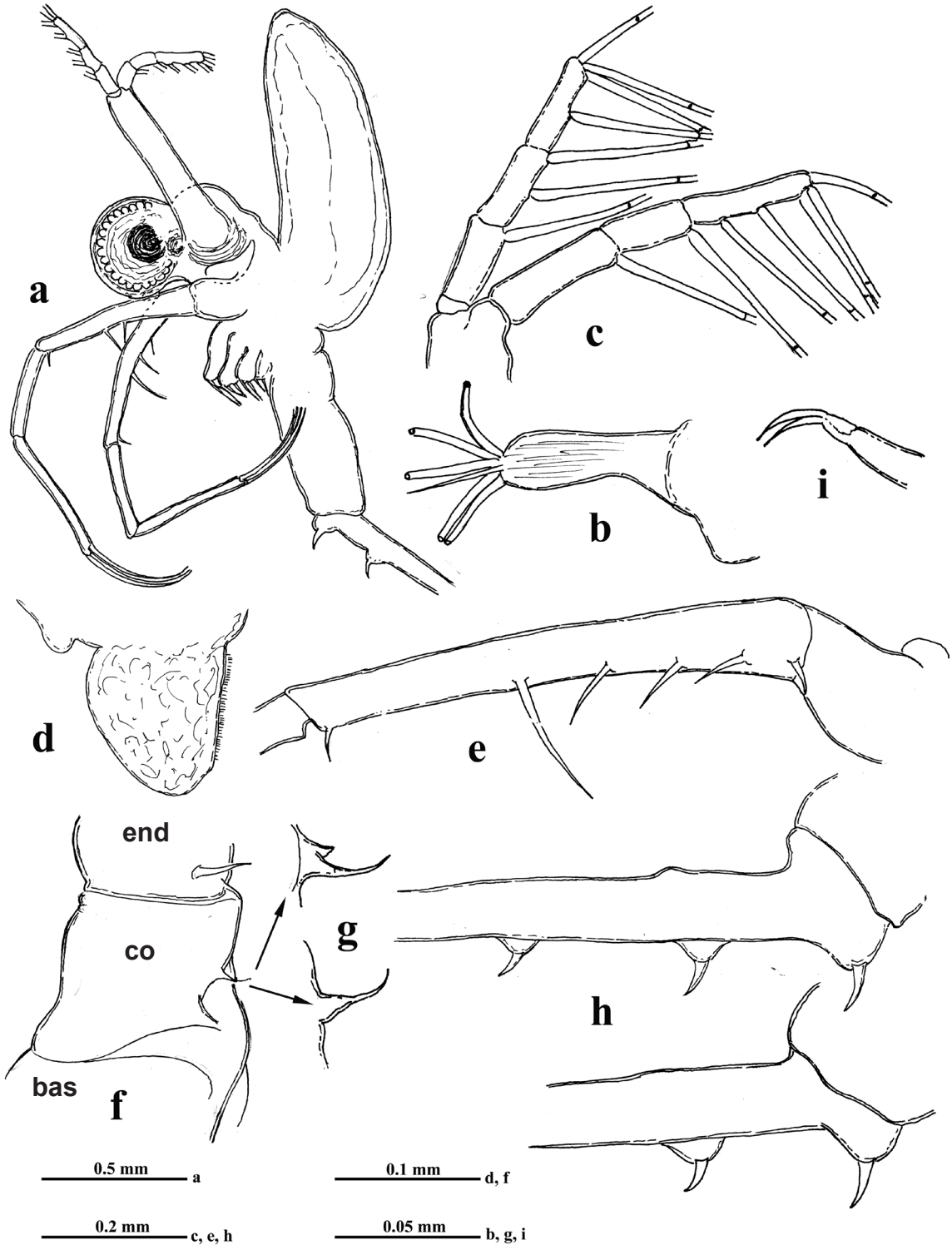

Fig. 2. *Cercopagis socialis* (Grimm, 1877), females, Caspian Sea: a — general lateral view; b — antennule; c — branches of swimming antenna; d — upper lip (labrum); e — first basal endopodital segment of the thoracic limb of first pair (tl I); f — protopodite of the same limb, inner side (bas — basis, co — coxa, end — endopodite); g — rudiments of pseudognathobase of different shape; h — postabdomen and proximal part of caudal process with claws; i — minute apical setae of caudal process.

Рис. 2. *Cercopagis socialis* (Grimm, 1877), самки, Каспийское море: a — общий вид сбоку; b — антеннула; c — ветви плавательной антенны; d — верхняя губа (лабрум); e — первый базальный членик эндоподита торакальной конечности первой пары (tl I); f — протоподит той же конечности, вид изнутри (bas — базис, co — кокса, end — эндоподит); g — рудименты псевдогнатобазы различной формы; h — постабдомен и проксимальная часть каудального выроста с когтями; i — мелкие апикальные щетинки каудального выроста.

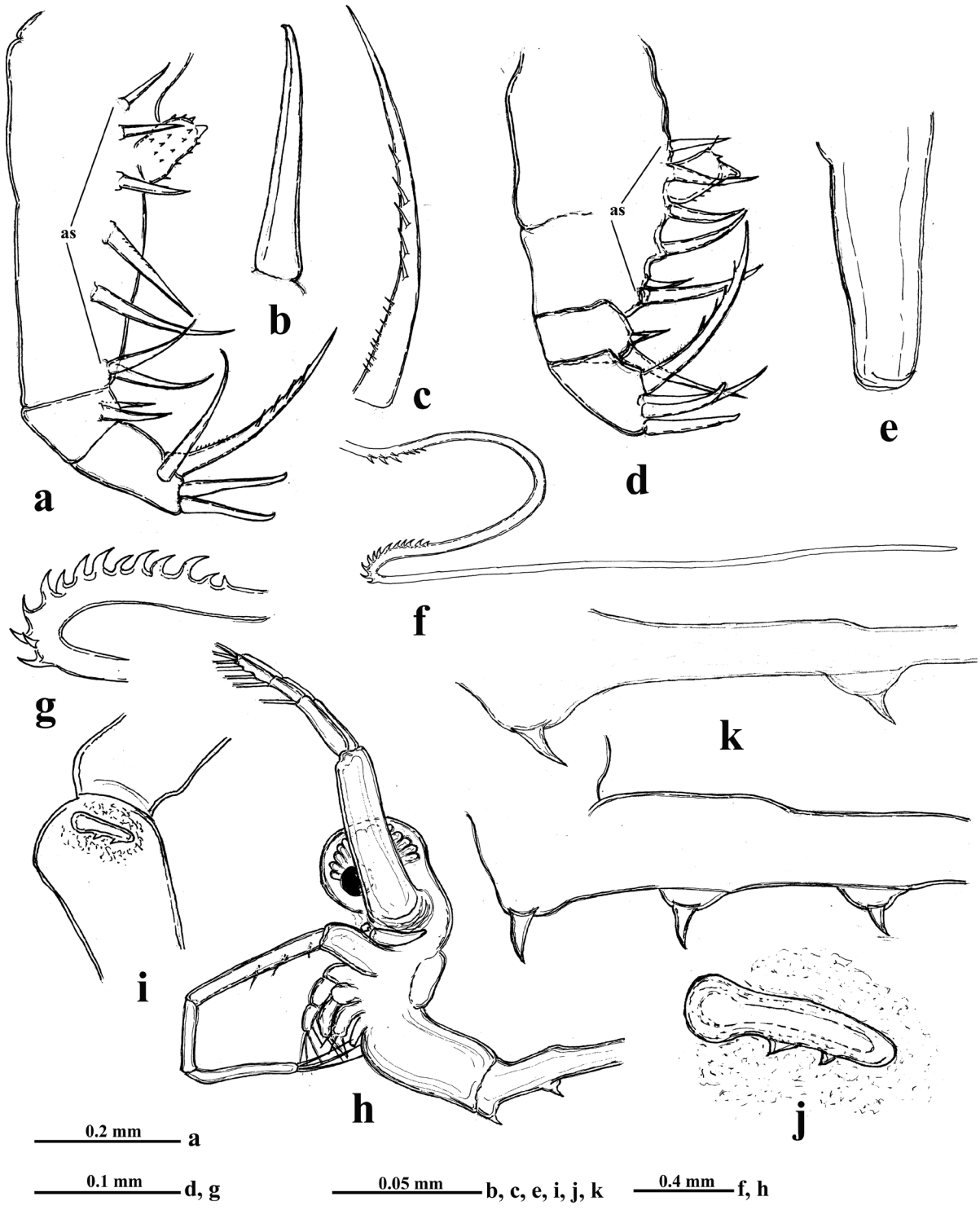

Fig. 3. *Cercopagic socialis* (Grimm, 1877), females (a–d, g) and males (e, h–k), Caspian Sea. Female: a — thoracic limb of second pair (tl II); b — anterior apical seta of tl II; c — posterior subapical seta of tl II; d — thoracic limb of third pair (tl III); f — end of caudal process with a denticulated bend; g — denticles of bend of caudal process; Male: e — copulatory appendage; h — general lateral view; i — distal part of thoracic limb of first pair with a hook; j — hook; k — claws of postabdomen and caudal process.

Рис. 3. *Cercopagic socialis* (Grimm, 1877), самки (a–d, g) и самцы (e, h–k), Каспийское море. Самка: a — торакальная конечность 2-й пары (tl II); b — передняя апикальная щетинка той же конечности; c — задняя субапикальная щетинка той же конечности; d — торакальная конечность 3-й пары (tl III); f — конец каудального выроста с зубчатым изгибом; g — зубчики изгиба каудального выроста; Male: e — копулятивный придаток; h — общий вид сбоку; i — дистальная часть торакальной конечности 1-й пары с хватательным крючком; j — хватательный крючок; k — когти постабдомена и каудального выроста.

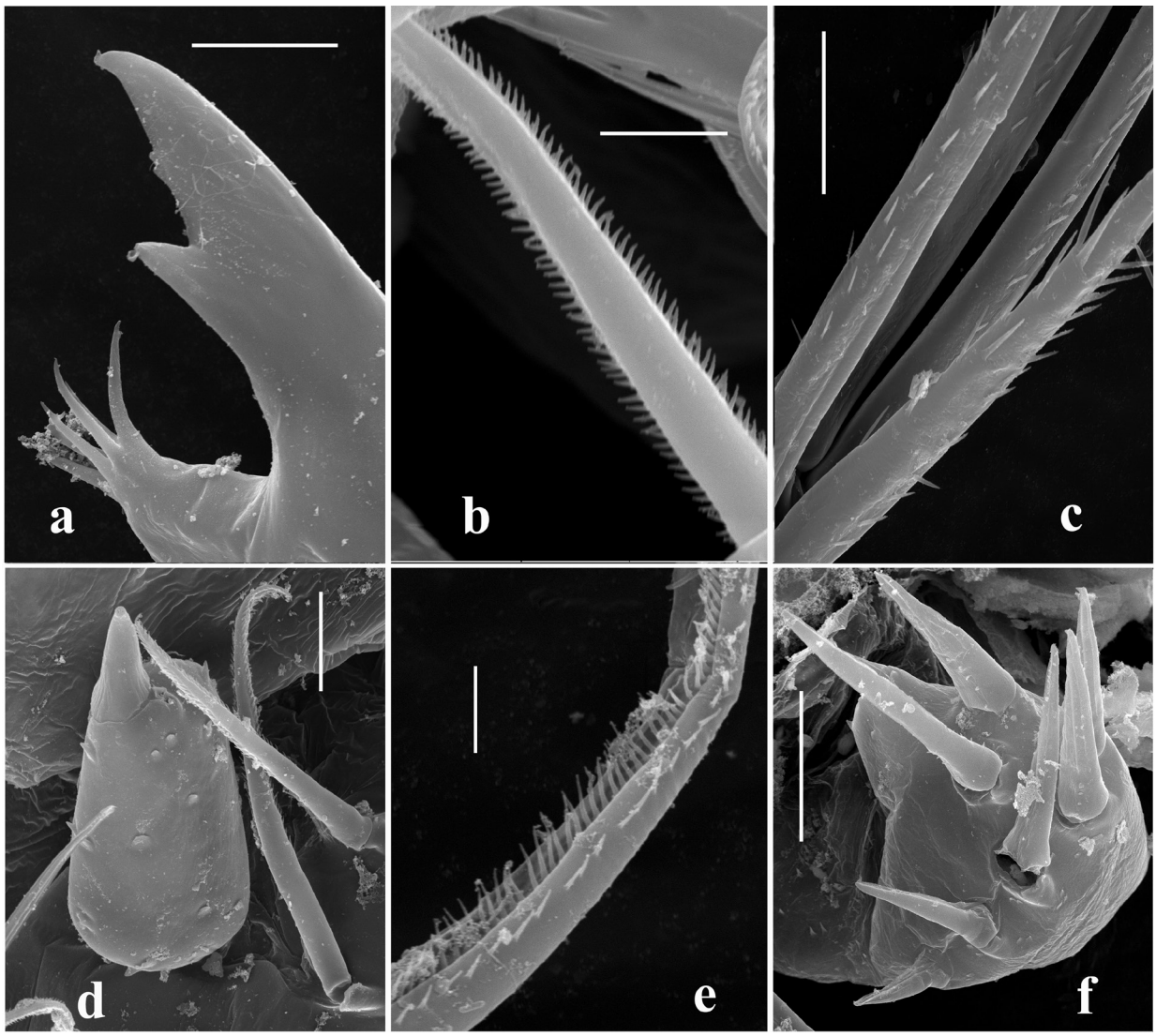

Fig. 4. *Cercopagic socialis* (Grimm, 1877), females, Caspian Sea: a — distal end of mandible; b, e — distal long seta of first endopodital segment of the thoracic limb of first pair (tl I); c — armament of long apical setae of tl I; d — pseudognathobase of the thoracic limb of third pair (tl III); f –thoracic limb of fourth pair (tl IV). Scale bars: a, d — 20 mμ; b, e — 5 mμ; c, f — 25 mμ.

Рис. 4. *Cercopagic socialis* (Grimm, 1877), самки, Каспийское море: a — дистальный конец мандибулы; b, e — дистальная длинная щетинка 1-го членика эндоподита торакальной конечности 1-й пары (tl I); c — вооружение длинной апикальной щетинки той же конечности; d — псевдогнатобаза торакальной конечности 3-й пары (tl III); f — торакальная конечность 4-й пары (tl IV). Размерная шкала: a, d — 20 mμ; b, e — 5 mμ; c, f — 25 mμ.

Limnocal. gr. + *Temorella gr.,* det. G.O. Sars; collected by Grimm 4 VII. 1876, Caspian Sea, st. No. 107, 0°26′ E; 40°57′ N, depth 75–80 sazh."; 2) ZIN, bottle No. 6965 with two labels: old one "*Bythotrephes socialis* Grimm, Caspian Sea, St. 108, 0°26′ E; 41°6′ N, 4.VII. 76, 80–90 sazh., Grimm" and new one: "*Cercopagis socialis* (Grimm) + *Limnocal. gr.* + *Temorella gr.,* det. G.O. Sars; collected by Grimm 4 VII. 1876, Caspian Sea, st. No. 108, 0°26′ E; 41°6″ N, depth 80–90 sazh."; 3) ZIN, bottle No. 9266, *Bythotrephes socialis* Grimm, Caspian Sea, St. 109, 0°26′ E; 41°16′ N, 4.VII. 76, depth 250 sazh., 4) 3 males (allotypes) from the Middle Caspian Sea collected in 1940–1962 (ZIN, "*Cercopagis socialis* (Grimm), No. 46740 from samples No. 59-1964) designated by Ph.D. Mordukhai-Boltovskoi"; 5) SMNH, two tubes with 3 ad, 5 juv, and 9 ad, respectively in a bottle No. 158440 (504) with a label: "*Cercopagis socialis* ("*Byhotrephes socialis*"), Caspe, Grimm 4/9 71".

