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A review of the marine and brackish-water species of *Testudinella* (Rotifera: Monogononta, Testudinellidae), with the description of two new species

WILLEM H. DE SMET
University of Antwerp, Department of Biology, Campus Drie Eiken, Universiteitsplein 1, B-2610 Wilrijk, Antwerpen, Belgium.
E-mail: willem.desmet@ua.ac.be

Abstract

Two new morphospecies of the rotifer genus *Testudinella* (Rotifera, Monogononta, Testudinellidae), *T. bicorniculata* **sp. nov.** and *T. elongata* **sp. nov.**, are described from marine psammon collected in the Mediterranean. *T. bicorniculata* **sp. nov.** is characterized by two antero-lateral lorica projections; dorsal and ventral anterior margins undulate with shallow median sinus; foot opening sub-terminal, inverted U-shaped; distal foot pseudosegment short; fulcrum with proximal opening. *T. elongata* **sp. nov.** is characterized by its strongly elongate and striate lorica; dorsal anterior margin tri-lobed; ventral margin projecting, almost straight; foot opening sub-terminal, inverted U-shaped; distal foot pseudosegment long; fulcrum with proximal opening. The new species are related to *T. obscura* Althaus, 1957, which is redescribed. Brief descriptions of the external morphology and trophi, as well as biogeographical information are provided for the other *Testudinella* species reported from marine and brackish environments. *T. pseudoclypeata* Bērziņš, 1943 is synonymized with *T. elliptica* (Ehrenberg, 1834).

Key words: Rotifera, Floscullariaceae, *Testudinella*, new species, marine, Mediterranean

Introduction

Rotifers inhabiting marine environments have been little studied taxonomically and ecologically, and are usually recognized as an inconspicuous taxon, although it is becoming obvious that rotifer diversity is much more relevant than generally accepted (e.g. Ricci & Fontaneto 2003; Fontaneto *et al.* 2006, 2008). Why such a cosmopolitan constituent of marine fauna received little attention is connected with difficulties in collecting sufficient material, the time-consuming and laborious techniques to extract them from sediment and vegetation, and to prepare them for study. Moreover, inaccurate and incomplete descriptions resulted in problems with marine rotifer taxonomy, and redescriptions of previously described species based on a broader spectrum of specific characters are needed. In this contribution two new species of *Testudinella* Bory de St. Vincent, 1826 (Testudinellidae: Monogononta, Floscullariaceae) are described from the Mediterranean, and additional information is presented on the other members of the genus reported from marine and brackish waters world-wide. Testudinellidae is a small family comprising three genera, *Anchitestudinella*, *Testudinella* and *Pompholyx*, of which *Testudinella*, with about 40 morphospecies considered valid in the recent annotated checklist of rotifers by Segers (2007), is the most species-rich. *Testudinella* is a benthic-periphytic genus of microphagous rotifers primarily inhabiting the littoral of freshwater lakes and ponds. To date seven species have been reported from marine, brackish or inland saline habitats, only two of which, *T. clypeata* (Müller, 1786) and *T. obscura* Althaus, 1957, are considered strictly marine, the others being euryhaline or occasionally introduced freshwater species (Fontaneto *et al.* 2006, 2008).

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Materials and methods

Sampling (Fig. 1) was done in the Mediterranean (northern Spain, 7 samples; eastern France, 5 samples; Italy: island Elba, 7 samples), the Red Sea (southern Egypt, 7 samples) and the Mindanao Sea (the Philippines, 10 samples). Samples were collected during SCUBA diving by scraping the uppermost centimetre of sand using 250 ml plankton bottles, at depths of 8 to 70 m and distances from the shore varying from ~10 m to 10 km. Fixation followed by adding 35% formalin up to a final concentration of ~4%. The rotifers were extracted in the laboratory using the swirl-decantation technique: the sand is added to filtered seawater and stirred, and after momentary setting the supernatant is poured off through a 40 µm net.

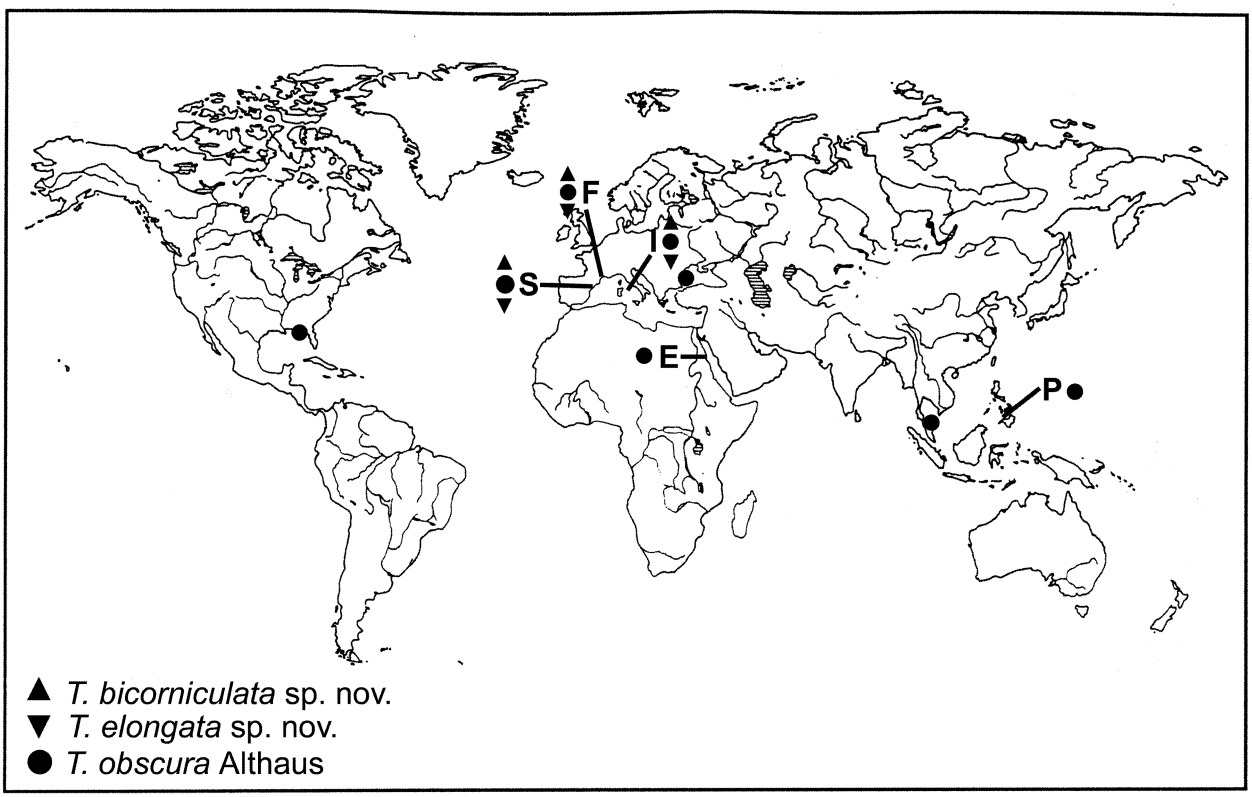

FIGURE 1. Map indicating sampling areas and distribution of *Testudinella bicorniculata* **sp. nov.**, *T. elongata* **sp. nov.** and *T. obscura* Althaus. S, Spain; F, France; E, Egypt; I, Italy; P, Philippines.

Specimens of *T. clypeata* were collected in littoral psammon or vegetation from the Channel (Audresselles and Wimereux, France), the Zwin (Belgium), the Eastern Scheldt and Veerse Meer (the Netherlands), and from the Amurskii Bay, Sea of Japan (Russia). Specimens of *T. elliptica* (Ehrenberg, 1834) came from different ponds in Belgium.

Animals were examined and drawn using a Leitz Orthoplan microscope equipped with camera lucida. Trophi were isolated by dissolving the animals in NaOCl and then prepared for scanning electron microscopy (SEM) following De Smet (1998). For SEM a Philips SEM 515 microscope operated at 20 kV was used.

Systematics

Phylum ROTIFERA Cuvier, 1812

Class EUROTATORIA De Ridder, 1957

Subclass MONOGONONTA Plate, 1889

Order FLOSCULARIACEAE Harring, 1913

Family TESTUDINELLIDAE Harring, 1913

Genus *Testudinella* Bory de St. Vincent, 1826

***Testudinella bicorniculata* sp. nov.**
(Figs 2 & 3)

Diagnosis. *Testudinella bicorniculata* **sp. nov.** is characterized by two antero-lateral lorica projections; dorsal and ventral anterior margins undulate with shallow median sinus; foot opening sub-terminal, inverted U-shaped slit; distal foot pseudosegment short; manubria with well developed sub-ventral chamber; fulcrum with proximal opening.

Type locality. Mediterranean, Parc national Port-Cros, Île de Bagaud, Pointe de Montrèmian, France: depth 25 m, distance from shore ~8 km, 27 July 2006.

Holotype. A female in a permanent, glycerine glass slide mount deposited in the Royal Belgian Institute of Natural Sciences (RBINS), Brussels, Belgium, No. IG. 30986, RIR 190.

Paratypes. 8 females from type locality. One female in RBINS (RIR 191); one female in ANSP 1973; one mounted paratype and 5 SEM trophi preparations in department of Biology, University of Antwerp.

Additional material. 16 females collected in psammon from Mediterranean: Spain, Bègur, Bay of Aiguafreda, Furio de Aiguaxelida (3), depth 28 m, distance from shore ~250 m, water temperature 24 °C, 17 August 2006; Italy, Elba Island: Punta Madonna (1), La Fonza Esterna (4), La Formiche di Ponente (5), Scoglietto di Portoferraio (2), Scoglio della Nave Enfola (1), depth 30–40 m, distance from shore ~50–1000 m, 25–30 September 2006.

