

Comparative biology of the predatory cladoceran *Cercopagis pengoi* from Lake Ontario, Baltic Sea and Caspian Sea

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With 8 figures and 3 tables

Abstract: *Cercopagis pengoi*, an onychopod cladoceran native to the Ponto-Caspian-Aral region, was first found in the Baltic Sea in 1992 and in Lake Ontario in 1998. Morphological studies of *C. pengoi* from Lake Ontario, Baltic Sea and Caspian Sea revealed a high degree of variability in body length, structure and length of the caudal process, and shape and size of the brood pouch. The female brood pouch changed dramatically in size and shape between instar stages, resulting in distinctive appearances. Males had significantly shorter body length, caudal process length and distances between adjacent articular spines than did females. Instar III parthenogenetic females dominated populations of *C. pengoi* from all geographical localities. Body length of all instar stages, genders, and reproductive modes from Lake Ontario was smaller than that of comparable individuals from European localities. The ratio of caudal process length to body length also varied geographically, with highest values observed for individuals from Lake Ontario. Clutch size for instar III parthenogenetic females from Lake Ontario was lower than values reported from the Baltic Sea and Caspian Sea. Observed differences in morphological and reproductive characteristics of geographically remote populations may reflect *C. pengoi*'s vulnerability to zooplanktivory or responses to environmental conditions.

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Introduction

The Great Lakes have been invaded by a large number of species, including those from the Ponto-Caspian (Black, Azov and Caspian Seas) region (MILLS et al. 1993). Ponto-Caspian species that have recently become established in the Great Lakes include zebra mussels (*Dreissena polymorpha*), quagga mussels (*D. bugensis*), round gobies (*Neogobius melanostomus*), tube-nose gobies (*Proterorhinus marmoratus*), amphipods (*Echinogammarus ischnus*), and onychopod cladocerans (*Cercopagis pengoi*) (MACISAAC & GRIGOROVICH 1999). Zebra and quagga mussels, round gobies, and *Echinogammarus* amphipods are now ecologically dominant species in the lower Great Lakes, particularly in Lake Erie.

Cercopagis pengoi (OSTROUMOV, 1892) is native to the Black, Azov, Caspian and Aral sea basins (SARS 1897, 1902, MEISNER 1908, MORDUKHAI-BOLTOVSKOI 1960, 1968 a). In 1959, the species was first recorded in the Kakhovka reservoir and in other downstream localities in the Dnieper River, Ukraine (TSEEB 1963, 1964). Damming and construction of reservoirs and canals on the Dnieper, Don and Manych rivers has facilitated *C. pengoi* dispersal in eastern Europe (TSEEB 1964, ZHURAVEL 1965, MORDUKHAI-BOLTOVSKOI & GALINSKIY 1974, MORDUKHAI-BOLTOVSKOI 1979). This expansion was likely aided by shipping traffic and by intentional stocking of invertebrates (TSEEB 1964, ZHURAVEL 1967, MORDUKHAI-BOLTOVSKOI & GALINSKIY 1974). The species' current distribution in the Black and Azov sea basins includes all reservoirs on the Dnieper River, the Tsimlyansk and Veselovsk reservoirs in the Don River drainage, and numerous canals in southern Ukraine (ZHURAVEL 1965, 1967, GLAMAZDA 1971, KAFTANNIKOVA & BAZILEVICH 1972, VOLVICH 1978, GUSYNSKAYA & ZHDANOVA 1978, GUSYNSKAYA 1989, ZIMBALEVSKAYA 1989, SHEVTSOVA & PRIMAK 1990).

C. pengoi was first reported outside of the Ponto-Caspian basin in coastal waters of the eastern Baltic Sea during 1992 (OJAVEER & LUMBERG 1995). The species has since been reported from other coastal and open-water regions of the sea (reviewed by KRYLOV et al. 1999). The first report of *Cercopagis* in North America was made during summer 1998 in Lake Ontario, where the species was reported in relatively high numbers throughout the lake (MACISAAC et al. 1999). Lake Ontario was previously invaded in 1985 by a related cercopagid, *Bythotrephes*, though this species occurs rarely in the plankton (JOHANSSON et al. 1998). Both cercopagid species are believed to have been transported to the Great Lakes from Europe via ocean-going vessels (SPRULES et al. 1990, MACISAAC et al. 1999).

C. pengoi occurred at an average density of 170 ind./m³ in western Lake Ontario during August 1998 (MACISAAC et al. 1999). Ecologically, the species is a voracious predator on crustacean plankton (MORDUKHAI-BOLTOVSKOI

1968 a, RIVIER 1998). Given its diet and abundance in this lake, *C. pengoi* could potentially impact the native plankton assemblages including carnivorous onychopods. For example, *Bythotrephes* and *Cercopagis* have inverse patterns of abundance in the Neva River estuary (Baltic Sea) (V. E. PANOV, pers. observation).

Knowledge of *Cercopagis*' life history is essential to the development of predictive models of population growth and to evaluate the potential impact of this species on invaded ecosystems. Some aspects of *C. pengoi* biology and ecology have been reported for the Caspian Sea (e.g. RIVIER 1967, 1998, MORDUKHAI-BOLTOVSKOI & RIVIER 1971, 1987) and Baltic Sea (KRYLOV & PANOV 1998). For example, *C. pengoi* may reproduce both parthenogenetically and sexually, respectively producing embryos or resting eggs which develop in a dorsal brood pouch (see RIVIER 1969, 1974). However, *Cercopagis* morphology and phenotypic variability have not been studied as extensively. Species boundaries in the genus *Cercopagis* are not clearly understood, as some diagnostic morphological features such as the structure and length of the caudal process and brood pouch shape exhibit variability (RIVIER 1998). As a result, there is no clear consensus as to the geographical distribution of representatives of the genus. The valid records beyond the Ponto-Caspian-Aral region have been provided only for two taxa of *Cercopagis* – *C. pengoi* (in the Baltic Sea and Lake Ontario) and *C. ossiani* MORDUKHAI-BOLTOVSKOI, 1968 (in the Baltic Sea) (OJAVEER & LUMBERG 1995, MACISAAC et al. 1999, SIMM & OJAVEER 1999). Six other species and intraspecific forms of *Cercopagis* which are endemic to the Ponto-Azov-Caspian-Aral region, namely *C. socialis* (GRIMM, 1877), *C. cylindrata* SARS, 1897, *C. longicaudata* SARS, 1902, *C. neonilae* SARS, 1902, *C. pengoi gracillima* SARS, 1902, and *C. pengoi aralensis* MORDUKHAI-BOLTOVSKOI, 1974, have also been reported from localities beyond their native ranges (TSEEB et al. 1971, IVANOV & MAKARTSEVA 1982, N. V. ALADIN, pers. observation). However, to date, no evidence has been presented to confirm these distributions.

