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Trends in Cladocera and Copepoda taxonomy[1]

Тенденции в систематике Cladocera и Copepoda[1]

N.M. Korovchinsky
Н.М. Коровчинский

A. N. Severtsov Institute of Ecology and Evolution of Russian Academy of Sciences, Leninsky prospect 33, Moscow 117071 Russia.
e-mail: nmkor@orc.ru
Институт проблем экологии и эволюции им. А. Н. Северцова РАН, Ленинский проспект 33, Москва 117071 Россия.

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КЛЮЧЕВЫЕ СЛОВА: Cladocera, Copepoda, континентальные воды, систематика.

ABSTRACT: During recent decades investigation on the morphology and taxonomy of cladocerans (Ctenopoda and Anomopoda) and copepods (Calanoida and Cyclopoida) of continental waters has much intensified. This is evident from the description of a large number of new taxa, primarily at the species level, along with the publication of many summary monographs. The taxonomy of Calanoida is comparatively more developed but needs further elaboration. Progress in the taxonomy of Ctenopoda and Anomopoda mostly results from the revisions of many "species" which have appeared to be actually species-groups; this is also evident for Cyclopoida. For all groups under consideration reevaluation of the species which may have only slight morphological differences is characteristic. The new taxonomic approaches are mostly based on detailed morphological studies supplemented by new genetic, cytogenetic, or ecological methods.

РЕЗЮМЕ: В последние десятилетия исследования по морфологии и систематике кладоцер (Ctenopoda и Anomopoda) и копепод (Calanoida и Cyclopoida) континентальных вод значительно интенсифицировались, судя по описанию большого числа новых таксонов, прежде всего видового уровня, и публикации многих монографий. Систематика Calanoida относительно лучше разработана, но требует дальнейшего совершенствования. Прогресс в систематике Ctenopoda и Anomopoda в основном базируется на ревизии многих "видов", которые в действительности оказались группами таковых. Это также характерно для Cyclopoida. Для всех исследуемых групп характерна переоценка видов, которые могут иметь лишь малые морфологические отличия. Новые подходы в систематике в основном базируются на детальных морфологических исследованиях, дополненных новыми методами — генетическими, цитогенетическими и экологическими.

[1] This paper is dedicated to 110th anniversary of the first Russian hydrobiological station "Lake Glubokoe" (Moscow Area".
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Introduction

Cladocera and Copepoda are some of the most important invertebrates in continental waters. The latter group is morphologically, taxonomically, and ecologically diverse [Fryer, 1998] but represents a monophyletic assemblage at the subclass/class level. The status of the 'Cladocera' is, however, controversial. Based on traditional detailed morphological analysis 'Cladocera' is regarded as an artificial group representing four orders of Branchiopoda (Ctenopoda, Anomopoda, Onychopoda, and Haplopoda) or even incorporated in different subclasses of Crustacea [Starobogatov, 1986; Fryer, 1987]. In contrast, modern cladistic analysis [Martin, Cash-Clark, 1995; Olesen, 1998; Negrea et al., 1999] and genetic studies [e.g. Hebert, Taylor, 1997] support monophyly of the group.

The representatives of cladocerans, Ctenopoda (47 spp.), Anomopoda (ca. 560 spp.), Onychopoda (34 spp.) and Haplopoda (1 sp.), mostly or exclusively inhabit continental waters [Korovchinsky, 1996 and unpubl. data]. While ca. 95 % of cladocerans live in continental waters, Copepoda are much more diverse in the seas and oceans. Only three of their orders (suborders) (Calanoida, Cyclopoida, and Harpacticoida) with free-living representatives inhabit continental water bodies. Calanoida and Cyclopoida number here about 1200 species [Stepanova, Alexeev, 1995] which is approximately 10% of 11500 known Copepoda species [Humes, 1994]. In spite of their superiority in genera and species richness, the Calanoida and Cyclopoida of continental waters (mostly representatives of nine families and ca. 120 genera) are roughly comparable with cladocerans (11 families, 77 genera) with respect to habitat diversity.

All data available clearly demonstrate poor knowledge of the taxonomy and biology of groups under consideration [Humes, 1994; Korovchinsky, 1996]. On the other hand, studies on the subject have recently greatly intensified and developed qualitatively. This feature is directly connected with the possibility to recognize good species determining the interspecific separation. The latter may be different as it has been

Table 1. The summary monographs on Cladocera and Copepoda of continental waters published during some recent decades.
Таблица 1. Монографии по Cladocera и Copepoda континентальных вод, опубликованные в последние десятилетия.