Etymology. The name of the species is composed of the Latin *bis*, meaning twice, and the Latin adjective *corniculata*, meaning provided with a small horn, and refers to the small antero-lateral projections of the lorica.

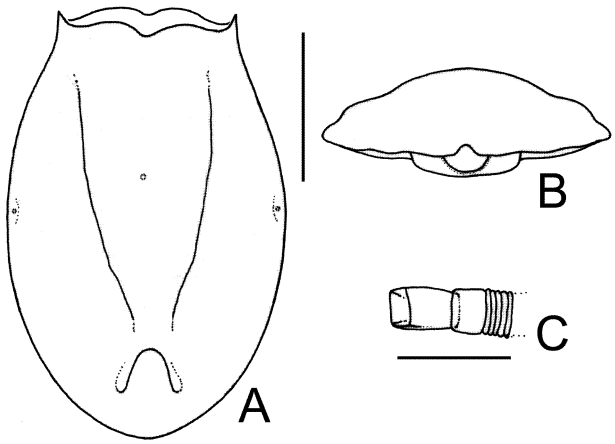

FIGURE 2. *Testudinella bicorniculata* s**p. nov. A.** Lorica, ventral view. **B.** Lorica, caudal view. **C.** Foot pseudosegments. Scale bars: A, B: 50 µm, C: 25 µm.

Description of female. The smooth lorica (Fig. 2A) is vase-shaped, truncate anteriorly with acute antero-lateral projections; ratio length/width 1.39–1.55 (average 1.50). The dorsal and ventral anterior margins are undulate with shallow median sinus; the dorsal anterior margin is slightly projecting beyond the ventral margin. The posterior margin is smoothly rounded or very weakly rounded-angular. Ventrally two longitudinal furrows delimit a protruding median part. In cross-section (Fig. 2B) the lorica is slightly arched dorsally with shallow elevation near the lateral margins; ventrally almost flat with median part weakly

protruding. The foot opening is an inverted U-shaped slit widening distally, situated near posterior 1/5 on the ventral side. The foot is composed of a long wrinkled proximal part, a short penultimate pseudosegment, and a slightly longer distal pseudosegment ending in a ciliated cup (Fig. 2C). The ratio lorica length/position of antennae relative to dorsal anterior margin varies between 2.50–3.04 (average 2.72) for the dorsal antenna and 2.03–2.36 (average 2.18) for the lateral antennae. Two red eyespots.

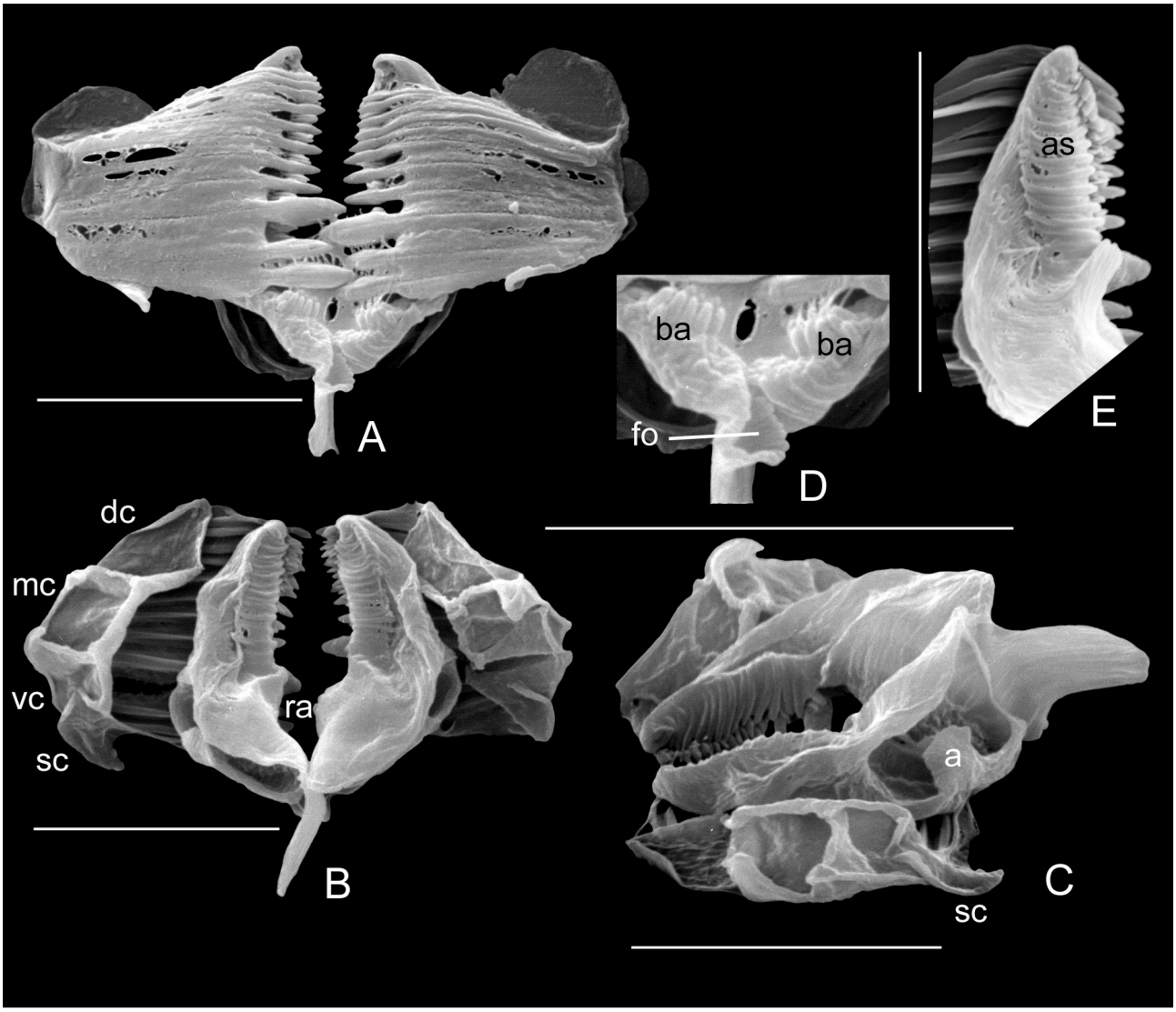

FIGURE 3. *Testudinella bicorniculata* **sp. nov.**, scanning electron microscope photographs of trophi. **A.** Complete set, frontal view. **B.** Complete set, caudal view. **C.** Complete set, lateral view. **D.** Detail proximal fulcrum opening and basal apophyses. **E.** Detail left ramus with arched scleropili. Scale bars 10 µm. a: alula, as: arched scleropili, ba: basal apophyses, dc: dorsal chamber, fo: fulcrum opening, mc: median chamber, sc: sub-ventral chamber, vc: ventral chamber

Trophi malleoramate (Fig. 3). The rami are elongate-triangular with rounded latero-ventral margins, and short caudally recurved blunt alulae (Fig. 3C: a). Basal and subbasal chambers not separated by partition, forming a large chamber opening latero-ventrally by a large common fenestra. Asymmetrical and interlocking median rami apophyses (Fig. 3B: ra) are apparent in caudal view. The inner margins of the distal rami sections bear 11–14/11–16 (left/right) arched and fairly strongly webbed rami scleropili (Fig. 3E: as). The basal apophyses (Fig. 3D: ba) are moderately developed ridges, composed of a series of fused scleropili. The fulcrum is short and plank-shaped, more or less trapezoid in lateral view. It is composed of a double layer of longitudinally oriented and appressed sclerite bodies, the caudal series of which is involved in the formation of the junction with the rami, and an anterior series which border a distinct opening proximally (Fig. 3D: fo).

The unci plates consist of 10–11/10–11 (right/left) straight teeth, running parallel and strongly webbed, with interlocking heads; space between teeth fairly large. Each uncus has three major teeth, the midst distinctly the smallest, with strongly clubbed head (Fig. 3A). The head of the minor teeth is weakly offset, relatively long and more or less cylindrical. The crescent shaped manubria are composed of the superimposed dorsal, median and ventral chamber, and moreover show a well developed sub-ventral chamber (Figs B, C: sc).

Male unknown.

Measurements. Lorica length 124–143 µm (mean=135 µm, N=12), lorica width 87–93 µm (mean=90 µm, N=12), antero-lateral spine 4–6 µm (mean=5, µm, N=20), penultimate foot pseudosegment 7–8 µm (mean=8 µm, N=5), distal foot pseudosegment 14–16 µm (mean=15, N=5); trophi: length × width 16.0–16.5 × 22.0–23.0 µm, ramus 12.0–12.5 µm, fulcrum 4.5–5.5 µm, largest major tooth 11.5–12.0 µm, manubrium 12.0–12.5 µm.

Comments. The new species superficially resembles *T. robertsonae* Koste, 1990 (in Koste & Robertson, 1990) and *T. truncata* (Gosse, 1886) which also bear antero-lateral projections. *T. robertsonae* is more squat (ratio lorica length/width 1.1–1.2 versus 1.4–1.6 in the new species), and shows a transversal elliptical foot opening (inverted-U shaped split in *T. bicorniculata* **sp. nov.**). *Testudinella truncata* is more slender anteriorly, resulting in a more elongate vase-shaped lorica; its foot opening is terminal and more or less rectangular instead of subterminal and U-shaped. A median fold as present at the antero-ventral lorica margin in *T. robertsonae* and *T. truncata* is absent in *T. bicorniculata* **sp. nov.** The trophi of *T. truncata* (De Smet, 2005; no SEM data available for *T. robertsonae*) display a higher number of teeth (12/12) and arched rami scleropili (~22/25), and the heads of its major teeth are more slender and only weakly offset. The most characteristic differences in trophi structure concern the subventral manubrium chambers and proximal fulcrum opening present in the new taxon, but absent in *T. truncata*. Both *T. robertsonae* and *T. truncata* (except for a single specimen record from slightly saline (328 mg $Cl^{-}.L^{-1}$) inland water by Althaus (1957a)), are inhabitants of freshwater.