In this study, we describe morphology, size patterns, fecundity, and demography of *Cercopagis pengoi* from Lake Ontario, and compare these characteristics with those of populations from the Baltic Sea and Caspian Sea. Furthermore, we examine morphological characters used in the taxonomy of *C. pengoi* across instar stages, genders, reproductive modes and geographical localities to clarify the extent of ontogenetic (i.e. age) and geographical variability in this species. We also assess weight-length relationships for *C. pengoi* from Lake Ontario. As well, we review the systematic history of the species and its intraspecific forms, and discuss morphological differences among the forms.

Systematic history

Cercopagis pengoi (OSTROUMOV, 1892) belongs to the family Cercopagidae (Crustacea: Cladocera: Onychopoda), which comprises two genera, *Bythotrephes* and *Cercopagis*. Members of this family are characterized by the following combination of morphological features, many of which reflect their predatory lifestyle (MORDUKHAI-BOLTOVSKOI 1968 a, 1968 b): 1) the cephalon, or head, is composed primarily of a compound eye; 2) antennae I, or antennules, are reduced to small appendages positioned beneath the eye; 3) antennae II constitute well developed, biramous appendages used for swimming (Fig. 1); 4) the mandibles possess a sharp cutting edge and terminal denticles and are adapted for biting; 5) the trunk bears four pairs of grasping thoracopods, lacking exopods; 6) thoracopods I are tremendously longer than thoracopods II–IV and differ in shape; and 7) the well-developed abdomen bears an elongate caudal process, extending at least one body length (MORDUKHAI-BOLTOVSKOI & RIVIER 1987).

The number of setae on rami of antennae II is used as a distinguishing feature in separating the genus *Cercopagis* from *Bythotrephes* (SARS 1897, MORDUKHAI-BOLTOVSKOI & RIVIER 1987). There are seven natatory setae on each ramus of antennae II in *Cercopagis*, whereas there are eight setae on the outer (four-segmented) ramus and seven setae on the inner (three-segmented) ramus in *Bythotrephes* (SARS 1897) (Fig. 2). Members of the genus *Cercopagis* lack a gnathobasic process on thoracopod I (SARS 1897). The shape and structure of the penis differ between *Cercopagis* and *Bythotrephes* (MORDUKHAI-BOLTOVSKOI & RIVIER 1987). In *Bythotrephes*, the penes are shorter and covered with minute setae, whereas, in *Cercopagis*, the penes are rather long and smooth (MORDUKHAI-BOLTOVSKOI & RIVIER 1987). In addition, the two genera differ in the shape of the labrum, the condition of the anterior mandibular process, the length of spines on the external face of the thoracopods I–III, and proportion between the length of abdomen and the combined length of the thorax and cephalon (MARTIN & CASH-CLARK 1995).

Systematics in the genus *Cercopagis* has been revised since its original description in 1897 (MORDUKHAI-BOLTOVSKOI 1968 b, MORDUKHAI-BOLTOVSKOI & RIVIER 1987). Two former genera erected by SARS (1897), *Cercopagis* and *Apagis*, were later recognized by MORDUKHAI-BOLTOVSKOI & RIVIER (1987) as subgenera treated within the genus *Cercopagis*. The two taxa differ in the length and structure of the caudal process and the presence (in *Cercopagis*) of a loop (SARS 1987, MORDUKHAI-BOLTOVSKOI 1968 a, MORDUKHAI-BOLTOVSKOI & RIVIER 1987). The systematics of *Cercopagis* and *Apagis* and relationships between these taxa are poorly understood. It has been suggested that *Cercopagis* (*Apagis*) *ossiani* may represent the first generation of *Cercopagis* (*Cercopagis*) *pengoi* that emerge from resting eggs (SIMM & OJAVEER 1999, I. RIVIER, unpubl. data).

Several species of *Cercopagis* established by SARS (1897, 1902) were thought to be intraspecific forms of the single polymorphic species *C. pengoi* (MORDUKHAI-BOLTOVSKOI 1960, 1965) and were, therefore, combined into the '*Cercopagis pengoi* group' (MORDUKHAI-BOLTOVSKOI 1968 a). This group comprises four taxa including the typical form (i.e. *C. pengoi* sensu stricto), *C. neonilae*, *C. pengoi gracillima*, and *C. pengoi aralensis*. Members of this group can be distinguished from all other species