FEMALE

General body appearance and segmentation. Body elongated and divided into four parts — head, thorax, abdomen, and postabdomen with long caudal process (Figs 1, 2a). Its longitudinal axes are conspicuously incurved when head is located at different angle, frequently at almost right angle, to the thorax. Also highly movable abdomen can be either at straight line with the thorax or stays at different angle to it. Head large with rounded anterior part filled by the enormously developed compound eye and bearing small antennules ventrally. Posterior part of head bears long swimming antennae and mouth parts consisting of mandibles, maxillules (mx I), and upper lip (labrum). Thorax with strongly developed muscular ventral side bearing four pairs of thoracic limbs of different size directed antero-ventrally. Dorsally, thorax bears sack-like carapace transformed into a brood pouch sometimes reaching large size. Abdomen (metasoma) is elongated, cylindrical, not-segmented and flexible, connected with small postabdomen, bearing ventrally a pair of curved claws and posteriorly very long straight caudal process with one or two pair of similar but usually smaller claws proximally. General body length of females (without caudal process) may reach 2.4 mm or slightly more (in the examined specimens it

Table 1. Data on body measurements of the representatives of *Cercopagis socialis* (20 specimens) from Caspian Sea (in columns, from top to bottom: range, M, SD, CV) (abbreviation see above).
Таблица 1. Данные по измерению тела представителей *Cercopagis socialis* (20 особей) из Каспийского моря (в колонках сверху вниз: разброс данных, средняя, среднее квадратичное отклонение, коэффициент вариации) (сокращения см. выше).

BL	AbL : BL, %	CPL : BL, %	TlL : BL, %	E3L : E1L, %
1.57–2.43	28.5–40.0	494–644	87.2–114.0	68.0–84.2
2.02	33.8	566	99.9	76.5
	2.7		7.5	3.3
	7.3		6.9	4.0
PCL : BL, %	**CPCL : BL, %**	**ICLD : BL, %**	**ICTh : BL, %**	
3.4–4.4	2.4–4.3	9.6–19.6	4.0–6.6	
4.0	2.9	15.4	5.5	
0.3	0.5	3.0	0.8	
7.3	13.9	17.7	13.0	

ranges from 1.57 to 2.43 mm) while the length of caudal process may surpass the body length considerably.

Head. Comparatively large and subdivided into two parts — rounded anterior part mostly filled by large compound eye (15–20% of body length) and posterior part bearing dorsally a large saddle-shaped neck organ, swimming antennae and mouth parts. Eye contains numerous ommatidia, not accurately calculated but probably as numerous as in *Bythotrephes* (200–300) and have comparatively small pigment spot which occupies about one-fifth or at most one-fourth of the eye's volume (in fixed individuals, it appears to be larger). Ocellus (naupliar eye) is absent.

Antennules. Small and situated on the ventral side of the anterior head part beneath the eye. They are elongated, slightly bulbous distally (Fig. 2b) and sit on the joined basis. Terminally they bear five aesthetascs and one short and thin sensory seta of regular type.

Swimming antennae. Comparatively long, with elongated cylindrical basipodite (Fig. 2c). Of two antennal branches, the lower three-segmented (endopodite) one is slightly longer than upper branch. The upper branch (exopodite) is four-segmented (length of segments from the second one to distal (not counting the smallest proximal) — 1 : 1.14 : 1.3. Small proximal-most segment of upper branch lacks setae, while other segments possess a row of two-segmented swimming setae of more or less similar size except distal of them which are shorter; the same is true for the setae of lower branch. All setae are bilaterally armed with rows of uniform thin setules. General formula of antennal setae: 0–1–2–4/ 1–1–5.

Mouth parts. They are represented by upper lip (labrum), mandibles, and maxillules (maxilla I). The upper lip (Fig. 2d) looks laterally like a thick rounded-triangular lobe bearing numerous papillae along its posterior-internal (oral) margin. Mandibles are bilobed and adapted for biting (Fig. 4a), with a toothed, blade-like posterior lobe and small anterior lobe (mandibular process) armored with a cluster of six-seven long prominences, bearing a tiny outgrowth distally. Posterior lobe is strongly sclerotized and divided in two tooth-shaped parts, the larger (posterior) of which has a small double additional tooth about midway along its border. Maxillules (mx I) look like two cylindrical structures situated posterior to mandibles. Distally, they bear short central seta and some papillae near it. Maxillae (mx II) are absent; the openings of maxillar glands are probably situated near the bases of tl I laterally as it is known for *Bythotrephes* (see Olesen *et al*. [2003]).

Carapace. It looks like a bag-like structure, strongly modified into closed brood pouch (Fig. 2a). It is attached to the dorsal side of thorax and reaching sometimes rather big size (length 73–87% and width — 30–40% of body length). It is of elongated-oval shape without a terminal prominence.

Thoracic limbs. Four pairs of strongly chitinized, stenopodous limbs are densely situated along the muscular ventral side of thorax and directed antero-ventrally (Fig. 2a). All of them have complex and variously setaceous armament along their inner side. Limbs of three anterior pairs are five-segmented and those of the last fourth pair are three-segmented. Protopodites of all of them, covered by comparatively softer cuticle, are inconspicuously delimited into two parts (segments) — coxa and basis (Fig. 2f) while the endopodites of limbs of three anterior pairs are composed of three well developed segments and those ones of the fourth pair are unisegmented (Figs 2a, e, 3a, d, 4f).

Limbs of first pair (tl I) are especially long and strong, their length is often either equal or surpasses body length (82.0–114.0, av. 99.9% of body length) (Fig. 2a, j). Terminally, the inner side of their protopodite bears a small seta or seta and small prominence near it (Fig. 2g), which probably represent a remnant of pseudognathobasic process. The first segment of endopodite is especially long and bears normally five, sometimes four, lateral setae (Fig. 2e) the distal of which is longest and densely pubescent (Fig. 4b, e). Distally, this segment bears short seta. The second segment of endopodite is conspicuously shorter lacking any armament. The terminal, third segment of endopodite is also long, only slightly shorter than first segment (68–84% of its length), and bears apically four long roughly spinulated setae (Fig. 4c), two of them terminally and two subterminally.

The limbs of second pair (tl II) are considerably shorter (17–20% of body length). The first, basal segment of their endopodite bears a row of five, rarely four, rather long anterior lateral setae (Fig. 3a). Two terminal setae of the segment are of the same type. Internally, this segment bears stout cylindrical pseudognathobasic process, possessing one large apical prominence and some small denticles and spinules laterally. The second segment is short with only two smaller setae, the anterior of which is longer. The distal, third segment of endopodite of the limb bears four setae, two terminal and two subterminal ones (Fig. 2a). Of the latter, the neighboring posterior subterminal seta (Fig. 3c) is especially long and roughly armed with some large denticles. The anterior terminal seta (Fig. 3b) is thick, comparatively short and naked with longitudinal ribs. Both terminal setae are slightly hooked apically.

The limbs of the third pair (tl III) are generally similar to those of the previous ones, differing in some details. Their lateral anterior setae of first segment of endopodite are fewer (3–4) (Fig. 3d), posterior terminal seta of the segment is much shorter than the neighboring anterior one. The pseudognathobasic process is similar to that one of tl II (Fig. 4d). Of setae of second

segment, the anterior one is again longer than the posterior seta. Terminal and subterminal setae of third segment are similar to those of tl II but shorter.

The limbs of the fourth pair (tl IV) (Fig. 4f) are considerably reduced, their protopodite bears externally a seta sited on a short cylindrical base. The only segment of endopodite has two rows of rather long and stout spine-like setae armed laterally by few minute spinules. The internal row always consists of two larger setae and the external row of 5–6 setae, which differ in their appearance. Almost the whole internal part of terminal segment is occupied by the reduced but nevertheless rather large pseudognathobasic process armed by one large apical prominence and a number of lateral spinules.

Abdomen (metasoma) (Fig. 2a) is moderately long (29–40% of body length), cylindrical and devoid of even traces of segmentation.

Postabdomen is comparatively small (about 7–8% of body length) and separated from the abdomen by a fold or distinct segmental suture (Fig. 2h). The anal opening is situated between postabdominal claws. The latter are comparatively small (3.4–4.4, av. 4.0% of body length) and curved backwards (Fig. 2h).

Caudal process is directly and invisibly connected with postabdomen (Fig. 2a, h) and then proceeds as a very long and straight spine-like structure variable in its length (494–644% of body length), thus surpassing the body length in about five–six times (Fig. 1). Basally, it bears one or two pairs of claws similar to those of postabdomen (those of proximal pair: 2.4–4%, av. 2.9% of body length) and apically — two minute setae arose from common base (Fig. 2i). Near its end, caudal process creates a prominent bend (loop) with two groups of curved denticles (Fig. 3f, g). Pairs of claws sit rather closely (distance between them 9.6–19.6%, av. 15.4% of body length). Between them, the thickness of the structure is considerable, reaching 4.0–6.6, av. 5.5% of body length.

Gamogenetic females were found for the first time by Mordukhai-Boltovskoi [1967]: "Females with winter eggs, two in number, have been found by me in the central Caspian Sea in autumn samples; they differ from the parthenogenetic ones in a considerable broader and more chitinized brood pouch, sometimes being angular at the top".

MALE

Only three adult males from the Middle Caspian Sea were at my disposal (Fig. 3h) which were first described by Mordukhai-Boltovskoi [1967]: "The males have been found also as single specimens in the central Caspian in the autumn" [Mordukhai-Boltovskoi, 1967]. They had body length 1.0–1.30 mm (however, Mordukhai-Boltovskoi sad that "the males do not exceed 1.5 to 1.8 mm"), length of tl I — 58.0–66.7%, length of caudal process — 525.0–764%, and interclaw distance — 12.3–23.8% of body length. There is only a rudiment of the brood pouch. As well as females, males could have two or three pairs of claws on postabdomen and caudal process. The proximal bend of a loop of caudal process is usually inconspicuous, nearly straightened, and bears only three or four denticles. The distal segment of tl I is slightly swollen proximally and bears on its inner side a small strongly chitinized hook with two inner denticles (Fig. 3i, j). The copulatory appendages (penises), set just after tl IV, are small, smooth and slightly conic in shape (Fig. 3e).

TYPE MATERIAL. The original specimens of the species under consideration described by Grimm [1877] and Sars [1897] were fortunately preserved, but the type specimens were not designated due to the absence of the tradition to designate and store the type materials at that time. Meanwhile, the rules of ICZN [2000] require the correct designation of type specimens of the preserved type series, which the studied individuals (all of them are syntypes) undoubtedly represent (ICZN 72.4, 73.2).For this reason, the lectotype of *Cercopagis socialis* was designated from specimens collected in the type locality (a parthenogenetic female with body length 1.95 mm, Caspian Sea, St. 107, 0°26′ E; 40°57′N, 4.VII.1876 g., 75–80 sazheney, coll. by O. Grimm) and deposited in the Zoological Museum of Moscow State University (ZMMU Ml-277). Respectively, all other specimens of the type series, which include both specimens from the present sample and specimens from other samples collected by Dr. O. Grimm (see Nos 1–3 in the "Material examined"), are parelectotypes (ICZN 74.1.3); they are partly deposited (10 specimens) also in the Zoological Museum of Moscow State University (ZMMU Ml-278), others in the collection of Zoological Institute (ZIN) in St.-Petersburg. The type specimens of males (three allotypes) were collected in 1940–1962 in the Middle Caspian Sea and designated by Ph.D. Mordukhai-Boltovskoi. They are stored in the collection of Zoological Institute, St.-Petersburg (ZIN, *Cercopagis socialis* (Grimm), No. 46740 from samples No. 59-1964).

REMARKS. Dr. O. Grimm [1877], the first investigator of the genus *Cercopagis,* took only a brief look at these crustaceans. In his description of the species *C. socialis* he made a mistake by specifying four segments of the endopodite of the first pair of limbs (tl I) and making an unrealistic conclusion about the lifestyle of these crustaceans (see above).

Unlike Grimm, Sars [1897] provided a very extensive description of both the external and internal structure of this species. Only females were examined, males were absent in the samples. The latter were described many years later by Mordukhai-Boltovskoi [1967]. Generally, this description was quite correct except for a few details. Thus, Sars indicated six aesthetasks in the antennules missing the sensory seta as well as only four prominences of mandibular process, though there are actually six or seven of them. Also, he did not notice the remains of the pseudognathobasic process on the inner side of the protopodite of tl I. Of course, Sars rejected Grimm's fantastic assumption about the functional role of the enormously long caudal process armed with a special loop-like bend and gave a more realistic explanation: "…I am therefore of opinion, that the caudal process, besides acting in the usual manner as a balancing apparatus, has the additional significance of a preying organ, by the aid of which, other Entomostraca may be grasped. The flexibility of the caudal process in connection with the very movable articulation of the urosoma with the metasoma, will allow the animal, in such cases, so to turn itself, as to seize the captive prey with its long anterior pair of legs, and thus bring it within reach of the other legs and the oral parts" [Sars, 1897: 13].

Cercopagis pengoi (Ostroumov, 1892)

Figs 5–8.

Pengo, 1880: 47–48, Tab. I (*Bythotrephes* sp.); Ostroumov, 1892: 12 (*Bythotrephes*); Sars, 1897: 20–22, Pl. 2, figs 4, 4a (*C. tenera*), 1902: 35–36 (*C. tenera*), 36–37, Pl. I, figs 1–4 (*C. neonilae*); 37, Pl. I, figs 5–9 (*C. gracillima*); Sovinsky, 1902: 374 (*C. tenera*), 375 (*C. Pengoi*); Zernov, 1903: 13–14, figs 19–21, 32, 33; Meissner, 1908: 53–55; Valkanov, 1951: 66–81, Tab. 12–16; Manuilova, 1964: 297, fig. 166 (*C. neonilae*), 298, fig. 167 (*C. gracillima*), 299, fig. 168 (*C. tenera*); Mordukhai-Boltovskoi, Negrea, 1965: 197–199; Mordukhai-Boltovskoi, 1967: 114, figs 1–4, 1968b: 130–131, fig. 140 (*C. pengoi*), 132, fig. 141 (*C. neonilae*), 132–133, fig. 142 (*C. gracillima*), 142, Fig. 152 (*Apagis ossiani*); 1969: 20, Tab. 2–1, 1974: 133–134 (*C. pengoi aralensis*); Mordukhai-Boltovskoi, Rivier, 1971: 3–5, fig. 2 (*C.* (*Apagis*) *ossiani*), 1987: 154, fig. 94-A (*C. neonilae*), 156–158, fig. 94, B–G (*C. pengoi*), D (*C. gracillima*), E (*C. pengoi aralensis*), 163, fig. 102 (*C.* (*Apagis*) *ossiani*); Rivier, 1998: 175–177, figs 217–223 (*C. neonilae*), 178–179, figs 218, 220, 221, 224 (*C. pengoi*), fig. 219 (*C. pengoi gracillima*), 226 (*C. pengoi aralensis*), 187, figs 249, 250 (*C.* (*Apagis*) *ossiani*); Plotnikov, 2016 (*C. pengoi aralensis*); Korovchinsky *et al*., 2021: 473–476, fig. 147.

Data on body and body parts measurements of the representatives of the species are presented in Table 2.