The morphology of the trophi and shape of the foot opening suggest a relationship with *T. clypeata*, *T. obscura* and *T. elongata* **sp. nov.**

Distribution and ecology. The species was to date only sampled in small numbers from psammon collected in the Mediterranean, at depths of 25–40 m and distances from the shore varying from 50 m to 8 km, during July–September. Water temperatures varied from 21–24 °C. It occasionally co-occured with the related *T. obscura* and *T. elongata* **sp. nov.**

***Testudinella elongata* sp. nov.**

(Figs 4 & 5)

Testudinella sp. n. in De Smet (2005)

Diagnosis. *Testudinella elongata* **sp. nov.** is characterized by its strongly elongate and striate lorica; dorsal anterior margin with broad, flat median part and rounded lateral parts; ventral margin almost straight, rounded laterally; foot opening sub-terminal, inverted U-shaped; distal and penultimate foot pseudosegments long; manubria with well developed sub-ventral chamber; fulcrum with proximal opening.

Type locality. Mediterranean, Bay of Hyères, Île Porquerolles, France: near wreck of Prosper Schiaffino (Donateur), depth 50 m, distance from shore ~4 km, 31 December 2001.

Holotype. A female in a permanent, glycerine glass slide mount deposited in the Royal Belgian Institute of Natural Sciences (RBINS), Brussels, Belgium, No. IG. 30986, RIR 192.

Paratypes. One female from type locality in RBINS (RIR 193); two females from Bègur, Bay of Aiguafreda, Furio de Aiguaxelida, Spain in ANSP 1974; 5 SEM trophi preparations in department of Biology, University of Antwerp.

Additional material. 20 females collected in psammon from Mediterranean: Spain, Bègur, Bay of

Aiguafreda, Furio de Aiguaxelida (2), depth 28 m, distance from shore ~250 m, water temperature 24 °C, 17 August 2006; Italy, Elba Island: Punta Madonna (1), Scoglio della Nave Enfola (7), La Fonza Esterna (1), La Formiche di Ponente (4), Punta della Madonna di Ponente (2), Scoglietto di Portoferraio (3), depth 30–40 m, distance from shore ~50–1000 m, 25–30 September 2006.

Etymology. The species name *elongata* is a Latin adjective, and refers to the elongate lorica.

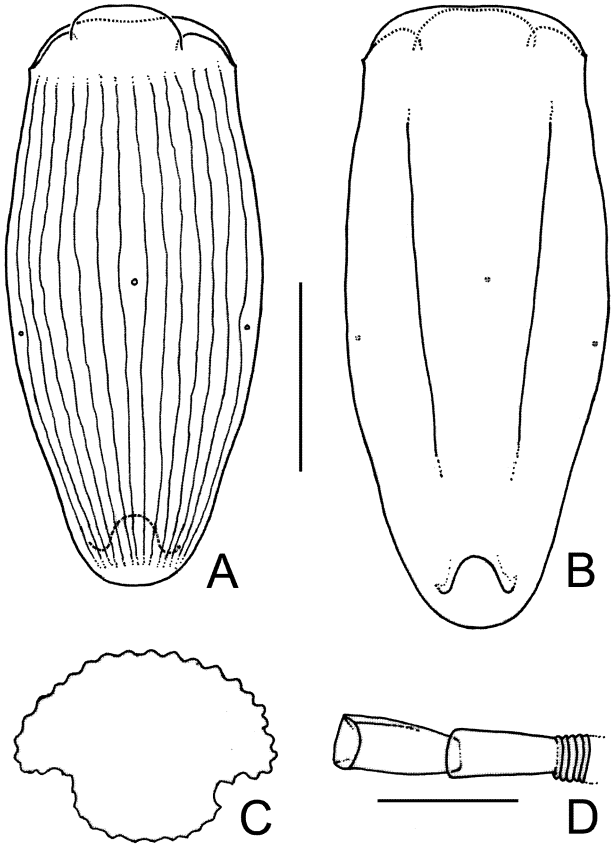

FIGURE 4. *Testudinella elongata* **sp. nov. A.** Lorica, dorsal view. **B.** Lorica, ventral view. **C.** Lorica, cross-sectional view. **D.** Foot pseudosegments. Scale bars A–C: 50 µm, D: 25 µm.

Description of female. The lorica (Fig. 4) is strongly elongate, truncate anteriorly and rounded posteriorly. Ratio length/width 2.22–2.72 (average 2.41). The dorsal surface is ornamented with ~15–20 faint longitudinal ridges. The dorsal anterior margin shows a broad, flat median part connected by shallow folds to smaller rounded lateral lobes. The ventral margin is almost straight with a very broad and shallow median sinus, and rounded lateral edges. The dorsal anterior margin does not or only slightly projects beyond the ventral margin. Ventrally two longitudinal furrows delimit a protruding median part, which is ornamented with very faint longitudinal ridges as well. In cross-sectional view (Fig. 4C) both the dorsal and ventral margin appear arched. The sub-terminal foot opening is a wide inverted U-shaped slit on the ventral side. The foot (Fig. 4D) is composed of a long wrinkled proximal part, and a relatively long penultimate and somewhat longer distal pseudosegment ending in a ciliated cup. The ratio lorica length/position of antennae relative to dorsal anterior margin varies between 2.11–2.40 (average 2.22) for the dorsal antenna and 1.77–1.93 (average 1.83) for the lateral antennae. Two red eyespots.

Trophi malleoramate (Fig. 5). The rami are relatively short elongate-triangular with rounded latero-ventral margins. Alulae (Fig. 5B: a) very weakly developed, pointing caudally. Basal and sub-basal chambers forming a single chamber, opening latero-ventrally by a large common fenestra. Median apophyses shallow, asymmetrical and interlocking. The inner margins of the distal rami sections bear ~13–14/11–12 (left/right)

strongly webbed arched rami scleropili. The basal apophyses are moderately developed ridges, composed of a series of fused scleropili. The fulcrum is short, plank-shaped, and more or less trapezoid in lateral view. It is composed of a double layer of long and appressed sclerite bodies, the caudal series of which is involved in the formation of the junction with the rami, and an anterior series which proximally border a distinct opening (Fig. 5A: fo). The unci plates consist of 9–10/9–10 (right/left) strongly webbed teeth. There are three straight major teeth with distinctly offset head in each uncus; the head of the midst teeth is only slightly smaller than the others. The minor teeth are weakly curved and lie close to each other; their head is elongate-lanceolate. The crescent shaped manubria are weakly sclerotized and composed of the superimposed dorsal, median, ventral and well developed sub-ventral chamber (indistinct in the SEM photographs due to crumpling up of weak manubria).

Male unknown.

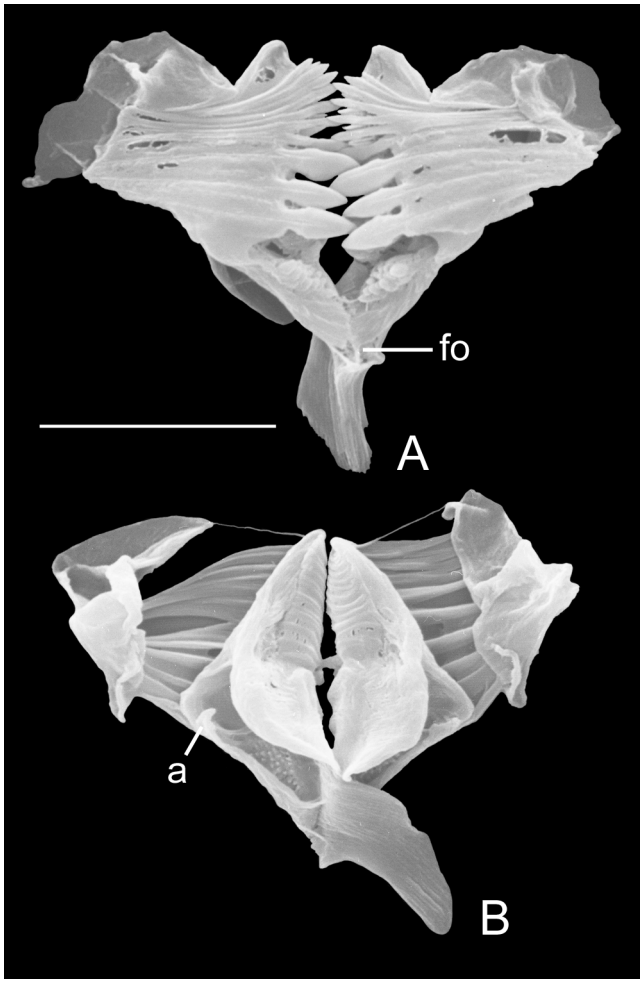

FIGURE 5. *Testudinella elongata* **sp. nov.**, scanning electron microscope photographs of complete set of trophi. **A.** Frontal view. **B.** Caudal view. Scale bar 10 µm. a: alula, fo: fulcrum opening.

Measurements. Lorica length 144–166 µm (mean=159 µm, N=12), lorica width 61–72 µm (mean=66 µm, N=12), penultimate foot pseudosegment 13–18 µm (mean=15 µm, N=9), distal foot pseudosegment 18–20 µm (mean=19, N=10); trophi: length × width 14.5–20.5 × 19.5–23.5 µm, ramus 10.5–14.0 µm, fulcrum 4.0–7.0 µm, largest major tooth 10.5–12.5 µm, manubrium 12.0–12.5 µm.