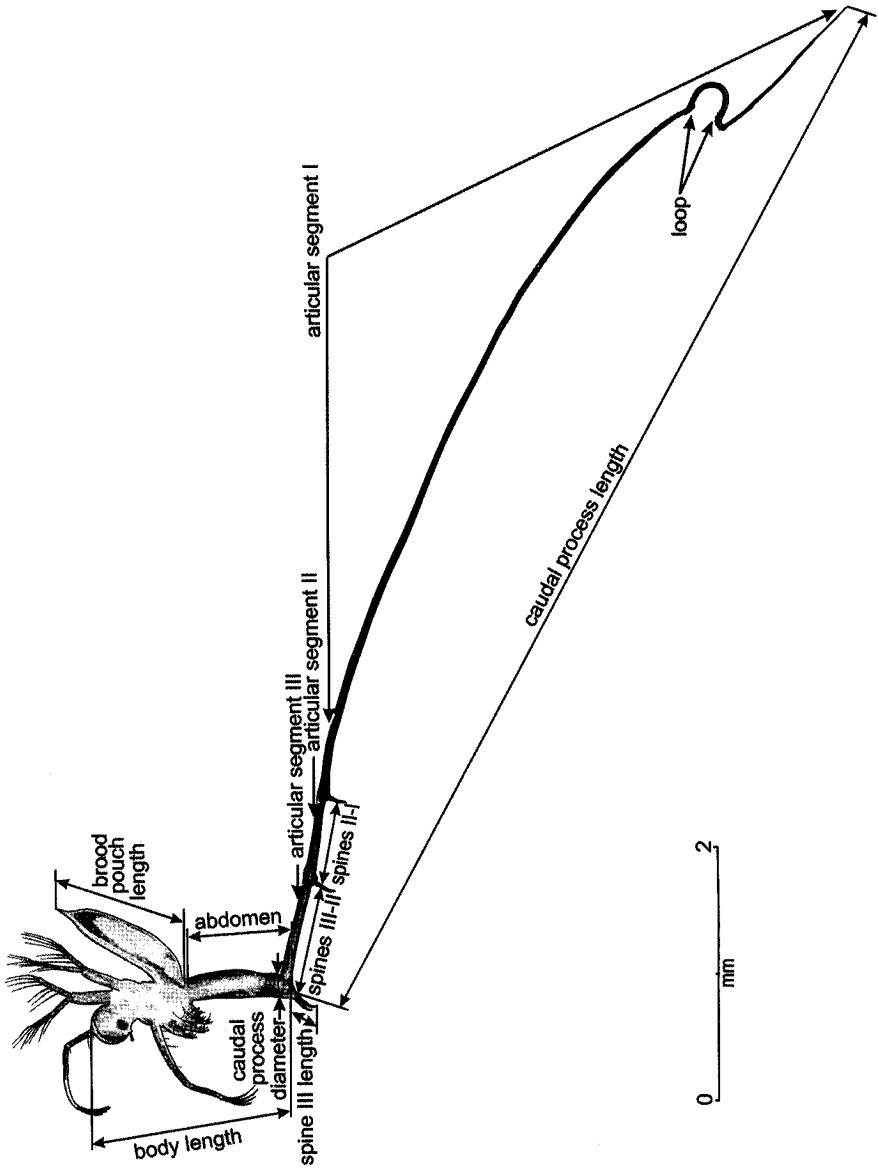


Fig. 1. Lateral view of instar III parthenogenetic female of *Cercopagis pengoi* from Lake Ontario showing body dimensions. Body length is 1.62 mm and caudal process length is 9.59 mm.

of the subgenus *Cercopagis* based on the following set of characters: 1) the presence of a pointed apex on the brood pouch; 2) the proximal articular spines of the caudal process are well-developed and extend at least $\frac{3}{4}$ the distance between the base of these spines on the caudal process and attachment point of the caudal process on the abdo-

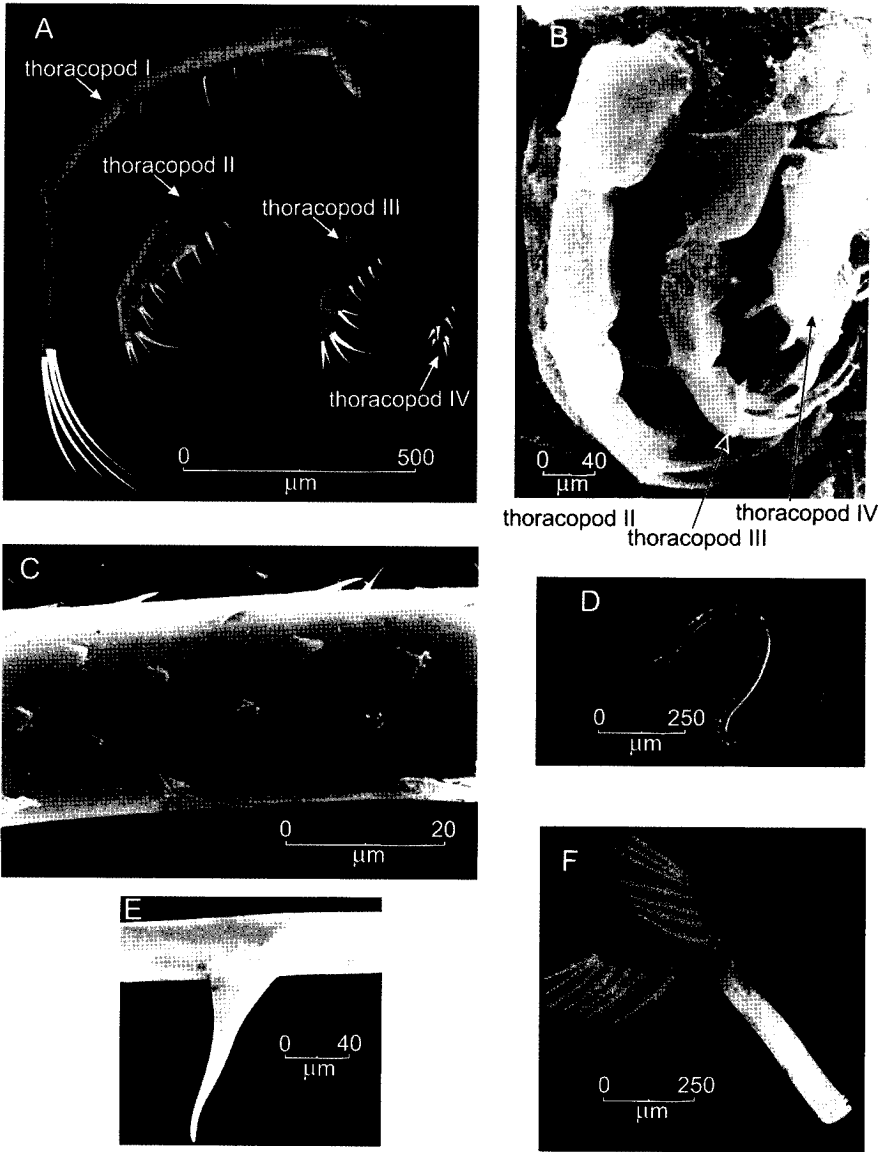


Fig. 2. Details of the structure of *Cercopagis pengoi* parthenogenetic female from Lake Ontario: lateral view of the thoracopods under a dissection microscope (A) and S.E.M. (B) microscopy; cuticle covering of caudal process at high magnification, showing minute spines, S.E.M. (C); loop of caudal process (D); articular spine II, S.E.M. (E); antenna II, showing seven plumose natatory setae on each ramus.

men; 3) the distances between adjacent pairs of articular spines are relatively large and more or less comparable to the abdomen length in females (MORDUKHAI-BOLTOVSKOI 1968 a). It is not entirely clear whether members of the *Cercopagis pengoi* group represent a number of morphologically similar species or a single, variable species. In addition to morphological differences, members of this group have different geographical distributions and slightly different salinity preferences (RIVIER 1967, MORDUKHAI-BOLTOVSKOI & RIVIER 1987).