Years	Cladocera	Copepoda
1950s	Johnson, 1952; Brooks, 1957, 1959 (3)	Lindberg, 1957; Wilson, Yetman, 1959 (2)
1960s	Sramek-Husek et al., 1962; Herbst, 1962; Roen, 1962; Olivier, 1962; Manuilova, 1964; Brooks, 1966; Scourfield, Harding, 1966; Goulden, 1968 (8)	Harding, Smith, 1960; Bayly, 1961, 1964; Damian-Georgesku, 1963, 1966; Dussart, 1967, 1969 (7)
1970s	Smirnov, 1971, 1976, 1977; Flцssner, 1972; Pennak, 1978; Chiang, Du, 1979 (6)	Monchenko, 1974; Einsle, 1975; Kiefer, 1978; Pennak, 1978; Mazepova, 1978; Shen, Tai, 1979 (6)
1980s	Negrea, 1983; Smirnov, Timms, 1983; Idris, 1983; Margaritora, 1985; Mordukhai-Boltovskoi, Rivier, 1987; Michael, Sharma, 1988 (6)	Dussart, 1982, 1989; Dussart, Defaye, 1983, 1985; Stella, 1983; Petkovsky, 1983; Reid, 1985 (7)
1990s	Smirnov, 1992, 1996; Korovchinsky, 1992; Korovchinsky et al., 1995; Lieder, 1996; Alonso, 1996; Rivier, 1998 (7)	Bayly, 1991; Borutsky et al., 1991; Einsle, 1993; Reddy, 1994; Dussart, Defaye, 1995; Stepanova, Alexeev, 1995; Karaytug, 1999; Rayner, 1999 (8)
General number	30	30

Remark: The above mentioned references on Cladocera may be also obtained in Korovchinsky, 1992, 1996, 1997 and those on Copepoda in Dussart, Defaye, 1995 and in present paper.

suggested in cladocerans represented both by morphologically rather peculiar taxa and sibling species [Korovchinsky, 1992]. Taxonomic investigation of Cladocera and Copepoda specialized long ago and has developed more or less separately. Specialists on the groups are mostly not aware of the results of neighbours, neither are hydrobiologists who use taxonomic information as a basis for their research. Integral knowledge about the taxonomic diversity of these crustaceans would seem to be critical for both. The aim of this paper is to compare and briefly summarize modern taxonomic studies on Cladocera and Copepoda (except Harpacticoida) of continental waters to reveal trends in their development, thus following discussion initiated by J. Reid [1997/98]. The main information has been taken from fundamental monographs and many current papers of which only the most important are cited below.

The rate of species richness studies

According to Humes [1994] 4141 species of Copepoda (freshwater and marine) were described from 1964 to 1991 (27 years, ca. 153 species per year) which comprise 37% of their known number (there are no data on continental water's representatives alone). About 180 cladoceran species (30% of known species) were described during the similar period of 30 years from 1964 to 1994. These data show, taking into consideration the large difference in general species richness of the groups and number of specialists, similar intensified rates of studies on these crustaceans during the few recent decades.

Summary publications

Until the mid-20th century the information on taxonomic diversity of Cladocera was mostly scattered in numerous publications, while summaries on the subject appeared occasionally [Korovchinsky, 1997]. The next period, however, beginning in the 1960s, was dedicated in large part to summing up the results of prior publications in many books (see Korovchinsky [1996]) (Table 1).

A similar trend may be observed in the Copepoda of continental waters. The equal numbers of large revisions, identification books and taxonomic reviews were published post-1950s [e.g., Lindberg, 1957; Wilson, Yeatman, 1959] to the present [Einsle, 1993; Reddy, 1994; Dussart, Defaye, 1995; Karaytug, 1999] (Table 1).

It is interesting to note in both groups that regional taxonomic-faunistic reviews predominate over taxonomic revisions of particular groups although in Cladocera the latter became more numerous in the 1990s.

Character of current studies

The significant changes in cladoceran taxonomy started in the 1970s are mostly connected with the name of Professor D.G. Frey and his followers [Frey, 1982, 1987 and references cited in Korovchinsky, 1996]. They used a population approach, the study of large groups of specimens, numerous characters, morphological variability, ontogenetic changes, experimental crosses, electron microscopy, and electrophoresis. The population-genetic and taxonomic studies by Professor P. D. N. Hebert and his co-workers, recently combined with more detailed morphology [e.g., Korinek & Hebert, 1996; Hebert & Finston, 1996; Hebert & Wilson, 2000], also contributed much to this field.