MATERIAL EXAMINED: **Sea ofAzov**: 1) ZIN, samples N 490-936, Azov expedition on the ship "Besstrashnyi", st. 33b, 4.8.1923, 15 ad collected by N.L. Chugunov and V.M. Arnoldi; 2) ZIN, sample without a number, 2 deformed ad. **Caspian Sea (northern part)**: 3) St. 34, quadrat 258, 21.8.1981, coll. CaspNIRH, 5 ad, 4) St. 4, quadrat 372, 09.6.1990, CaspNIRH, 3 ad, 5) 1991, CaspNIRH, 3 ad, 6) 20.8.2018, CaspNIRH, 15 ad, 7) ZIN, N 46739, two males (alotypes) from samples N 59-1964 collected by Ph.D. Mordukhai-Boltovskoi; 8) ZIN, N 1/57515, 1 ad with a label "*Cercopagis* (*Apagis*) *ossiani,* Caspian Sea, det. Mordukhai-Boltovskoi, holotype"; 1 ad with a label: "*Apagis ossiani* M.-Bolt., ZIN, paratype N 1/46893, det. Mordukhai-Boltovskoi; coll. by an expedition on the ship "Abo", st. 71, 10.5.1913", 1 ad, label: "Caspian expedition on the ship "Abo" (209-29). 27.4.1913, st. 71, r. 116". 9) ZIN, sample N 6877 with a label: "*Cercopagis neonilae* G.O. Sars, Caspian Sea, collected by Maksimovich, determined by Sars", two very deformed ad; 10) ZIN, sample N 9259 with a label: "*Cercopagis neonilae* G.O. Sars, Caspian Sea, received from the University of Christiania in 1930", 4 ad. **Aral Sea**: 11) ZIN (N 342-1961), Aralo-Caspian expedition, two tubes in a bottle, one of them with a label: "Aral, st. 6, 24.9.1935, coll. A.L. Behning, *Cerc*.", 3 ad. **Volga and Kama rivers:** 12) Saratovskoje reservoir on the River Volga near Balakovo, 24.6.2011, coll.A.I. Popov, 11 ad; 13) Kamskoje reservoir on the River Kama, coll. R.S. Sabitova, August 2016, 4 ad; 14) Votkinskoje reservoir on the River Kama, coll. V.I. Lazareva and R.S. Sabitova, summer 2016, 2 ad. **Baltic Sea:** 15) Vislinsky Bay, 2.06.2000, coll. Yu.Yu.Polunina, 33 ad; 17) Baltic Sea, 12.8.2001, coll. Yu.Yu. Polunina, some ad; 18) Baltic Sea, August 2010, coll. A.S. Semenova, numerous ad; 19) Kurshu-mares bay (Curonian lagoon), 23.7.2006, coll. A.S. Semenova, numerous ad.

FEMALE

General body appearance and segmentation. Generally as in previous species (Fig. 5a). General body length of females (without caudal process) may reach 2.4 mm or slightly more, in the examined specimens it ranges from 1.14 mm to 2.46 mm.

Head. Comparatively large and subdivided into two parts — rounded anterior part mostly filled by large compound eye (14–18% of body length) and posterior part bearing dorsally a large saddle-shaped neck organ, swimming antennae and mouth parts. Eye contains numerous ommatidia, not accurately calculated but probably as numerous as in *Bythotrephes* (200–300) and has comparatively small pigment spot which occupies about one-fifth or at most one-fourth of the eye's volume (in fixed individuals, it appears to be larger) (Fig. 5a). Ocellus (naupliar eye) is absent.

Antennules. Small and situated on the ventral side of the anterior head part beneath the eye. They are elongated, slightly bulbous distally (Fig. 5b) and sit on the joined basis. Terminally they bear five aesthetascs in two groups (two and three in each one, respectively) and short, thin sensory seta of regular type.

Swimming antennae. Comparatively long, with elongated cylindrical basipodite (Fig. 5a) bearing proximally a small setulated seta on its dorso-posterior side (Fig. 5d). Of two antennal branches, the lower three-segmented one (endopodite) is slightly longer than upper branch. The upper branch (exopodite) is four-segmented (relative length of segments from the second one to distal (not counting the smallest proximal) — 1 : 0.9 : 1.2 and in lower branch — 1 : 0.7 : 1.2. Small proximal-most segment of upper branch lacks setae, whereas other segments possess a row of two-segmented swimming setae of more or less similar size except distal of them which are shorter; the same is true for the setae of lower branch. All setae are bilaterally armed with rows of uniform thin setules. General formula of antennal setae: 0–1–2–4/ 1–1–5. Some segments bear small, thin apical denticles (Fig. 5e, f).

Mouth parts. They are represented by upper lip (labrum), mandibles, and maxillules (maxilla I) (Fig. 5c). Mandibles are bilobed and adapted for biting (Fig. 8a), with a toothed, blade-like posterior lobe and small anterior lobe (mandibular process) armored with a cluster of six-ten long prominences, bearing the tiny outgrowths distally. Posterior lobe is strongly sclerotized and divided in two tooth-shaped parts, the larger (posterior) of which has a small additional tooth about midway along its border.

Maxillules (mx I) look like two cylindrical structures situated posterior to mandibles (Fig. 5c). Distally, they bear short central seta. Maxillae (mx II) are absent; the openings of maxillar glands are probably situated near the bases of tl I laterally as it is known for *Bythotrephes* (see Olesen *et al.* [2003]).

Carapace. It looks like a bag-like structure, strongly modified into closed brood pouch (Fig. 5a). It is attached to the dorsal side of thorax and reaching sometimes rather big size (length up to 75–98% and width — 18–47%, usually 20–32% of body length). It has elongated-oval shape with rather big terminal prominence (Figs 5a, 7a, b).

Thoracic limbs. Four pairs of strongly chitinized, stenopodous limbs are densely situated along the muscular ventral side of thorax and directed antero-ventrally (Fig. 5a). All of them have complex and variously setaceous armament along their inner side. Limbs of three anterior pairs are five-segmented and those of the last fourth pair are three-segmented. Protopodites of all of them, covered by comparatively softer cuticle, are inconspicuously delimited into two parts (segments) — coxa and basis (Fig. 5i) while from the outside they bear small terminal prominences (Fig. 5l). The endopodites of limbs of three anterior pairs are composed of three well developed segments and those ones of the fourth pair are unisegmented (Fig. 5a, m, n, o).

Limbs of first pair (tl I) are especially long and strong, though their length is shorter than body length (49.0–80.0%). Terminally, the inner side of their protopodite bears small prominences (Fig. 5i, j), which probably represent a remnant of a pseudognathobasic process. The first segment of endopodite is especially long and bears normally 5 lateral setae (Fig. 5k) the distal of which is longest, all of them are densely pubescent, fine setules are arranged in three longitudinal rows (Fig. 8d, e). Distally, this segment bears short seta, which sometimes may be strongly reduced (Fig. 5g, h). The second segment of endopodite is conspicuously shorter lacking any armament. The terminal, third segment of endopodite is also long, but shorter than first segment (58–75% of its length), and bears apically four long and strong roughly spinulated setae (Fig. 8c), two of them terminally and two subterminally.

The limbs of second pair (tl II) are considerably shorter (Fig. 5m). The first, basal segment of their endopodite bears a row of five, rarely four, rather long anterior lateral setae variously setulated (Fig. 8f). Two terminal setae of the segment are of the same type, posterior of them is shorter. Internally, this segment bears stout cylindrical pseudognathobasic process, possessing one large apical prominence and numerous small denticles laterally (Fig. 8g). The second segment is short with only two smaller setae, the anterior of which is longer again. The distal, third segment of endopodite of the limb bears four setae, two terminal and two subterminal. Of the latter, neighboring posterior subterminal seta (Fig. 8c) is especially long and roughly armed with some large denticles. The anterior terminal seta is thick, comparatively short and naked with longitudinal ribs. Both terminal setae are slightly hooked apically.

The limbs of the third pair (tl III) are generally similar to those of the previous pair, differing in some details. Their lateral anterior setae of first segment of endopodite are fewer (2–3) (Fig. 5n), posterior terminal seta of the segment is shorter than the neighboring anterior one. The pseudognathobasic process is similar to that one of tl II (Fig. 8h). Of setae of second segment, the anterior one is again longer than the posterior seta.

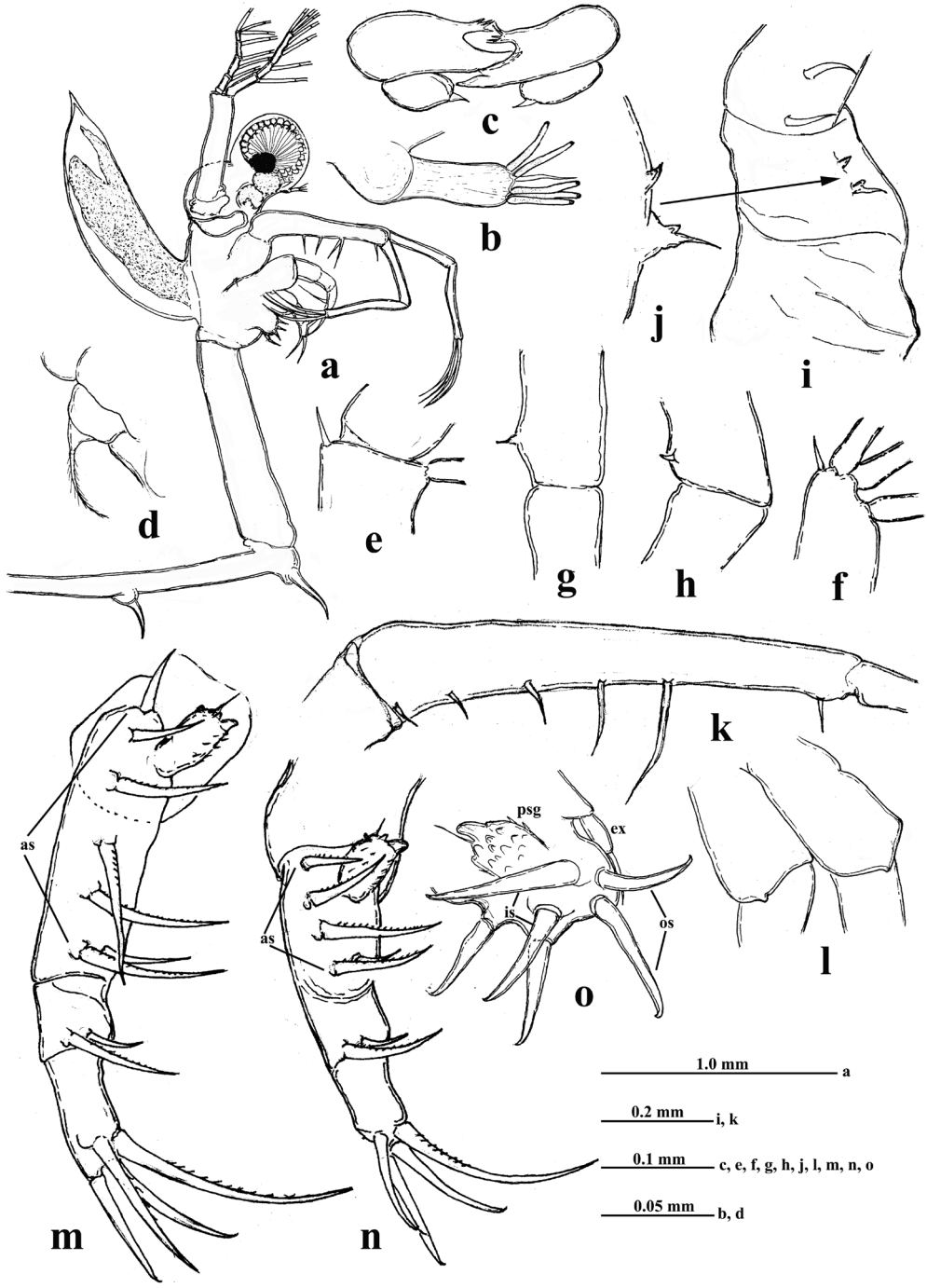

Fig. 5. *Cercopagis pengoi* (Ostroumov, 1892), females, Baltic Sea (a–g, i–o), Aral Sea (h): a — general lateral view; b — antennule; c — mandibles and maxillules (mx I); d — seta on dorso-lateral proximal side of protopodite of swimming antennae; e — apical end of second segment of upper antennal branch; f — apical end of distal segment of upper antennal branch; g, h — unusually reduced distal seta of first endopodital segment of tl I; i — protopodite of tl I, inner side; j — remnants of pseudognathobasic process on protopodite of tl I; k — first endopodital segment of tl I; l — basal part of thoracic limbs tl II and tl III, outer side; m — thoracic limb of second pair (tl II); n — thoracic limb of third pair (tl III); o — thoracic limb of fourth pair (tl IV) (as — anterior setae, ex — remnant of exopodite, is — inner setae, os — outer setae, psg — pseudognathobase).

Рис. 5. *Cercopagis pengoi* (Ostroumov, 1892), самки, Балтийское море (a–g, i–o), Аральское море (h): a — общий вид сбоку; b — антеннула; c — мандибулы и максиллы (mx I); d — щетинка на дорсо-латеральной стороне проксимальной части протоподита плавательной антенны; e — апикальный конец 2-го членика верхней ветви плавательной антенны; f — апикальный конец дистального членика верхней ветви плавательной антенны; g, h — необычно редуцированная дистальная щетинка 1-го членика торакальной конечности 1-й пары; i — протоподит той же конечности с внутренней стороны; j — остатки псевдогнатобазы на протоподите той же конечности; k — первый членик эндоподита той же конечности; l — базальная часть торакальных конечностей 2-й и 3-й пар с внешней стороны; m — торакальная конечность 2-й пары (tl II); n — торакальная конечность 3-й пары (tl III); o — торакальная конечность 4-й пары (tl IV) (as — передние щетинки, ex — рудимент экзоподита; is — внутренние щетинки, os — внешние щетинки, psg — псевдогнатобаза).

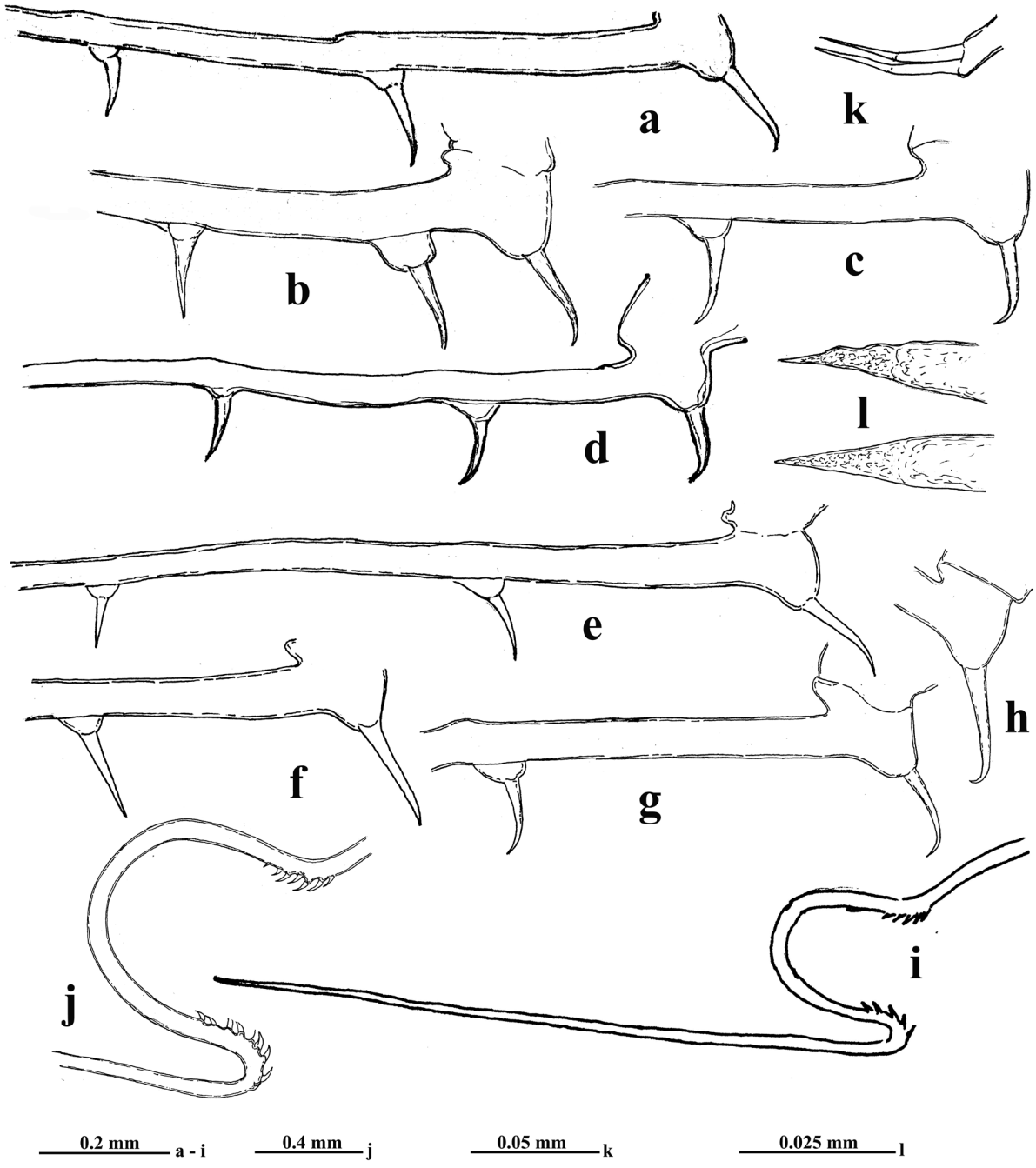

Fig. 6. *Cercopagis pengoi* (Ostroumov, 1892), females, Baltic Sea (a, b, l), Aral Sea (c, d), Sea of Azov (e, f, i, j) and Caspian Sea (g, h, k): a–h — claws of postabdomen and caudal process; i — distal end of caudal process; j — distal denticulated bend of caudal process; k — apical sensory setae of caudal process; l — apical ends of caudal process (probably in case of loss of apical sensory setae).