Cercopagis pengoi was first found in the Azov Sea on 27 July 1876 by Russian scientist K. K. PENGO (PENGO 1879). Owing to similarities in gross morphology, animals were originally identified as marine representatives of *Bythotrephes*, but no specific name was given. The species *B. pengoi* was formally established by OSTROUMOV in 1892 (OSTROUMOV 1892). Presumably unaware of OSTROUMOV's report, SARS described this form as a new species *Cercopagis tenera* from Caspian Sea material (SARS 1897), and the two species were later recognized to be identical (ZERNOV 1903, MEISNER 1908). Subsequent workers adopted this arrangement (MORDUKHAI-BOLTOVSKOI 1960, 1968 a, MORDUKHAI-BOLTOVSKOI & RIVIER 1987). *C. pengoi* ranges widely over eastern Europe as native or introduced populations. It occurs over a broad spectrum of salinity, from 0.1 to 14.0‰ (VALKANOV 1957, MORDUKHAI-BOLTOVSKOI 1969, MORDUKHAI-BOLTOVSKOI & RIVIER 1971).

Cercopagis gracillima was originally described by SARS (1902) based on Caspian Sea specimens. It is identified by an extremely extended pointed apex at the tip of the brood pouch, the length of which is greater than the maximum width of the brood pouch, an elongate abdomen that exceeds in length the combined length of the thorax and cephalon, and lengthened, abruptly curved articular spines that far exceed in length the distance between the base of the proximal pair of articular spines and the point of attachment of the caudal process on the abdomen (MORDUKHAI-BOLTOVSKOI 1968 a). Because various transitional phenotypes were observed between the typical forms *C. pengoi* and *C. gracillima* in the northern Caspian Sea, the latter is today considered an intraspecific form of *C. pengoi* (MORDUKHAI-BOLTOVSKOI & RIVIER 1987; RIVIER 1998). Relative to *C. pengoi*, *C. gracillima* occupies a restricted distribution range in the northern Caspian Sea and tolerates restrained salinity values between 1–12‰ (RIVIER 1967).

In erecting *C. neonilae* from Azov Sea specimens, SARS (1902) described only minor differences between the new species and *C. tenera* (= *pengoi*), which caused some doubts with respect to the validity of the former taxon (MEISNER 1908, MORDUKHAI-BOLTOVSKOI 1960, 1965). MEISNER (1908) placed *C. neonilae* in synonymy with *C. pengoi*. *C. neonilae* is distinguished from *C. pengoi* in that it has a shorter pointed apex on the brood pouch, an abdomen which is shorter than the combined length of the thorax and cephalon, and articular spines which are shorter than the distance between the base of the proximal pair of articular spines and the point of attachment of the caudal process on the abdomen (SARS 1902, MORDUKHAI-BOLTOVSKOI 1968 a, MORDUKHAI-BOLTOVSKOI & RIVIER 1987). It remains to be determined whether these features are sufficient to warrant designation of *C. neonilae* as a separate species, but it has been assigned to the *Cercopagis pengoi* group (MORDUKHAI-BOLTOVSKOI 1968 a, MORDUKHAI-BOLTOVSKOI & RIVIER 1987). Its distribution encompassing the Caspian Sea, Azov Sea and Black Sea estuaries overlaps with that of *C. pengoi* (MORDUKHAI-

BOLTOVSKOI & RIVIER 1987). In the Caspian Sea, *C. neonilae* appeared to exhibit a preference to mild salinity of 1–12.5‰ (RIVIER 1967).

The subspecies *C. pengoi aralensis* was first described by MORDUKHAI-BOLTOVSKOI (1974) based on specimens collected in the Aral Sea. This form is distinguished from typical *C. pengoi* by its possession of a considerably smaller caudal process (less than 3.5 times the body length) and a variously reduced loop on the caudal process (MORDUKHAI-BOLTOVSKOI & RIVIER 1987). Variation in shape of the loop in this form results in a variety of appearances, from bent, bearing fields of minute spines, to a straight, kinkless process. Owing to a drastic increase in salinity (to levels over 18‰) since the 1980s in the Aral Sea, *Cercopagis* spp. were likely extirpated from the sea proper and now occur only in adjacent Lake Sudochie in the Amudarya River estuarine region (ALADIN 1996, N. V. ALADIN, pers. observation).

Materials and methods

Cercopagis was collected on 27 August 1998 at eight sites (43° N and 79° W) in western Lake Ontario using bottom to surface hauls (≤ 27 m) of a 0.5-m-diameter, 253- μ m mesh plankton net. Additional *C. pengoi* were collected from Lake Ontario by trawling offshore in ≤ 20 m with weighted Trilene fishing line (5.4 kg test). Animals snagged on fishing lines by their caudal process were recovered as a fibrous mass. *C. pengoi* was collected during July 1997 from the Neva River estuary (60° 18' N and 28° 43' E), Baltic Sea, Russia, by 10 m vertical hauls of a 0.2-m-diameter, 150- μ m mesh plankton net. An additional collection was made on the northern Caspian Sea about 75 km from the Volga River delta (45° 03' N and 48° 17' E), near Zhemchuzhnyi Island, during 22–24 August 1998. The sample was collected using a 0.39-m-diameter, 74- μ m mesh plankton net, and is a composite of one horizontal surface tow and one 10 to 3 m vertical tow. All samples were preserved in 70% ethanol or in 4% sugar-formalin. In the laboratory, *Cercopagis* was separated from other material and transferred to 70% ethanol within a few days after sampling.

All surveys were conducted during relatively calm periods. Water column temperature in all surveyed basins ranged within the limits of 17–24 °C. In Lake Ontario, water temperature at the collections sites varied from 23.9 °C at surface to 17.4 °C at bottom. Less marked temperature variation was recorded during sampling in the Baltic Sea, from 18 to 21 °C. Salinity differed greatly among surveyed basins, ranging between 0.14–0.20‰ in Lake Ontario, 2.0–3.4‰ in the Baltic Sea and 6–7‰ in the Caspian Sea.

