Thematic set:
Cyprideis torosa

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On the modern distribution of the euryhaline species *Cyprideis torosa* (Jones, 1850) (Crustacea, Ostracoda)

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Abstract: The modern distribution of the euryhaline ostracod *Cyprideis torosa* (Jones, 1850) is illustrated on three geographical maps, visualizing its occurrence in Europe, Africa and Asia. The presence of other *Cyprideis* species, within the distribution area of *C. torosa*, is discussed. The species has also been recorded from Australia, but it appears now that its presence and that of other *Cyprideis* species, is a complex issue, that requires new research. Passive transport by migratory birds is briefly dealt with, by mentioning some interesting new examples from the literature, and by linking the distribution in China to the Central Asian Flyway of waterfowl. *Cyprideis torosa* is a single, highly variable, polymorphic and widely distributed species, with locally different populations. This variability is commented upon and put in a broader context. An imaginary line, connecting the peripheral records, delineates the distribution area of the species. The most interesting aspect is the very pronounced north–south distribution. The species occurs above the Arctic Circle in Europe and Asia but also in South Africa, illustrating that it is a eurythermal species that has adapted to very divergent temperature regimes.

Keywords: Ostracoda; Recent; zoogeography; dispersal

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Cyprideis torosa (Jones, 1850), described from Pleistocene sands of Grays, Essex, SE England, and type-species of the genus *Cyprideis* Jones, 1857, is a common brackish-water species with a very wide distribution, occurring in Europe, west and central Asia, and in Africa, as well in polar and in temperate, subtropical and tropical regions. It is a euryhaline species found in a wide range of salinities, from almost freshwater to fully marine and even hypersaline water (over 60‰). It has its optimal development in oligo-mesohaline waters, with salinities ranging from 2–16.5‰ (Meisch 2000).

In previous papers the distribution of the species in Africa has already been discussed (Wouters 2002, 2003). The distribution in Africa is updated and the same approach is used for Europe and Asia (it is generally accepted that the species does not occur in the Americas). As many records as possible were sought in the literature in order to obtain a view on the global distribution. These records were plotted on geographical maps. The three resulting maps constitute the core of this article. The purpose is to visualize the distribution of *Cyprideis torosa*, probably the best-known ostracod species, on a general distribution map, to discuss the distribution patterns and to detect distributional and/or taxonomical uncertainties.

Since this study is based on records found in the literature, it has an extensive bibliographical section. The references used in this article are cited at the end of the paper. The publications used for the composition of the distribution maps (Figs 2–4) can be consulted online.

Origin

The euryhaline ostracod *Cyprideis torosa* first appeared in the Late Miocene (van Harten 2000). The species was also reported later from other Miocene deposits; it is figured in only three of the twelve papers with *C. torosa* records published after 2000 and consulted by the present author (not exhaustive). It is therefore difficult to ascertain whether all these Miocene records are, indeed, *C. torosa*. In a well-documented study on *Cyprideis* species in the Neogene of Italy, using a geometrical morphometric approach, Ligios & Gliozzi (2012) recognized twelve species, six of them being new. The new species are confined both geographically and stratigraphically, suggesting endemic speciations similar to those occurring in ancient lakes.

According to van Harten (2000), *C. torosa* is supposed to be the only survivor of a large number of fossil species and subspecies that have been recorded from the Neogene of the Mediterranean area, the Paratethys in particular, and it may well be a daughter species of the ubiquitous species in the 'Lago Mare' of the Mediterranean Messinian, *Cyprideis agrigentina* Decima, 1964 (van Harten 1990). This hypothesis was not sustained by the results of a recent paper by Grossi *et al.* (2015). After close examination of *C. agrigentina* and *C. torosa*, the authors concluded that there were significant differences between the ecophenotypical behaviour of the two species.

The studies of Ligios & Gliozzi (2012) and Grossi *et al.* (2015) clearly illustrate that detailed morphological analysis is required to distinguish between *Cyprideis* species. This was also the case for research carried out by Gross *et al.* (2008), who demonstrated that *Cyprideis* species from Lake Pannon (Austria) with strong resemblance to each other could be separated only by applying elaborate morphometric techniques. The citation of the species named *Cyprideis torosa* in stratigraphical and/or palaeoecological studies of Miocene and, by extension, Pliocene, Quaternary and Recent ostracods, must therefore be interpreted with some caution, certainly when the species is only listed, and not described or figured.

Variability of some important characters

When describing *C. torosa* from the Seychelles (Wouters 2002), the material was compared with material from The Netherlands, Belgium, southern France and Egypt.

The valves of *Cyprideis torosa* from Silhouette Island (Seychelles) differ in some respects from other *C. torosa* populations. First, the valves are somewhat more oblong (especially the males), and have parallel dorsal and ventral margins. In the Belgian and French material the dorsal margin tapers towards the posterior. The Egyptian material (Lake Quarun, Faiyum), however, takes a somewhat intermediate position, in having nearly parallel dorsal and ventral margins. Some specimens of *C. torosa*, figured by previous authors, have valve shapes which are more or less similar to that of *C. torosa* from Silhouette Island, such as those figured by Slack *et al.* (1995) from the Nile Delta in Egypt, by Basha (1987) from Quaternary deposits in the Jordan Rift Valley, by Boukhari & Guernet (1985) from Pleistocene deposits in the Faiyum, Egypt and by Pugliese & Stanley (1991) from Late Quaternary deposits in the Nile Valley. The West African *Cyprideis torosa*, figured by Carbonnel (1982, as *C.* cf. *mandviensis* Jain, 1978), Carbonel *et al.* (1984) and Witte (1993) apparently show more resemblance to 'European' *C. torosa*. In this respect, the valve shape of *C. torosa* from Silhouette Island could be interpreted as unusual, within a highly variable species.

All specimens from the Seychelles lack the postero-ventral spine in the right valve. When studying numerous valves of the species from Italy, Decima (1964) noticed that all right valves possessed a postero-ventral spine. Analysis of specimens from Lake Qarun (Egypt) (Wouters 2002), however, revealed that on 25 specimens (with soft parts), 3 specimens completely lacked a postero-ventral spine, the other 22 specimens having a more or less developed spine. This indicates that in a single population there may be specimens with and without a spine, illustrating that the presence of such a spine is perhaps a less important diagnostic feature of *C. torosa* than is generally accepted. Gross *et al.* (2008) disagree with this point of view and consider the number of spines as a valuable feature for species discrimination. This may well be the case for the three *Cyprideis* species mentioned in their paper, but not for *C. torosa*. Schornikov (2015, pl. 1, fig. 16) even figures a right valve (from the North Caspian Sea) with two postero-ventral spines.