Рис. 6. *Cercopagis pengoi* (Ostroumov, 1892), самки, Балтийское море (a, b, l), Аральское море (c, d), Азовское море (e, f, i, j) и Каспийское море (g, h, k): a–h — когти постабдомена и каудального выроста; i — дистальный конец каудального выроста; j — дистальный зубчатый изгиб каудального выроста; k — апикальные чувствительные щетинки каудального выроста; l — апикальный конец каудального выроста (вероятно, в случае утраты апикальных чувствительных щетинок).

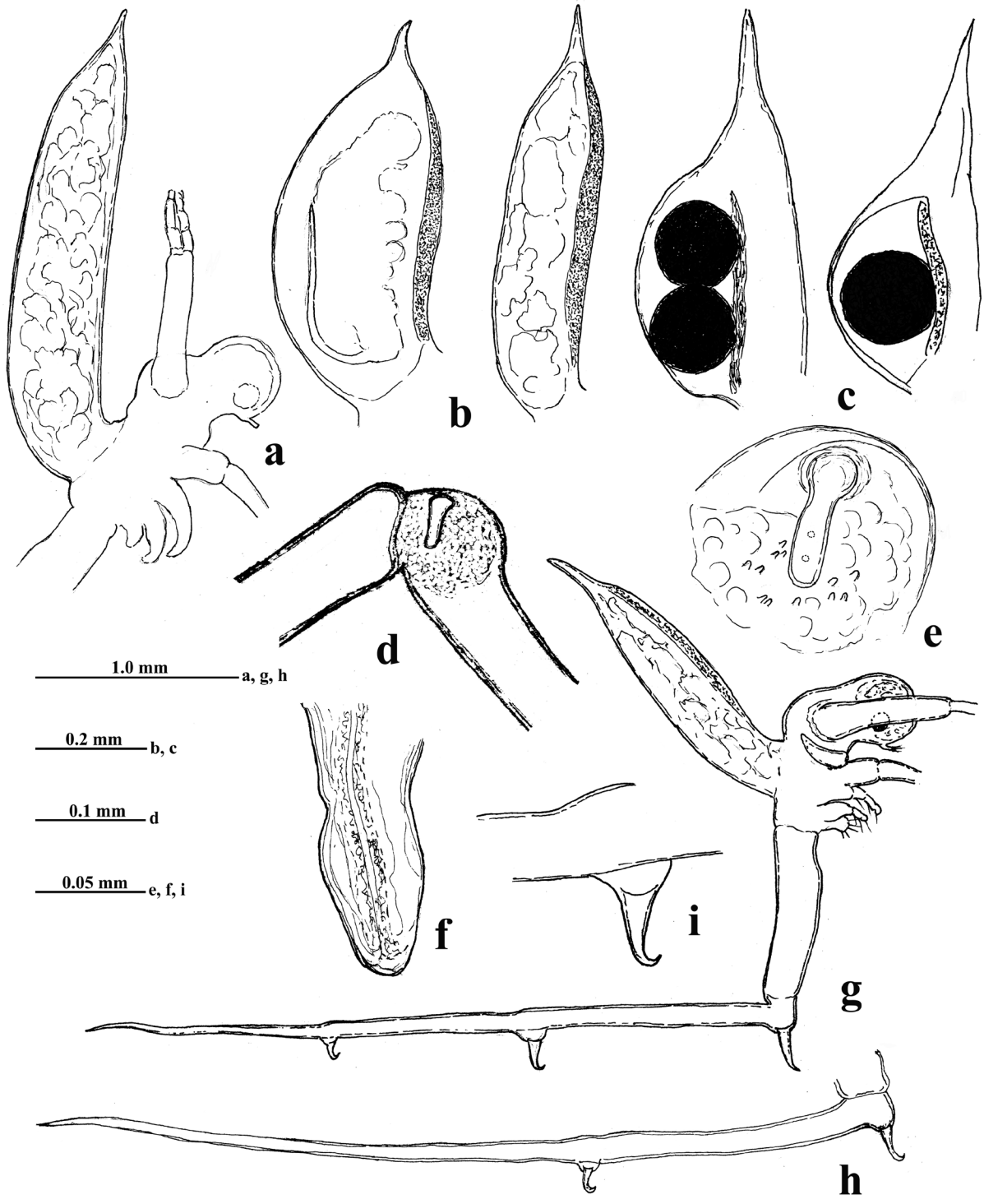

Fig. 7. *Cercopagis pengoi* (Ostroumov, 1892), females and males, Baltic Sea (a, d–f) and Caspian Sea (b, c): a — schematic drawing of a female with a large brood pouch; b — brood pouches of different shape; c — brood pouches of gamogenetic females with resting eggs; d — proximal part of male's distal endopodital segment of tl I with clasping hook; e — male's clasping hook, f — copulatory appendage. Females of the first generation hatched from resting eggs ("*Apagis ossiani*"), Caspian Sea: g — general lateral view; h — postabdomen and caudal process; i — claw of caudal process.

Рис. 7. *Cercopagis pengoi* (Ostroumov, 1892), самки и самцы, Балтийское море (a, d–f) и Каспийское море (b, c): a — схематичный рисунок самки с крупной выводковой камерой; b — выводковые камеры различной формы; c — выводковые камеры гамогенетических самок со стойкими яйцами; d — проксимальная часть дистального членика эндоподита 1-й пары конечности самца с хватательным крючком; e — хватательный крючок самца, f — копулятивный придаток. Самки первого поколения, вышедшие из стоких яиц ("*Apagis ossiani*"), Каспийское море: g — общий вид сбоку, h — постабдомен и каудальный вырост; i — коготь каудального выроста.

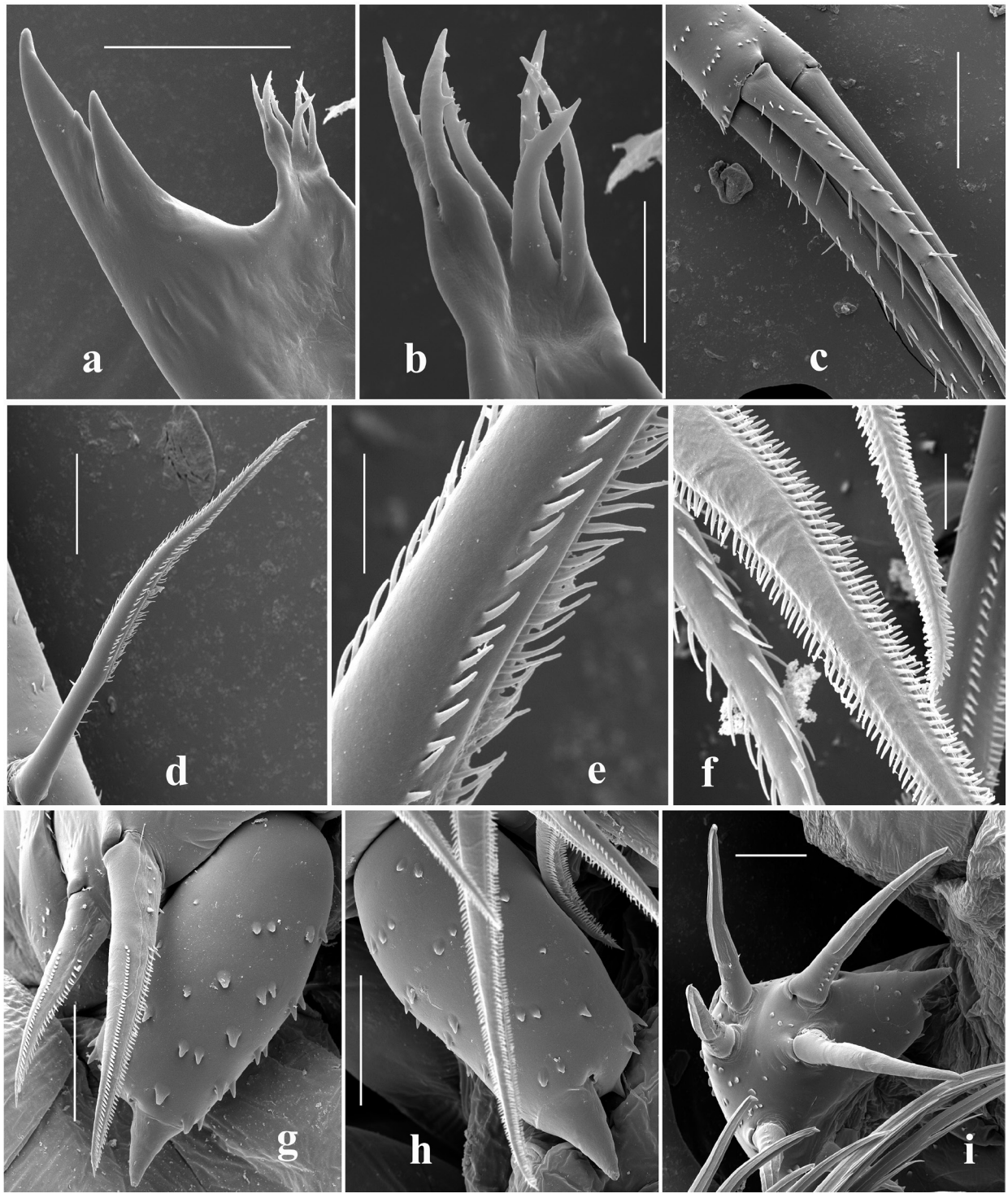

Fig. 8. *Cercopagis pengoi* (Ostroumov, 1892), females, Baltic Sea: a — distal part of mandible; b — prominences of mandibular process; c — armament of apical setae of tl I; d — lateral seta of first endopodital segment of tl I; e — armament of this seta; f — armament of lateral setae of tl II; g — pseudognathobase of tl II; h — pseudognathobase of tl III; i — thoracic limb of fours pair (tl IV). Scale bars: a — 20 μm, b — 5 μm, c — 25 μm, d, g, h, i — 10 μm, e — 2 μm, f — 2.5 μm.

Рис. 8. *Cercopagis pengoi* (Ostroumov, 1892), самки, Балтийское море: a — дистальная часть мандибулы; b — выросты мандибулярного выроста; c — вооружение апикальных щетинок торакальных конечностей 1-й пары; d — боковая щетинка 1-го членика эндоподита торакальной конечности 1-й пары; e — вооружение той же щетинки; f — вооружение боковой щетинки торакальной конечности 2-й пары (tl II); g — псевдогнатобаза той же конечности; h — псевдогнатобаза торакальной конечности 3-й пары (tl III); i — торакальная конечность 4-й пары (tl IV). Размерная шкала: a — 20 μm, b — 5 μm, c — 25 μm, d, g, h, i — 10 μm, e — 2 μm, f — 2,5 μm.

Table 2. Data on body measurements of the representatives of *Cercopagis pengoi* from four populations (in columns, from top to bottom: range, M, SD, CV; the absence of the latter parameters means that the number of measurements was too small) (abbreviations see above).

Таблица 2. Данные по измерению тела представителей *Cercopagis pengoi* из четырех популяций (в колонках сверху вниз: разброс данных, средняя, среднее квадратичное отклонение, коэффициент вариации; отсутствие данных по последним параметрам означает, что число измерений было слишком мало) (сокращения см. выше).

BL, mm	AbL : BL, %	CPL : BL, %	TlL : BL, %	E3L : E1L, %	PCL : BL, %	CPCL : BL, %	ICID : BL, %	ICITh : BL, %
1. Sea of Azov (n = 15)								
1.14–1.80	37.8–47.1	443–606	63.5–72.6	58.9–68.2	8.7–14.0	8.3–12.5	27.9–38.9	3.5–5.7
1.40	43.1	551	68.1	60.9	12.1	9.8	33.3	4.7
	2.7		3.6	5.2	1.6		3.7	0.7
	5.8		4.9	8.5	11.9		10.2	14.0
2. Northern part of Caspian Sea (n=18)								
1.16–2.12	33.3–48.2	420–583	48.6–64.3	57.9–70.8	7.3–15.0	3.7–10.5	31.9–60.0	3.4–5.3
1.57	37.4	550	58.2	59.7	10.7	7.8	47.8	4.3
	5.2		4.3	6.1	2.3	2.0	7.4	0.5
	13.9		6.8	10.2	20.0	23.4	14.3	11.5
3. Reservoirs of the Volga and Kama rivers (n=17)								
1.71–2.34	35.5–49.3	386–501	66.3–80.0	62.9–75.0	9.3–17.8	6.9–11.9	20.2–29.5	3.4–5.0
2.0	40.3	442	73.0	69.6	12.3	8.9	24.5	4.1
	3.3		5.1	3.5	2.3	1.3	2.6	0.5
	8.2		6.4	5.0	17.3	13.7	9.7	10.0
4. Baltic Sea (n=15)								
1.70–2.46	35.8–48.7	427–600	66.9–79.2	63.6–75.0	8.7–12.3	7.2–10.7	30.4–43.5	3.2–5.8
2.22	41.6	494	72.9	70.6	9.9	7.3	37.9	4.4
	3.4		3.8		1.0		4.3	0.7
	8.1		5.2		10.0		11.2	15.0

Terminal and subterminal setae of third segment are similar to those of tl II but shorter.

The limbs of the fourth pair (tl IV) (Figs 5o, 8i) are considerably reduced, their protopodite bears externally a seta sited on a short cylindrical base which may be considered as a remnant of exopodite (5o: ex). The only segment of endopodite has two rows of rather long and stout spine-like setae armed basally by few minute spinules. The internal row always consists of two larger setae (is) and the outer row of four setae (os), which differ in their appearance. Almost the whole internal part of the terminal segment is occupied by the reduced but nevertheless rather large pseudognathobasic process armed by one large apical prominence and a number of lateral spinules (Fig. 8i).

Abdomen (metasoma) (Fig. 5a) is moderately long (35–49%, av. 42% of body length), cylindrical and devoid of even traces of segmentation.

Postabdomen is comparatively small (7–11% of body length) and separated from the abdomen by a fold or distinct segmental suture (Fig. 5a). The anal opening is situated between postabdominal claws. The latter are comparatively long (7.3–17.8, av. 9.9–12.3% of body length), curved apically backwards (Fig. 6a–h).

Caudal process is directly and invisibly connected with postabdomen (Fig. 5a) and then proceeds as a very long and straight spine-like structure variable in its length (386–606% of body length), thus surpassing the body length in about 4–6 times. Basally it bears one or two pairs of claws similar to those of postabdomen (those of proximal pair: 3.7–12.5, av. 7.3–9.8% of body length) and apically — two minute setae arose from common base (Fig. 6k) (if the apical setae are broken, then the caudal process ends with a conically cut edge (Fig. 6l). Near its end, caudal process creates a prominent bend (loop) with two groups of curved denticles (Fig. 6i, j). Pairs of claws sit usually rather distantly (distance between them 20.2–60.0, av. 24.5–47.8% of body length). Between them, the thickness of the structure is considerable, reaching 3.2–5.8, av. 4.1–4.7% of body length.