Only the typical *C. pengoi* 'form' was detected in all localities. We employed both light (12 \times to 50 \times) and scanning electron microscopy (S.E.M.; 60 \times to 2000 \times) to examine morphological characters of *C. pengoi*. However, because some structures showed evidence of severe distortion after coating with gold, we limit use of S.E.M. images in this study.

We used only intact animals with a complete caudal process to evaluate the relationship between body length and caudal process length. Damaged animals were utilized for body length measurements only if both the entire body and proximal portion

of the caudal process were present. In total, we examined 4550 *Cercopagis* specimens from Lake Ontario, >73 animals from the Baltic Sea and >43 animals from Caspian Sea.

Gender was determined by the presence (in males) or absence (in females) of paired penes on the ventral surface of the thorax, behind the base of the last thoracic limbs. Mature sexual females were discriminated from parthenogenetic females by their possession of resting egg(s) in the brood pouch or ovary (see Results). The term 'non-ovigerous females' was used to define females without eggs or embryos in the brood pouch. The caudal process is typically comprised of one articular segment in instar I animals, while two and three articles are present in instars II and III, respectively. According to studies of postembryonic development in *Bythotrephes* (ZOZULYA 1977, YURISTA 1992), the caudal process in cercopagids likely grows by addition of a new articular segment from a growth zone, thereby pushing the retentive, older portion of caudal process in the posterior direction. Instars of *C. pengoi* were distinguished by the number of articular segments and paired spines positioned on the caudal appendage. We recorded the presence of parthenogenetic and sexual females, males, instar stages, and stages of brood development.

Images of *Cercopagis* were outputted from a Leica Wild M8 dissecting microscope via a Hitachi VK-C370 videocamera and Flashpoint 128 framegrabber, to Optimas 6.2 image analysis software on a personal computer. We measured: 1) body length as the distance from the tip of the eye to the anus, located between the proximal pair of articular spines on the caudal process (after BURKHARDT 1994); 2) total length of the caudal process as the distance from the anus to the distal end of the caudal process (after BURKHARDT 1994); 3) diameter of the caudal process at the point of its attachment on the abdomen; 4) length of the articular spine III; 5) distances between adjacent articular spine pairs; 6) brood pouch size as the distance from the tip of the brood pouch to the inferior point of insertion of the brood pouch on the trunk; and 7) clutch size. All comparisons among Lake Ontario, Baltic Sea, and Caspian Sea populations were made using alcohol-preserved specimens.

In order to assess weight-length relationships, 334 *Cercopagis* from Lake Ontario, preserved in sugar-formalin, were sorted according to gender, instar stage and mode of reproduction (parthenogenetic vs. sexual), and categorized into the following body length groups: 0.81–1.00, 1.01–1.20, 1.21–1.40, 1.41–1.60, 1.61–1.80, and 1.80–2.00 mm. Each group included between 5 and 30 individuals, and were dried for 24 h at 60 °C and held over silica gel prior to weighing. Dry mass was measured with a Cahn 4700 electrobalance to a precision of 1 µg. The relationship between body mass and body length was assessed for different parthenogenetic female instars using ANCOVA, with body length as a covariate and instar stage as a categorical variable. The initial model revealed no interaction between mass and length, thus the models presented here lack an interaction term.

Differences in size dimensions and structural indexes among instars and populations of *C. pengoi* were examined using one-way ANOVA, followed by Bonferroni's multiple comparisons test when ANOVA was significant. Two-way ANOVA (instar, basin) test was utilized only for the analysis of differences in body length of instar II and III parthenogenetic females from Lake Ontario, Caspian Sea and Baltic Sea. Differences between genders and among reproductive modes (parthenogenetic vs. sexual)

were examined using t-tests. The relationships between caudal process length and body length and between clutch size and body length in all instars of parthenogenetic females from Lake Ontario were examined using linear regression analysis. This analysis was repeated for the population from the Caspian Sea. All data were transformed as $\log_{10}(x+1)$ prior to statistical analysis to stabilize variance. All tests were conducted using Systat 8.0.

Results

Morphological characteristics

Morphometric characteristics of *C. pengoi* varied among localities, instar stages and genders (Table 1). We limit descriptions of the ratio of caudal process length to body size, and the length and structure of the caudal process, largely to instar III parthenogenetic females, as these individuals were numerically dominant in all samples. Body length of instar III females was significantly different among all surveyed basins (ANOVA, $P < 0.05$). The smallest mean body size of instar III parthenogenetic females was recorded in Lake Ontario (1.45 mm), followed by that in Caspian Sea (1.73 mm) and Baltic Sea (1.99 mm). A similar pattern of geographical variation in body size was established for instar II parthenogenetic females (ANOVA, $P < 0.05$).

Caudal process length and body length were positively correlated in instar III females from Lake Ontario ($R^2 = 0.19$; $P < 0.001$; $n = 338$) (Fig. 3). This relationship was weaker for comparable individuals from the Caspian Sea ($R^2 = 0.23$; $P = 0.096$; $n = 13$), possibly owing to small sample size. A significant relationship between caudal process length and body length was also established

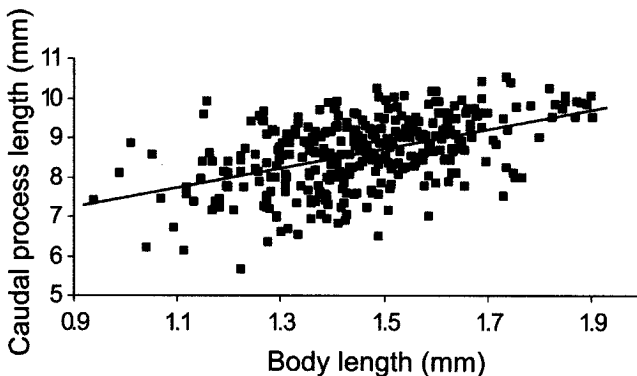


Fig. 3. Relationship between caudal process length and body length in instar III parthenogenetic females of *Cercopagis pengoi* from Lake Ontario in August, 1998. Line represents least-squares linear regression ($y = 2.5x + 5.0$; $R^2 = 0.19$) relating the caudal process length (y in mm) to body length (x in mm).

