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## Rotifera from the Mediterranean Sea, with description of ten new species

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## Abstract

A total of 43 rotifer taxa, belonging to 14 genera, was identified in 47 psammon and periphyton samples collected in the northern part of the western basin of the Mediterranean Sea. Of these, 10 previously described species are new to the Mediterranean, 10 species are new to science and could be described, and 5 others are potential new ones of which insufficient material was available to warrant a full description.

Rotifers formed a constant component of meiofauna, from the eulittoral to at least 8 km off shore and a depth of 66 m. A clear zonation was apparent with one to two species only found in the eulittoral zone and sublittoral fringe, and 42 taxa occurring in the sublittoral zone.

The trophi of seven previously known species are redescribed based on scanning electron microscopy. *Dicranophorus bulgaricus* Althaus, 1957 is redirected to *Allodicranophorus* **gen. nov.** and *Lepadella pontica* Althaus, 1957 to *Halolepadella* **gen. nov.**

**Key words:** *Allodicranophorus*, *Halolepadella*, marine, Mediterranean, biodiversity, psammon, Rotifera

## Introduction

Rotifera are among the least known taxonomic groups in marine and brackish water habitats, to date accounting for a total number of about 115 strictly thalassic species reported world-wide (Fontaneto *et al.* 2006; Appeltans *et al.* 2012). Besides a general lack of knowledge on marine rotifer species diversity, our information on their biogeographical distribution is also very patchy since huge areas of the world remain unexplored, and even for the European seas, which belong to the most intensively studied areas, geographical coverage is incomplete (Costello *et al.* 2006). Information on the thalassic rotifer fauna of the Mediterranean is scarce, and mostly restricted to brackish habitats. Reviews of the rotifer fauna of the Mediterranean Sea were compiled by Ahlrichs (2003), Ricci & Fontaneto (2003), and Fontaneto *et al.* (2006, 2008a), reporting about 90 species with only 21 of them being strictly marine, and seven of them occurring in both marine and inland saline waters. Since then several new species have been described: *Myersinella longiforceps* and *M. uncodonta* from the Tyrrhenian Sea (De Smet 2007), *Lecane insulaconae* from the Northern Adriatic Sea (Fontaneto *et al.* 2008b), and *Testudinella bicorniculata* and *T. elongata* from the Hyères Archipelago (De Smet 2009). Ten new species are described in the present contribution. Morphological and distributional data, as well as the descriptions of the trophi based on scanning electron microscopy, are provided for several other species.

## Material and methods

Samples of algal vegetation and psammon were hand-collected in the eulittoral zone, the sublittoral fringe, and the sublittoral zone; psammon was obtained by scraping ~200 ml of the uppermost centimetre of sand; the sublittoral samples were taken during scuba-diving. Fixation was done on the spot, by adding 35% formalin up to a final concentration of ~4%. The rotifers were extracted in the laboratory by washing the algae or by multiple swirling and decantation of the psammon using filtered seawater, and consequent filtering on a 40 µm mesh width net (Fontaneto *et al.* 2008). Specimens were examined and drawn using a Leitz Orthoplan microscope equipped with camera lucida. Rotifer trophi were prepared with dilute NaOCl according to De Smet (1998). Scanning electron microscopy (SEM) of the trophi was done with a Philips SEM 515, operated at 20 kV.

The areas sampled (Fig. 1) are restricted to the northern part of the western subregion of the Mediterranean Sea, and located in the Balearic Sea at the Costa Blanca and Costa Brava (Spain), the Golfe du Lion, the Hyères Archipelago and the Côte d'Azur (France), and the Tyrrhenian Sea, Elba Island (Italy). The naming of the larger Mediterranean subregions is according to the database MarineRegions.org. by Claus *et al.* (2015). The annotated list of samples is shown in Table 1.

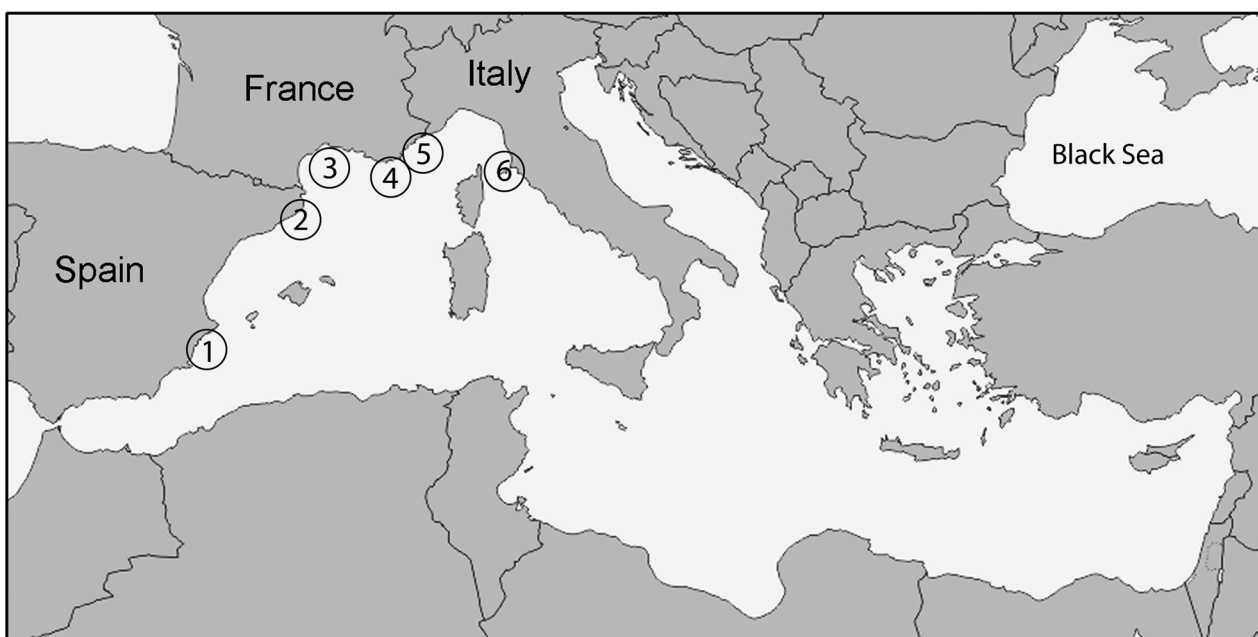
Three major zones are recognized in the discussion on the distribution of the species: the eulittoral zone or part of the shore between high and low tides, the sublittoral fringe extending from the lower limit of the eulittoral to a depth of 5 m, and the sublittoral extending seaward of the sublittoral fringe.

Nomenclature of rotifers follows the candidate 'List of Available Names (LAN) for Phylum Rotifera' (Segers *et al.* 2012; Jersabek & Leitner 2013).