Gamogenetic females were found occasionally by some authors [Zernov,1903; Valkanov, 1951; Mordukhai-Boltovskoi, 1967; Negrea, 1983] in the Aral Sea, Sea of Azov, and Caspian Sea, as well as in the near shore Gebeje Lake in Bulgaria. In the material studied in the present paper, these females were found occasionally as well in samples from the Caspian Sea. They had specific brood pouches with a high pointed top bearing either one or two large black resting eggs (diameter 0.32–0.38 mm) (Fig. 7c).

Parthenogenetic females of first generation hatched from resting eggs (the form "*Apagis ossiani*")

The three individuals studied (Fig. 7g, h, i) were of moderately body size (1.40 –1.90 mm) and possessed rather large, narrow carapace (80–83% of body length) strongly pointed distally and shortened tl I (50–57% of body length). Their abdomen is of a regular size (44.2–49.6%) while the caudal process is shortened (133–198%) (according to Mordukhai-Boltovskoi and Rivier [1971] it is longer: "it is 2 to 2.5 times as long as the body"), slightly thickened proximally (5.1–6.4%) then tapering distally. Two or three claws of postabdomen and the caudal process are curved forward, comparatively small (8.7–9.4 and 5.0–6.4%, respectively) and stay far apart (60.5–69.0%). Only five such adult females have been found during the entire study of the Caspian Sea [Mordukhai-Boltovskoi, Rivier, 1971, 1987; Rivier, 1998].

MALE

Only three rather deformed adult males from the Caspian Sea were at my disposal, two of which were first described by Mordukhai-Boltovskoi [1967] and designated as allotypes. Another male was encountered from material from the Baltic Sea. They had body length 0.73–1.33 mm (however, Mordukhai-

Boltovskoi said that "the males do not exceed 1.3 to 1.8 mm"), length of tl I — 66.0–88.0%, length of caudal process — 360–464%, and interclaw distance — 14.5–29.0% of body length. There is only a rudiment of the brood pouch. As well as females, males can have two or three pairs of claws on the postabdomen and caudal process. The distal segment of tl I is slightly swollen proximally and bears on its inner side a small strongly chitinized hook with two inner denticles and some tiny denticles under it (Fig. 7d, e). The copulatory appendages (penises) set just after tl IV are small, smooth and slightly conic (Fig. 7f).

TYPE MATERIAL. This species was first described as *Bythotrephes* sp. by Mrs. N. Pengo [1880] from the Sea of Azov near Mariupol' City. This material has definitely not been preserved. Then the species was described again from the Caspian Sea under the name *Cercopagic tenera* Sars [Sars, 1897]. This material also could not be found by the author of the present paper in the collection of Zoological Institute (ZIN). More precisely, there is a small bottle in the collection with a label: "No. 6881, *Cercopagis tenera* G.O. Sars, det. by G.O. Sars, sp. orig!, coll. by Maksimovitch, Caspian Sea, No. 2, 3 specimens" which previously contained three males designated as allotypes by Mordukhai-Boltovskoi, which, however, turned out to be empty. Only two other allotypes (No. 46739 in the ZIN collection) designated later by Mordukhai-Boltovskoi, mentioned above, have been preserved.

Due to the absence of type specimens and specimens of the type series (in a note kept in the ZIN collection, Mordukhai-Boltovskoi specifically pointed out that the holotype of *C. pengoi* is not in the collection) and taxonomic uncertainty regarding forms close to the species, *C. neonilae, C. tenera,* and *C. gracillima,* the author of the present paper designated a neotype [ICZN, 75.3] which is deposited in the collection of Zoological Museum of Moscow State University (ZMMU No. 279). This is a female with a body length 1.39 mm and with an entire caudal process stored in a small jar with a formalin and labeled: "*Cercopagis pengoi* (Ostroumov, 1892). NEOTYPE.Sea of Azov (ZIN N 490-936), Azov expedition, st. 33b, 4.08.1923, coll. Chugunov and Arnoldi".

REMARKS. As was noted above, Mrs. N. Pengo [1880] made the first detailed description of the representatives of the genus *Cercopagis* from the Sea of Azov ("*Bythotrephes* sp.") which undoubtedly belonged, judging by her description and drawings, to the species *C. pengoi.* She only made a mistake in the number of the aesthetasks of antennules, prominences of the maxillary outgrowth of the mandibles and in the number of thoracic limbs' segments; also, the pseudognathobasic processes of tl II – tl IV were incorrectly described and abdomen and postabdomen were not separated. At the same time, this researcher noticed a number of subtle details that were not observed by the following authors. In particular, she described "two tiny setae" which are situated on the protopodite of tl I, which in fact represent the remnant of the pseudognathobasic process.

However, with all the attention to detail, the drawing of the general appearance of the crustacean from the Sea of Azov was made by N. Pengo rather roughly, schematically, which obviously mislaid the following researchers. In particular, Sars [1897] used Pengo's drawings and did not recognize the identity of *Cercopagis* individuals from the Sea of Azov and *C. tenera* from the Caspian Sea, which were depicted by him in a much more natural way. On the contrary, he found [Sars, 1902] that some individuals from the Caspian Sea, generally close to *C. pengoi*, are identical to the Sea of Azov's representatives and named them *C. neonilae*.

The author of the present paper studied six individuals identified by Sars *C. neonilae* (Fig. 9), two of them strongly deformed. In general, most of their features, including the length of abdomen (metasoma) are similar to those of *C. pengoi*, only the claws of most of them are shorter and stouter (5.1–5.5% and 3.5–4.5% of body length on postabdomen and caudal process, respectively) (Fig. 9d–f), although one individual had the latter ones exactly like in *C. pengoi* (relatively thin and long: 10.5–7.0% of body length) (Fig. 9g). Also, some individuals of the latter species had a relatively wide brood pouch (up to 47.0% of its length), which is comparable to that of *C. neonilae* (e.g., see Fig. 7b, left). The latter feature probably depends on the size and number of embryos contained in the brood pouch.

In the studied material, there were no individuals that could definitely be attributed to the species *C. gracillima* (later the form *gracillima*) described by Sars [1902] for one adult female and especially characteristic of the Northern Caspian Sea [Mordukhai-Boltovskoi, Rivier, 1987; Rivier, 1998]. Representatives from this area did not differ significantly from others in the length of the abdomen and claws of the postabdomen and caudal process (see Table 2).

Based on the above scant data, we can agree at this point with the assumptions of previous authors [Meissner, 1908; Mordukhai-Boltovskoi, 1965, 1968a, b; Mordukhai-Boltovskoi, Rivier, 1987; Rivier, 1998] that the taxa *C. neonilae* and *C. gracillima* are the extreme forms of the morphologically variable species *C. pengoi* and should be attributed to its synonyms.

In the Aral Sea, cercopagidids were first described by Zernov [1903] under the name *C. tenera*, which, according to this author, is very close, if not identical to the species *C. pengoi.* Later, Meissner [1908] quite definitely identified the Aral individuals as *C. pengoi.* At the same time, both authors do not present any specific morphological features of the Aral specimens, in particular, Zernov [1903] depicted them with a long caudal process having a loop characteristic of representatives of the genus. Later, Mordukhai-Boltovskoi [1974] noticed several distinctive features of the Aral representatives of the species (shortened caudal process with an underdeveloped or missing posterior loop, closely situated claws of postabdomen and caudal process, and unusually long tl I) and suggested that they should be classified as a new subspecies *C. pengoi aralensis* (however, the type specimens of the taxon have not been designated).

The author of the present paper had a possibility to investigate three adult females from the Aral Sea collected in 1935 (Fig. 6c, d). Indeed, these individuals had comparatively long tl I (102–108% of body length) (however, their large length could also be due to deformity of the trunk), as well as a relatively short caudal process (410–479% of body length) without a posterior loop. Thus, the relative length of the caudal process turns out to be larger than was indicated earlier in the Aral Sea individuals ("only 3–3.5 times longer than the body" [Mordukhai-Boltovskoi, Rivier, 1987; Rivier, 1998], which is quite comparable with that one of the individuals of the species from the reservoirs of the Volga and Kama Rivers (see Table 2). It is also difficult to accept the idea that "The special traits of the Aral *Cercopagis* obviously evolved during the last period of existence of the lake in relation to changes in its conditions, including increased salinity. *C. pengoi* which lived in the Aral Sea earlier did not differ from the typical form [Zernov, 1903]" [Mordukhai-Boltovskoi, Rivier, 1987; Rivier, 1998]. As was indicated above, the Aral Sea specimens collected in 1935 when this water body had a reduced salinity, also possessed a straight, without a loop, caudal process.

Of all the named above diagnostic features, the morphology of the caudal process is the most unambiguous in terms of taxonomic specificity of the Aral Sea population of *C. pengoi*. However, not everything is clear about it either, because according to Zernov's [1903] drawing, the Aral individuals may also have a caudal process of a regular shape. This point, as well as the ambiguity with other diagnostic features, the lack of a

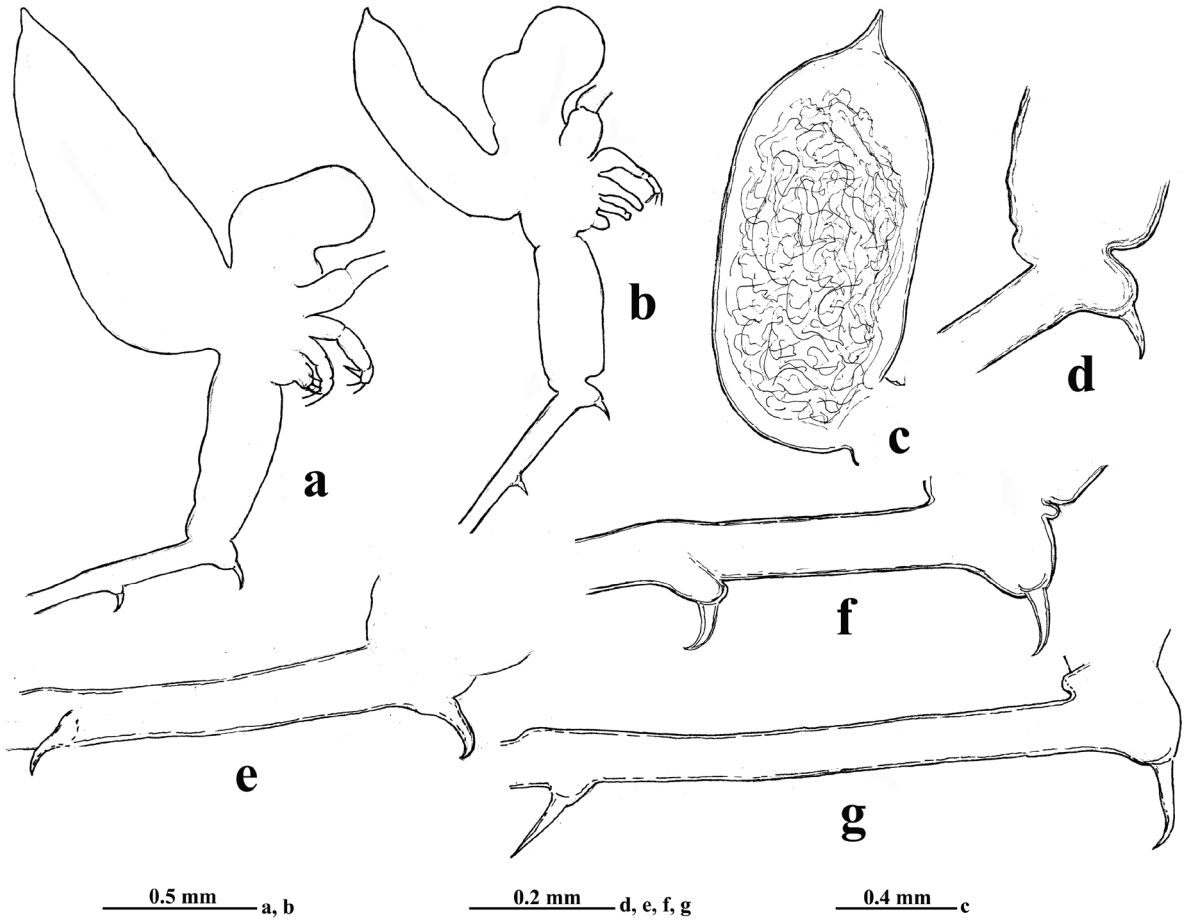

Fig. 9. "*Cercopagis neonilae* Sars, 1902", females, Caspian Sea: a, b — body contours; c — brood pouch; d–g — claws of postabdomen and caudal process.

Рис. 9. "*Cercopagis neonilae* Sars, 1902", самки, Каспийское море: a, b — контуры тела; c — выводковая камера; d–g — когти постабдомена и каудального выроста.

sufficient number of individuals for research, so far prevent me from making an unambiguous conclusion about the validity of the Aral Sea's subspecies.

As for other populations of *C. pengoi,* the Baltic and the river reservoirs' populations are noticeably larger than those from the Sea of Azov and Caspian Sea (the especially large body size of the Baltic specimens was also noted by Grigorovich *et al.* [2000]), the former ones also have longer tl I and their distal segment (see Table 2) ($p < 0.001$). In the Caspian specimens, the claws of the postabdomen and caudal process are especially widely spaced. The Sea of Azov's specimens differ from the Caspian ones in the presence of more straight and more closely situated claws (Fig. 6) and longer tl I ($p < 0.001$). These morphological differences probably coincide with the fact that the Caspian and Ponto-Azov populations of the species exhibit marked genetic divergence (see Cristescu *et al.* [2001]).

The most variable features (CV = 10–23) are the size of the claws, distance between them, and thickness of the caudal process (see Table 2).

Cercopagis micronyx Sars, 1897
Fig. 10.

Sars, 1897: 18–19, Pl. 2, figs 2, 2a, 1902: 35; Sovinsky, 1902: 374; Manuilova, 1964: 296–297, fig. 164; Mordukhai-Boltovskoi, 1967: 116, figs 10–12, 1968b: 137–138, fig. 147; Mordukhai-Boltovskoi, Rivier, 1987: 161–162, fig. 100; Rivier, 1998: 184–185, figs 241–243; Korovchinsky *et al*., 2021: 481–482, fig. 149, 7–10.

MATERIAL EXAMINED: Caspian Sea, females: 1) one adult specimen (1 ad) (ZIN, No. 6875, a small bottle with a label: "*Cercopagis micronyx* G.O. Sars, det. G.O. Sars, sp. orig., coll. O. Grimm, three paratypes" (in fact there was only one specimen in the bottle); 2) two specimens (ZIN, No. 46738 from sample No. 59-1964, a small bottle with a label: "*Cercopagis micronyx* G.O. Sars, 2 males, allotypes, det. by Ph.D. Mordukhai-Boltovskoi, coll. by the expedition on the ship "Professor Soldatov", the Middle Caspian Sea, August 1963".