Table 1. Morphometric characteristics of *Cercopagis pengoi* in Lake Ontario, Baltic Sea and Caspian Sea. All dimensions are in mm. Numbers represent mean and standard deviation (in parentheses) and sample size (N). Instar I–III parthenogenetic females are designated as pI–pIII, instar I–III sexual females as sI–sIII, instar I–III males as mI–mIII. Caudal process diameter is identified at the point of its attachment on the abdomen. One or no observation of specific attributes is indicated with * (caudal process broken; see text for more details). NA specifies not applicable characteristic. Spines III–II distance refers the distance between articular spines III and II, spines II–I distance specifies the distance between articular spines II and I, and spines I–tip distance defines the distance between articular spines I and distal end of the caudal process.

Water Body	Instar Sex	N	Body Length	Brood pouch Size	Caudal process Diameter	Caudal process Length	Spines III–II Distance	Spines II–I Distance	Spines I–tip Distance	Spine III Length
Lake Ontario	pIII	395	1.45 (0.19)	0.84 (0.19)	0.17 (0.06)	8.57 (0.94)	0.74 (0.18)	0.65 (0.12)	7.16 (0.98)	0.22 (0.04)
	pII	171	1.29 (0.18)	0.55 (0.18)	0.15 (0.02)	7.66 (0.82)	NA	0.65 (0.18)	7.03 (0.86)	NA
	pI	42	1.02 (0.13)	0.25 (0.13)	0.14 (0.02)	6.26 (0.92)	NA	NA	6.26 (0.96)	NA
	sIII	42	1.58 (0.13)	0.83 (0.16)	0.18 (0.02)	8.81 (0.82)	0.79 (0.16)	0.71 (0.09)	7.32 (0.82)	0.25 (0.04)
	sII	12	1.34 (0.18)	0.68 (0.19)	0.15 (0.04)	7.74 (1.15)	NA	0.65 (0.20)	7.07 (1.23)	NA
	sI	45	1.00 (0.10)	0.19 (0.03)	0.13 (0.02)	6.27 (0.88)	NA	NA	6.27 (0.88)	NA
	mIII	30	1.37 (0.17)	NA	0.16 (0.03)	5.40 (0.60)	0.29 (0.04)	0.33 (0.06)	4.75 (0.70)	0.21 (0.02)
	mII	18	1.15 (0.18)	NA	0.15 (0.02)	4.82 (0.73)	NA	0.32 (0.05)	4.50 (0.58)	NA
	mI	9	0.98 (0.11)	NA	0.11 (0.02)	4.45 (0.69)	NA	NA	4.45 (0.69)	NA
	Baltic Sea	pIII	22	1.99 (0.19)	1.54 (0.42)	0.19 (0.04)	9.65	0.96 (0.14)	0.82 (0.15)	7.90 (*)
pII		7	1.53 (0.21)	1.22 (0.38)	0.18 (0.03)	7.83	NA	0.93 (0.09)	6.90 (*)	NA
sIII		4	1.90 (0.20)	1.30 (0.30)	0.22 (0.03)	*	0.85 (0.91)	0.80 (0.14)	*	0.36 (0.03)
mIII		2	1.60 (0.20)	NA	0.18 (0.02)	*	0.30 (0.06)	0.35 (0.06)	*	0.22 (0.02)
mI		4	1.10 (0.10)	NA	0.12 (0.02)	4.7	NA	NA	4.7 (*)	NA
pIII		31	1.73 (0.27)	1.70 (0.19)	*	7.48 (0.72)	0.84 (0.11)	0.80 (0.12)	6.13 (0.69)	0.26 (0.03)
Caspian Sea	pII	6	1.51 (0.19)	1.09 (0.55)	*	7.19 (0.82)	NA	0.82 (0.07)	6.43 (0.09)	NA
	sII	1	1.10	0.80	*	7.60	NA	0.70 (*)	6.92 (*)	NA

for in instar II ($R^2 = 0.39$; $P < 0.001$; $n = 150$) and instar I ($R^2 = 0.20$; $P = 0.005$; $n = 36$) parthenogenetic females from Lake Ontario.

The Lake Ontario population also differed from other populations in terms of caudal process length (see Table 1). Length of the caudal process in instar III females from Lake Ontario was significantly greater than that in Caspian Sea (t -test, $P < 0.001$). Comparison with animals from the Baltic Sea could not be made because only one instar III female had an intact caudal process. The ratio of caudal process length to body length was distinguishable for each population (Table 2). The highest value of this index for instar III females was reported in Lake Ontario (5.9), followed by the Baltic Sea (4.9) and Caspian Sea (4.3). In the Caspian Sea, *C. pengoi* populations from northern and central basins were in turn different with respect to relative length of caudal process (I. K. RIVIER, unpubl. data). For example, the ratio of caudal process length to body length for instar III parthenogenetic females from the central basin of Caspian Sea averaged 6.5 ($n = 14$) (I. K. RIVIER, unpubl. data) and exceeded the values (4.3) that we reported from the northern basin.

Spacing and relative development of articular spines on the caudal process are additional characters used in *Cercopagis* taxonomy (MORDUKHAI-BOLTOVSKOI & RIVIER 1987). The ratio of the distance among articular spines II and III to body length in females averaged 0.50 and did not differ significantly between surveyed basins (ANOVA, $P = 0.16$). Length of articular spine III (available in instar III animals) was variable both within (up to 18 %) and among (64 %; ANOVA, $P < 0.001$) basins. The ratio of size of articular spine III to diameter of the caudal process typically exceeded 1.0 in males and females (Table 2).

Table 2. Indexes of adult *Cercopagis pengoi* in Lake Ontario, Baltic Sea and Caspian Sea. Abbreviations as in Table 1. Indexes are determined based on average magnitudes. Caudal process diameter is identified as the point of its attachment on the abdomen. Caudal-process ratio denotes the relative lengths of articular segments III, II, and I of the caudal process (see Fig. 1).