**TABLE 1.** Details of samples.

1. France, Golfe du Lion, Port Vendres, Ansa de l'Espeluga, 15.08.1994, sublittoral fringe, depth 0.5 m, *Enteromorpha* sp.
2. France, Golfe du Lion, Port Vendres, Ansa de l'Espeluga, 15.08.1994, sublittoral fringe, depth 0.5 m, cyanobacterial Aufwuchs.
3. France, Golfe du Lion, Port Vendres, Ansa de l'Espeluga, 18.08.1995, sublittoral fringe, depth 4 m, *Codium fragile* (Suringar) Hariot.
4. France, Golfe du Lion, Port Vendres, Ansa de l'Espeluga, 18.08.1995, sublittoral fringe, depth 4 m, *Corallina* sp.
5. Spain, Balearic Sea, Costa Brava, Cadaqués, 07.1997, sublittoral fringe, depth 3 m, water temperature 17 °C, *Ceramium* sp.
6. Spain, Balearic Sea, Costa Brava, Cadaqués, 07.1997, sublittoral fringe, depth 3 m, water temperature 17 °C, *Cladostephus* sp.
7. Spain, Balearic Sea, Costa Blanca, Benidorm, Punta de Pinet, 22.03.1996, low-eulittoral, psammon.
8. Spain, Balearic Sea, Costa Blanca, Benidorm, Punta de Pinet, 22.03.1996, low-eulittoral, *Enteromorpha* sp.
9. France, Côte d'Azur, Agay, Rade d'Agay, 08.2000, sublittoral fringe, depth 5 m, *Ceramium* sp.
10. France, Golfe du Lion, Marseille, Îles de Riou, La Pierre de Cassis, 30.10.2001, sublittoral, ~5 km off shore, depth -50 m, water temperature 17 °C, psammon.
11. France, Golfe du Lion, Marseille, Îles de Riou, La Pierre de Cassis, 30.10.2001, sublittoral, ~5 km off shore, depth 40 m, water temperature 17 °C, psammon.
12. France, Hyères Archipelago, Côte d'Azur, near wreck Donateur (Prosper Schiaffino), 31.10.2001, sublittoral, 4 km off shore, depth 45 m, water temperature 17 °C, psammon.
13. France, Hyères Archipelago, Côte d'Azur, near wreck Donateur (Prosper Schiaffino), 31.10.2001, sublittoral, 4 km off shore, depth 50 m, water temperature 17 °C, psammon.
14. France, Golfe du Lion, Port Vendres, shore, 42.518021, 3.113359, 02.04.2005, low-eulittoral, psammon.
15. France, Golfe du Lion, Port Vendres, shore, 42.517971, 3.113230, 02.04.2005, mid-eulittoral, psammon.
16. France, Golfe du Lion, Port Vendres, Ansa de l'Espeluga, shore, 42.520585, 3.118962, 02.04.2005, mid-eulittoral, psammon.
17. France, Golfe du Lion, Port Vendres, Ansa de l'Espeluga, shore, 42.520635, 3.118924, 02.04.2005, low-eulittoral, psammon.
18. France, Côte d'Azur, Hyères Archipelago, Parc National Port Cros, Île de la Gabinière, La Gabinière Est, 26.06.2006, sublittoral, 10 km off shore, depth 43 m, water temperature 22 °C, psammon.
19. France, Côte d'Azur, Hyères Archipelago, Parc National Port Cros, Île de Bagaud, Pointe de Montrémian, 27.06.2006, sublittoral, 8 km off shore, depth 25 m, water temperature 22 °C, psammon.
20. France, Côte d'Azur, Hyères Archipelago, Parc National Port Cros, Île de Port Cros, Pointe du Vaisseau, 29.06.2006, sublittoral, 9 km off shore, depth 40 m, water temperature 19 °C, psammon.
21. France, Côte d'Azur, Hyères Archipelago, Cavalaire-sur-Mer, wreck Espingole, 01. 07. 2006, sublittoral, 500 m from shoreline, depth 39 m, water temperature 20 °C, psammon.
22. Spain, Balear Sea, Costa Blanca, Bégur, Canyons de Tamariu, 13.08.2006, sublittoral, 250 m from shoreline, depth 30 m, water temperature 27 °C, psammon.
23. Spain, Balearic Sea, Costa Blanca, Bégur, Illa de Fito, 14.08.2006, sublittoral, 250 m from shoreline, depth 21 m, water temperature 26 °C, psammon.
24. Spain, Balearic Sea, Costa Blanca, Bégur, Illa Negra, 14.08.2006, sublittoral, 250 m from shoreline, depth 22 m, water temperature 25 °C, psammon.
25. Spain, Balearic Sea, Costa Blanca, Bégur, Pointa des Plom, 15.08.2006, sublittoral, 250 m from shoreline, depth 15 m, water temperature 26 °C, psammon.
26. Spain, Balearic Sea, Costa Blanca, Bégur, Furio de Fito, 16.08.2006, sublittoral, 250 m from shoreline, depth 28 m, water temperature 16 °C, psammon.
27. Spain, Balearic Sea, Costa Blanca, Bégur, Furio de Aiguaxelida, 17.08.2006, sublittoral, 50 m from shoreline, depth 28 m, water temperature 24 °C, psammon.
28. Spain, Balearic Sea, Costa Blanca, Bégur, Furio de Fito, 18.08.2006, sublittoral, 250 m from shoreline, depth 45 m, water temperature 15 °C, psammon.
29. Italy, Tyrrhenian Sea, Elba, Punta della Madonna, 25.09.2006, sublittoral, 50 m from shoreline, depth 30 m, water temperature 21 °C, psammon.

30. Italy, Tyrrhenian Sea, Elba, Scoglio della Nave Enfolà, 25.09.2006, sublittoral, 50 m off shore, depth 40 m, water temperature 21 °C, psammon.
31. Italy, Tyrrhenian Sea, Elba, Il relitto di Pomonte (wreck of Elviscott), 26.09.2006, 100 m from shoreline, sublittoral, depth 10 m, water temperature 23 °C, psammon.
32. Italy, Tyrrhenian Sea, Elba, La Fonza Esterna, 27.09.2006, sublittoral, 50 m from shoreline, depth 30 m, water temperature 23 °C, psammon.
33. Italy, Tyrrhenian Sea, Elba, La Formiche di Ponente, 28.09.2006, sublittoral, 50 m from shoreline, depth 40 m, water temperature 21 °C, psammon.
34. Italy, Tyrrhenian Sea, Elba, Punta della Madonna di Ponente, 28.09.2006, sublittoral, 50 m from shoreline, depth 40 m, water temperature 22 °C, psammon.
35. Italy, Tyrrhenian Sea, Elba, Picco Giallo, 29.09.2006, sublittoral, 50 m from shoreline, depth 35 m, water temperature 22 °C, psammon.
36. Italy, Tyrrhenian Sea, Elba, Scoglio Fino, 30.09.2006, sublittoral, 1 km off shore, depth 35 m, water temperature 23 °C, psammon.
37. Italy, Tyrrhenian Sea, Elba, Scoglietto di Portoferraio, 30.09.2006, sublittoral, 1 km off shore, depth 35 m, water temperature 23 °C, psammon.
38. France, Côte d'Azur, Golfe de Fréjus, Baie de St. Raphaël, St. Raphaël, Le Jardin, 23.10.2008, sublittoral, 400 m from shoreline, depth 66 m, water temperature 20 °C, psammon.
39. France, Côte d'Azur, Golfe de Fréjus, Baie de St. Raphaël, St. Raphaël, 23.10.2008, sublittoral, 500 m from shoreline, depth 20 m, water temperature 17 °C, psammon.
40. France, Côte d'Azur, Golfe de Fréjus, Baie de St. Raphaël, St. Raphaël, 23.10.2008, sublittoral, 400 m from shoreline, depth 15 m, water temperature 17 °C, psammon.
41. France, Côte d'Azur, Le Lavandou, Cap Bénat, 01.06.2010, sublittoral, 50 m from shoreline, depth 20 m, water temperature 17 °C, psammon.
42. France, Côte d'Azur, Le Lavandou, Îlot de la Fourmigue, 02.06.2010, sublittoral, 3.5 km off shore, depth 15 m, water temperature 16°C, psammon.
43. France, Côte d'Azur, Le Lavandou, Îlot de la Fourmigue, 03.06.2010, sublittoral, 3.5 km off shore, depth 17 m, water temperature 17 °C, psammon.
44. Spain, Balearic Sea, Costa Brava, Rosas, Raco de Sant Pere, Punta de Sa Figuera, 22.07.2012, sublittoral, 20 m from shoreline, depth 26 m, water temperature 21 °C, psammon.
45. Spain, Balearic Sea, Costa Brava, Rosas, Golf of Rosas, El Fraire, 23.07.2012, sublittoral, 50 m from shoreline, depth 15 m, water temperature 21 °C, psammon.
46. Spain, Balearic Sea, Costa Brava, Rosas, Golf of Rosas, Bau Cap Trencat de Fora (1&2), 24.07.2012, 50 m from shoreline, depth 26 m, water temperature 21 °C, psammon.
47. Spain, Balearic Sea, Costa Brava, Rosas, Badia de Jóncols, La Piscina, 25.07.2012, 50 m from shoreline, depth 28 m, water temperature 21 °C, psammon.



**FIGURE 1.** Map indicating sampling areas. 1. Costa Blanca, Balearic Sea; 2. Costa Brava, Balearic Sea; 3. Golfe de Lion; 4. Hyères Archipelago; 5. Côte d'Azur; 6. Elba Island, Tyrrhenian Sea.

## Results

The list of rotifers found is provided in Table 2. A total of 43 taxa, 2 Bdelloidea and 41 Monogononta, was found in the 47 samples. Twenty six of them could be fully identified, and 10 are described as new to science. Judging from the trophi at least some five more species were new to science, but complete description was not warranted by scarcity of specimens or state of contraction. The undescribed species belong to the genus *Cephalodella* (1 sp.), *Encentrum* (2 spp.) and *Paradicranophorus* (3 spp.), and are included in the results of species richness and distribution. Of the previously described species, 10 are new for the Mediterranean Sea.

The only species of Bdelloidea that could be fully identified, *Rotaria laticeps* Wulfert, was present in 45% of the samples. The species of Monogononta belong to 14 genera distributed over 8 families, with Dicranophoridae containing 21 species in 4 genera as most species-rich and accounting for 51% of monogonont taxa encountered. The most species-rich genus *Encentrum* (Dicranophoridae) is represented by 14 species (34% of total monogonont species). The second most important family, only accounting for 12% of monogononts, is Proalidae, with 5 species belonging to *Proales*.