FEMALE

General body appearance and segmentation as in previous species (Fig. 10a). Body length of the female examined is 1.18 mm. Head comparatively large (40.5% of body length). Carapace looks like a bag-like structure, strongly modified into closed brood pouch (Fig. 10a). In the examined female, it has elongated-oval shape with the narrowed, rounded distal part. The thoracic limbs of first pair (tl I) are rather long (105%) having the seta armament of regular type. Abdomen (metasoma) (Fig. 10a) is comparatively short (31% of body length) and wide (48% of its length), cylindrical. Postabdomen is small as usual and bears small claws (2% of body length) widened at base, it imperceptibly turns into a caudal process thickened proximally (6.1% of body length) (Fig. 10a, b). The latter is long (626% of body length) and proximally bears one pair of claw-like

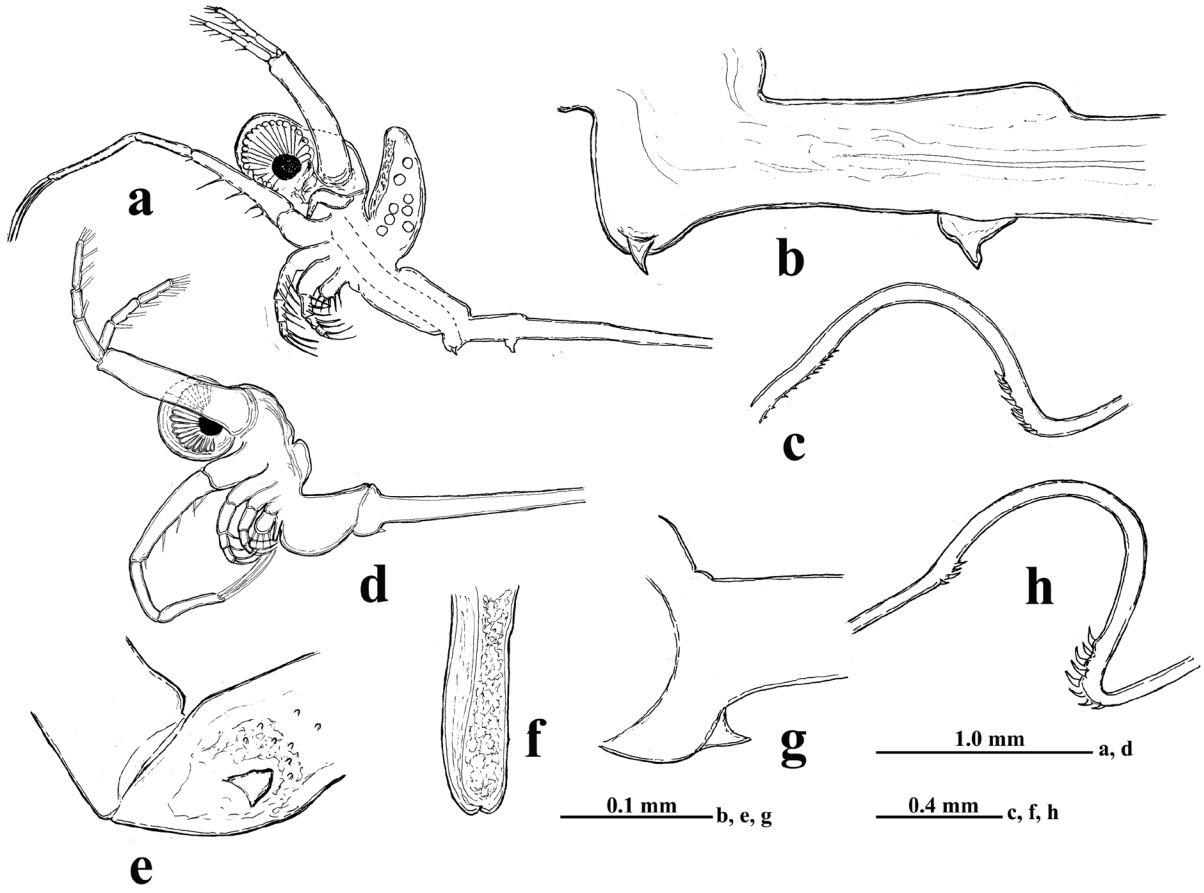

Fig. 10. *Cercopagis micronyx* Sars, 1897, females (a–c) and males (d–h), Caspian Sea: a, d — general lateral view; b — claws of postabdomen and caudal process; c, h — denticulated bend of caudal process; e — undeveloped clasping hook on distal segment of tl I; f — copulatory appendage, g — claw of postabdomen.

Рис. 10. *Cercopagis micronyx* Sars, 1897, самки (a–c) и самцы (d–h), Каспийское море: a, d — общий вид сбоку; b — когти постабдомена и каудального выроста; c, h — зубчатый изгиб каудального выроста; e — недоразвитый хватательный крючок дистального членика торакальной конечности 1-й пары; f — копулятивный придаток, g — коготь постабдомена.

prominences (2% of body length) (Fig. 10b). Near its end, the caudal process creates a prominent bend (loop) with two groups of curved denticles, proximal and distal (Fig. 10c). Pairs of claws sit rather closely (17.6% of body length).

MALE

Two studied males (Fig. 10d) were probably juveniles, judging by their small body size (0.67–0.70 mm), the presence of claws only on postabdomen and underdeveloped hooks on tl I. Abdomen (metasoma) (Fig. 10a) is also short (30–31% of body length), convex ventrally and wide (73–77% of its length). Postabdominal claws are also small (2.3–2.4% of body length). Caudal process is long (795– 838% of body length), thickened at base (9.5–10.2% of body length) and also creates a prominent bend (loop) with two groups of curved denticles (Fig. 10h). The clasping hooks on tl I are underdeveloped (Fig. 10e), copulatory appendages small, cylindrical (Fig. 10f).

REMARKS. Sars [1897, 1902] found only few specimens of the species. In the ZIN collection, these specimens (or only some of them) were designated by an unknown person (probably by Ph.D. Mordukhai-Boltovskoi) as paratypes but most likely they can be considered syntypes. Unfortunately, only one specimen of them has been preserved.

Mordukhai-Boltovskoi [1967, 1968b] had rather abundant parthenogenetic females of the species which were described rather briefly. At the same time, very few males were obtained. Adult males bear two or three pairs of small close-sitting denticles on the postabdomen and proximal part of the caudal process. Only two juveniles were found by the author in the ZIN collection, while the gamogenetic females were absent.

According to Mordukhai-Boltovskoi [1968b], *C. micronyx* is mostly abundant and widely distributed species of the genus in the Middle and South Caspian Sea. Generally, its representatives are very polymorphic in some features, especially in the shape of the metasoma and brood pouch, in the degree of development and location of the claws on the postabdomen and caudal process.

Cercopagis longiventris Mordukhai-Boltovskoi, 1962
Fig. 11a–b.

Mordukhai-Boltovskoi, 1962: 131; 1964: 24–25, fig. 3; 1968b: 130, fig. 139; Mordukhai-Boltovskoi, Rivier, 1987: 159, fig. 98; Rivier, 1998: 181, figs 237–239; Korovchinsky *et al*., 2021: 479, fig. 149, 1–3.

MATERIAL EXAMINED: 1 ad (ZIN No. 1/46736) supplied with a label: "*Cercopagis longiventris* nov. sp. (holotype), det. F.D. M.-Boltovskoi, expedition on the ship "Professor Soldatov", the eastern part of the Middle Caspian Sea, 1961 (from sample N 59-1964)".

FEMALE. Body generally long and narrow, its length 1.39 mm. Tl I is comparatively short (63% of body length). Abdomen (metasoma) is unusually long (59% of body length) and

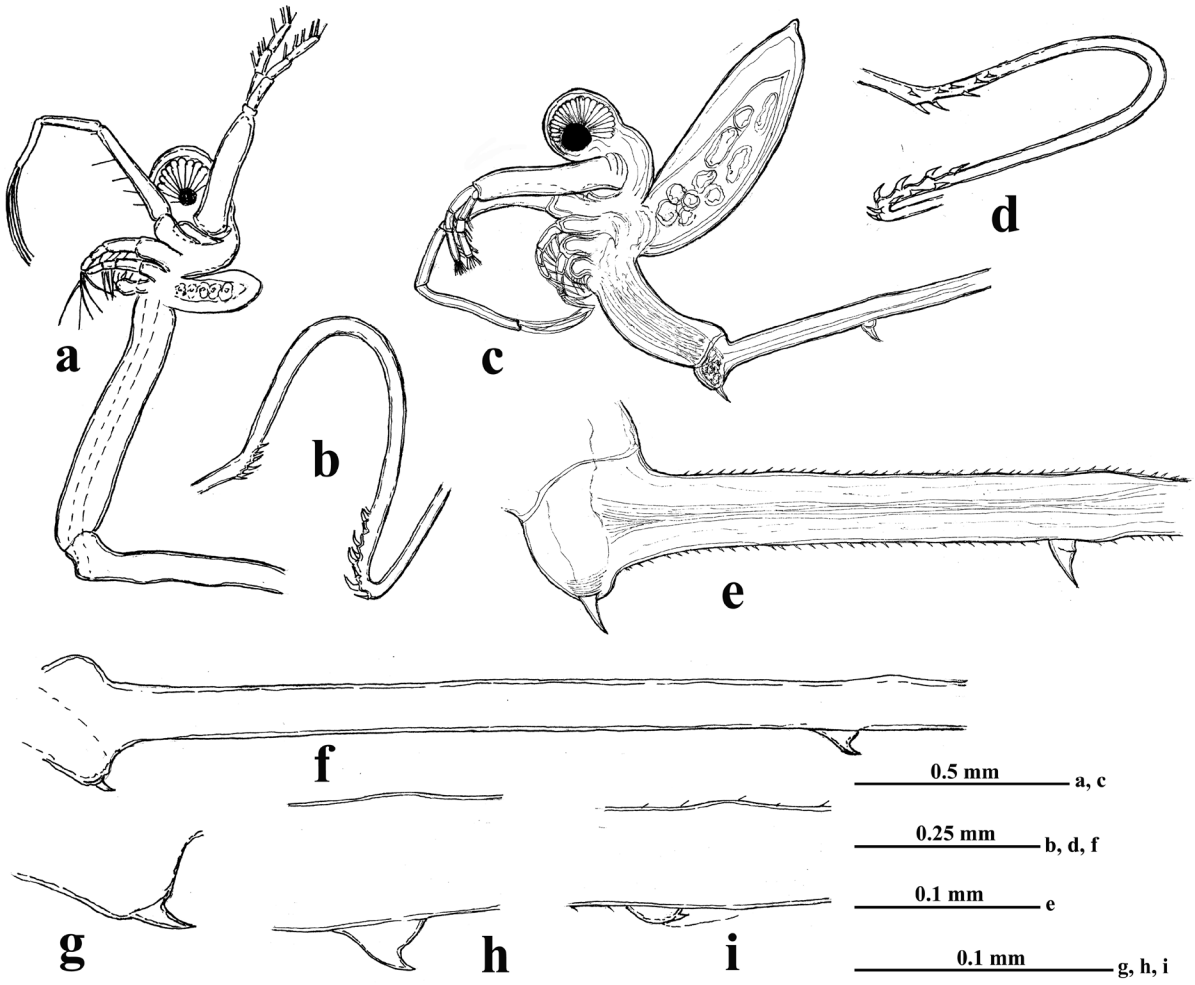

Fig. 11. *Cercopagis longiventris* Mordukhai-Boltovskoi, 1962, female, Caspian Sea (a, b). *Cercopagis spinicaudata* Mordukhai-Boltovskoi, 1962, females (c–i): a, c — general lateral view; b, d — denticulated bend of caudal process; e–i — claws of postabdomen and caudal process.

Рис. 11. *Cercopagis longiventris* Mordukhai-Boltovskoi, 1962, самка, Каспийское море (a, b). *Cercopagis spinicaudata* Mordukhai-Boltovskoi, 1962, самки (c–i): a, c — общий вид сбоку; b, d — зубчатый изгиб каудального выроста; e–i — когти постабдомена и каудального выроста.

narrow (18% of its length). Brood pouch is small, rounded on the top and bears some small eggs. Caudal process is of moderate length (440% of body length), thickened basally, almost as thick as abdomen (7% of body length), then it narrows (3.4% of body length) and posteriorly forms a typical denticulated bend. Postabdomen and caudal process lack any claws.

REMARKS. Mordukhai-Boltovskoi [1962] presented the first very brief diagnosis of the species, so this date should be used instead of "Mordukhai-Boltovskoi,1964" as it was previously presented by the author in his more extensive description of the taxon [Mordukhai-Boltovskoi, 1964]. In the latter, however, the typification of specimens has not been provided.

In particular, the author mentioned that "Caudal claws reduced to scarcely detectable spinules near the anus or altogether lacking". Just the absence of these spinules was observed in the above-described specimen. In contrast to Mordukhai-Boltovskoi [1964], who mentioned that "The caudal process forms an immediate prolongation of the metasoma, the whole animal being stretched usually in one straight line", the studied specimen possesses its caudal process directed almost at right angle to the rest of the body which probably indicates its real ability to bend. Also, the previously studied specimens were larger, having body length of 1.65–2.10 mm. In total, for all the time only few (four or five) specimens (parthenogenetic females) of the species were found, whereas gamogenetic females and males are unknown.

Cercopagis spinicaudata Mordukhai-Boltovskoi, 1962
Fig. 11c–i.

Mordukhai-Boltovskoi, 1962: 131, 1968b: 133, fig. 143; Mordukhai-Boltovskoi, Rivier, 1971: 1–3, fig. 1; 1987: 159, fig. 97-B, C; Rivier, 1998: 180–181, figs 234–236; Korovchinsky *et al*., 2021: 478–479, fig. 148, 6–9.

MATERIAL EXAMINED: 1) 1 ad (ZIN No. 1/57513) supplied with a label: "*Cercopagis spinicaudata* sp. n. (holotype), det. Ph.D. M.-Boltovskoi, Caspian"; 2) 2 ad (ZIN No. 1/46894) supplied with a label: "*Cercopagis spinicaudata,* paratypes, det. Mordukhai-Boltovskoi, Middle Caspian Sea, expedition on ship "Professor Soldatov", 09.1962 and 08.1963".

FEMALE. In fact, only two specimens were examined, holotype and one paratype, because another paratype specimen was strongly deformed being deprived of caudal process.

Abdomen is either of moderate (38% of body length in holotype specimen) or of considerable length (59.5% of body length in paratype specimen) and width (about 48% of its length).

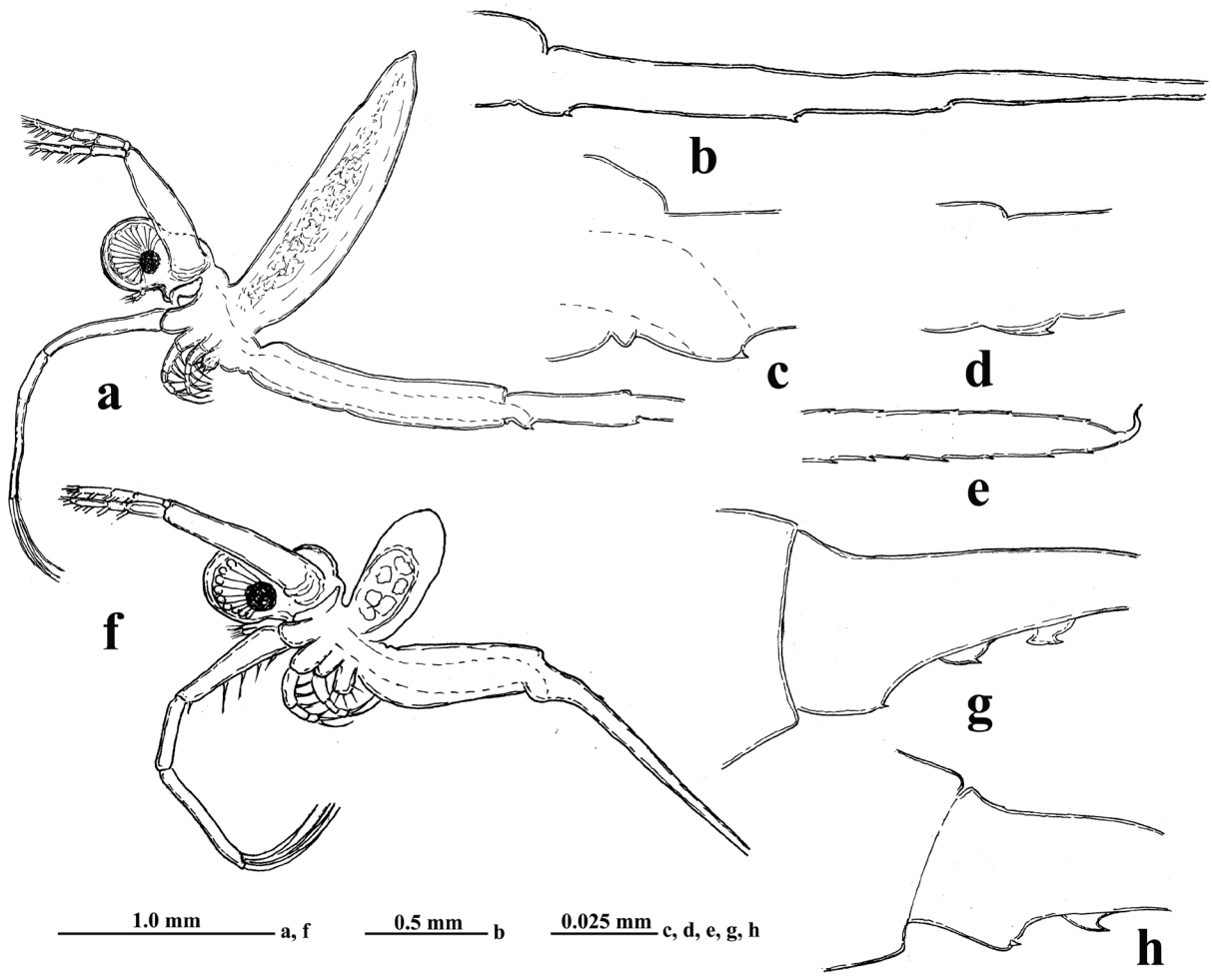

Fig. 12. "*Apagis cylindrata* Sars, 1897", females, Caspian Sea (a–e) and "*Apagis beklemishevi* Mordukhai-Boltovskoi, 1962", females, Caspian Sea (f–h): a–f — general lateral view; b–d, g, h — claws of postabdomen and caudal process; e — apical end of caudal process.