Water Body	Instar Stage	N	Ratio of caudal process length to body length	Ratio of distance between Spines III–II to body length	Ratio of Spines III size to caudal process diameter	Caudal-process ratio III:II:I
Lake Ontario	pIII	395	5.9	0.51	1.3	1.1:1.0:11.0
	sIII	42	5.6	0.50	1.4	1.1:1.0:10.3
	mIII	30	3.9	0.22	1.3	1.0:1.1:16.4
Baltic Sea	pIII	22	4.9	0.48	1.9	1.2:1.0:9.6
	sIII	4	*	0.45	1.6	*
	mIII	2	*	0.19	1.2	*
Caspian Sea	pIII	31	4.3	0.48	*	1.1:1.0:7.7

Sexual females of *Cercopagis* produce only resting eggs. Resting eggs developing in the ovary or brood pouch are visible with light microscopy as a dark-contrast mass shielded by yolk granules (Fig. 4). Instar III sexual females from Lake Ontario possessed significantly larger body size and caudal process length than did parthenogenetic females (t-test, $P < 0.001$) (Table 1). In instar III sexual females, the ratio of the distance between articular spines III and II to body length was approximately 0.50 (Table 2). Mean body length of instar III sexual females in Lake Ontario (1.58 mm) was significantly smaller than that of individuals from the Baltic Sea (1.90 mm; t-test, $P = 0.019$).

Males were rare in the Baltic Sea collection and absent in the Caspian Sea sample. Therefore our treatment of males is limited primarily to individuals from Lake Ontario. Thoracopod I of males is of a grasping type and bears a toothed hook (MORDUKHAI-BOLTOVSKOI 1968 a). Males also possess paired penes behind thoracopods IV. On the dorsal side of the trunk, males bear a tubercle outgrowth, resembling the brood pouch of newborn females (Fig. 5). The loop of the caudal process in males is bent much less than that of females (see Fig. 4C, 5C).

Based on Lake Ontario data, the mean body length of males was significantly smaller than that of parthenogenetic and sexual females for instar II and III animals (ANOVA, $P < 0.005$), but not for instar I individuals (ANOVA, $P = 0.58$). All male instars had significantly shorter caudal process lengths and distances between adjacent articular spines than did comparable females (t-tests, $P < 0.001$). Males also had a lower ratio of caudal process length to body length and ratio of distance between articular spines III and II to body length (Table 2). Males further differed from females in terms of the relative length of articular segments III and II of the caudal process. The mean distance between articular spines I and II (0.33 mm) was significantly greater (t-test, $P = 0.048$) than the distance between articular spines II and III (0.30 mm). These distances respectively correspond with the sizes of articular segments II and III of the caudal process (Fig. 5). The mean distance between articular spines II and III in parthenogenetic and sexual females was greater than that between articular spines I and II (t-test, $P = 0.049$). Trends in size variation of males from Lake Ontario and the Baltic Sea were similar to patterns established for females.

Significant instar-related differences existed with respect to body length and caudal process length for all reproductive groups from Lake Ontario (Table 2). Increases in body length between moults exceeded increases in caudal process length in parthenogenetic females, sexual females and males, resulting in a slightly reduced spiniferous appearance with increasing instar stage. Mean body length increased by 42.2 % and the caudal process length increased by 36.9 % from instar I to III in parthenogenetic females. In sexual females, comparable increases between instars I to III were 58.0 % in body length and

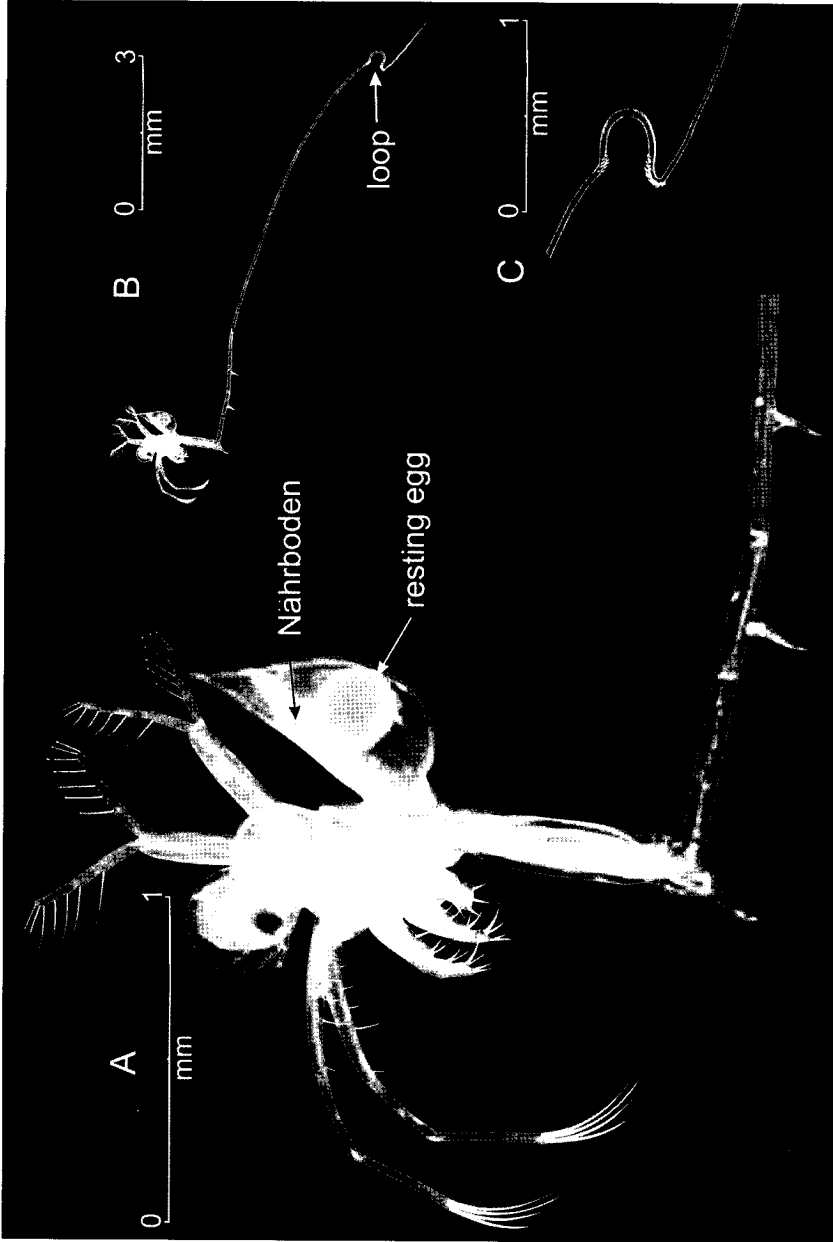


Fig. 4. Instar III sexual female of *Cercopagis pengoi* from Lake Ontario. (A) Lateral view of anterior region showing brood pouch containing Nährboden and resting egg. (B) Same animal with complete caudal process. Body length is 1.70 mm and caudal process length is 9.82 mm. (C) Loop of caudal process illustrating extensive curvature.