**TABLE 2.** Rotifer taxa collected at the different sampling stations. Numbers refer to the sampling stations (Tab. 1). Taxa marked with an asterisk are new to the fauna of the Mediterranean Sea.

### BDELLOIDEA

Bdelloidea indet. : 19, 32, 33, 34, 35, 36, 43

### Philodinidae

*Rotaria laticeps* Wulfert, 1942 : 19, 21, 24, 27, 28, 29, 30, 31, 32, 33, 34, 35, 37, 39, 40, 41, 42, 43, 44, 45, 46

### MONOGONONTA

#### Brachionidae

*Notholca bythnoma* sp. nov. : 29, 30, 33, 34, 37, 39, 41

#### Dicranophoridae

*Allodicranophorus bulgaricus* (Althaus, 1957) : 10, 13, 24, 27, 29, 30, 31, 32, 33, 34, 37, 42, 43

*Encentrum algente* Harring, 1921 : 44

*E. aluligerum* sp. nov. : 13, 28, 32, 34, 37, 41, 42, 45, 46

*E. astridae* Sørensen, 2001\* : 34

*E. foroiuliense* sp. nov. : 33, 38, 39, 41, 42

*E. kutikovae* De Smet & Chernyshev, 2006\* : 42

*E. loefgreni* sp. nov. : 33, 41, 42

*E. longirostrum* Tzschaschel, 1978\* : 31, 41, 42, 43

*E. marinum* (Dujardin, 1841) : 24, 41, 42

*E. pugiodigitatum* sp. nov. : 24, 27, 29, 30, 31, 33, 34, 41, 42

*E. psammophilum* Althaus, 1957\* : 34, 42, 43, 44

*E. striatum* Althaus, 1957\* : 42

*E. uncinatoides* sp. nov. : 30, 33, 41, 43

*E. valkanovi* Althaus, 1957\* : 19, 21, 24, 29, 30, 33, 34, 41, 43, 45

*Encentrum* spp. (2 spp.) : 10, 24, 30, 32, 35, 37, 42, 43, 46

*Myersinella longiforceps* De Smet, 2007 : 29, 30, 33, 34, 41

*M. uncodonta* De Smet, 2007 : 30, 33, 34, 41, 42

*Paradicranophorus halophilus* sp. nov. : 27, 29, 30, 33, 34, 35, 37, 39, 42, 45, 46

*Paradicranophorus* sp. 1 : 27, 33, 34, 37

*Paradicranophorus* sp. 2 : 12

*Paradicranophorus* sp. 3 : 41

#### Lepadellidae

*Cohurella adriatica* Ehrenberg, 1831 : 3, 4, 5, 6, 9, 11, 19, 24, 27, 28, 39, 41, 42

*C. colurus* (Ehrenberg, 1830) : 13, 24, 27, 29, 30, 31, 33, 34, 37, 41, 45, 46

*Halolepadella pontica* (Althaus, 1957) : 12, 13, 19, 28, 31, 41, 42, 43

#### Lindiidae

*Lindia aequorea* sp. nov. : 31, 32

*L. elsae* De Smet, 2006\* : 31

*L. gravitata* Lie-Pettersen, 1905 : 29, 39, 42, 46

#### Notommatidae

*Cephalodella* sp. : 29, 43

*Pleurotrocha fontanetoi* sp. nov. : 29, 30, 33, 34, 35, 37, 41

### Proalidae

- Proales francescae* sp. nov. : 11, 13, 19, 33, 40, 41, 44, 46  
*P. halophila* Remane, 1929 : 19, 31, 33  
*P. litoralis* De Smet, 1996\* : 8  
*P. similis* Beauchamp, 1907 : 3, 5, 6, 9, 10, 11, 12, 13, 19, 24, 28, 41, 43, 45, 46  
*P. syltensis* Tzschaschel, 1978\* : 24, 41

### Testudinellidae

- Testudinella bicorniculata* De Smet, 2009 : 19, 27, 29, 32, 33, 37, 40, 41, 43, 46  
*T. elongata* De Smet, 2009 : 13, 29, 30, 32, 34, 37, 41, 43, 44, 46  
*T. obscura* Althaus, 1957 : 10, 11, 12, 13, 19, 21, 22, 24, 27, 28, 29, 30, 31, 32, 33, 34, 35, 37, 38, 40, 41, 42, 43, 44, 45, 46, 47

### Trichocercidae

- Trichocerca marina* (Daday, 1889) : 13  
*T. pediculus* Remane, 1949\* : 30, 31

## Description of new species

### Subclass MONOGONONTA Plate, 1889

### Order PLOIMA Hudson & Gosse, 1886

### Family BRACHIONIDAE Ehrenberg, 1838

### Genus *Notholca* Gosse, 1886

#### *Notholca bythonoma* sp. nov.

(Figs 2, 3)

**Diagnosis.** Lorica 115–150 µm long, widest at anterior margin, dorsal plate tapering to rounded end with acute or cut-off caudal extension; antero-dorsal margin with six short spines; dorsal plate with longitudinal striation; two weak lateral folds running from base of caudal extension towards anterior; ventral plate protruding.

**Type locality.** Scoglio della Nave Enfola, Elba Island, Tyrrhenian Sea, Italy. In sublittoral psammon collected on 25.09.2006, 50 m seaward from shoreline and 40 m deep; water temperature 21°C.

**Holotype.** A female in a permanent, glycerine glass slide mount deposited in the Royal Belgian Institute of Natural Sciences (RBINS), Brussels, Belgium, No. IG 33082, RIR 216.

**Paratypes.** One female from type locality in RBINS, No. IG 33082, RIR 246; 7 mounted paratypes and 6 SEM trophi preparations in Department of Biology, University of Antwerp.

**Additional material.** 18 specimens collected at the Côte d'Azur, and Elba Island, Tyrrhenian Sea (see Tab. 2 species list).

**Etymology.** The specific name *bythonoma* (Greek *buthos*, meaning depth, *nomos*, meaning dwelling-place, home) is an adjective referring to the environment the species was found.

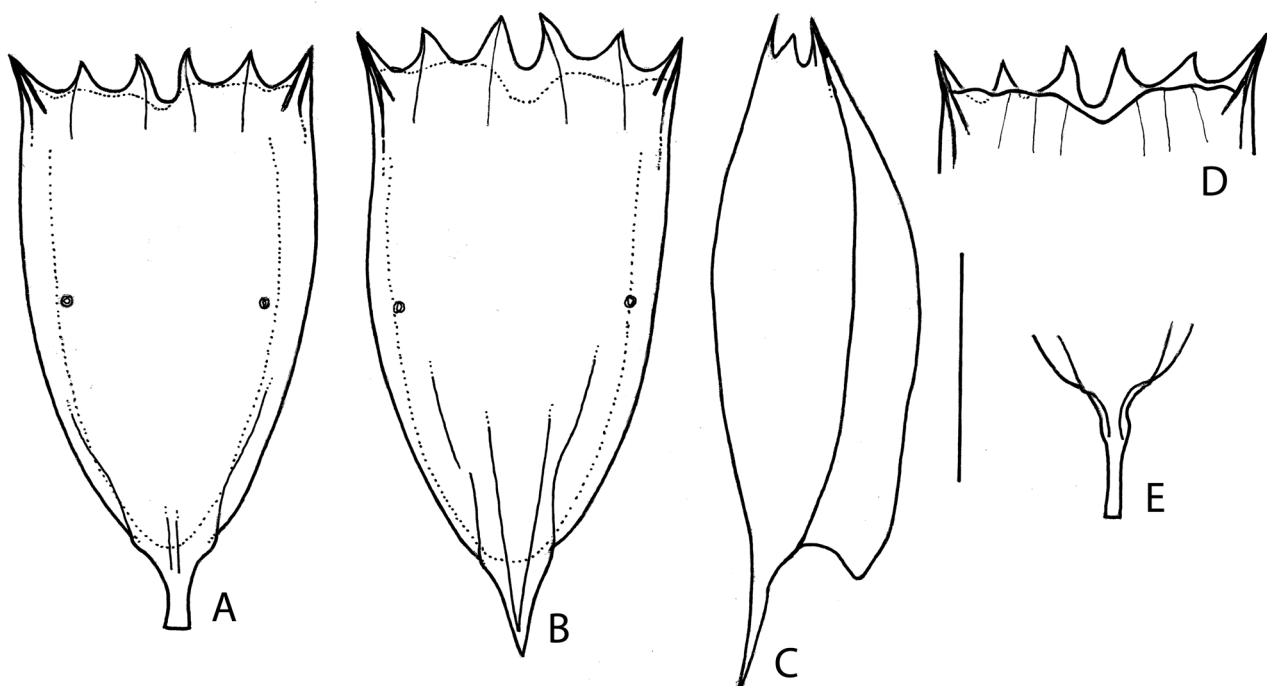
**Description of female.** Lorica (Fig. 2) longer than wide, ratio length:width *c.* 2, widest at anterior margin, gradually tapering towards rounded posterior end; dorsal plate prolonged into short to fairly long, acutely tapering or rectangular-truncate extension. Posterior extension not set off from trunk, occasionally marked off by basal swelling; laterally from base of caudal extension two folds run parallel over a short distance, and afterwards diverge, continuing laterally to anterior somewhat less 1/3 lorica length. Antero-dorsal margin with six short, fairly broad spines, median and lateral spines almost equally long, intermediate spines somewhat smaller; lateral spines with two reinforced ridges; antero-ventral margin with broad median notch, and arched or weakly undulate lateral edges. Dorsal plate with longitudinal striation. In lateral view fairly thick with protruding ventral plate. Ratio lorica length:position of lateral antennae to antero-dorsal margin 2.15–2.30.