Comments. *Testudinella elongata* **sp. nov.** can not be confused with any congener. It is a close relative of *T. obscura* by its generally similar shape of the dorsal anterior lorica margin, foot opening and trophi shape, but is easily differentiated from the latter by its elongate lorica and the absence of a distinct V-shaped antero-median notch of the ventral plate. Minute differences in trophi morphology concern the minor teeth which

appear slightly curved in the new species and straight in the latter. With *T. clypeata* and *T. bicorniculata* **sp. nov.** it shares a similar foot opening and fulcrum with proximal opening.

Distribution and ecology. The species is known only from psammon collected in the Mediterranean, at depths of 28–50 m and distances from the shore varying from 50 m to ~4 km, during August, September and December. Water temperatures varied from 18–24 °C. It was always present in small numbers and occasionally co-occurred with the related *T. obscura* and *T. bicorniculata* **sp. nov.** .

***Testudinella obscura* Althaus, 1957**
(Figs 6 & 7)

Material examined. Hundreds of specimens collected in psammon samples from the Mediterranean, Mindanao Sea and Red Sea were examined. The localities at which I found *T. obscura* are as follows:

Mediterranean. (1) France, Bay of Hyères: Île Porquerolles, near wreck of Prosper Schiaffino (Donateur), depth 50 m, distance from shore ~4 km, 31 December 2001; Port Cros, La Gabinière Est, depth 43 m, distance from shore 10 km, water temperature 22 °C, 26 June 2006; Cavalaire, wreck of Espignole, depth 29 m, distance from shore 500 m, water temperature 20 °C, 1 July 2006; (2) Spain, Bègur: Canyons de Tamariu, Illa de Fito, Furio de Fito, depth 21–45 m, distance from shore 250 m, 15–27 °C, 13, 14 and 18 August 2006. (3) Italy, Elba Island: Ligurian Sea: Punta della Madonna, Scoglio della Nave Enfola, La Formiche di Ponente, Punta della Madonna di Ponente, Picco Giallo, Scoglietto di Portoferraio; Tyrrhenian Sea: Il Relitto di Pomonte (wreck of Elviscott), La Fonza Esterna; depth 10–40 m, distance from shore ~50 m to 1 km, water temperature 21–23 °C, September 2006.

Mindanao Sea, the Philippines: Bohol Island (Garden Eel), Balicasag Island, Siquijor Island (Tubod Sanctuary, Sawang), Apo Island (Cogon, The Chapel), Negros Island (Dauin); April 2007, depth 8–30 m, distance from shore ~10 m to 5 km, water temperature 28 °C, April 2007.

Red Sea, Egypt: Sha'ab Maksour, Abu Galawa Sougair, Sha'ab Marsa Alam, Abu Dabbab, El Shona; depth 15–30 m, water temperature 29 °C, October 2006.

Description of female. The lorica (Fig. 6) is more or less elliptical, weakly truncate anteriorly, smooth or occasionally very weakly striated (Fig. 6F). Ratio lorica length/lorica width 1.43–1.71 (average 1.54). The dorsal anterior margin shows a broad, flat median part connected by shallow folds to smaller rounded lateral lobes. The ventral margin is slightly convex (Fig. 6D, F) to weakly undulate (Fig. 6A–C, E), with shallow median indentation. The dorsal anterior margin is not or slightly projecting beyond the ventral margin. The posterior margin is smoothly rounded or very weakly rounded-angular. In cross-section (Fig. 6G) the lorica is slightly arched dorsally with shallow elevation near the lateral margins; ventrally almost flat with median part protruding. The foot opening is sub-terminal, on the ventral side; it takes the shape of an inverted U-shaped slit, the lateral margins of which sometimes appear undulate (Fig. 6C). The foot is composed of a long wrinkled proximal part, a short penultimate and a longer distal pseudosegment ending in a ciliated cup. The ratio lorica length/position of antennae relative to the antero-dorsal margin varies between 2.40–2.88 (average 2.60) for the dorsal antenna and 1.97–2.23 (average 2.07) for the lateral antennae. Two red eyespots.

Trophi malleoramate (Fig. 7). The rami are elongate triangular with rounded latero-ventral margins, and very short blunt alulae (Fig. 7D: a). Basal and subbasal chambers forming single large chamber, opening latero-ventrally by a large common fenestra. Asymmetrical and interlocking median apophyses are apparent in caudal view. The inner margins of the distal rami sections bear 10–16/11–16 (left/right) arched and strongly webbed rami scleropili. The basal apophyses are moderately developed ridges, composed of a series of fused scleropili. The fulcrum is short, plank-shaped, and more or less trapezoid in lateral view. It is composed of a double layer of long and appressed sclerite bodies, the greatest part of which is involved in the formation of the junction with the rami, and another series situated anteriorly which border a distinct proximal opening (Fig. 7A: fo). The unci plates are composed of 10–12/11–12 (left/right) straight and strongly webbed teeth, lying parallel. There are three major teeth with distinctly offset club-shaped head in each uncus; the head of

the midst tooth is distinctly smaller than the others. The space between the minor teeth is fairly large, and their weakly offset head is cylindrical to elongate-lanceolate. The crescent shaped manubria are composed of a superimposed dorsal, median, ventral and well developed subventral chamber (Fig. 7B: sc).

Male unknown.

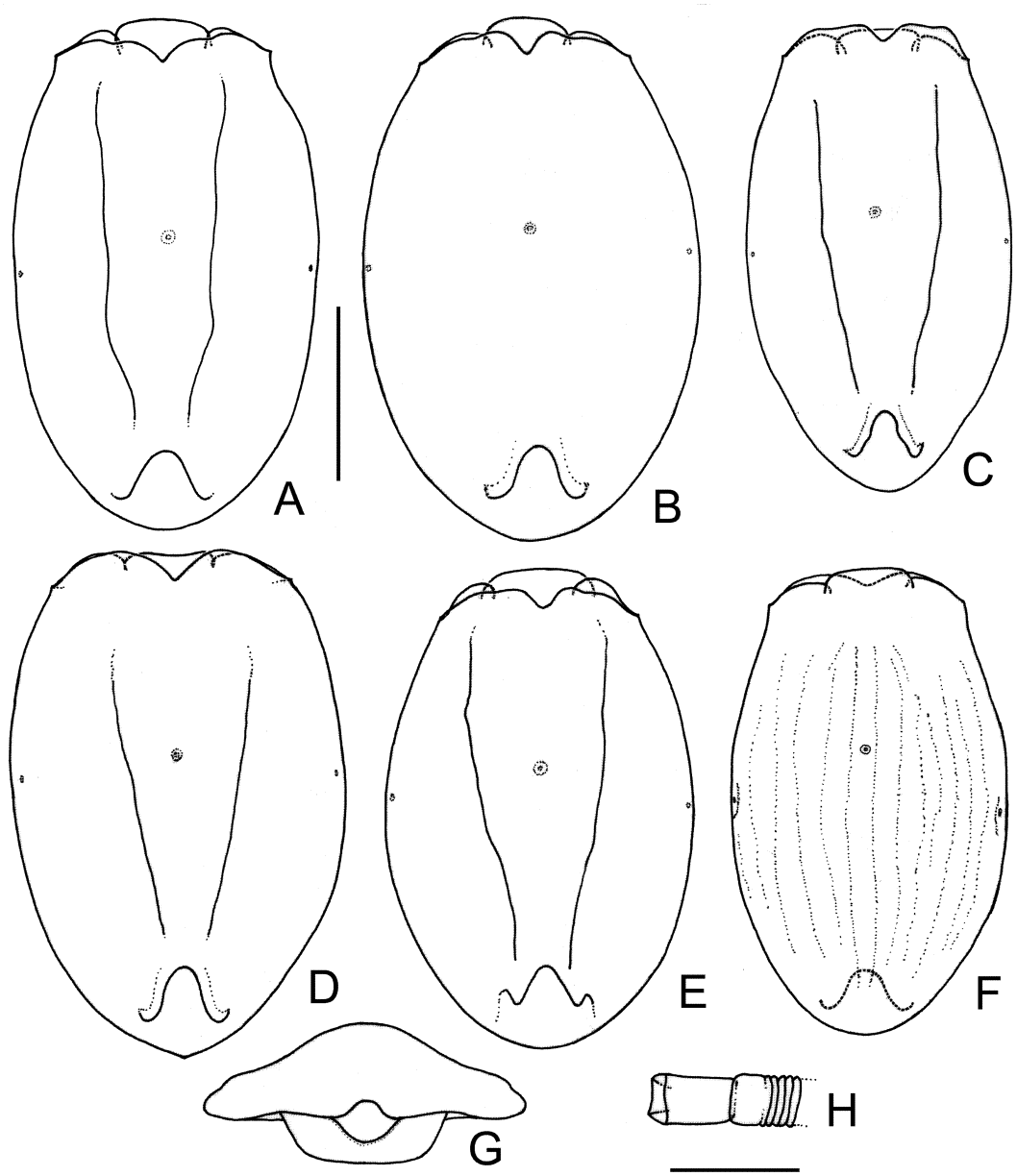

FIGURE 6. *Testudinella obscura*. **A–E.** Loricae, ventral view. **F.** lorica, dorsal view. **G.** Lorica, caudal view. **H.** Foot pseudosegments. Scale bars: A–G: 50 µm, H: 25 µm.