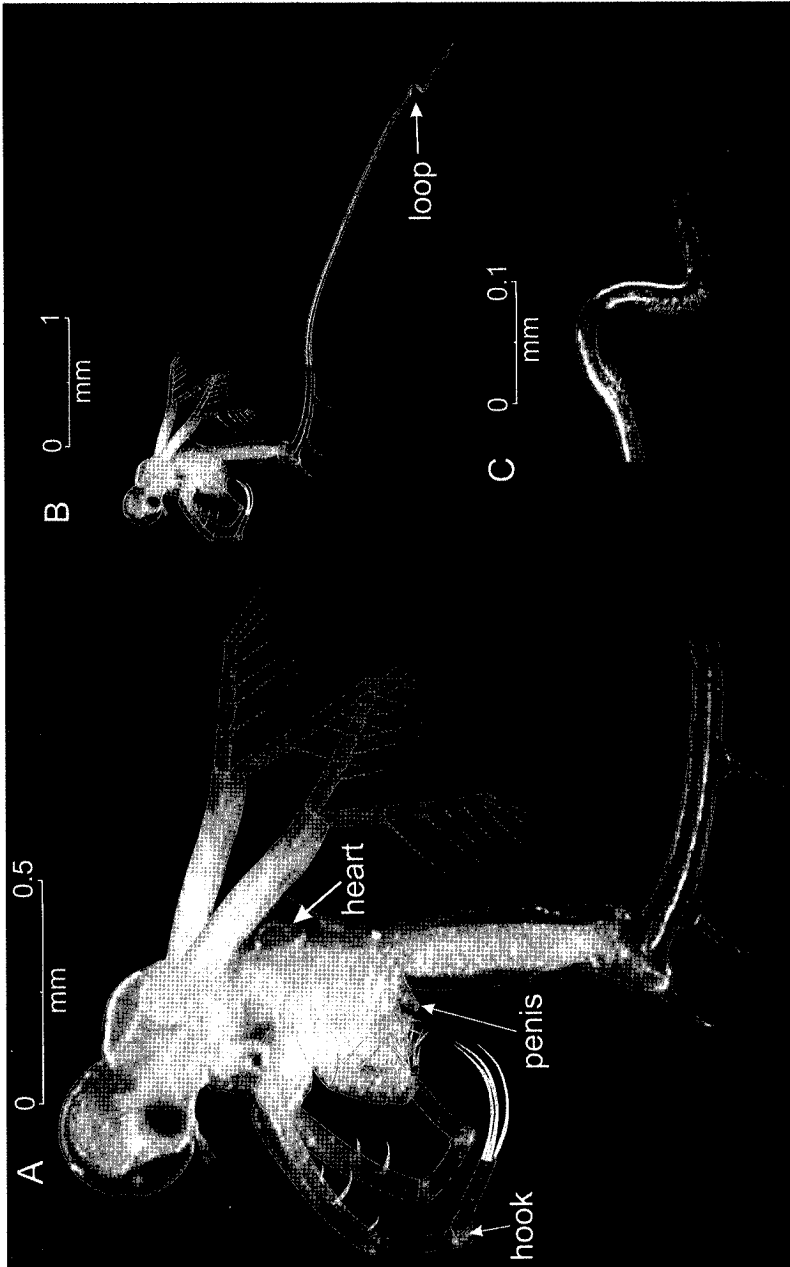


Fig. 5. Instar III male of *Cercopagis pengoi* from Lake Ontario. (A) Lateral view of anterior region showing hook, penis and dorsal out-growth containing heart. (B) Same animal with complete caudal process. Body length is 1.43 mm and caudal process length is 5.49 mm. (C) Loop of caudal process illustrating non-extensive curvature.

40.5 % in caudal process length. There was much less growth in males, as body length and caudal process length increased by only 39.8 % and 21.4 %, respectively, between these instars.

Shape and size of the brood pouch varied dramatically between instars (Fig. 6). Instar I parthenogenetic females typically possessed a small brood pouch with a rounded to somewhat angular apex (Fig. 6 A–B). Between instars I and II, the pouch lengthens dramatically to accommodate the growing embryos, and becomes pointed at the apex. In parthenogenetic females from Lake Ontario, brood pouch length increased by 120 % between instars I and II. However, a small number (5 of 171 specimens) of instar II parthenogenetic females examined from Lake Ontario had a divergent brood pouch shape. In these individuals, the brood pouch was rounded and lacked a pointed apex (see Fig. 6C) similar to that described for *C. socialis* (SARS 1897). The brood pouch of instar III parthenogenetic females was 236 % larger than that of instar I individuals and was always distinctly pointed at the apex (Fig. 6 E–F). Inter-instar changes in the shape and size of the brood pouch of sexual females were similar to those described for parthenogenetic females (Table 1). Brood pouch size of sexual females from Lake Ontario increased by an average of 337 % between instars I and III. All instar II and III sexual females from Lake Ontario always had a pointed apex on the brood pouch.

Population structure

Instar III parthenogenetic females dominated populations of *C. pengoi* from all geographical localities (Fig. 7). In the Baltic Sea, there was an apparent modal peak of parthenogenetic females with a body length of 1.8–2.0 mm, comprising 25.0 % of the population in July 1997. Instar III parthenogenetic females of 1.6–1.8 mm constituted the predominant size group in Caspian Sea, accounting for 26.2 % of the population in August 1998. In Lake Ontario, there was a modal peak of instar III parthenogenetic females with body length of 1.4–1.6 mm, accounting for 20.8 % of the population in August 1998. The Lake Ontario population differed from others by the absence of individuals with body length >2.0 mm and by a considerably higher proportion of animals <1.00 mm.

Males made up ca. 9.5 and 3.8 % of the total population of *C. pengoi* in the Baltic Sea and Lake Ontario, respectively. No males were collected from the Caspian Sea.

Reproductive characteristics

Fecund individuals of parthenogenetic females were observed at all instars, whereas sexual females were not in a reproductive condition at instar I. Fecun-