Trophi of typical *Notholca*-type (Fig. 3). Rami triangular, almost symmetrical in outline; right rostellum (Fig. 3F: r) slightly more robust than left one; alulae well developed, symmetrical, rounded; subbasifenestrae large, almost symmetrical; basifenestrae minute, rounded; medial surface of rostellum with opening, the fenestrula (Fig. 3F: f); apophyses and teeth on inner margin of rami strongly asymmetrical, left stronger than right; sclerite

elements composing apophyses and teeth stout, strongly fused, hardly recognizable individually; both ramus apophyses tricuspidate; rami teeth composed of two groups of four basally fused tooth-shaped projections, fitting into the spaces between the two major uncinal teeth; inner margin of rami anterior to right rostellum with two separate small blunt prominences, and a comb of about 8 small blunt appressed sclerite bodies (Figs 3B, F: cs), anterior to left rostellum a similar configuration of elements but comb-forming sclerite bodies less distinct. Fulcrum short, lamelliform, distal margin only weakly expanded, almost parallel-sided in lateral view with distal end strongly oblique. Unci almost symmetrical and equally developed; ventral margin with fairly pronounced outward bend proximally; two major teeth, the first and third the most robust, and two distinct minor teeth; left dorsal uncinal margin with three additional strongly reduced teeth, right dorsal margin with 1–2 additional reduced teeth; first tooth of major teeth slightly smaller than other major one (third teeth). Subunci a bundle of elongate-fusiform scleropili. Manubria as usual for the genus, composed of large elongate dorsal chamber with large elongate opening, a long medial chamber with minute opening, and smaller ventral chamber with small, elongate-triangular opening. A strong ligament connects the lateral margin of the basal apophyses with the ventral margin of the head of the manubria, and a weaker one with the ventral margin of the unci.

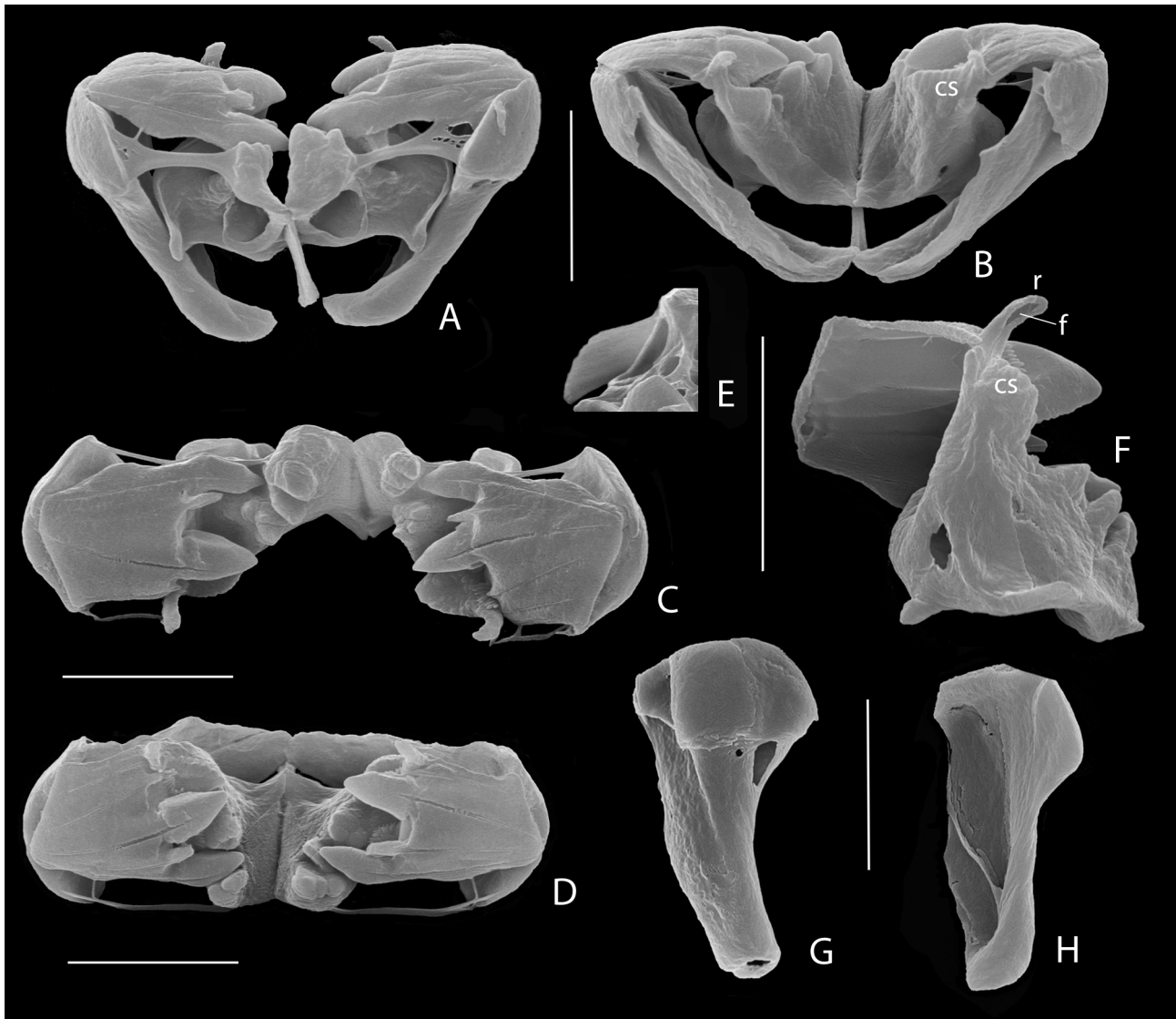
**Measurements.** Lorica (N=10): length 115–150  $\mu\text{m}$ , width 50–68  $\mu\text{m}$ , median antero-dorsal spine 10–13  $\mu\text{m}$ , lateral antero-dorsal spine 10–12  $\mu\text{m}$ , intermediate antero-dorsal spine 6–8  $\mu\text{m}$ , caudal extension 8–30  $\mu\text{m}$ ; trophi (N=5): length  $\sim$ 18  $\mu\text{m}$ , ramus 13.1–14.2  $\mu\text{m}$ , fulcrum 3.7–4.8  $\mu\text{m}$ , unci 12.2–13.9  $\mu\text{m}$ , manubrium 18.0–19.8  $\mu\text{m}$ .

**Comments.** *Notholca bythonoma* **sp. nov.** shows a superficial resemblance with *N. intermedia* Voronkov, 1917, a freshwater species described from Lake Baikal. The latter species is larger, 200–220  $\mu\text{m}$  (data from Kutikova 1970) vs. 115–150  $\mu\text{m}$  in *N. bythonoma*, with the lorica broadest near its posterior half vs. lorica widest at anterior margin; its antero-lateral and antero-median spines are longer vs. spines short and only slightly different in length in the new species; the two weak lateral folds running from the base of the caudal extension towards anterior in *N. bythonoma* **sp. nov.** are lacking in *N. intermedia*. Varga (1939: p. 335, Fig. 9) pictured a *Notholca* sub *N. heptodon* Perty from freshwater Lake Balaton, Hungary, with the lorica widest at the anterior margin and narrowing caudally. He claims the species identical with the *N. heptodon* (Perty, 1850) as pictured in Brauer (1912), and actually considered an invalid junior subjective synonym of *Notholca foliacea* (Ehrenberg, 1838), although his specimens apparently lacked the characteristic anteriorly pitted collar and dorsal pattern of striae of the latter. Varga's animal differs from *N. bythonoma* **sp. nov.** by its undulate lateral lorica margins and the absence of the two caudo-lateral folds.