Distribution and ecology. The species was originally described (Althaus 1957b) from littoral mesopsammon (3 mm), 15–20 m from the shore, of the Bulgarian part of the Black Sea at Spatnite pjasatzi near Varna, July, salinity ~18 %. Only a few more, but undocumented records exist from Russia (White and Barents Sea), Europe (the Channel, Mediterranean), USA (Gulf of Mexico) and a tidal river on Peninsular Malaysia. Studying zooplankton in 104 arctic rockpools of different salt content along the shores of the islands in the White and Barents Sea, Ghilarov (1967) reports the species from (percentages of water bodies the species was found in the areas of the respective seas bracketed) fresh (14 and 25 %), brackish (3 and 17 %) and marine (25 and 60 %) waters. The records from the Channel, Europe are by d'Hondt (1970), who found in

total four specimens among *Enteromorpha* in a puddle at Roc'h kroum and the harbour of Roscoff, and in a nursery tank of the Station Biologique (July, October). Menéndez & Comín (1986) and Forés *et al.* (1986) reported *T. obscura* from coastal lagoons of the Ebro Delta (N. E. Spain), located at the western part of the Mediterranean. Studying rotifer distribution in interstitial sand of a small brackish-water beach in Florida, USA (Okalossa Isl., Santa Rosa Sound), Turner (1993) collected *T. obscura* in the top 4 cm of sand of the intertidal zone (August, water temperature 38 °C, pH 6.5). Green (1995) found a single specimen in plankton of the Chukai river estuary opening into the South China Sea, Malaysia (28.2 °C, 3,800 µScm at high tide). Speaking from my experience with marine rotifers, I have not found yet the species in samples, both psammon or periphyton, from the North Sea, the Channel, and arctic rockpools or littoral from Svalbard (Spitsbergen) and Greenland, and neither did Godske Eriksen (1968), Godske Björklund (1972) observe it in rock-pools and shore-pools, or among sub-littoral algae and bottom sediments from western Norway and southern Finland. I therefore consider the observations by Ghilarov (1967) and d'Hondt (1970) as misidentifications of e.g. young *T. clypeata* (Müller, 1786).

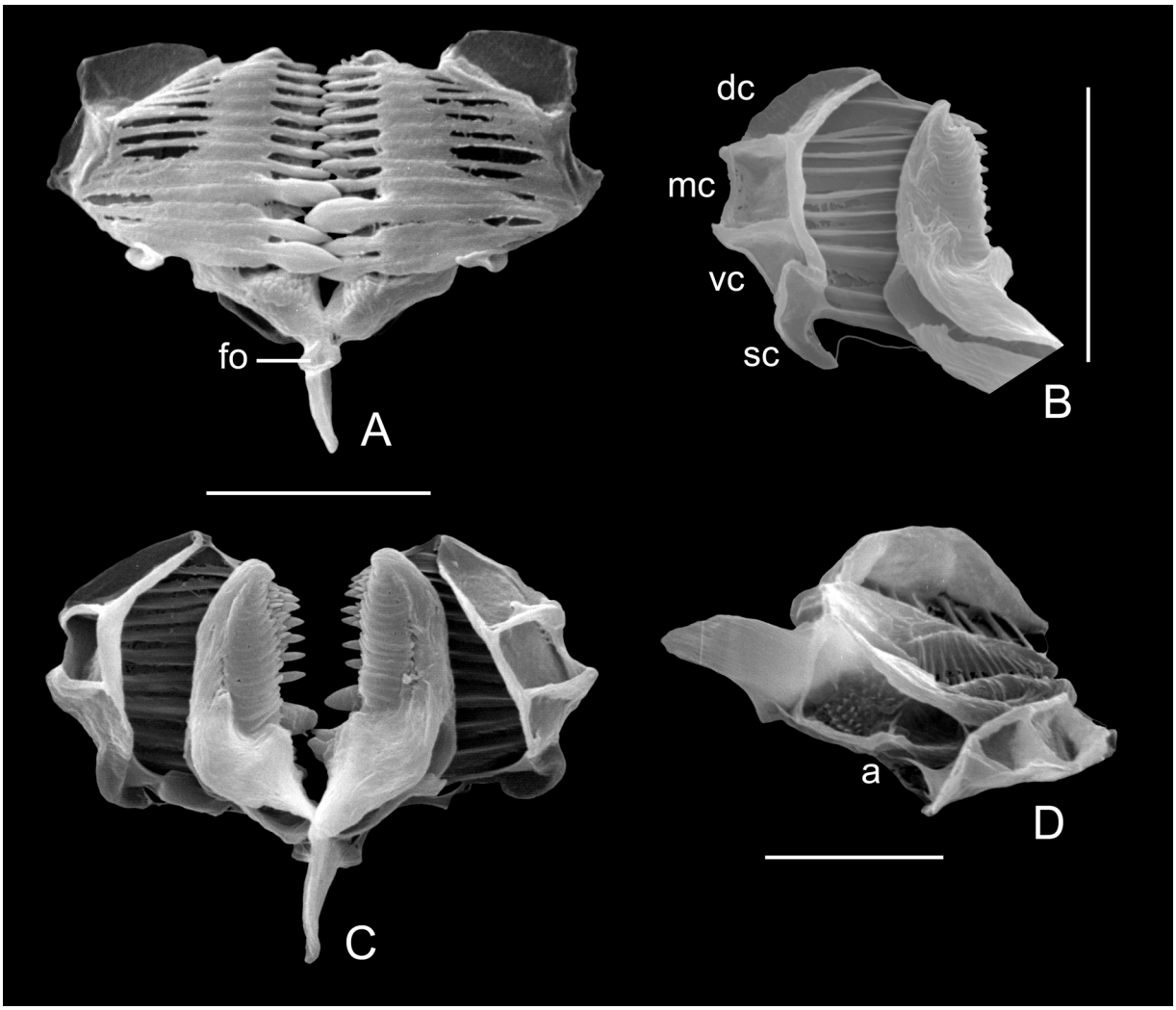

FIGURE 7. *Testudinella obscura*, scanning electron microscope photographs of trophi. **A.** Complete set, frontal view. **B.** Detail left manubrium. **C.** Complete set, caudal view. **D.** Complete set, lateral view. Scale bars: 10 µm. a: alula, dc: dorsal chamber, fo: fulcrum opening, mc: median chamber, sc: sub-ventral chamber, vc: ventral chamber.

From the observations considered valid it follows that the species is widespread (Fig. 1) and apparently perennial. The water temperatures of 15–38 °C it was found, suggest that it prefers warm waters. It occurs from the intertidal zone to at least 10 km off shore, up to a depth of 50 m, and I agree with Turner (1993) that *T. obscura* appears to be an interstitial element and may live only in that habitat (the single specimen report

from plankton by Green (1995) must be considered as an accidental introduction). *Testudinella obscura* was present in 24 of the 38 subtidal psammon samples studied here and as such it was the most frequent, and often even only species observed. It usually was also the most abundant rotifer and only outnumbered locally by the monogonont *Lindia gravitata* (Lie-Pettersen, 1905) and the bdelloid *Rotaria laticeps* Wulfert, 1942.

The variation of the lorica (Fig. 6) was not related to any sampling locality or area.

***Testudinella clypeata* (Müller, 1786)**
(Figs 8–10)

T. clypeata typica after Voigt (1957), *T. elliptica* after Jersabek *et al.* (2003, ANSP Catalog Number 1828)
? non *T. clypeata* after Rousselet (1898), Dieffenbach & Sachse (1912) and Bartoš (1951, Figs 7, 8), *T. crassa* after Harring (1913), *T. clypeata* var. *crassa* after Remane (1929) and Voigt (1957), *T. clypeata crassa* after Wiszniewski (1954) and Bērziņš (1960)
non *T. clypeata* after Bartoš (1951, Figs 3, 4), *T. clypeata dentata* after Wiszniewski (1954), *T. clypeata* f. *pseudoclypeata* Koste (1978)

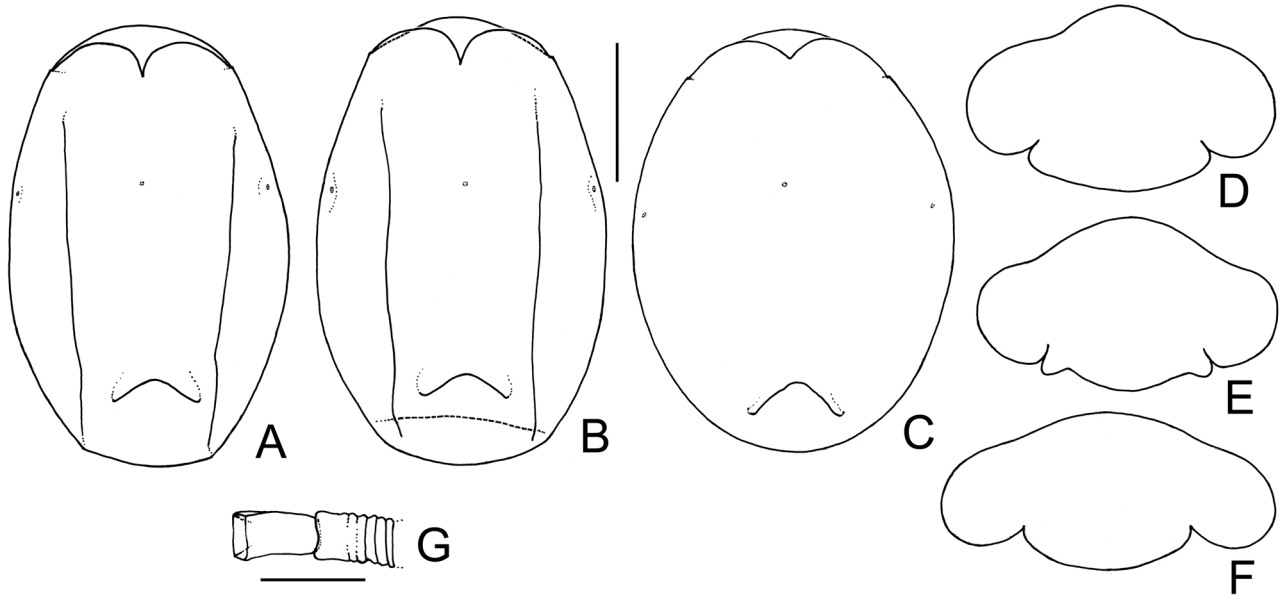

FIGURE 8. *Testudinella clypeata*. **A–C.** Loricae, ventral view. **D–F.** Loricae, cross-sectional view. **G.** Foot pseudosegments. Scale bars: A–F: 50 µm, G: 25 µm.