Wouters (2002) compared three soft part characters, namely the morphology of the hemipenis, the medial seta of the fourth segment of the antennule, and the morphology of the male right first leg, more particularly the length of the terminal claw. The morphology of the hemipenis is generally accepted to be a good discriminating character between *Cyprideis* species. The importance of hemipenis morphology was underlined by Sandberg & Plusquellec (1974, p. 14), stating that 'it allows rapid determination of specific placement of any given C*yprideis* male'. The significance of hemipenis morphology for species discrimination was also experienced when describing species of the *Cyprideis* species flock in Lake Tanganyika (Wouters & Martens 1994, 1999, 2001, 2007, 2008).

In *C. torosa* the two hemipenes are asymmetrical. The dorsal shield is distally rounded in the left hemipenis and pointed in the right one. The dorsal lobe is long, and straight or nearly straight, with parallel lateral margins and a rounded or bluntly pointed distal extremity. The copulatory process is a large, broadly rounded lobe and the copulatory lobe has a hammer-like appearance, with a slightly curved shaft. When comparing each of these elements in specimens from different localities (The Netherlands, Egypt, the Seychelles and Belgium), it appeared that there are no significant differences between them (Wouters 2002). In relation to the left–right asymmetry of the dorsal shield, it must be emphasized that this feature is difficult to compare with other populations or with other species, because this asymmetry is not mentioned in the descriptions of *C. torosa*. In a recent publication by Schornikov (2015) it was shown that *Cyprideis pedashenkoi* (Daday, 1909) exhibits left–right asymmetry in the copulatory appendage, but for many other *Cyprideis* species this character state is unknown. None of the seven *Cyprideis* species hitherto described from Lake Tanganyika exhibit left–right asymmetry in the hemipenis.

The morphology of the male right first leg and especially the length of the terminal claw is another useful feature in *Cyprideis* taxonomy. The length of this claw shows a large variability. By calculating the length of the claw v. the combined lengths of the second, third and fourth segments of the leg (in %), the shortest claw can be found in specimens from Lake Qarun (50%), followed by the material from The Netherlands (51%), the material from Belgium (54%) and the material from the Seychelles (from 67.8 to 70.5%). The specimens from Lake St Lucia have the longest claws (88%). It is surprising, however, that the specimens from Lake Qarun, geographically intermediate between Europe and the Seychelles, have the shortest claws of all.

The male right first leg shows another interesting feature, namely a 'split' seta on the antero-distal margin of the second segment (Fig. 1). This seta also occurs in some other *Cyprideis* species, such as *Cyprideis edentata* Klie, 1939*b*. The latter author interpreted this seta as (Klie 1939*b*, p. 13) a large claw-like seta on which a sensory hair is inserted. This is a correct interpretation of the structure, which is called here 'split' seta, for practical purposes. This remarkable seta can also be seen in *Cyprideis stenopora* Triebel, 1956, *Cyprideis gelica* Sandberg & Plusquellec, 1974 and *Cyprideis americana* (Sharpe, 1908). In none of these species is the 'split' seta as strongly developed as in *C. torosa*. There are two other species, however, in which the 'split' seta very much resembles that of *C. torosa*, namely *Cyprideis australiensis* Hartmann, 1978 and *Cyprideis pedashenkoi* (Daday, 1909) (Schornikov 2015).

Jain (1978) described *Cyprideis mandviensis* from the NW coast of India. As far as the valve shape is concerned this species is very similar to the specimens of *C. torosa* from the Seychelles. *Cyprideis mandviensis* has elongate valves and lacks a postero-ventral spine in the right valve. Jain (1978) emphasized that the difference between *C. torosa* and *C. mandviensis* is not only in the shape of the valves, but also in the number of anterior marginal pore canals. *Cyprideis mandviensis* has fewer anterior pore canals, namely 25–30, whereas *C. torosa* has 33–40 (according to Decima 1964). The specimens from the Seychelles have 32–39 pore canals. Material from Belgium, restudied for this paper, has 29–33 pore canals. Unfortunately, the appendages of *C. mandviensis* remain unknown.

The material from False Bay in Lake St Lucia (KwaZulu Natal, South Africa) has appendages that are very similar to European

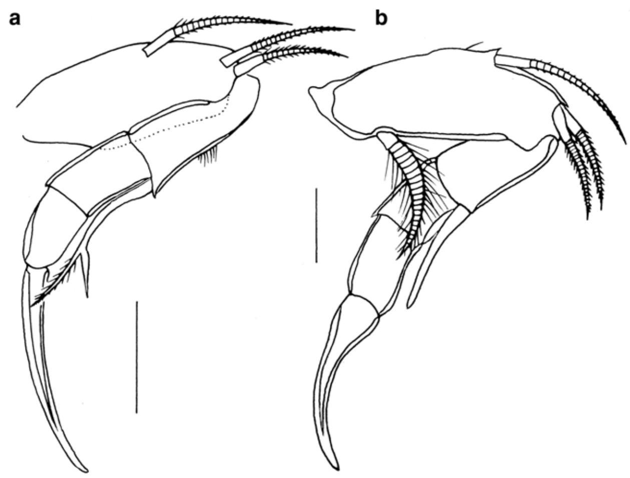

Fig. 1. Right first leg of male: (**a**) *Cyprideis torosa* (Jones, 1850), with 'split' distal seta on second segment, Lake St Lucia, False Bay, KwaZulu-Natal, southern Africa (O.C. 2819, RBINSc., Brussels); (**b**) *Cyprideis remanei* Klie, 1940, with simple distal seta on second segment, Knysna Estuary, southern Africa (O.C. 2817, RBINSc., Brussels). Scale bars 50 µm.