**FIGURE 2.** *Notholca bythonoma* **sp. nov.** A, B. Loricae, dorsal view; C. Lorica, lateral view; D. Lorica, anterior margins, ventral view; E. Lorica, caudal extension. Scale bar: 50  $\mu\text{m}$ .

**Distribution and ecology.** The species was found in low numbers in sublittoral psammon samples from the Côte d'Azur and Tyrrhenian Sea, at distances of 50 m to 1 km from the shoreline, and depths between 20 and 40 m. It was present in samples of June, September, and October, at water temperatures of 17–23 °C.



**FIGURE 3.** *Notholca bythonoma* sp.nov., SEM photographs of trophi. A. Complete set, ventral; B. Complete set, dorsal; C. complete set, ventro-frontal; D. complete set, dorso-frontal; E. fulcrum, lateral; F. left ramus, oblique dorsal (uncus at the back); G. right manubrium, outer view; H. left manubrium, inner view. cs: comb of sclerite bodies; f: fenestrula; r: rostellum. Scale bars: 10  $\mu$ m.

## Family DICRANOPHORIDAE Harring, 1913

### Genus *Encentrum* Ehrenberg, 1838

#### *Encentrum aluligerum* sp. nov.

(Figs 4, 5)

**Diagnosis.** Medium-sized (120–140  $\mu$ m) *Encentrum* with oblique-frontal corona; rostrum broad, anteriorly almost straight; tail broad, rounded; trophi of subgenus *Isoencentrum*-type; rami outline more or less hexagonal; median rami opening pyriform; intramallei short; rami with single apical tooth; preuncinal teeth single, stout, set at right angle to trophi axis; outer margin of basal rami chambers with proximal, short ventral alula; inner margin of subbasal rami chambers with distal tooth.



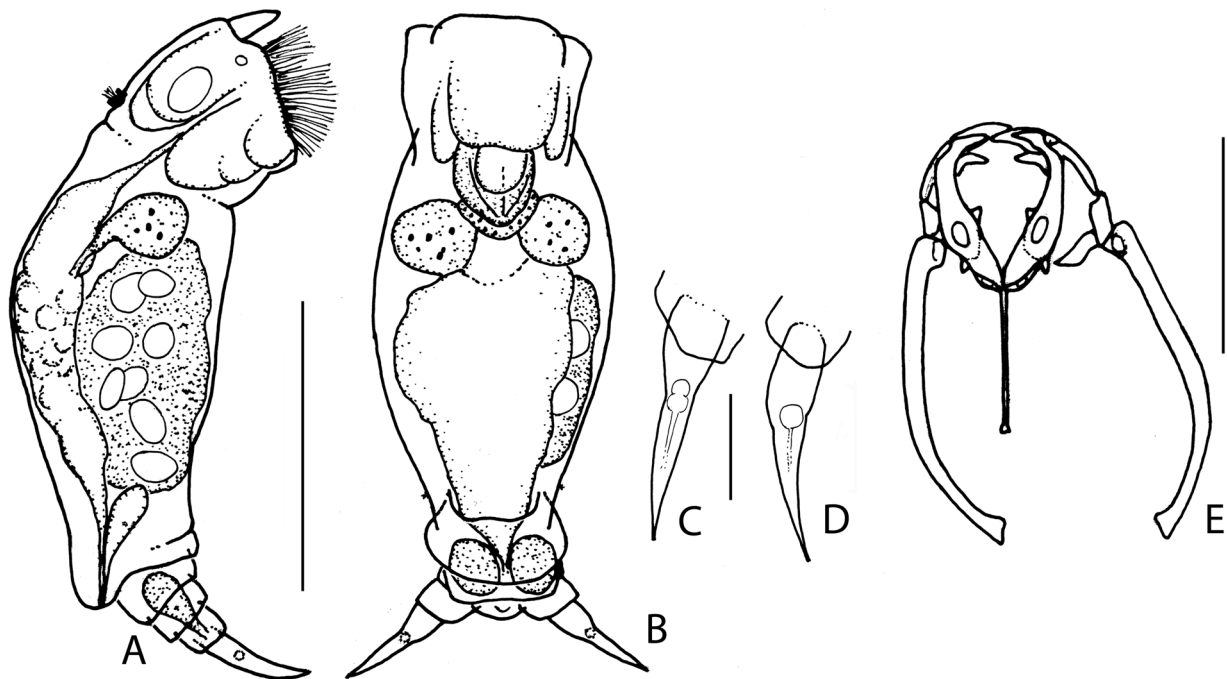
**Type locality.** Cap Bénat, Baie du Lavandou, Côte d'Azur, France. In psammon collected on 03.06.2010, 50 m from shoreline, and depth of 20 m; water temperature 17 °C.

**Holotype.** A female in a permanent, glycerine glass slide mount deposited in the Royal Belgian Institute of Natural Sciences (RBINS), Brussels, Belgium, No. IG 33082, RIR 217.

**Paratypes.** One female from type locality in RBINS, No. IG 33082, RIR 247; 5 mounted paratypes and 6 SEM trophi preparations in Department of Biology, University of Antwerp.

**Additional material.** Several specimens from sublittoral of the Costa Blanca and Costa Brava, Balearic Sea, the Côte d'Azur, and Elba Island, Tyrrhenian Sea (see Tab. 2 species list).

**Etymology.** The name of the species is composed of the Latin *alula*, a diminutive of *ala* meaning small wing, and the Latin *gerere*, to bear, and refers to the ventral alulae on the basal rami chambers.



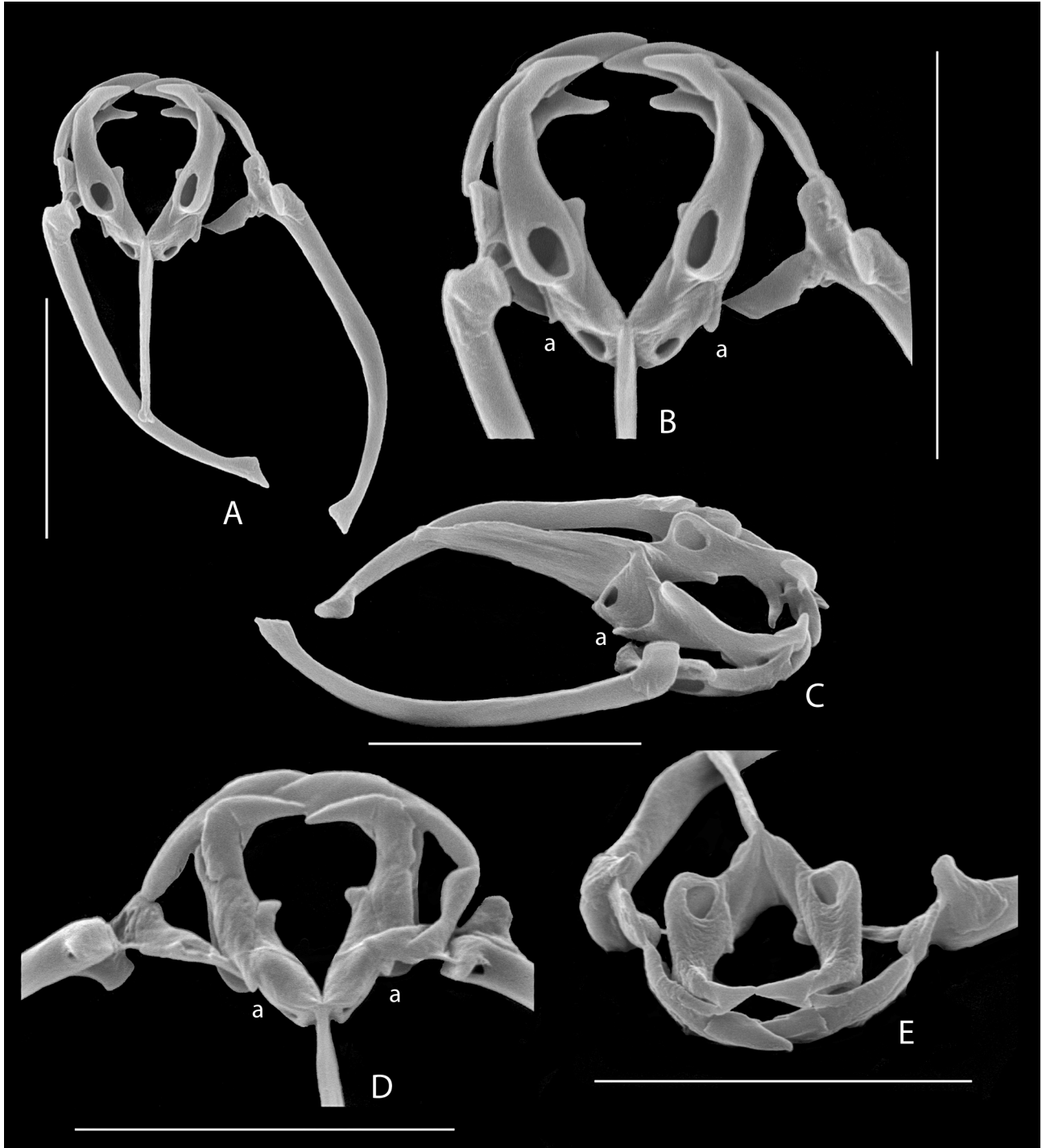
**FIGURE 4.** *Encentrum aluligerum* sp. nov. A. Female, lateral view; B. female, dorsal; C. toe, dorsal; D. toe, lateral; E. trophi, dorsal. Scale bars: A, B: 50  $\mu$ m; C–E: 10  $\mu$ m.