This species is easily recognized by the elliptical lorica (length/width ratio 1.30–1.55, average 1.45), which is often slightly angular postero-laterally (Figs 8A, 9C) apparently depending on the state of contraction or fixation (Fig. 9). The dorsal anterior margin is convex, and the ventral anterior margin shows a broad V-shaped sinus; a dorsal transversal fold is often present at the end of the lorica. In cross-sectional view (Fig. 8D–F) the dorsal margin appears convex, the lateral edges are broadly rounded and separated by a shallow sulcus from a convex median part ventrally. The characteristic foot-opening is a wide inverted U-shaped slit, situated ventral and sub-terminal. The foot (Fig. 8G) is composed of a long and wrinkled proximal part, a clearly offset slender distal pseudosegment and a less defined short penultimate pseudosegment. The dorsal and lateral antennae are situated somewhat posterior to the anterior third of the lorica: ratio lorica length/position of antenna(e) relative to antero-dorsal margin varying from 2.70–2.85 (average 2.75) and 2.35–2.75 (average 2.58) respectively. Two red eyespots.

The trophi (Fig. 10 and De Smet (2005)) are characterized by 14–16/14–16 (left/right) unci teeth. The three major teeth show a slender and distinctly offset head. The manubria are composed of three large

superimposed chambers, the dorsal, median and ventral, and a strongly reduced sub-ventral chamber (Fig. 10B: sc). About 28–30/25–26 arched rami scleropili are apparent in caudal view. The fulcrum shows a distinct proximal opening frontally (Fig. 10: fo).

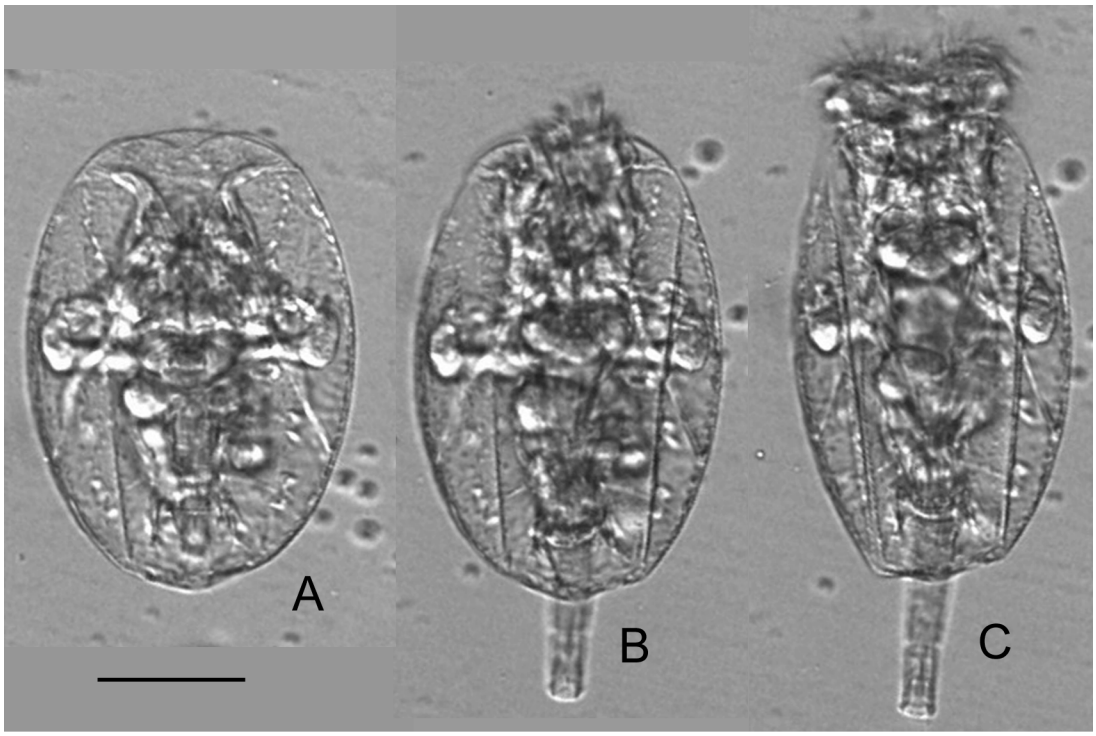

FIGURE 9. *Testudinella clypeata*, variation in shape of specimen. **A, B.** Contracted. **C.** Swimming. Scale bar: 50 µm.

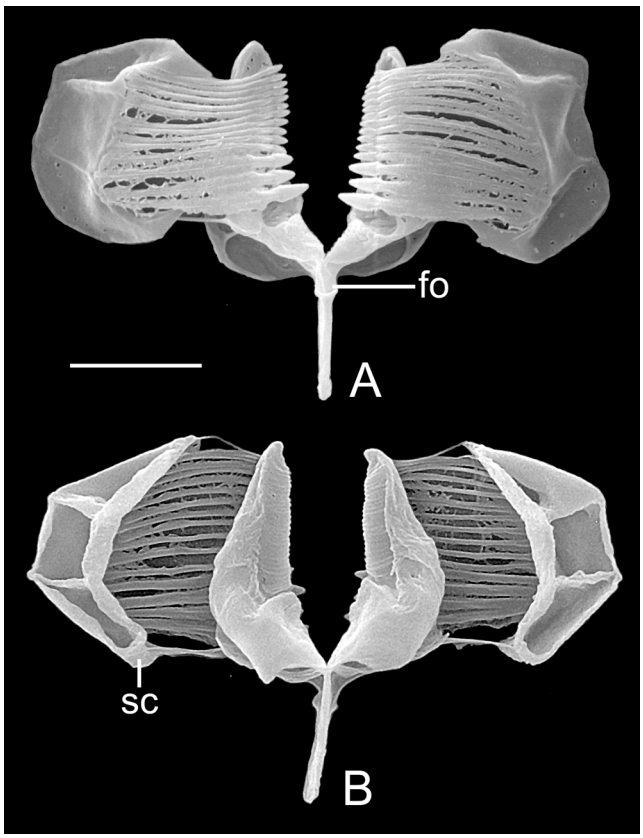

FIGURE 10. *Testudinella clypeata*, scanning electron microscope photographs of complete set of trophi. **A.** Frontal view. **B.** Caudal view. Scale bar: 10 µm. fo: fulcrum opening, sc: sub-ventral chamber.

Measurements. Lorica length 150–170 µm, lorica width 100–130 µm, distal foot pseudosegment 18–22 µm.

According to De Ridder & Segers (1997), *T. clypeata* is a widespread species occurring in the marine littoral and brackish waters all over the Palaearctic region. The species has apparently often been confused with *T. elliptica*, however, the reliable illustrated records by De Manuel et al. (1992), De Maeseneer (1980), De Ridder (1957a, b, 1967, 1972), Gillard (1947), Hudson & Gosse (1886), Seehaus (1930), von Hofsten (1911), Wulfert (1942) and personal observations confirm this general distribution. The reports from freshwater habitats are probably misidentifications concerning *T. elliptica*. De Ridder & Segers (1997) also report the species from the Nearctic region (Cap Breton Island, Nova Scotia, Canada), incorrectly referring to Chengalath & Koste (1988). However, the specimens mentioned sub *T. elliptica* by Jersabek et al. (2003; ANSP Catalog Number 1828) and originating from a brackish pool near Atlantic City, New Jersey, USA are distinctly *T. clypeata*, illustrating the species' presence in the Nearctic.

***Testudinella elliptica* (Ehrenberg, 1834)**
(Figs 11 & 12)

Synonym: *T. pseudoclypeata* Bērziņš, 1943, *T. clypeata* f. *pseudoclypeata* after Koste (1978)
non *T. elliptica* after Bartoš (1951, Figs 7, 8) and Jersabek *et al.* (2003, ANSP Catalog Number 1828)

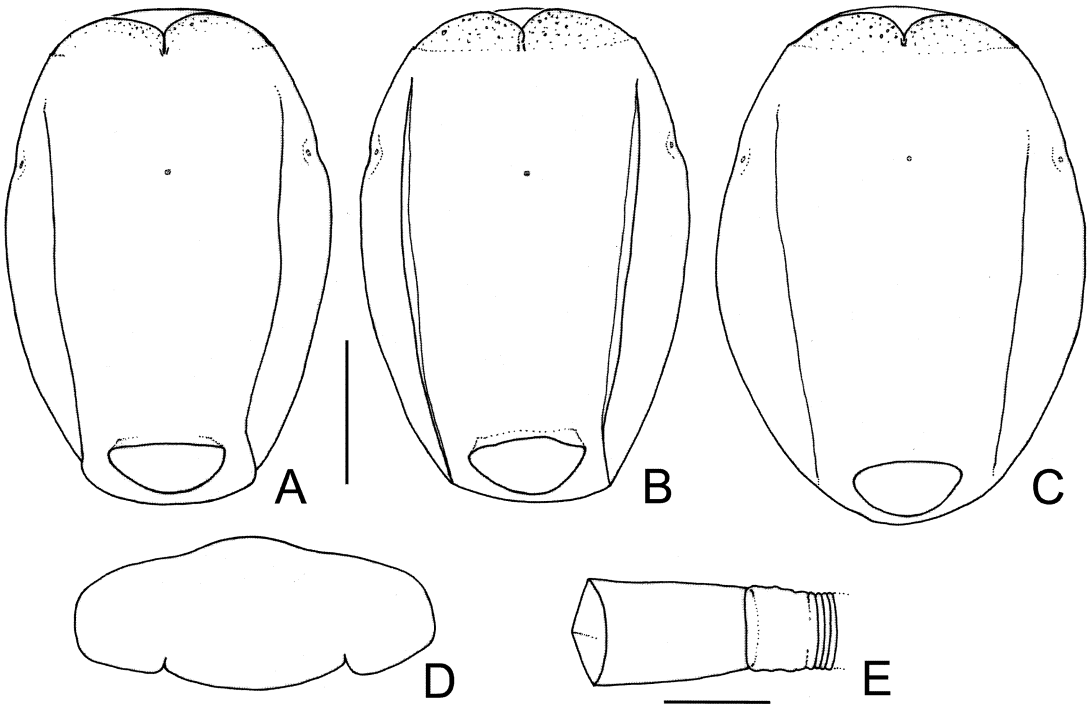

FIGURE 11. *Testudinella elliptica*. **A–C.** Loricae, ventral view. **D.** Lorica, cross-sectional view. **E.** Foot pseudosegments. Scale bars: A–D: 50 µm, E: 25 µm.