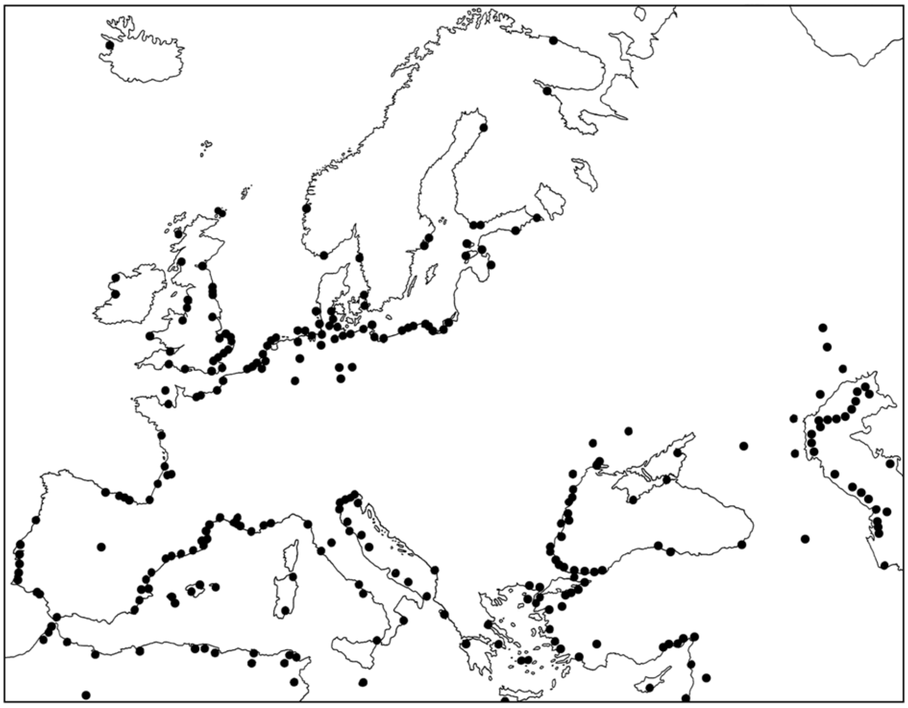

Fig. 2. Distribution of *Cyprideis torosa* in Europe and SW Asia.

material (Wouters 2003). The male right first leg exhibits the typical 'split' seta, but has a long terminal claw. As a matter of fact, when comparing specimens from False Bay with material from The Netherlands, Belgium, Egypt and the Seychelles, the South African specimens have the longest claws of all. The distal shield, with its curved chitinized structure, the dorsal lobe, the copulatory process and the central lobe are all very similar to specimens from Europe. Even the small ventro-central triangular process, also observed in other European and African populations of the species, is present in the False Bay material. The valves are more elongate than European *C. torosa*, but less than the specimens from the Seychelles. They are faintly punctate, and the male right valve shows a small postero-ventral spine. As a whole, one could say that valves of the False Bay material are externally more similar to European specimens than the Seychelles material.

Distribution

The composition of the distribution maps of *Cyprideis torosa* (Figs 2–4) is based on records found in the literature. In many cases, the species is only listed, without description or figures, but these records were nevertheless used to compose the maps. The present author is well aware that this exercise is incomplete and that there is probably an unknown number of unseen publications. It is felt, however, that despite this impediment, the final result gives a fairly good idea of the global distribution of the species.

Europe and SW Asia

Figure 2 illustrates the distribution of *C. torosa* in Europe and SW Asia.

Cyprideis torosa occurs in the northern coastal zone of the Kola Peninsula. It is common in the Baltic Sea, the Gulf of Bothnia, the Gulf of Finland, the Gulf of Riga, the Øresund, the coasts of Germany and Poland, and in some inland localities in Germany. *Cyprideis torosa* occurs in the North Sea area, in the German and Dutch part of the Wadden Sea, including on some Frisian islands. It is very common in The Netherlands, where it is the second most common non-marine species after *Cypria ophtalmica* (Jurine) (this paper). In the UK the species has been repeatedly reported from the coastal area of East Anglia. Elsewhere it is known from southern England, Wales and the coastal zone of NE England, Scotland and the Irish Sea coastal area. The northernmost point in the UK is a brackish lake on Mainland, the Orkney Islands, Scotland (D. Horne, pers. comm. 2015). Only two localities are known from the west coast of Ireland, and one from west Iceland, where the species was found living in water associated with thermal springs. The species was found regularly in brackish waters and estuaries along the North Sea and Atlantic coasts of Belgium, France, Spain and Portugal. In the Mediterranean part of Europe, the species occurs in coastal areas of all countries, and on the islands of Mallorca, Minorca, Ibiza, Formentera (Baleares), Sardinia, Malta, Paros, Naxos, Cyprus and Gokçeada. The species was found repeatedly as empty valves in sediments of the Adriatic Sea. The distribution of *C. torosa* in Turkey is very well documented. It occurs in the southern. and westen Mediterranean coastal zone, along the south coast of the Black Sea, in the Sea of Marmara and occasionally in inland saline lakes. More to the north, the species was found in the Black Sea, in and near the Danube delta, the delta of the river Dnieper, brackish-water bodies near Ochakov, near Chernavska, the Donets river near Charkov, Kakhovka Reservoir, the lower Dniester (Ukraine) and in the Sea of Azov and the Kuban Delta, the Yahorlyk River (Moldova). It was found in Lake Manych-Gudilo, a large saltwater reservoir lake in Kalmykia (Russia), in Lake Sevan (Armenia), in the Caspian Sea, tributaries of Lake Elton (western Russia, near Volgograd) and the saline pond Ilmen Gorchichny, west of Astrakhan.

In a publication on the genetic differentiation in *C. torosa*, based on material from localities in England, The Netherlands and Poland, Sywula *et al.* (1995) concluded that the studied European populations are genetically similar to each other to such a degree that they should be treated as sets of subpopulations, rather than as separate units. One can wonder if the same conclusion would be reached when studying populations from a much wider geographical area, including far eastern and southern localities. According to Sywula *et al.* (1995), this similarity is largely due to the passive dispersal of *C. torosa* by aquatic birds.

Africa

Figure 3 illustrates the distribution of *C. torosa* and other *Cyprideis* species in Africa (and in Southern Europe and SW Asia).