**Description of female.** Body short fusiform (Figs 4A, B). Head *c.* 1/4 total length, offset by neckfold, narrower than trunk, slightly decurved ventrally. Corona oblique-frontal. Rostrum large, broad, anterior margin weakly rounded to almost straight. Dorsal antenna in posterior half of head. Trunk weakly arched dorsally, flattened ventrally, in dorsal view with constriction before tail. Tail broad, rounded. Lateral antennae near posterior margin of trunk. Foot short, broad, 3 pseudosegments. Toes short (Figs 4C, D), *c.* 1/6 total length; in dorsal view almost straight, tapering, more or less strongly indented before mid-length, with reservoir at indentation, tips acute; toes in lateral view weakly decurved ventrally. Shallow caudal antenna between bases of toes. Two colourless rostral eyespots? Brain saccate; small retrocerebral sac. Proventriculus offset from stomach; stomach and intestine weakly offset. Gastric glands spherical, with fairly long stalks. Pedal glands club-shaped. Vitellarium with 8 nuclei.

Trophi (Figs 4E, 5) of subgenus *Isoencentrum*-type (De Smet 1997). Rami outline rounded-hexagonal; median rami opening pyriform. Rami each with stout, slightly offset and incurved apical tooth set at oblique angle to trophi axis; cardal apophysis of apical teeth well developed; inner margin of subbasal rami chambers with short triangular tooth distally; basal chambers ventrally with short, caudally pointing alula (Figs 5B–D: a). Prior to each apical ramus tooth a stout preuncinal tooth ventrally, set at right angle to trophi axis, composed of short shaft and head forming right angle; cardal apophysis reduced. Fulcrum ramus length; narrow and parallel-sided in dorsal/ventral view; in lateral view weakly curved ventrally, with broad base tapering to obtuse distal end. Unci single-toothed, with offset head; head shaft length, expanded in plane of rami; dorsal apophysis well developed, ventral one reduced. Intramallei fairly short, thin, more or less rectangular. Supramanubria fairly short, elongate-trapezoidal. Manubria longer than incus, rod-shaped, straight, incurving and slightly tapering to crutched cauda; head with short, rounded dorsal expansion and acute ventral one.

**Measurements.** Body (N=5): total length 120–140  $\mu\text{m}$ , toe 20–23  $\mu\text{m}$ ; trophi (N=5): length 19–22  $\mu\text{m}$ , ramus 6.1–7.3  $\mu\text{m}$ , fulcrum 7.3–8.4  $\mu\text{m}$ , uncus 5.2–5.9  $\mu\text{m}$ , intramalleus 1.2–1.9  $\mu\text{m}$ , manubrium 14.8–16.1  $\mu\text{m}$ .

**Comments.** *Encentrum aluligerum* sp. nov. is easily distinguished from its congeners by the specific shape of the trophi. The only other marine *Encentrum* of the subgenus *Isoencentrum* bearing alulae known to date is *E. frenoti* De Smet, 2002, described from subantarctic Îles Kerguelen. Alulae of the latter are minute and dorso-lateral, and both the other trophi features as well as the species' external and internal morphology allow for an unequivocal distinction with the new species.



**FIGURE 5.** *Encentrum aluligerum* sp. nov., SEM photographs of trophi. A. Complete set, dorsal; B. detail, dorsal; C. complete set, dorso-lateral; D. detail, ventral; E. detail, dorso-frontal. a: alula. Scale bars: 10  $\mu\text{m}$ .

**Distribution and ecology.** The species was found in low numbers in sublittoral psammon samples from the Costa Blanca, Costa Brava, Côte d'Azur, and Tyrrhenian Sea, at distances of 50 m to 3.5 km from the shoreline, and depths between 15 and 50 m. It was present in samples of June, July, August, September, and October, at water temperatures of 15–23 °C.

***Encentrum foroiuliense* sp. nov.**

(Figs 6, 7)

**Diagnosis.** A fairly large *Encentrum* about 175 µm long (slightly contracted). Corona oblique; rostrum shallow, almost straight; large more or less rectangular tail; toes narrow basally, expanding for about 1/3 their length and tapering afterwards to ventrally curving tubular tip; large spherical proventriculus; trophi subgenus *Encentrum*-type; rami outline longer than wide, ratio length:width of closed rami 2.2–2.3; median rami opening elongate drop-shaped; carina rami present; fulcrum ramus length; preuncinal teeth in line with apical rami teeth; intramallei long, with broad, rounded medio-lateral basal expansion.

**Type locality.** Baie de St. Raphaël, Golfe de Fréjus, 'Le Jardin', Côte d'Azur, France. In psammon collected on 23.10.2008, 400 m from shoreline and depth of 66 m; water temperature 20 °C.

**Holotype.** A female in a permanent, glycerine glass slide mount deposited in the Royal Belgian Institute of Natural Sciences (RBINS), Brussels, Belgium, No. IG 33082, RIR 218.

**Paratypes.** One female from type locality in RBINS, No. IG 33082, RIR 248; 3 mounted paratypes and 4 SEM trophi preparations in Department of Biology, University of Antwerp.

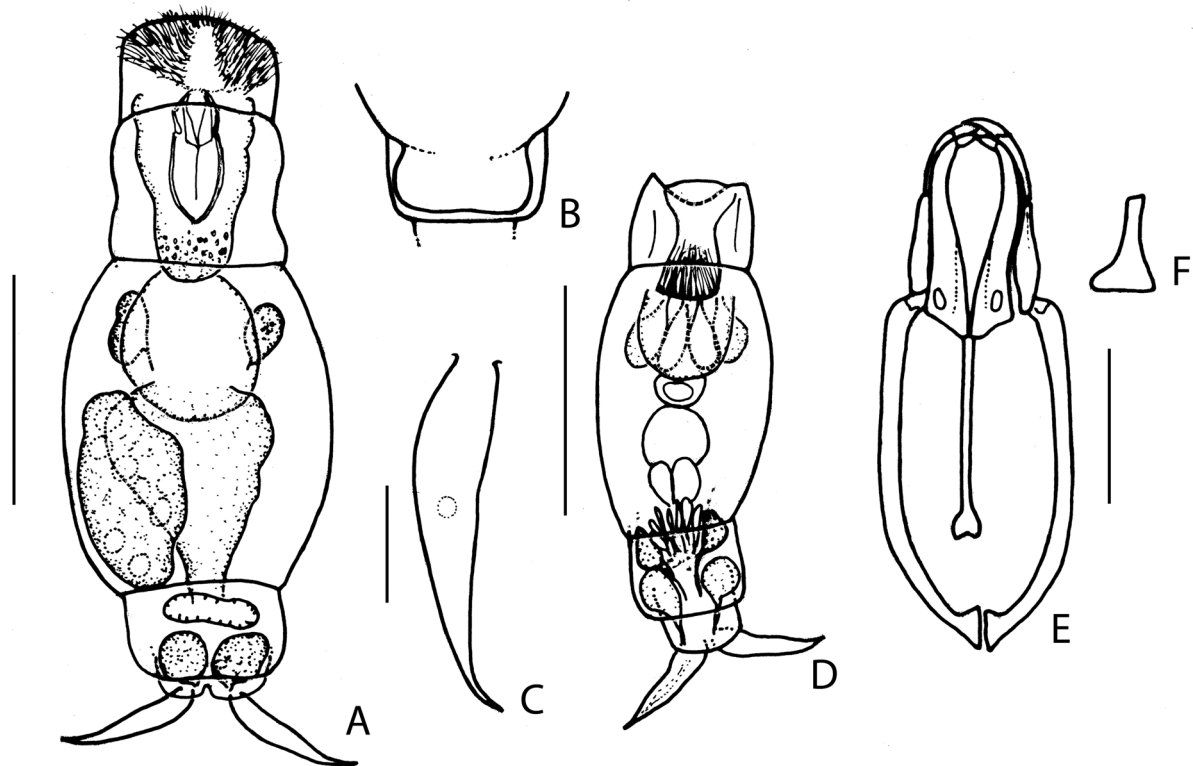
**Additional material.** Several specimens from sublittoral of Îlot de la Fourmigue and Cap Bénat, Baie du Lavandou, Côte d'Azur.