Testudinella elliptica has often been confounded with *T. clypeata*, due to the rather similar lorica outline and shape. The antero-dorsal margin is convex, the antero-ventral one shows a broad V-shaped sinus; the two antero-ventral lobes are finely granulated. Ratio lorica length/lorica width 1.40–1.65 (average 1.53). The most characteristic features distinguishing *T. elliptica* from *T. clypeata* are its large, more or less semi-lunar ventral foot opening situated close to the posterior edge (Fig. 11A–C), the massive distal (Fig. 11E) and short penultimate foot pseudosegment, and the more anteriorly placed dorsal and lateral antennae, with the ratio lorica length/position of antenna(e) relative to dorsal anterior margin varying between 3.00–3.40 (average

3.16) and 3.30–3.60 (average 3.43) respectively. The lorica is usually also slightly, more or less abruptly narrowing anteriorly at the height of the lateral antennae. In cross-sectional view (Fig. 11D) the dorsal margin appears convex, the lateral edges are broadly rounded continuing more or less strongly flattened ventrally, and becoming separated from a more or less convex median part by shallow sulci. Two red eyespots.

The trophi (Fig. 12, and De Smet (2005)) have 16–17/16–17 (left/right) uncinal teeth, with very slender and only weakly offset heads, bearing two small lateral knobs at their base. The manubria consist of three large superimposed chambers and a strongly reduced sub-ventral chamber. The number of arched rami scleropili is ~50/46–66 (left/right). The fulcrum lacks a proximal opening frontally.

Measurements. Lorica length 170–250 µm, lorica width 105–205 µm, distal foot pseudosegment 36–40 µm.

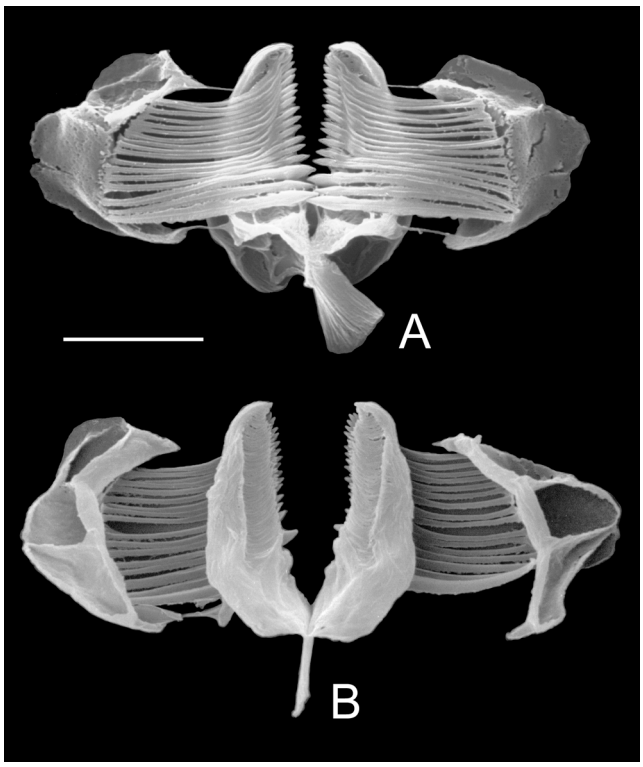

FIGURE 12. *Testudinella elliptica*, scanning electron microscope photographs of complete set of trophi. **A.** Frontal view. **B.** Caudal view. Scale bar: 10 µm.

Testudinella elliptica is a widespread species reported from the Palaearctic, Nearctic, Oriental and Neotropical regions (De Ridder & Segers 1997). It is primarily an inhabitant of fresh waters, living among submerged vegetation and in benthos, or as epibiont on *Asellus aquaticus* (Linnaeus, 1758) (Crustacea, Isopoda). The reports from marine and brackish habitats (see also Fontaneto et al. (2006)) have to be interpreted with caution and may concern occasional introductions or confusions with *T. clypeata*. In this respect it is interesting to mention that in culture experiments with *T. elliptica*, de Beauchamp (1928) observed that specimens died at a 0.2 % salt concentration, and he wonders claiming that ‘the species is euryhaline and living also in brackish waters’.

Bērziņš (1943) described *T. pseudoclypeata* from a freshwater pond in Lettland, and considered the species closely related to *T. clypeata*. According to Segers (2007) *T. pseudoclypeata* is a synonym of *T. clypeata*, occasionally considered an infrasubspecific variant of the latter. Bērziņš (1943) considered the transverse-oval foot opening and flattened shape of the ventro-lateral and medio-ventral margins as characters distinguishing it from *T. clypeata*. However, a large transversal foot opening, flattened ventro-lateral margins, as well as the ratio lorica length/position lateral antennae = 3.6 (which can be derived from Bērziņš’ Fig. 25) are typical for *T. elliptica.* The degree of flattening of the median ventral part largely depends on the state of

development of the vitellarium. Consequently there are no characters differentiating between *T. pseudoelliptica* and *T. elliptica*, and it is concluded that the two names are synonyms.

***Testudinella crassa* (Levander, 1894) sp. inq.**
(Fig. 13)

T. clypeata after Rousselet (1898), Harring (1913), Koste (1978) and Segers (2007), *T. clypeata* var. *crassa* after Remane (1929) and Voigt (1957), *T. clypeata crassa* after Wiszniewski (1954) and Bērziņš (1960)

This poorly described taxon is characterized by a convex dorsal anterior margin, and a slightly undulate ventral anterior margin with small rounded median sinus bordered by two acute projections (dorsal and ventral was wrongly interpreted in the original description). The lorica outline is oval with shallow lateral indentations at the height of the foot. The sub-terminal foot opening is a wide, inverted U-shaped slit. A specimen with similarly shaped anterior margins was figured by Rousselet (1898) sub *T. clypeata*. Its outline is elliptical instead of oval and the lateral margins of the foot opening show an indentation; the lateral antennae are situated a little above the middle. However, similar variations in shape of the lorica and foot opening are evident in other species as well, and I consider the animals described by Levander (1894) and Rousselet (1898) most likely identical.

Measurements (values by Rousselet (1898) bracketed). Lorica length 157–162 µm (150 µm), lorica width 113–121 µm (102 µm).

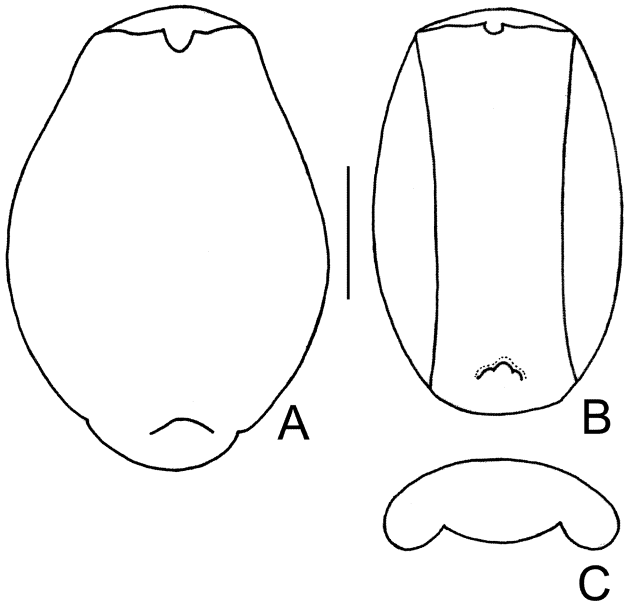

FIGURE 13. *T. crassa*, lorica. **A.** Ventral view. **B.** Ventral view, ? sub *T. clypeata*. **C.** Cross-sectional view, ? sub *T. clypeata*. Scale bar: 50 µm. A after Levander (1894); B, C after Gosse (1898).

The species was described from beach pools and seawater (Gulf of Finland), but freshwater ditches as well. The specimens studied by Rousselet (1898) originated from brackish tide pools of the Tay estuary, Scotland, UK. In her study on marine rotifers from beach pools in southern Finland Godske Björklund (1972) reported a population with forms corresponding to *T. crassa*, and clearly distinguished from populations of *T. clypeata* by lorica length and width as well. However, because of intermediate sizes of *T. clypeata* collected in western Norway, but without taking into consideration morphological aspects, she concluded that *T. crassa* does not seem to be a separate species.

Testudinella crassa has been synonymized with *T. clypeata* without convincing argumentation, but the

characteristic anterior margins suggest a valid species, and I suggest that it be treated as *species inquirenda* until more information becomes available.

Testudinella dentata **Myers, 1934**
(Fig. 14)

T. clypeata dentata after Wiszniewski (1954), *T. clypeata* after Koste (1978) and Segers (2007)

The lorica outline is oval and truncate anteriorly. The dorsal anterior margin is convex, projecting in the form of two lobes separated by a shallow and broad median sinus; the ventral anterior margin is weakly undulate and shows a rounded median sinus bounded by two acute projections. The lateral antennae are situated slightly above the middle. Foot opening a weakly arched transversal slit, located near the posterior 1/5th of the lorica. In cross-sectional view symmetrical both dorsally and ventrally, appearing much compressed, with rounded lateral margins and slightly inflated part in the middle.