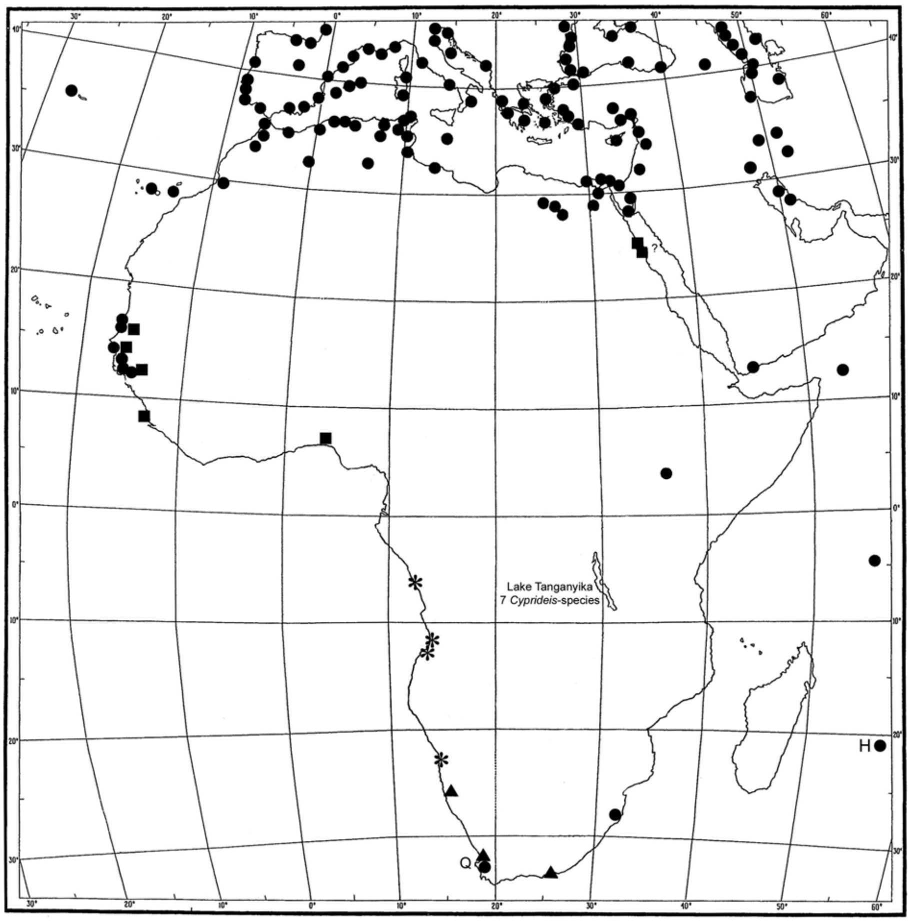

Fig. 3. Distribution of *Cyprideis torosa* and other *Cyprideis* species in Africa (and southern Europe and SW Asia). Circles, *C. torosa*; triangles, *C. remanei* Klie, 1940; asterisks, *C. limbocostata* Hartmann, 1974; squares, *C. nigeriensis* Omatsola, 1970; Q, South African locality, Draaihoek, with Quaternary *C. remanei* and *C. torosa* (described as *C. draaihoekensis*); H, occurrence of *C. torosa* in middle to late Holocene deposits of Mauritius.

General observations

The species is common to very common in northern Africa in a large number of Mediterranean and in some inland localities in Morocco, Algeria, Tunisia, Libya and Egypt. In Morocco the species occurs also along the Atlantic coast, with the Massa Lagoon, 40 km south of Agadir, as the most southern point (Badsi *et al.* 2010). In Egypt it is very common in the Nile Delta. Special localities in Egypt are the Siwa Oasis in the Libyan Desert (Harding 1955), nearly 50 km east of the Libyan border, and Lake Qarun (Faiyum), from which Bassiouni *et al.* (1985, 1986) reported *Cyprideis sohni* Bassiouni, 1979. Comparison of the appendages with European material showed that the *Cyprideis* species in Lake Qarun is *C. torosa* (Wouters 2002).

Along the western African coast, *C. torosa* occurs on the islands of Gran Canaria and Fuertaventura (Baltanás & Garcia-Avilés 1993; Beyer *et al.* 1997; Scharf & Meisch 2014). Further to the south, the species has been recorded from Senegal and Gambia (Carbonnel 1982; Carbonel *et al.* 1984; Witte 1993), with Sina, a village on the river Casamance (Senegal), as the southernmost point in West Africa (Debenay *et al.* 1990). In East Africa, the species is known from Lake Turkana, Kenya (Klie 1939*a*; Lindroth 1956; Kilenyi & Whittaker 1974; Cohen 1986). Kilenyi & Whittaker (1974, p. 31) restudied a male specimen with appendages, from the collections of the Zoological Institute and Museum in Hamburg, from Lake Turkana, and confirmed the identification as *Cyprideis torosa*. Finally, the species was found in the Dauban Marsh, on Silhouette Island (Seychelles) (Wouters 2002) and in False Bay, a side arm of Lake St Lucia, KwaZulu Natal (South Africa) (Wouters 2003).

Although numerous brackish and highly saline pools are present on the island Aldabra, McKenzie (1971) did not find the species after an intensive sampling campaign.

This paper deals with the modern distribution of *C. torosa*. An exception is made, however, for two fossil records, because they are both situated outside the modern distribution area of the species.

Dingle & Honigstein (1994) described the new species *Cyprideis draaihoekensis* from Quaternary coastal sequences in Draaihoek and Gypsum Quarry, St Helena Bay, north of Cape Town (Fig. 3, Q herein), where the new species occurs together (i.e. in the same samples) with *Cyprideis remanei* Klie, 1940. *Cyprideis draaihoekensis* was already synonymized with *C. torosa* by Mostafawi (2003). A second interesting record is the presence of the species in middle to late Holocene deposits of the island of Mauritius (Indian Ocean) (Fig. 3, H herein). In their study, de Boer *et al.* (2014) used valves of the species for stable isotope analysis. The youngest deposits in which the species was found are only 400 years old. It is, therefore, not to be excluded that it is still living on the island.

Other species

Apart from *C. torosa* there are several other *Cyprideis* species in Africa. *Cyprideis remanei* was described by Klie (1940) from the Bay of Lüderitz, Namibia. The species was found again in the same locality by Hartmann (1974). Later it was recorded from Knysna Estuary (Wouters 2003). It is somewhat surprising that it was not mentioned by Benson & Maddocks (1964) in their extensive monograph on ostracods of Knysna estuary. *Cyprideis remanei* was also found in Quaternary deposits in the southwestern Cape (Dingle & Honigstein 1994). Referring to this paper, Mostafawi (2003) wrongly synonymized *C. remanei* with *C. torosa*.

Cyprideis limbocostata Hartmann, 1974 was described from a mangrove area in Palmeirinhas, near Luanda (Angola), but other living populations were found in several localities between Cacuaco (north of Luanda, Angola) and Sandwich Harbour (south of Walvis

Bay, Namibia). Babinot & Kouyoumontzakis (1986) recorded it as *C.* cf. *limbocostata* in the estuary of the River Congo. According to Hartmann (1974), *C. limbocostata* is closely related to *C. remanei*.

Cyprideis nigeriensis Omatsola, 1970 was originally described from Ikorodu, in the Lagos Lagoon, Nigeria. In the same year it was found in Sierra Leone, near Black Johnson, south of Freetown and on the east side of Sherbro Island (Keen 1970). From Senegal it was recorded from Fanda, on the River Casamance, and from Lébar, on the River Senegal, not far from the river mouth by Carbonnel (1982), and from St Louis and Joal Beach by Witte (1993). Both *C. remanei* and *C. limbocostata* have a small and simple seta on the male right first leg (v. 'split' seta in *torosa*). In *C. nigeriensis* this character state is unknown. The first leg figured by Omatsola (1970, pl. 2, fig. 6) does not show sufficient detail to be conclusive.