**Etymology.** The name *foroiuliense* is a Latin adjective of Forum Iulii, name given to the city of Fréjus by the Romans, and refers to the area of the type locality.

**Description of female.** Body more or less cylindrical (Fig. 6A). Head offset by distinct transversal fold. Rostrum broad, shallow, almost straight. Corona oblique. Dorsal antenna in posterior third of head. Trunk elliptical. Tail prominent (Fig. 6B), more or less rectangular, somewhat narrower proximally, slightly expanding distally and rounding off to straight or weakly indented distal margin. Foot cylindrical, two broad pseudosegments. Toes *c.* 1/6 total length, divergent, narrow at base, expanding for about 1/3 their length and tapering afterwards to tubular tip, in dorsal view more or less straight, in lateral view (Fig. 6C) with curved dorsal margin and more or less straight ventral margin, tubular tips decurved ventrally; a small rounded reservoir near midlength. Brain saccate; retrocerebral sac broad. Two colourless eyespots? Proventriculus large, spherical. Gastric glands rounded-ovate, stalks short. Pedal glands clubbed, relatively small. Vitellarium with 8 nuclei.

Trophi (Figs 6E, F, 7) subgenus *Encentrum*-type (De Smet 1997). Trophi large, elongate, slender. Rami outline longer than wide, ratio length:width of closed rami 2.2–2.3; outer margin of rami weakly concave dorso-laterally, rounded-angular posteriorly; median rami opening elongate drop-shaped; latero-ventral margin of each ramus with shallow, rounded crest, the carina rami (Fig. 7E: cr), at 2/3 from ramus attachment to fulcrum; basifenestrae and subbasifenestrae small, elliptical to rounded. Each ramus with single, slightly offset incurved apical tooth set at obtuse angle to trophi axis; distinct cardal apophysis absent. Each ramus ventrally with single preuncinal tooth set at obtuse angle to trophi axis, in line with apical teeth; preuncinal teeth with short triangular head and short shaft forming obtuse angle; head without distinct cardal apophysis. Fulcrum ramus length, in dorsal/ventral view distal end slightly widening and indented; in lateral view with broad base, quickly tapering, continuing parallel-sided. Unci medium long, slightly curved; head less shaft length, with small dorsal apophysis, ventral apophysis vestigial; head expanded in plane of rami. Intramallei long, with broad, rounded, relatively short medio-lateral basal expansion ventrally, bearing small proximal opening; latero-ventral part expanded, fitting lateral concavity of rami. Supramanubria absent. Manubria slightly less incus length, stout, rod-shaped, more or less straight, distally incurved with crutched cauda, head short, triangular, with dorsal and ventral opening distally.

**Description of male.** Male (Fig. 6D) similar in habitus to female, but smaller and more slender; head distinctly offset; trunk elliptical; foot with broad penultimate pseudosegment and narrower distal one; toes similar to female ones, but with less pronounced tubular part; saccate brain and retrocerebral sac large; eyespot(s) and lateral antennae not observed. Trophi absent.



**FIGURE 6.** *Encentrum foroiuliense* sp. nov. A. Female, ventral; B. tail; C. toe, lateral; D. male, dorsal; E. trophi, dorsal; F. intramalleus. Scale bars: A, B, D: 50  $\mu$ m; C, E, F: 10  $\mu$ m.

**Measurements.** Female, body (N=5): length (slightly contracted) up to 175  $\mu$ m, toe 30–31  $\mu$ m; trophi (N=4): length 26  $\mu$ m, ramus 12.2–13.5  $\mu$ m, fulcrum 12.2–13.1  $\mu$ m, uncus 5.8–6.8  $\mu$ m, preuncinal tooth 2.5  $\mu$ m, intramalleus 7.0–7.4  $\mu$ m, manubrium 21.4–23.7  $\mu$ m. Male (N=3): length 120  $\mu$ m (slightly contracted), toe 24–26  $\mu$ m.

**Comments.** *Encentrum foroiuliense* sp. nov. can not be confused with any other member of the subgenus *Encentrum* by its characteristic shape of the toes and tail. The shallow crest at the ventro-lateral margins of the rami, the carina rami, has to date also been observed in *E. psammophilum* and *E. valkanovi* (Figs 31C, E: cr). The position of these crests near the junction uncus-intramalleus suggests a role in the functioning of malleus and incus by, e.g., helping to keep the intramalleus-uncus in position, or as attachment of mastax muscles interconnecting the distal end of the intramallei and/or proximal part of the unci with the antero-lateral part of the rami. The intramallei of the *Encentrum*-type are usually well developed and long ('sock-shaped'), and closely connected to the rami, in contrast to the small intramallei in the trophi of the *Isoencentrum*-type, which appear not connected directly to the rami (see Fig. 5). The intimate connection of the intramallei with the rami in the *Encentrum*-type comes about by their swollen latero-ventral part fitting into a long lateral cavity of the rami (e.g. Fig. 7D), and their wing-shaped medio-lateral basal part grasping ventrally the base of the rami (e.g. Fig. 7E), both moreover closely interconnected by strong ligaments (Figs 7E, 9C, 31C). These different trophi configurations suggest a different way of operating. In the *Encentrum*-type intramallei-unci and rami will act together to seize the prey (see Fig. 31A), and its engulfing will be achieved by withdrawal of the whole trophi set, whereas in the *Isoencentrum*-type, grasping of the prey will be primarily by the protruding unci, followed by pulling the prey back through an inward movement of these unci by pivoting on the rami tips, and added by the movement of the co-operating flexibly jointed manubria.

**Distribution and ecology.** The species was found at low numbers in the sublittoral psammon samples from the Côte d'Azur and Tyrrhenian Sea, at distances of 50 m to 3.5 km from the shoreline and depths between 15 and 66 m. It was present in samples of June, September, and October, at water temperatures of 20–21 °C. Males were present in June.



**FIGURE 7.** *Encentrum foroiuliense* sp. nov., SEM photographs of trophi. A. Complete set, dorsal; B. complete set, ventral; C. detail, oblique dorso-frontal; D. detail, dorsal; E. detail, ventral. cr: carina rami. Scale bars: 10  $\mu$ m.

***Encentrum loefgreni* sp. nov.**

(Figs 8, 9)

**Diagnosis.** Large-sized *Encentrum* about 200 µm long (slightly contracted). Trophi subgenus *Encentrum* type; rami smoothly curved; rami outline oboval; median rami opening lenticular; basal rami chambers with distinct triangular alula; apical ramus tooth indistinctly offset; preuncinal teeth in line with apical rami teeth; fulcrum broad basally, tapering to blunt end.

**Type locality.** Îlot de la Fourmigue, Baie du Lavandou, Côte d'Azur, France. In psammon collected on 02.06.2010, 3.5 km from the shoreline and depth of 15 m; water temperature 16 °C.