As a result, the degree of taxonomic recognition has reached the level of sibling species and interspecific hybrids. Many well known and widely distributed taxa considered as species were proved to be in fact groups of closely or even not closely related species with compar-

Table 2. Genera and species-groups (the latter are indicated by 1–2 principal species) of Cladocera and Copepoda effectively studied (at least partly) during recent decades (in parenthesis — the area of locally revised taxa, revisions supplemented by genetic analysis (*) and interpopulation crosses (**)).
Таблица 2. Роды и группы видов (последние обозначаются 1–2 основными видами) Cladocera и Copepoda, эффективно исследованные (по крайней мере частично) в последние десятилетия (в скобках — область локально ревизованных таксонов, ревизии, сопровождаемые генетическим анализом (*) и межпопуляционными скрещиваниями (**)).

CLADOCERA		COPEPODA
Family Sididae	Family Chydoridae	Calanoida
Sarsilatona	*Eurycercus* **	*Calamoecia*
*Diaphanosoma mongolianum*Ueno, 1938	*Pleuroxus* **	*Boekella*
D. orghidani Negrea, 1982	*Plurispina*	*Pseudoboekella*
D. celebensis Stingelin, 1900 – *D. volzi* Stingelin, 1905	*Archepleuroxus*	*Hemiboekella*
D. dubium Manuilova, 1964	*Planicirclus*	*Phyllodiaptomus*
	Disparalona	*Neodiaptomus*
Family Daphniidae	*Chydorus*	*Heliodiaptomus*
Daphnia pusilla (Serventy, 1929)	*Dunhevedia*	*Allodiaptomus*
D. similis Claus, 1876*	*Dadaya*	*Eodiaptomus*
D. carinata King, 1853* (Australia)	*Alona affinis* (Leydig, 1860)	*Sinodiaptomus*
D. mediterranea Alonso, 1985 – *D. hispanica* Glagolev et Alonso, 1985	*A. costata* Sars, 1862	*Spicodiaptomus*
D. pulex Leydig, 1860 * (North America)	*A. rectangula* Sars, 1862	*Megadiaptomus*
D. villosa Korinek et Hebert, 1996 *	*A. karua* King, 1853	*Leptodiaptomus**
Megafenestra	*Acroperus elongatus* (Sars, 1862) **	*Hesperodiaptomus arcticus* (Marsh, 1920)*
Scapholeberis	*Kurzia*	*Mixodiaptomus*
Simocephalus	*Kozhowia*	*Lovenula* (Africa)
	Oxyurella	*Paradiaptomus*
Family Ilyocryptidae	*Notoalona*	
Ilyocryptus	*Ephemeroporus*	Cyclopoida
	Celsinotum	*Mesocyclops* **
Family Macrothricidae	*Bryospilus*	*Cyclops** **
Macrothrix laticornis (Fischer, 1851)	*Spinalona*	*Acanthocyclops** **
	Family Bosminidae	*Megacyclops* *
	Bosmina (South and North America)	*Diacyclops*
	Bosminopsis (Amazon region)	*Tropocyclops*
		Paracyclops
		Thermocyclops
		Metacyclops (North and South America)
		Fimbricyclops
		Yansacyclops
		Ponticyclops
		Stolonicyclops

atively small ranges [e.g., Frey, 1973, 1980, 1991; Hann, 1982, 1990]. In general, over 160 species of 29 genera of Ctenopoda and Anomopoda were involved in modern detailed studies (Table 2).

A somewhat different situation was observed in Copepoda probably mainly due to permanent bisexuality of their populations (on the contrary, in most cladoceran populations unisexual parthenogenetic reproduction

predominates). It is not unlikely that thanks to this difference, taxonomy of Calanoida, in which mainly reliable secondary sexual characters were used, always remained at higher level , compared with that of Cladocera. This resulted in better elaboration of their zoogeography and revealing of significant endemicity of local faunas. The positive characters of taxonomy of Calanoida made them a good object for different limnological analyses [Hutchinson, 1967; Pejler, 1975].

Meanwhile, the modern revisions of some genera of Calanoida: *Mixodiaptomus, Neodiaptomus, Tropodiaptomus, Phyllodiaptomus* [Kiefer, 1982; Alonso, 1984; Dussart, Fernando; 1985; Dumont, Reddy, 1993, 1994; Reddy, 1994; Dumont et al., 1996; Reddy et al., 1998] and some others testify to the incompleteness of species richness of the group. Moreover, a new genus *Keraladiaptomus* was recently described from India [Santos-Silva et al., 1994]. The success of recent taxonomic revisions of Calanoida is based on detailed morphological studies, supplemented sometimes by genetic analysis [Boileau, Hebert, 1988; Boileau, 1991].