In a publication dealing with ostracods from two mangrove ecosystems along the Egyptian Red Sea coast, the Wadi Gemal area and the Abu Ghoson area, Helal & Abd El-Wahab (2012) mention the presence of *Cyprideis torosa* and (the junior synonym) *C. littoralis*. Their figured valves (Helal & Abd El-Wahab 2012, figs 7 and 12) do not resemble *C. torosa*, but are very similar to *C. nigeriensis*. Since no appendages are described, the identification of this Red Sea material remains uncertain (Fig. 3, two squares with question mark).

The *Cyprideis* species flock of Lake Tanganyika, consists of 23 species in 6 genera to date. Seven species belong to the genus *Cyprideis*. These species show a very distinct bathymetrical segregation and are listed here in two groups, the deep water fauna (1) and the littoral fauna (2), with their depth of occurrence: (1) *C. mastai* Wouters & Martens, 1994 (40–90 m), *C. rumongensis* Wouters & Martens, 1994 (50 m), *C. profunda* Wouters & Martens, 1999 (90 m); and (2) *C. spatula* Wouters & Martens, 1999 (5–9.5 m), *C. loricata* Wouters & Martens, 2001 (10–32 m), *C. aciculata* Wouters & Martens, 2007 (18 m) and *C. romei* Wouters & Martens, 2008 (9 m). When comparing *C. torosa* from different localities with the *Cyprideis* species flock of Lake Tanganyika, it can be observed that, among other differences, the Tanganyikan species all lack the left–right asymmetry in the dorsal shield of the copulatory appendage, and the 'split' seta on the male right first leg. This leads to the conclusion that species of the Tanganyikan *Cyprideis* species flock are not closely related to *Cyprideis torosa*. The ancestry of this flock must be sought elsewhere, maybe in one of the numerous fossil *Cyprideis* species described from Neogene deposits from the Mediterranean area and the Paratethys.

Asia, and some European and peripheral records

Figure 4 illustrates the distribution of *C. torosa* and *C. pedashenkoi* in Asia, with some European records and peripheral records of the global distribution of the species.

General observations

In the Middle East the species is known from Beirut, Jaffa, Port Said, Lake Kinneret, the Gavish Sabka, Solar Lake and Dahab lagoon (along Gulf of Aqaba), near Basrah (Iraq), reservoir Kuh Rand (SW of Isfahan), Lake Famur and Gavkaneh Area, Anzali Lagoon, Caspian Sea, Iranian coastal area of the Persian Gulf, tidal flat of the coast of Aden City and Socotra Island (Yemen). Furthermore, it has been found in lakes Sudochye and Kara-Teren (Uzbekistan), lakes Chalkar and Balkash (Kazakhstan) and Aral (Uzbekistan/Kazakhstan) and in different lakes between Chelyabinsk and Kurgan, and between Kurgan and Omsk, among others: lakes Lebyazhe, Gorkye, Travykul, Bolshoi, Utiche and Peshanoye. An important locality is the Yamal Peninsula (Kara Sea) (see further under 'Peripheral records' section below). The species was found in lakes in West Mongolia, and in China in the Qaidam Basin and adjacent areas and near Lake Qinghai (Prov. Qinghai), lakes Bosten and Ulungur (Prov. Xingjiang), and Tibetan salt lakes. Very few localities are known from India, namely Loharwada, 9 km east of Charki Dadri, Mandvi beach, Palaeolake Riwasa and the Gautami–Godavari estuary (east coast) (see further under 'Peripheral records' section).

Distribution in China

In the checklist of non-marine ostracods in China (Yu *et al.* 2009) only a few localities are mentioned: Qaidam basin and adjacent

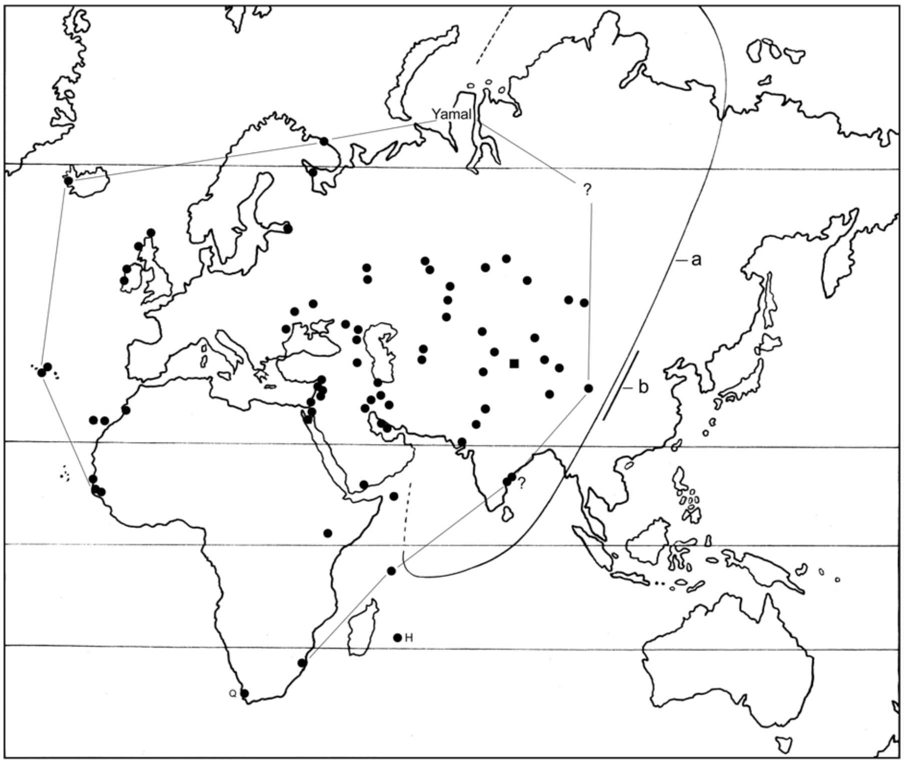

Fig. 4. Map showing distribution of *Cyprideis torosa* (circles) and *Cyprideis pedashenkoi* (square) in Asia, with some European records, and peripheral records of the global distribution of the species. 'a' denotes the eastern margin of the Central Asian Flyway of waterfowl (Anatidae) (redrawn from Miyabayashi & Mundkur 1999; Boere & Stroud 2006); 'b' the Zhao–Whatley boundary line (Zhao & Whatley 1992) between brackish-water ostracod faunas with *Cyprideis* and *Sinocytheridea* (redrawn); Yamal is the Yamal peninsula, northernmost locality of *C. torosa*; Q, Quaternary; H, Holocene.

areas, Qinghai, the salt lakes of Sinkiang and the salt lakes of Tibet, without further specifications. The species is mentioned from the 'Shallow Lake' on the Qinghai plateau by Yang (1988). Apparently it does not occur in Lake Qinghai itself, as can be concluded from a study by Li *et al.* (2010) on the distribution of Recent ostracod species in the lake. The species was also found in Lake Bangong, western Tibet (Song *et al.* 2014).