Рис. 12. "*Apagis cylindrata* Sars, 1897", самки, Каспийское море (a–e) и "*Apagis beklemishevi* Mordukhai-Boltovskoi, 1962", самки, Каспийское море (f–h): a–f — общий вид сбоку; b–d, g, h — когти постабдомена и каудального выроста; e — апикальный конец каудального выроста.

Tl I is also of moderate length (80–100% of body length). The brood pouch is oblong-oval with small prominence on the top. The length of caudal process is 460–585% of body length; it is comparatively thick proximally (4.3–7.4% of body length) and covered with numerous spinules. Claws of postabdomen and caudal process are small (0.4–4.9% of body length), curved, and situated distantly one from another (20.5–49.3% of body length). Body length 1.14 mm (holotype) and 1.86 mm (paratype).

REMARKS. Mordukhai-Boltovskoi [1962] presented the first very brief diagnosis of the species, so this date should be used again instead of "Mordukhai-Boltovskoi, 1968" as it was previously presented by the author in his first more extensive description of the taxon [Mordukhai-Boltovskoi, 1968b]. In the latter, the typification of specimens has not been provided either. This was made only in the next more detailed redescription of the species (see Mordukhai-Boltovskoi, Rivier [1971]).

The authors of the latter publication mentioned that the parthenogenetic females of the species occur rather commonly, whereas males are rare as usual. In particular, they found and described one male specimen of the species (allotype No. 2/57514 in the ZIN collection). Unfortunately, the latter was absent in the collection (it is noted that "it is in the author's possession"). Later on, some additional males were collected in the coastal and central regions of the Middle Caspian Sea [Mordukhai-Boltovskoi, Rivier, 1987; Rivier, 1998].

Forms of the "Genus *Apagis* Sars, 1897"

(parthenogenetic females of first generation hatched from resting eggs that cannot yet be attributed to any species)

"*Apagis cylindrata* Sars, 1897"

Fig. 12a–e.

MATERIAL EXAMINED: 1) sample No. 6828 (ZIN collection) with a label: "*Apagis cylindrata* G.O. Sars, collected by O. Grimm, No. 69, Caspian Sea, 2 ad"; 2) sample No. 6827 (ZIN collection) with a label: "*Apagis cylindrata* G.O. Sars, collected by Maksimovitch, Caspian Sea, No. 2, 10 specimens", 7 ad, 4 juv.

Abdomen is long (58.0–68.2% of body length) and comparatively narrow (13.0–17.0% of body length). Brood pouch is long and comparatively narrow, pointed on the top. Tl I is of moderate length (42.3–58.5% of body length). Caudal process is comparatively thick proximally (3.8–7.8% of body length), then it narrows (2.6–5.4%), its length is 96–152% of body

length. Proximally, it bears two or three tiny denticles, those on postabdomen are especially small and thin, more posterior of them have plate-like appearance with sharpened apical end; the distance between denticles is13.5–22.2 % of body length, apically caudal process bears two minute sensory setae [see Sars, 1897, fig. 3: 2]. Body length 1.84–2.51 mm.

REMARKS. Sars [1897] described this form as having only one individual, and then several others were added [Sars, 1902]. Striking distinguishing features of it are the presence of an unusually long abdomen and specific rudimentary denticles of the postabdomen and caudal process. It is a large-bodied form, reaching 3.0 mm.

The form is widespread in the Middle and Southern Caspian Sea, and enters the southern regions of the Northern Caspian Sea. This is the most common form of cercopagidids, often reaching a large number and entering shallow areas where other cercopagidids are not found [Mordukhai-Boltovskoi, 1968b; Mordukhai-Boltovskoi, Rivier, 1987; Rivier, 1998]. It was also recorded in the brackish Lake Chany in Western Siberia [Rivier, 1998] but this was later refuted [Rivier, 2007].

Judging by the especially long abdomen, the representatives of this form may refer to the species *C. longiventris* possessing similar diagnostic features which requires further confirmation.

"***Apagis becklemishevi*** Mordukhai-Boltovskoi, 1964" Fig. 12f–h.

MATERIAL EXAMINED: sample No. 1/46737 (ZIN collection) with a label: "*Apagis beklemishevi* nov. sp. holotype and paratypes, det. by Ph.D. Mordukhai-Boltovskoi, expedition on ship "Professor Soldatov", Middle Caspian Sea, 1961–1962, from sample No. 59-1964", 4 ad.

Abdomen is of moderate length (37.0–48.4% of body length) and comparatively thick (37.0–47.8% of body length). Brood pouch is comparatively small, rounded or slightly angular on the top. Tl I is comparatively long (68.4–100.0% of body length). Caudal process is straight, thick proximally (6.3–8.3% of body length), then it narrows (5.3%); comparatively it is long (280–400% of body length). Proximally, it bears two or three tiny denticles, those on postabdomen are especially small and thin, more posterior of them have plate-like appearance with sharpened apical end; denticles are closely situated (4.0–9.2% of body length). Body length 0.96–1.52 mm.

REMARKS. The form was described in sufficient detail, including thoracic limbs [see Mordukhai-Boltovskoi, 1964]. It is often found in the Middle Caspian Sea, but usually as single specimens. Judging by the studied specimens, the representatives of this form can reach a larger body size (up to 1.52 mm) than it was previously indicated (1.1–1.35 mm).

Discussion

PRELIMINARY NOTES. Generally, the representatives of the genus *Cercopagis* attracted less attention than other Onychopods, including the nearby genus *Bythotrephes*, due to its relatively local distribution in the past – exclusively in the Ponto-Caspian-Aral basin. As a result, they were generally less accessible for wide international research compared to Podonidae, Polyphemidae and *Bythotrephes,* although their initial detailed study was conducted, among others, by the leading Norwegian crustaceologist G.O. Sars [1897, 1902]. Later, these crustaceans have been studied in many ways by Russian researches — in respect of external and internal structure, taxonomy, species richness, spatial distribution, migrations, reproduction and development [see Mordukhai-Boltovskoi, Rivier, 1987; Rivier, 1998].

Only later, in very recent time, the representatives of the genus *Cercopagis*, rather only one of their species, *C. pengoi,* penetrated north into the river systems, and then into the Baltic Sea and further into the American lakes, and for this reason it has come into the field of closer attention of a wide range of hydrobiologists. At this time, they became the subject of molecular-genetic studies in order to determine their geographic dispersion, time and patterns of evolutionary development of the genus (e.g., Makarewicz *et al*. [2001]; Cristescu, Hebert [2002]). Now the main research work of the genus, mainly on its ecology, is provided in the Baltic Sea and North American lakes.

TAXONOMY. Initially, the representatives of the marine Cercopagididae were readily attributed to the genus *Bythotrephes* [Grimm, 1877; Pengo, 1880]. Then, since the 1890s, the family began to include three genera — freshwater *Bythotrephes* and brackishwater Ponto-Caspian *Cercopagis* and *Apagis,* two latter of which were established by Sars [1897]. This system remained for more than a century when it was finally shown that the representatives of the genus *Apagis* represent only individuals of a separate ontogenetic stage of particular species, namely females of the first generation, hatching from resting eggs [Simm, Ojaveer, 1999, 2006; Makarewicz *et al*., 2001]. Accordingly, the genus/subgenus *Apagis* was abolished [Korovchinsky *et al*., 2021].

Up to now, 11 species of the genus *Cercopagis* have been described but one of them, *C. tenera,* could be synonymized with *C. pengoi* [Zernov, 1903; Meissner, 1908; Mordukhai-Boltovskoi, Rivier, 1987; Rivier, 1998]. The validity of two other species, *C. neonilae* and *C. gracillima,* is poorly justified. These taxa were insufficiently described and required further investigation. Some authors, not without reason, believed that these taxa may represent the different morphological varieties of *C. pengoi* and can also be synonyms of this species [Meissner, 1908; Mordukhai-Boltovskoi, 1964, 1965, 1968b]. In the recent monographs on Onychopoda [Mordukhai-Boltovskoi, Rivier, 1987; Rivier, 1998], *C. neonilae* is considered valid, but this has not been proven. There is also an unresolved issue with the taxon *C. pengoi aralensis*. Originally, it was poorly described, and the very little material available to the author also does not allow to draw a reasonable conclusion. Due to the general reason for the lack of sufficient material, all the abovementioned taxa are provisionally classified as synonyms of morphologically variable *C. pengoi.*

Of the remaining eight species, the author managed to study five species, whereas the material for three species (*C. prolongata*, *C. robusta*, *C. anonyx*) was absent. The latter were originally described by a few individuals (see Sars [1897]) and later, with more material (see Mordukhai-Boltovskoi, Rivier [1987]; Rivier [1998]), they were not reinvestigated. As for five studied species, *C. socialis*, *C. pengoi*, *C. spinicaudata*, *C. longiventris*, *C. micronyx*, the material for the latter three species was minimal, only being represented by few type individuals.

Thus, only *C. socialis* and *C. pengoi* were studied in sufficient detail, the former species first by Sars [1897] and then in the present paper, as well as *C. pengoi*, a species in which several populations have been comparatively studied. All the remaining six species of the genus remain insufficiently taxonomically studied. It is precisely for this reason that the present revision of the genus *Cercopagis* should be considered partial.

As for the "*Apagis*" forms, they were usually found in small numbers, with the exception of "*A. cylindrata"*. The species identity of these forms is still definitely known only by "*A. ossiani*", which is related to *C. pengoi* [Simm, Ojaveer, 1999, 2006; Makarewicz *et al.,* 2001]. The species attribution of the remaining forms needs further investigation.

The diagnostic features important for the species identification include comparative size and shape of abdomen (metasoma), brood pouch, caudal process, denticles of postabdomen and caudal process, and their relative location. In contrast to the members of the nearby genus *Bythotrephes*, the size of tl I, their segments and segments' armament are not used due to the great uniformity of these structures in different species. The limbs of other pairs are also not used in taxonomy, as well as male's traits as it is also typical for the genus *Bythotrephes.*

COMPARATIVE MORPHOLOGY. Research work in this area, except for small notes by Sars [1897], practically did not affect the representatives of the genus.

The general body composition of *Cercopagis* compared to *Bythotrephes* looks more delicate and slender, the body size usually does not exceed 2.5 mm. As in the latter genus, the body is characterized by a conspicuous curve of its longitudinal body axis at which the head is situated almost at a right angle to the thorax. This places the eye in an extremely anterior position and the mouthparts appear close to the thoracic limbs, which hatch and manipulate prey before pushing it to the mouth. There is no data on the structure of the large compound eye, but it can be assumed that at least in many respects it is identical to that of the *Bythotrephes* except for the eye pigment, which is noticeably less developed.

Antennules. They are small, similar in females and males, as in *Bythotrephes,* and shifted far under the eye, where they do not prevent the functioning of the latter and, at the same time, retain their extremely anterior position. They are situated quite closely, thus their bases appear almost fully fused. Five antennular aesthetasks are well-developed (earlier, either four [Pengo, 1880] or six [Sars, 1897] aesthetasks were described); the sensory seta is somewhat smaller than aesthetasks and of regular appearance, whereas in *Bythotrephes* it is transformed into a smaller and thinner aesthetasks-like structure.

Swimming antennae. The basipodite of the antennae bears proximally, on a wrinkled base, a small feathered antero-dorsal seta similar to that of other Cladocera, which was never described before. As in other Cladocera, including *Bythotrephes*, this seta indicates an articulation, because in a strictly morphological sense, the antennal basipodite represents a protopod(ite), composed of two segments, a short coxa, and long basis.

The upper branch (exopodite) is four-segmented and the longer lower one (endopodite) is three-segmented, which is similar to that found in other Onychopoda and most Anomopoda families. Antennal setae are both terminal and lateral ones, which are especially numerous on distal segments of both branches. All antennal setae of *Cercopagis,* seven on both branches, not eight and seven as in *Bythotrephes,* on the upper and lower branch, respectively, are of similar structure and armament. They bear uniform setules of the "swimming" type and may be regarded as paddle setae. The longest setae are situated in the middle part of the branches, not terminally, which resembles the setae arrangement of *Bythotrephes* and may testify to a similar swimming mode of these planktonic predators.

Mouth parts. Among them, the upper lip (labrum) is especially distinctive, being large but not supplied with an anterior large proboscis–like outgrowth as in *Bythotrephes.* The labrum itself is quite large, wide and fleshy cone-like lobe, covering the mandibles and mouth. Its margin is densely covered by numerous small papillae.

Mandibles are bilobed and adapted for biting, with a toothed, blade-like posterior strongly sclerotized lobe and a small anterior lobe (mandibular process) armored with a smaller than in *Bythotrephes* cluster of only 6–10 long prominences with only few tiny spinules distally (Pengo [1880] and Sars [1897] counted only four prominences). Maxillules (mx I) are similar to those of *Bythotrephes.*

Carapace (brood pouch). Generally, this structure in *Cercopagis* species looks similar to that of *Bythotrephes*; like in the latter genus, its size and shape vary in different species.

Thoracic limbs. As in *Bythotrephes* and other onychopods, the representatives of the genus *Cercopagis* have similar pattern of limb's segmentation. Differences in the armament of the limbs are expressed in the absence of pseudognathobase on the protopodite of tl I, of which only small rudiments remain, as well as in a reduction in the number of setae. Of the latter, those on the distal end of the first segment have been reduced to one and on the second segment they have disappeared completely. Compared to the species of *Bythotrephes*, the thoracic limbs of second and third pairs have lost their posterior setae. On tl IV of *Cercopagis*, the setae arrangement compared to *Bythotrephes* is mutually opposite, namely, their inner row consists of only two setae, whereas the outer one is of a row of 5–6 setae.

Abdomen (metasoma) of *Cercopagis* is whole, without any traces of segmentation. There are no signs that its last third segment is transformed and functionally connected to the postabdomen, as observed in *Bythotrephes*. All segments are merged, which emphasizes the high degree of specialization of this large flexible structure.