Identification of Cyclopoida species has always been more difficult than in Calanoida mostly due to their strong morphological plasticity and indistinct diagnostic features. For this reason, some non-traditional methods such as complex biometric measurements, chromosomal characteristics, and experimental crosses were involved in their taxonomy long ago [e.g., Lowndes, 1932; Kozminski, 1936; Price, 1958; Monchenko, 1989; Dussart, Defaye, 1995]. Later they were supplemented by study of chromatine diminution [Einsle, 1975] and electrophoretic data [Einsle, 1988a].

These innovations are important but are limited in use [Fryer, 1985; Einsle, 1988a; Dahms, Schminke, 1995]. The necessity of studying fine morphological features, including those of larval stages, recently became more apparent in the taxonomy of Cyclopoida [Reid, 1991a] as it has been shown, for instance, in revisions of *Mesocyclops, Cyclops*, and *Paracyclops* [Kiefer, 1981; Van de Velde, 1984; Einsle, 1988b; Dahms, Fernando, 1993; Karaytug, Boxshall, 1998; Holynska, 2000]. The intercontinental comparison of populations of some Cyclopoida was ineffective in the past [Yeatman, 1944] due to poorly elaborated morphology, whereas at present small but constant morphological differences between supposed conspecific populations from Europe and North America [Chengalath, Shih, 1994] were found which suggests their taxonomic distinctness. The number of taxa shared between continents has been diminished upon continuing re-examination [Reid, 1997/98]. Similar patterns of intercontinental morphological and taxonomic differentiation of closely related taxa have been described in cladocerans [e.g., Korovchinsky, 1979; Frey, 1980, 1991; Michael, Frey, 1984].

Revisions of the *Mesocyclops leuckarti* (Claus, 1857) [Kiefer, 1981; Van de Velde, 1984], Australasian *Mesocyclops* (Holynska, 2000), *Cyclops strenuus* (Fischer, 1851) [Einsle, 1975; 1988b, 1996] species groups, and species of *Acanthocyclops* [Price, 1958; Fryer, 1985; Reed, 1986; Monchenko, 1989; Reid, 1997/98], which revealed frequent small morphological differentiation between species have clearly demonstrated a trend similar to that in cladocerans. In many of the latter the interspecific morphological separation has proved to be small or even inconspicuous as well [e.g., Frey, 1980, 1991; Hann,1982; Korovchinsky, 1987]. In the latter study the species status of two the closely related *Diaphanosoma mongolianum* (Ueno, 1938) and *D. lacustris* Korinek, 1981 was clarified by few cases of their co-occurrence in some water bodies. The same methodology was used to prove species status of some co-occurring forms of Cyclopidae [Monchenko, 1988].

Many other species of Cladocera, Calanoida and Cyclopoida need thorough reinvestigation. For example, the ratio of taxa of species rank of the latter group with very wide or cosmopolitan distribution (potential species groups) reaches more than 50 % in Europe (unpubl. author's data) and more than 70 % in North America [Shih, Chengalath, 1992]. According to Reid's [1997/98] data, North America and Eurasia share 27 % of their known species of cyclopids. Comparing with cladocerans, they are supposedly less investigated in detail (Table 2). Thus, about 45 % of the known species of Ctenopoda and Anomopoda may be considered as more or less taxonomically valid [Korovchinsky, 1996], while in the Cyclopoida of inland waters, with a close number of currently known species, such taxa seem less numerous. However, further study, especially in America [e.g., Reid, 1989, 1991b, 1993, 1997/98], is in progress.

Conclusion

During the last several decades the morphological, taxonomic, and faunistic studies of the Cladocera (Ctenopoda and Anomopoda) and the Copepoda (Calanoida and Cyclopoida) of continental waters have much intensified, resulting in the description of many new taxa and regular publication of summary monographs. Among the latter, however, the number of taxonomic revisions, strongly improving the classification of particular groups, is small compared with reviews of global or regional level.

The taxonomy of groups under consideration has been elaborated differently. However, in each case we find similar processes of re-evaluation of species resulted in discrimination of many species groups. Interspecific differences often appeared to be less pronounced (or inconspicuous in sibling species) than thought previously. The progress in taxonomy of Cladocera and Copepoda of continental waters is mostly based on detailed morphological studies, including the search of new features, variability, larval morphology, and SEM data as well as genetic and cytotaxonomic analysis.

Thus, in general the level of taxonomic studies of Cladocera and Copepoda, forming the bulk of microcrustaceans of continental waters, has increased significantly, apparently demonstrating deviation from typologic methodology. At the same time, the lack of specialists and difficulties in acceptance of a new taxonomic "ideology" may constrain the development of urgently needed finer resolution taxonomy.

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