Zhao & Wang (1988) commented on the presence of *Cyprideis torosa* in China. They emphasized (p. 812) that the species is conspicuously absent along the Chinese coast, and that it is probably replaced by the endemic species *Sinocytheridea latiovata* Hou & Chen. In 1993 the same authors reconsidered the distribution of *Cyprideis torosa* in China and concluded that this species has been widely encountered in W. China, such as in the Miocene of the Tarim Basin, and in the Pleistocene of the Qaidam basin, but never in East China. The eastern boundary of its distribution probably lies near Yunchen and Yuxian, where both *Sinocytheridea impressa* and *Cyprideis torosa* can occur in deposits, but rarely together in the same assemblage (Zhao & Wang 1993, p. 674).

Because of the absence of the euryhaline genus *Cyprideis* from both fossil and modern brackish-water faunas in eastern China, 'the late Cenozoic brackish water faunas can be divided into two types: the western type characterized by the presence of *Cyprideis* and the eastern type where *Cyprideis* is replaced by *Sinocytheridea* and other Chinese endemic genera' (Zhao & Whatley 1992, p. 157). In the same publication the authors drew a boundary line between the two types of fauna (Zhao & Whatley 1992, fig. 5), here called the 'Zhao–Whatley boundary line', between brackish-water ostracod faunas with *Cyprideis* and *Sinocytheridea* (Fig. 4, line b, herein). When position and orientation of this line are compared with the delineation of the Central Asian Flyway of waterfowl (Miyabayashi & Mundkur 1999; Boere & Stroud 2006), a remarkable convergence can be observed, indicating that bird migration probably plays an important role in the distribution of both *Cyprideis* and *Sinocytheridea* (see further under the 'Transport' section below).

Distribution in India

Only four localities are known from India. The southernmost and easternmost locality is the Gautami–Godavari estuary on the east coast (Bhandari & Singh 2006). Two subrecent localities: Loharwada, 9 km east of Charki Dadri (28° 26′ N, 76° 16′ E), District Mahendragarh, northern India, where the species occurs abundantly in subrecent deposits (Bhatia & Khosla 1977) and palaeolake Riwasa at the NE edge of the Thar Desert in NW India (Dixit *et al.* 2015). The fourth locality is Mandvi Beach, in NW India, the type-locality of *Cyprideis mandviensis* Jain, 1978. Other records of *Cyprideis* sp. or *C.* sp. cf. *C. mandviensis* published by Gopalakrishna *et al.* (2007), Elumalai *et al.* (2010) and Hussain & Mohan (2000) are probably not *Cyprideis torosa.* As a matter of fact, the valves figured by Hussain & Mohan (2000, pl. 1, fig. 11) show that this genus has a cypridoidean muscle scar pattern (v. cytheroidean in *C. torosa*).

Other species

There is at least one other *Cyprideis* species in Asia, namely *Cyprideis pedashenkoi* (Daday, 1909) from Lake Issyk-Kul, in NE Kyrgyzstan (Fig. 4, square herein). This species was originally described by Daday (1909) as *Cytheridea pedashenkoi*. Later it was considered a subspecies of *C. torosa* by Akatova (1972) and Jankovskaja (1972) or a junior synonym of *C. torosa*, by Klie (1939*a*), Sandberg (1964), Hartmann (1964) and Kilenyi & Whittaker (1974). In a very recent paper, Schornikov (2015) reaffirms that *C. pedashenkoi* is a separate species, endemic to Lake Issyk-Kul. According to the same author it can be distinguished from *C. torosa* by its double frontal muscle scar, the pronounced fossa-mural ornamentation, with punctate sculpture grouped into polygonal fields, as well as by the proportions of some parts of the appendage armature and details of the copulatory appendage.

Bate (1971, p. 252) mentions *Cyprideis* sp. from the Abu Dhabu Lagoon (Persian Gulf). He emphasizes that the species is not conspecific with the European *Cyprideis torosa* and that it is adapted to a hyperhaline rather than a brackish to marine environment. The figures (Bate 1971, pls 1–3, figs nn) are small and give insufficient information to gain more insight into this taxonomical uncertainty.

When studying material from the Caspian Sea, in the neigbourhood of the Pahlavi lagoon (now named Anzali Lagoon), Hartmann (1964) identified an ostracod instar in his material as *C. torosa* cf. *pedashenkoi*, and questioned the validity of the species *pedashenkoi* as defined by Bronstein (1947).

Yassini & Ghahreman (1976) mention two species from the Pahlavi (=Anzali) Lagoon (northern Iran, Caspian Sea coast), namely *Cyprideis toros*a and *Cyprideis* sp. The latter has smaller and shorter valves than *torosa*. The authors presume that the material came from reworked sediments of the Quaternary Würm cold interval in the study area. In two subsequent papers, however, Schornikov (2011, 2012) refers to *Cyprideis* sp. *sensu* Yassini & Ghahremann, for material collected in the Caspian Sea, the basins of the river Don and Taganrogsky Bay and the bottom of the Black Sea. In Schornikov's paper (2015) on *C. pedashenkoi*, drawings of the central muscle scar pattern (Schornikov 2015, text-figs 1, 14) and of the hinge (Schornikov 2015, text-figs 1, 23) of *Cyprideis* sp. *sensu* Yassini & Gahreman are published. The appendages and the valves remain to be described in detail in order to establish whether there is still another *Cyprideis* species present in Asia.