Postabdomen and caudal process. The latter structure is completely and imperceptibly connected to the postabdomen, which is indicated only by the presence of the posterior gut and anus. The claws of the postabdomen and caudal process are conspicuously less developed than in *Bythotrephes*, they are usually smaller and less numerous. These claws are comparatively larger in *C. socialis* and

C. pengoi, slightly weaker in *C. prolongata*, *C. robusta*, and *C. spinicaudata*, poorly developed in *C. micronyx*, and practically reduced in *C. longiventris* and *C. anonyx.* The latter two species have tiny claws, if any, only on the postabdomen and not in all individuals. In general, there is obviously an evolutionary trend towards a decrease in size and disappearance of claws.

In *Bythotrephes,* the caudal process is long, massive, and functionally very active organ, surpassing the body length by two–five times. One species, *B. cederstroemii,* and some representatives of the hybrid forms have a prominent denticulated bend on it, which is situated either in the middle part of the caudal process or somewhat proximal or distal; this bend serves to strengthen the caudal process. In *Cercopagis,* the caudal process turns out to be much more elaborated and functionally specialized organ, since it is relatively longer (surpasses body length usually at five-six, sometimes up to ten times) and has a very peculiar part — the distal bend, which looks like a real loop. This bend (loop) creates an additional strong fulcrum, thanks to which the body of *Cercopagis* specimens can take a more comfortable (probably more vertical) position, when the long hunting limbs of first pair (tl I) can stretch forward to grasp prey. *Bythotrephes* specimens seem less specialized in this regard, having at their disposal only a long caudal process sometimes strongly reinforced by a bend.

Generally, the members of the genus *Cercopagis* show clear signs of oligomerization in their morphological structure, which can be noted in the armament of swimming antennae, mandibles, thoracic limbs, and caudal process. Probably this is partly due to the relative decrease in body size in these crustaceans compared to members of the genus *Bythotrephes*. But, on the other hand, the presence of the whole long abdomen and especially the long caudal process with a very specific loop-like bend indicates the highest degree of specialization achieved by representatives of the family Cercopagididae.

NOTES ON GAMOGENETIC REPRODUCTION. According to the Caspian cercopagidids, it is known that their "gamogenesis is weakly expressed, and even in October males and females are present in solitary specimens only. In most of Cercopagididae… males are even completely unknown" [Rivier, 1998]. Indeed, single gamogenetic individuals are known only in five Caspian species, *C. socialis*, *C. pengoi*, *C. anonyx*, *C. micronyx*, and *C. spinicaudata*; in two latter species only males were recorded.

At the same time, numerous males of *C. pengoi* were recorded in the Bulgarian coastal lake Gebedje [Valkanov, 1951]. Later, numerous gamogenetic individuals, both females and males, were studied in the populations of *C. pengoi* that invaded the Baltic Sea and American Lake Ontario [Krylov, Panov, 1998; Grigorovich *et al*., 2000; Simm, Ojaveer, 2006].

The reason for the differences in sexual reproduction between different populations of *Cercopagis*, in particular *C. pengoi,* remains unclear. Rather recently it became known that this species populated the Baltic Sea and then the American Great Lakes from the Ponto-Azov basin, not from the Caspian Sea, and those populations from these two basins exhibit marked genetic divergence [Cristescu *et al.,* 2001]. So the differences in the intensity of gamogenetic reproduction in the Caspian Sea and Ponto-Azov basin and further in new northern habitats may be due to genetic differences. It should also be taken into account that the environmental conditions in the new northern Baltic and American habitats are significantly different from the original ones in many respects, including more severe temperature background, which could probably have a stressful effect on the invaders, leading to increased sexual reproduction.

It is also necessary to pay attention to the "*Apagis*" forms of the Caspian Sea, the presence of which is also associated with sexual reproduction, the laying of resting eggs from which they hatch. In total, four such forms are known belonging to different species of the genus, of which only one ("*A. ossiani*") is assigned to a particular species, *C. pengoi.* The species definition of other forms remains unknown. Of them, "*A. cylindrata"* from the Caspian Sea is characterized by "mostly distributed species of all cercopagids, it often develops in very large numbers and enters coastal shallow waters where other cercopagids are not found" [Mordukhai-Boltovskoi, 1968b; Rivier, 1998]. Also, *A. beklemishevi* is considered common. All this means that the species to which these forms belong produce numerous resting eggs. So far, this fact has not been noted. Before, researchers found only single gamogenetic females of the species with eggs [Mordukhai-Boltovskoi, 1967; Mordukhai-Boltovskoi, Rivier, 1971]. With a very small number of males found by these researchers in the population of the Caspian cercopagidids, this fact can be considered as the presence of obligate parthenogenesis in them, in which the resting eggs are produced parthenogenetically without fertilization [Hebert, Crease, 1983; Korovchinsky *et al.,* 2021: Vol.I: 185–186]. So far, no examples of obligate parthenogenesis have been known among Cercopagididae and Onychopoda in general. Of course, this hypothesis requires further verification.

GEOGRAPHICAL DISTRIBUTION. Originally, the representatives of the genus *Cercopagis* were known distributed all over the Ponto-Caspian-Aral region [Sovinsky, 1902; Mordukhai-Boltovskoi, 1960]. Of them, the comparatively euryhaline *C. pengoi* was especially widely distributed, being known as the only species of the genus in the Ponto-Azov basin and in the Aral Sea. In the Pontic area its occurrence is limited by estuaries, lagoons, and coastal lakes, in the Sea of Azov it was recently recorded in Taganrog Bay [Afanasjev *et al.,* 2019], possibly it occurs here in other bays, while in the Caspian Sea it prefers to occur in its desalinated northern area. All other species exclusively inhabit the Middle and South Caspian Sea with increased salinity.

In the Aral Sea, *C. pengoi* (see above for the taxonomic status of the local population of the species) was earlier quite common and widely distributed all over its area [Mordukhai-Boltovskoi, 1974]. Due to the salinization of the water body, this species had disappeared from its fauna by 1981 and was no longer found in the future.

There is a possibility of the natural reintroduction of this species into the Small Aral Sea from the lakes located in the lower reaches of the River Syr Darya [Plotnikov, 2016] if its representatives still live there.

In the 1950–1960s, *C. pengoi* began to populate reservoirs of the Dnepr and Don Rivers, then in the 1990s it populated the Baltic Sea from the area of the Black Sea [Cristescu *et al*., 2001], and in 1998 this species was first found in Great American Lakes [MacIsaak *et al*., 1999] from which it began to spread to neighboring lakes. Thus, *C. pengoi*, despite its disappearance in the Aral Sea, has recently proved to be extremely successful, incredibly expanding its range. In this, it is similar to *Bythotrephes cederstroemii* Schoedler, which is very widespread in Eurasia and also penetrated North American lakes [Korovchinsky, Arnott, 2019].

MODERN SPECIES RICHNESS OF CERCOPAGIS OF THE CASPIAN SEA. In their last summary work on Onychopoda, the authors [Mordukhai-Boltovskoi, Rivier, 1987] reported the occurrence of 13 species of the genera *Cercopagis* and *Apagis* in the Caspian Sea. Of them, five species (C. *socialis*, *C. pengoi*, *C. prolongata*, *C. micronyx*, *A. cylindrata*) were known numerous, four others were considered common (*C. spinicaudata*, *C. longiventris*, *C. anonyx*, *A. beklemishevi*) and three were rare (*C. robusta*, *A. ossiani*, *A. longicaudata*).

Dumont [1998a, 2000] was surprised by such a high species diversity of similar forms living in the upper layers of the pelagic zone of one, albeit a huge continental water body. He suggested that either the number of species is overestimated greatly or we do not know the species specialization. Now we can say for sure that the taxonomic richness was noticeably overestimated: the genus *Apagis* with its four species is being abolished, its "species" are only morphologically peculiar forms of the life cycle of species of the genus *Cercopagis*, of which only one is unambiguously known (see above), the other three still require the search for species to which they belong. Also, the taxon *C. neonilae*, apparently, is only a variety of *C. pengoi* (see above). Thus, at the end of the 20th century, eight valid *Cercopagis* species inhabited the Caspian Sea, the number of which also seems to be significant.

In the last decades, the biota of the Caspian Sea has been strongly influenced by a variety of alien species. Of the latter, the comb gellyfish *Mnemiopsis leidyi*, discovered here in 1999, had the greatest negative effect on zooplankton [Shiganova *et al.*, 2005; Shiganova, 2010].

Unfortunately, data on zooplankton at this time turned out to be mostly rather scarce and superficial. The author of the present paper reviewed 20 Russian research works on zooplankton collected in the Middle and South Caspian Sea published in 1999–2021. In some of them, the representatives of the genus *Cercopagis* are not mentioned at all. In most other works, only *C. pengoi* is recorded, *C. micronyx* is recorded in two articles, and once each — *C. socialis* and *C. prolongata*; the rest of four species of the genus have completely disappeared from the lists. Of four "*Apagis*" forms, the data on only two have been encountered — "*A. cylindrata*" (more often) and "*A. beklemishevi*". Data on Iranian waters also indicate catastrophic changes in the species richness of zooplankton. Thus, according to Roohi *et al.* [2008], after the introduction of *Mnemiopsis leidyi*, only one cladoceran species (*Pleopis polyphemoides* (Leuckart, 1859)) survived out of 24 ones earlier known. In another case, two *Cercopagis* species (*C. pengoi, C. prolongata*) noted in the late 1990s did not occur further after the appearance of this invader [Bagheri, Sabkara, 2013]. Also, from the rich fauna of the genus *Cercopagis*, known in the 1997–97s (*C. longiventris*, *C. pengoi*, *C. prolongata*, *C. socialis*, *C. spinicaudata*, *C. robusta*, *C. macronyx*, "*A. ossiani*", "*A. cylindrata*"), in 2008–2011 only one species (*C. pengoi*) was infrequently found in the Iranian waters of the Caspian Sea [Saravi *et al.,* 2017].

Based on the available data, it can be concluded (considering also that not all identifications of species under consideration could be accurate enough) that by now the unique, endemic fauna of the genus *Cercopagis* of the Caspian Sea has suffered greatly. Most species and forms have clearly greatly reduced their numbers; some, possibly, even become extinct. Further studies should provide a more accurate conclusion, taking into account the most recent changes, namely the introduction of another comb jellyfish, *Beroe ovata* Broguiére, 1789, reducing the number of *Mnemiopsis leidyi* and thus giving the ecosystem of the Caspian Sea a chance to recover [Vostokov *et al*., 2020; Shiganova *et al*., 2023].

ON THE ORIGIN AND SUBSEQUENT DISTRIBUTION PATHS OF THE GENUS *CERCOPAGIS*. Beginning from Sars [1902], researchers considered this genus as a descendant of the genus *Bythotrephes* as having rather recent freshwater origin (since the Khvalynian transgression, 35–10 ka) [Mordukhai-Boltovskoi, 1965; Potts, Durning, 1980; Mordukhai-Boltovskoi, Rivier, 1987; Rivier, 1998, 2007; Aladin *et al*., 1999].

Subsequently, it was believed that the endemic fauna of the Caspian Sea, to which the genus *Cercopagis* belongs, has a much older origin – from the Miocene, from the time of the existence of the brackish-water Sarmatian See, which is one of the stages of the evolution of Parathetis existed more than 7 million years ago [Dumont, 1998a, b, 2000].This was soon confirmed by the application of molecular-genetic methods [Cristescu, Hebert, 2002; Cristescu *et al.*, 2003] which showed that the divergence of genera *Cercopagis* and *Bythotrephes* occurred within 10–20 million years, more precisely about 12 million years ago.

The center of the genus' habitat has probably always been the current Southern Caspian, which existed in various forms all the time, having survived the epochs of many transgressions and regressions and salinity fluctuations. The expansion of the genus' range obviously occurred during transgressions, the most extensive of which were Akchagylian (3.6–2.6 million years ago) and Apsheronian (1.8–1.0 million years ago) [Krijgsman *et al*., 2018]. During these events there were faunistic contacts with the Ponto-Azov and Aral basins. The occurrence of *C. pengoi* in Ponto-Azov and the Aral Sea is obviously a consequence of these events. The lineage divergence of

the species from the Black Sea and Caspian Sea occurred about 0.8 million years ago [Cristescu *et al*., 2001].

The latest research [Pereboev *et al*., 2024] sheds new light on the evolution of Onychopoda, greatly correcting the previous scenario. In this work, the representatives of the Podonidae family are considered, but since the latter are also much evolved in the Caspian Sea biota being largely its endemics, their example, at least in part, can be applied to the family Cercopagididae as well.

According to new hypothesis, the evolution of Podonidae at the family-genus level appeared much earlier than it was regarded before — in Late Mesozoic–Early Cenozoic times, even before the formation of Paratethys. The same scenario can be applied, purely preliminarily, to the Cercopagididae, linking their origin with the brackish lagoons and estuaries of Tethys, and later evolution in the Paratethis and Ponto-Caspian refugia. Subsequently, representatives of the genus *Cercopagis* continued to live safely in the Ponto-Caspian basin, while the members of the genus *Bythotrephes*, having probably undergone significant extinction, abruptly changed their habitats, entering the Eurasian freshwaters [Korovchinsky, 2020]. Only recently the existence of *Cercopagis* in the Caspian Sea and the Aral Sea underwent a sharp deterioration due to anthropogenic influence, which, in the former case, led to the massive appearance of hostile alien species, and in the latter case, to the drainage of the Aral Sea. The release of the genus *Cercopagis* into freshwaters is associated with the formation of convenient ways for its widespread distribution — the construction of a chain of river reservoirs and the possibility of long-distance migrations with the ships' ballast waters.

Conclusion

Previously, significant attention was paid to the study of the genus *Cercopagis* during the period of Sars' work (1897–1902), and then, after a long break, in a series of works by Mordukhai-Boltovskoi (1962–1974). The following publications on the topic of that time (e.g., Mordukhai-Boltovskoi, Rivier [1987]; Rivier [1998]) can only be assessed mainly as useful compilations. Subsequently, only one species, *C. pengoi,* was studied, which attracted much attention as a widely distributed alien form, readily penetrated both brackish waters and freshwaters.

A lot has changed since then. The Aral Sea has practically disappeared; the fauna of the Caspian Sea has changed very much, subject to the massive introduction of alien forms under the pressure of which the native fauna has either disappeared or greatly reduced. Thus, we are faced with the situation of a complete or very significant loss of endemic faunas of huge and unique natural Eurasian lakes which remained, on the whole, insufficiently studied.

On the other hand, faunistic collections, in particular those on zooplankton, were collected in these reservoirs rather rarely and incompletely. And the saddest thing is that they have practically not been preserved. The rich collection of Prof. Ph.D. Mordukhai-Boltovskoi from the Caspian Sea and other water bodies, stored previously in the Institute of Biology of Inland waters (Borok, Russia), has been completely lost (Dr. V.I. Lazareva, personal information), and its fragments in the form of type specimens, of course, cannot make up for the losses. Viewing of several dozens of old samples from the Caspian and Aral Seas stored at the Zoological Institute (St.-Petersburg, Russia) gave minimal results: most of the samples were empty, while in the rest only single individuals of *Cercopagis* were present. With the loss of collections, the last evidence of the former fauna of reservoirs is lost. One can only hope for the possibility of finding additional samples in museum collections.

Representatives of the genus *Cercopagis* remain poorly explored, firstly taxonomically. Most species are superficially described, only for two of them, *C. socialis* and *C. pengoi*, described in this article, the descriptions are relatively complete. Regarding the last species, the attitude of taxa *C. neonilae* and *C. gracillima* to it remains not entirely clear. The other six species need thorough redescription, but for three of them the material is absent at all; for three others the available material is quite scarce (see above). The taxonomic affiliation of most of the "*Apagis*" forms is not determined.

The ecological relationships of the eight species of the genus that inhabit the pelagic zone of the Caspian Sea remain unknown, including the features of their specializations that allow coexistence in a vast but, at the same time, homogeneous environment.

The unique biota of the Caspian Sea seems to be lost mostly forever. In the future, it seems, under favorable conditions, only some of its features can be restored. Along with this, it is also possible that, perhaps, the species richness of the genus *Cercopagis* will be restored in some form, which will make it possible to continue the study of its representatives.

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