Measurements. Lorica length 150 µm, lorica width 90 µm.

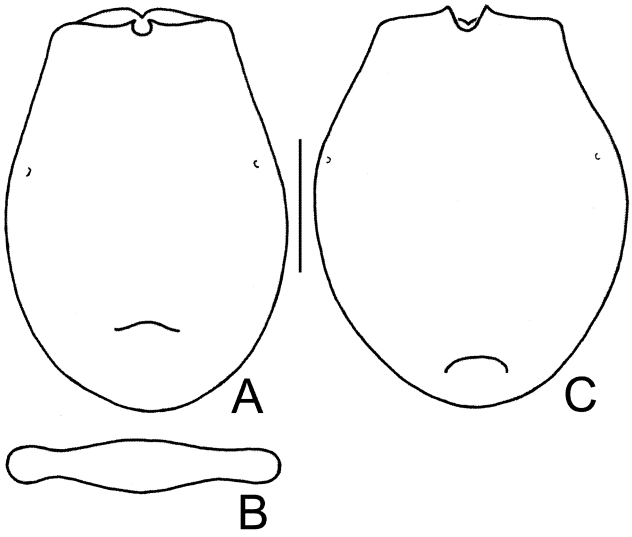

FIGURE 14. *Testudinella dentata*, lorica. **A.** Ventral view. **B.** Cross-sectional view. **C.** Ventral view. Scale bar: 50 µm. A, B after Myers (1934); C after Chengalath & Koste (1988).

The species was originally described from brackish water near the outlet of the Barcelona at Thomas Cove, and brackish water in Powell's Creek, Atlantic County, New Jersey, USA. Chengalath & Koste (1988) found it in temporary water bodies of Cape Breton Island, Nova Scotia, Canada.

Koste (1978) and Jersabek *et al.* (2003) doubt on the taxonomic status of *T. dentata* and suggest that it may be a synonym of *T. clypeata.* However, on close examination Chengalath & Koste (1988) conclude that both species are quite distinct, based on the general shape, the shape of the anterior margins, the position of the lateral antennae, foot opening and size, and consider *T. dentata* to be a valid species.

Testudinella patina **(Hermann, 1783)**
(Figs 15 & 16)

The lorica outline (Fig. 15A) is almost circular or very weakly elliptical: ratio length/width 1.05–1.20. The ventral anterior margin has a broad and shallow median sinus; the dorsal anterior margin is weakly convex to

almost straight, or shows three more or less pronounced shallow lobes. In dorsal/ventral view the lorica bears a band of irregular stipples of unequal diameter laterally and caudally, which in cross-sectional view appear to be the junctures of rod-shaped structures connecting the dorsal and ventral parts of the lorica. In cross-sectional view (Fig. 15B) the lorica margins are more or less sharp and protruding, the dorsal margin is flat or weakly convex, and the ventral margin is broadly arched and usually higher than the dorsal one. The foot opening is circular, situated ventrally near the middle or somewhat below the middle of the lorica. The distal foot pseudosegment (Fig. 15C) is relatively short and only weakly offset from the wrinkled proximal part of the foot; penultimate pseudosegment absent or indistinct. The dorsal and lateral antennae are located at almost the same height: ratio lorica length/distance antennae from antero-dorsal margin 3.25–3.55. Two red eyespots.

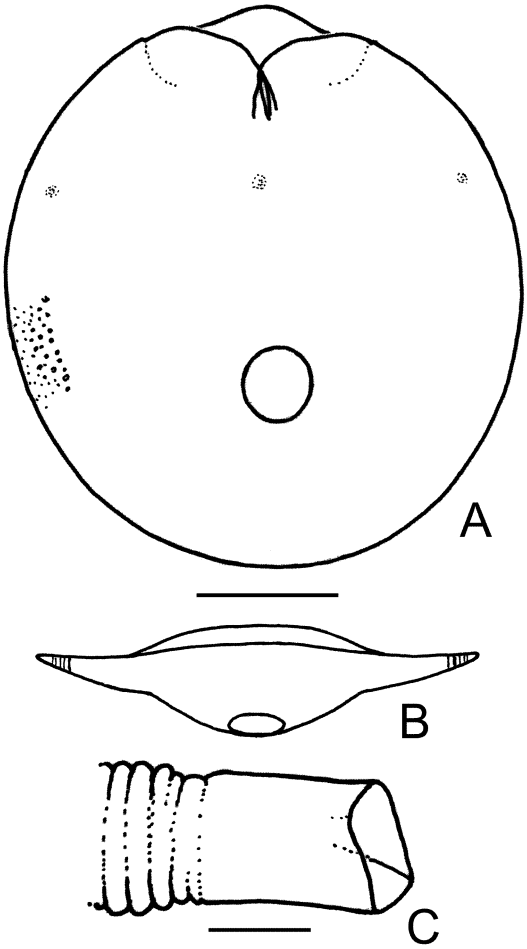

FIGURE 15. *Testudinella patina*. **A.** Lorica, ventral view. **B.** Lorica, caudal view. **C.** Distal foot pseudosegment. Scale bars: A, B: 50 µm, C: 25 µm.

The trophi (Fig. 16, and De Smet (2005) have 12–16/12–16 (left/right) unci teeth, with very slender and only weakly offset heads; heads of major teeth fairly small. The manubria consist of three large superimposed chambers; sub-ventral chamber vestigial. The number of arched rami scleropili is ~31–32/30–31 (left/right). The fulcrum lacks a proximal opening frontally.

Measurements. Lorica length 120-350 µm, lorica width 100-236 µ, distal foot pseudosegment 15–20 µm.

Testudinella patina is an euryhaline cosmopolitan species, common in freshwaters rich in submerged vegetation, but also regularly reported from the marine littoral, and brackish and inland saline waters (De Ridder & Segers 1997; Fontaneto *et al.* 2006).

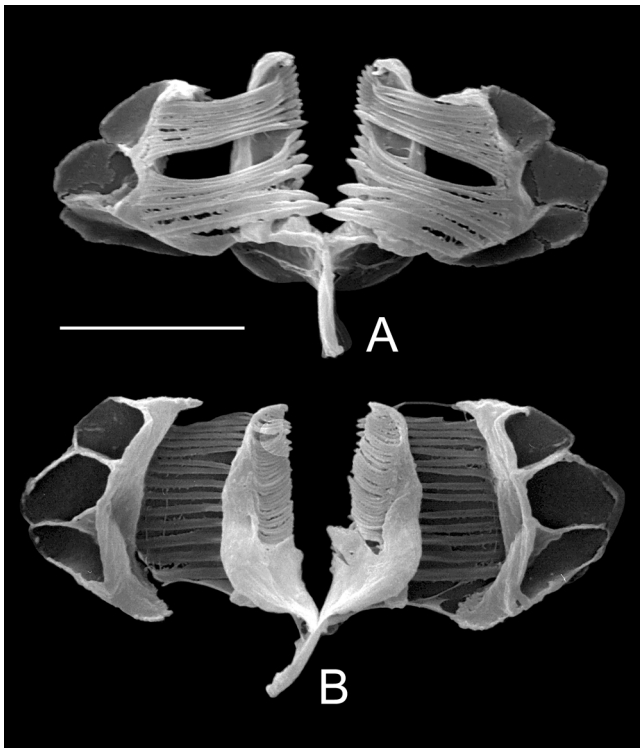

FIGURE 16. *Testudinella patina*, scanning electron microscope photographs of complete set of trophi. **A.** Frontal view. **B.** Caudal view. Scale bar: 10 µm.

Discussion

The similarity in trophi morphology and shape of the foot opening in *Testudinella bicorniculata* **sp. nov.**, *T. elongata* **sp. nov.** and *T. obscura* allow the conclusion that they are closely related. Another close relative may be *T. clypeata* which shares a similarly shaped slit-like foot opening and a proximal fulcrum opening. Such a fulcrum opening is absent in the other *Testudinella* species studied by SEM to date (De Smet, 2005). To date, *Testudinella bicorniculata* **sp. nov.**, *T. elongata* **sp. nov.**, *T. clypeata* and *T. obscura*, are also the only species of the genus occurring in strictly marine habitats. Based on the general morphology, and shape of the foot opening in particular, *T. crassa* and *T. dentata* may be related taxa as well, but a scanning electron microscopic study of the trophi morphology is needed.

The trophi of the new species and *T. obscura* are characterized by the presence of a well developed extra manubrial chamber, the sub-ventral chamber, which was so far not recognized in the malleoramate trophi type. This sub-ventral chamber is apparently weakly developed in the other *Testudinella* species and more or less strongly reduced to an inwardly directed projection, connected by a ligament to the latero-frontal corners of the rami. As such it is probably also present in other Flosculariaceae, for example Conochilidae (Segers & Wallace 2001).

Besides the classically used features used in the taxonomy of *Testudinella*, *viz.* shape of the lorica, shape and position of the foot opening, and position of the lateral antennae, the position of the dorsal antenna and shape of the distal and penultimate foot pseudosegments prove useful additional elements for the differentiation of the species.

Benthic-periphytic marine rotifers are primarily known from inshore habitats, living in intertidal and subtidal psammon and among vegetation. Planktonic species are mainly found in the littoral as well, with only some *Synchaeta* spp. and *Trichocerca marina* (Daday, 1890) being reported from the open oceans (Fontaneto *et al.* 2006). The present findings of rotifers in psammon up to 10 km out of the coastline and a depth of 50 m indicate that they are part of the infauna of offshore habitats as well.

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