Cyprideis torosa *in Australia?*

In 1978 McKenzie described the new species *Cyprideis westraliensis* from the causeway at Lake Preston, Western Australia. In the same year (1978) Hartmann had already described the new species *Cyprideis australiensis* from the mouth of the rivers Greenough and Chapman near Geraldton in Western Australia. One year later the same author (Hartmann 1979) records the species from more localities: the Mandyrah estuary, Leschenault-inlet Bunburry, Wonnerup-inlet Busselton, Prevelly Park near river Margareth, Hardy-inlet Augusta, Irwin-inlet near Peaceful road and Wilson-inlet Denmark. One year later Hartmann (1980) mentioned the species again from the Spencer Gulf, north of Point Augusta and from The Coorong, 3 km north of Policeman Point, and synonymized (with a question mark) *C. westraliensis* with *C. australiensis*. De Deckker *et al.* (1982, 1988*a*) followed this point of view and considered (1988*b*, p. 233) 'that all Australian specimens discussed here (Recent or fossil) are synonymous with *C. torosa*'. However, when the figures of the male right first leg of both species are compared, it appears clearly that in *C. westraliensis* the distal seta on the second segment is a strong, but short, simple seta (McKenzie 1978, fig. 24), whereas in *C. australiensis* this distal seta is a long, 'split' seta (Hartmann 1978, fig. 152). This important difference indicates that there are probably two different species involved. All later records were named *C. australiensis* by McKenzie *et al.* (1990): near Woodswell, The Coorong; Behrens (1991): among mangroves on Lizard Island; Yassini & Jones (1995): southwestern part of Lake Macquarie; Cale *et al.* (2004): Lake Wheatfield, SW Australia; De Deckker & Yokoyama (2009): Quaternary in Bonaparte Gulf, southern Australia; Gouramanis *et al.* (2010): Holocene of Blue Lake (southern Australia); De Deckker (1988), Yassini *et al.* (1993), Reeves *et al.* (2007) and L.S. J. Devriendt (2011, 'Late Quaternary environment of paleolake Carpentaria inferred from the chemistry of ostracod valves', Thesis, University of Wollongong, available at http://ro.uow.edu.au/theses/3319): Quaternary of the Gulf of Carpentaria. On one of the inside covers of the book published by De Deckker *et al.* (1988*b*), a SEM picture of an internal view of *C. australiensis* (no locality mentioned) is published, with a clear view of the male right first leg. The length of the distal seta on the second segment suggests that it is a 'split' seta.

Cyprideis australiensis was also recorded from localities outside Australia: by Hoibian *et al.* (2000) from the Néra Delta, New Caledonia; and by Titterton & Whatley (2006), as *Cyprideis* sp. cf. *C. australiensis*, from Quaternary and Recent sediments from Guadalcanal (Solomon Islands).

There is still another, somewhat overlooked species, namely *Cyprideis consobrina* (Brady, 1890), described from Nouméa (New Caledonia) as *Cytheridea consobrina*. According to Brady (1890, p. 505), this species 'differs very decidedly' from the European *C. torosa* 'in the character of its surface markings, the fossae being much larger; the shell is also more elongated, and in the female much more tumid behind'. McKenzie (1986) designated and illustrated a female carapace from the Brady collection as lectotype. Davis & Horne (1988) added the correct Hancock Museum registration of the specimen: lectotype, female carapace, 1.55.23 (B457). Maddocks (2007) also mentions *C. consobrina* in a checklist of Ostracoda from New Caledonia.

When the SEM photograph of the lectotype of *C. consobrina* published by McKenzie (1986, pl. 1, fig. 9) is compared with the SEM pictures of *C. australiensis* published by Hartmann (1978, pl. 5, figs 1–5; 1979, pl. 4, figs 3–11; 1980, pl. 8, figs 4, 5), it is clear that there are many similarities. It is, therefore, suggested here that *C. australiensis* Hartmann, 1978 may well be a junior synonym of *C. consobrina* (Brady, 1890). However, when the SEM pictures of *C. australiensis* from Palaeolake Carpentaria, of Devriendt (2011, unpublished thesis, p. 23, figs 2.3 and 2.4), are compared with those of *C. australiensis*, published by Hartmann (1978, 1979, 1980), some differences can be observed, indicating that both 'species' may not be conspecific.

It is not to be excluded that, instead of one species, there are three *Cyprideis* species in Australia: *Cyprideis consobrina* (Brady) (with *C. australiensis* Hartmann as a possible junior synonym), *Cyprideis westraliensis* McKenzie, and maybe *C. australiensis* sensu Devriendt and other authors dealing with Quaternary ostracods from the Gulf of Carpentaria. *Cyprideis consobrina* and *C. westraliensis* need to be resampled and the valves and appendages to be redescribed and figured in detail. This is also the case for *C. australiensis* recorded from Lizard Island by Behrens (1991). Only then will it be possible to conclude how many *Cyprideis* species there are in Australia, and whether one of them is *C. torosa*.

Peripheral records

The peripheral localities are discussed in a clockwise direction, starting in the north (Fig. 4).

Until recently (Wouters 2002), the northernmost locality of the species was Dalnye Zelentsy, some 280 km above the Arctic Circle, at 69° 06′ 31″ N, 36° 06′ 04″ E (east of Murmansk), Kola Peninsula, Barents Sea (Aladin 1989), but Schornikov (2011) mentions a more northerly locality on the Yamal Peninsula, situated in the Kara Sea (Russia), but without giving a locality or coordinates. He also reports a more easterly locality in the Krasnoyarsk region (Russia), but without more information.

The easternmost record is the Qinghai Plateau (NW China), *c*. 36° 54′ N, 100° 37′ E (Yang 1988). The southernmost and easternmost locality in India is the Gautami–Godavari estuary, east coast of India, 16° 36′ 03″ N, 82° 27′ 45″ E, where the species was recorded as *C. mandviensis*, but without description or picture (Bhandari & Singh 2006).

On the south coast of the Arabian Peninsula, the species was identified from shallow-marine tidal flat sediments, ranging in depth from 0.40 to 1 m collected along the coast line of Aden City (Yemen). Coordinates of the southernmost locality are 12° 46′ 36″, N 44° 52′ 55″ E (Mohammed & Keyser 2012).

Cyprideis torosa was sampled in Recent shallow-marine sediments collected along the northern coastline on Socotra Island (12° 39′ 15.7″ N, 54° 00′ 54.0″ E) (Mohammed *et al.* 2012), and from samples collected from the bottom of permanent streams running along the NNE part of Socotra Island, Indian Ocean. Coordinates of the southernmost locality are 12° 35′ 51.5″ N, 53° 46′ 40.1″ E (Mohammed *et al.* 2014).

In a previous paper the present author (Wouters 2002) already discussed the presence of *C. torosa* on the Seychelles, coordinates: 4° 29′ 11″ S, 55° 15′ 12″ E. It was, at that time, the southernmost known locality. One year later (Wouters 2003), however, material from a still more southerly situated locality was described from Lake St Lucia, an estuarine lake with changing salinity regime in KwaZulu Natal. Coordinates from K. Martens, who collected the material are 28° 00′ 39″ S, 32° 21′ 58″ E.

The species was found in a sediment core from the Tatos basin in the lowland of Mauritius (de Boer *et al.* 2014), coordinates 20° 12′ 48″ S, 57° 46′ 30″ E. The youngest deposits in which it was found are only 400 years old. It is, therefore, possible that it is still living on the island.

The species seems to be absent from southern and SW Africa, where it is replaced by other species.

In west Africa the southernmost locality is Sina, an inland village on the river Casamance, Senegal, 12° 32′ 48″ N, 15° 36′ 12″ W (Debenay *et al.* 1990).

On the Canary Islands, the species is known from Fuertaventura and Gran Canaria. The southernmost locality is a shallow lake situated between Maspalomas and the dune area, on the south coast of Gran Canaria, 27° 44′ 16″ N, 15° 35′ 40″ W (Scharf & Meisch 2014).

The most western locality of *C. torosa* is Pico Island (Azores archipelago), where it was found in Recent sediments, *c*. 38° 28′ N, 28° 20′ W (Meireles *et al.* 2014).

Klie (1938) recorded the species from Iceland, where it was found living in waters associated with hot springs, at *c*. 64° 58′ N, 21° 28′ W.

Finally, it was collected on Cape Kartesh, in the White Sea, at 62° 20′ 41″ N, 33° 37′ 36″ E, some 23 km below the Arctic Circle (Aladin 1989), and mentioned from the White Sea (without further detail) by Schornikov (2015).

The distribution area of *Cyprideis torosa* can be delineated by an imaginary line (Fig. 4, in a clockwise direction), connecting the following points: Kola Peninsula, Yamal Peninsula, an unknown locality in the Krasnoyarsk region (Russia), the Qinghai Plateau (NW China), the Gautami–Godavari estuary (east coast of India), Silhouette Island (Seychelles), Lake St Lucia on the east coast of Africa, no records on the coast of southern and SW Africa, Sina on the Casamance River (Senegal), Pico Island (Azores) and west Iceland. The most interesting aspect is the very pronounced north–south distribution. The species occurs above the Arctic Circle, in moderate and Mediterranean climatic zones, in subtropical regions, in tropical Africa, including islands in the Indian Ocean, and finally in South Africa, *c*. 4° 34′ 25″ below the Tropic of Capricorn. From this it can be concluded that *C. torosa* is a eurythermal species that has adapted to very divergent temperature regimes.

Transport

As discussed above, a remarkable convergence can be observed between the delineation of the Central Asian Flyway of waterfowl and the Zhao–Whatley boundary line, indicating that bird migration plays an important role in the distribution of both *Cyprideis* and *Sinocytheridea*. This is not surprising, since the potential for dispersal of ostracods by migratory birds is an often mentioned topic in the literature (e.g. Löffler 1964; Sandberg & Plusquellec 1974; De Deckker 1977; Neale 1984; van Harten 1990; Grigg & Siddiqui 1993, and others). When discussing the disjunct distribution of *Potamocypris humilis* (Sars), Horne & Smith (2004) argue that although some ostracod distributions have been shown to match the routes of bird migrations, the evidence for such dispersal remains circumstantial. It is not the goal of this article to discuss passive migration further, but two examples where *C. torosa* may well be involved, are worth citing. Frisch *et al.* (2007) studied the dispersal capacity of aquatic invertebrates, including ostracods, via water birds, from a pond in Veta la Palma (SW Spain). Faeces of Coot, Teal and Shoveler were used in hatching experiments, and viable ostracods were found. The species was not identified, but the authors add in a footnote (Frisch *et al.* 2007, p. 571) that *Cyprideis torosa* is the only ostracod species recorded in the Veta la Palma pond. In a similar study on the dispersal of invertebrates, including ostracods, in the Camargue (southern France), Brochet *et al.* (2010) collected invertebrate propagules from the plumage, feet and rectum of Teal. Ostracods were recorded in both internal and external samples. Hatching confirmed their viability and resulted in at least four ostracod species (*Potamocypris* cf. *producta* (Sars), Cyprididae, unidentified Ostracoda and *Paralimnocythere* cf. *psammophila* (Flössner)). *Cyprideis torosa* is a common species in the Camargue and it is, therefore, very possible that it is one of the 'unidentified Ostracoda'. The authors conclude that Teal may be important vectors of ostracod dispersal both within the Camargue and along migratory flyways.

A single variable species

In a remarkable paper on the effects of genotype and environment on phenotypic variability in *Limnocythere inopinata* (Baird), Yin *et al.* (1999) threw a new light on this widely distributed species. They concluded that both valve shape and the absolute and relative length of limb setae can be affected by environmental factors and by genotype, and this in parthenogenetic as well as in bisexual populations, and that *L. inopinata* is a variable, polymorphic species, consisting of a (semi-)continuous cluster. The final conclusion of the article is that it is impossible to single out population(s) as separate and recognizable clusters (Yin *et al.* 1999, p. 111). All specimens investigated are, therefore, maintained within *L. inopinata*, which can thus be considered a very variable species. Having studied and compared *Cyprideis torosa* from different localities, the present author presumes that for this species the situation may well be comparable, namely that it is a single, very variable and widely distributed species, with locally different populations.

The application of molecular methods in the last decade revealed cryptic diversity in ostracods, where species cannot be differentiated by morphological but only by genetic characters (Schön *et al.* 2014). In *Eucypris virens* (Jurine), close to 40 cryptic species have been described from Europe and North Africa (Bode *et al.* 2010), while Schön *et al.* (2012) found three cryptic species in *Darwinula stevensoni* (Brady & Robertson) and eight in *Penthesilenula brasiliensis* (Pinto & Kotzian). Analysis of DNA sequence data of *Romecytheridea* species of Lake Tanganyika, revealed a high cryptic diversity with allopatric distribution. If most morphospecies of Lake Tanganyika hold similar amounts of cryptic diversity, the *Cyprideis* species flock of the lake might very well consist of more than 100 endemic ostracod species (Schön *et al.* 2014), v. the actually known 23 species (Wouters & Martens 2008).

A high degree of intraspecific variation or the presence of cryptic diversity are two extremes of the taxonomical spectrum. Up to now it appears that *C. torosa* is a highly variable, polymorphic species, comparable with the variability described and illustrated for *Limnocythere inopinata* by Yin *et al.* (1999). However, many questions regarding the intraspecific variability of *C. torosa* remain unanswered, among others, by the absence of a sufficient number of detailed descriptions and illustrations of soft parts and valves from geographically different localities, and of the variability analysis of taxonomically relevant features.

The application of molecular methods on new material would be an interesting research topic to determine whether the amount of variability observed on the basis of morphological features can be confirmed or refined, or whether this variability is much more complex than is now believed.

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