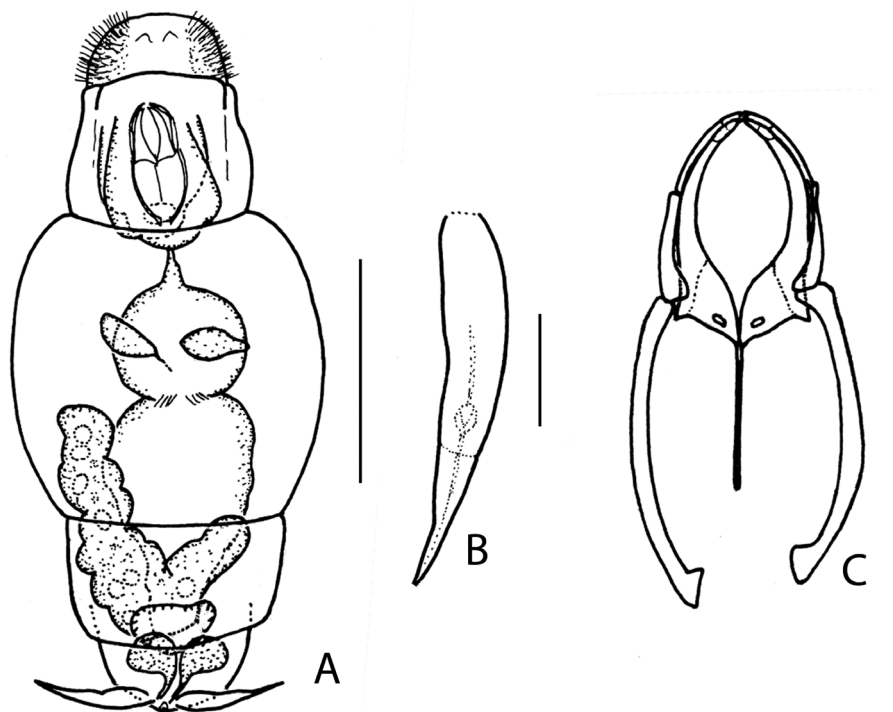
**Holotype.** A female in a permanent, glycerine glass slide mount deposited in the Royal Belgian Institute of Natural Sciences (RBINS), Brussels, Belgium, No. IG 33082, RIR 219.

**Paratypes.** One female from type locality in RBINS, No. IG 33082, RIR 249; 3 mounted paratypes and 3 SEM trophi preparations in Department of Biology, University of Antwerp.

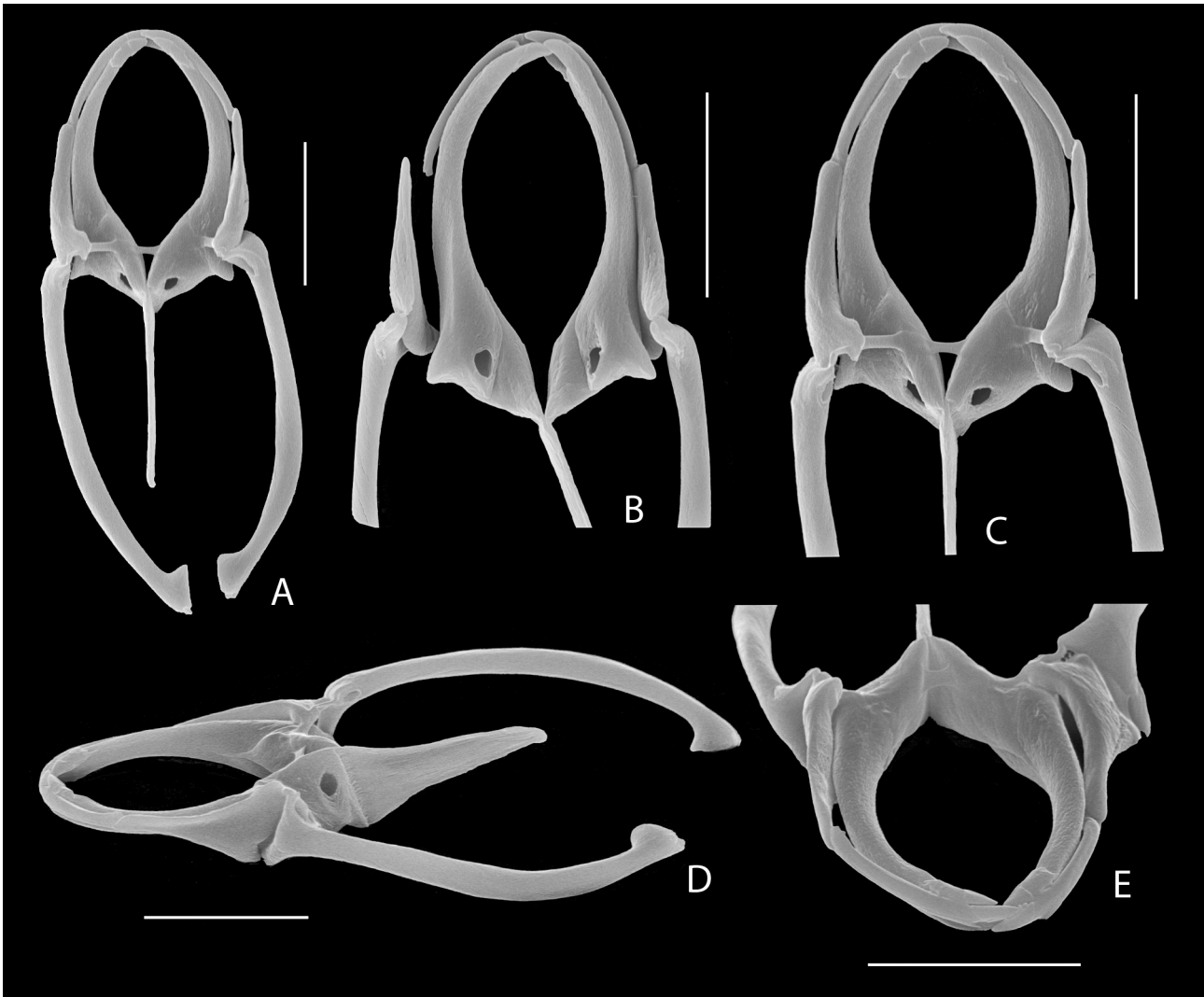
**Additional material.** A single specimen from sublittoral of Cap Bénat, Baie du Lavandou, Côte d'Azur, and 2 from La Formiche di Ponente, Elba Island, Tyrrhenian Sea.

**Etymology.** The species is named for Mr. Bart Löfgren, in recognition of his much appreciated sampling effort during scuba diving.

**Description of female.** Body plump fusiform (Fig. 8). Head offset by distinct neckfold, *c.* 1/4–1/3 total length. Rostrum indistinct, almost straight to broadly rounded. Corona strongly oblique to ventral. Dorsal antenna near neckfold. Trunk with two pseudosegments, widest near mid-length. Tail short, broadly rounded. Foot broad, a single pseudosegment. Toes (Fig. 8B) *c.* 1/7 total length, divergent, base narrower, dorsal margin slightly curved, ventral margin weakly undulate, indented near mid-length, near tip converging to more or less tubular point; a very weak transversal fold at about 1/3 from tip; a small rounded reservoir somewhat above mid-length. Small caudal antenna between bases of toes. Eyes not observed, possibly absent. Brain saccate; retrocerebral sac present. Proventriculus large, spherical, distinctly offset from stomach. Gastric glands ovate, without ? stalks. Pedal glands small, clubbed. Vitellarium with 8 nuclei.



**FIGURE 8.** *Encentrum loefgreni* sp. nov. A. Female, ventral; B. toe, lateral; C. trophi, ventral. Scale bars: A: 50 µm; B, C: 10 µm.



**FIGURE 9.** *Encentrum loefgreni* sp. nov., SEM photographs of trophi. A. Complete set, ventral; B. detail, dorsal; C. detail, ventral; D. complete set, ventro-lateral; E. detail, ventro-frontal. Scale bars: 10  $\mu$ m.

Trophi (Figs 8C, 9) subgenus *Encentrum*-type (De Smet 1997). Rami outline oboval with triangular postero-lateral alulae on basal chambers; median rami opening lenticular; basifenestrae and subbasifenestrae small, rounded. Rami curved, broad at base, tapering to indistinctly offset short apical tooth. Preuncinal teeth small, with short shaft and head, in line with apical rami teeth; apical rami teeth and preuncinal teeth without cardal apophysis. Fulcrum short, *c.* 2/3 ramus length, narrow and parallel-sided in dorsal/ventral view; in lateral view broad basally, gradually tapering to narrow blunt tip. Unci long, *c.* 1/2 ramus length, slender; shaft very long, head very short *c.* 1/4 uncus length, very weakly offset from shaft. Intramallei long, slightly longer than uncus, more or less sock-shaped, base broad with short, rounded medio-lateral basal expansion ventrally; distal half narrow. Supramanubria absent. Manubria *c.* 3/4 incus length, rod-shaped, more or less evenly curved with crunched cauda; head with small dorsal and ventral expansion with small caudal opening.

**Measurements.** Body (N=3): total length (slightly contracted) up to 255  $\mu$ m, toe 34–35  $\mu$ m; trophi (N=3): length 41–44  $\mu$ m, ramus 18.8  $\mu$ m, fulcrum 11.2–12.6  $\mu$ m, uncus 8.6–9.4  $\mu$ m, preuncinal tooth 3.0–3.5  $\mu$ m, intramalleus 9.8–10.8  $\mu$ m, manubrium 24.6–26.8  $\mu$ m.

**Comments.** *Encentrum loefgreni* sp. nov. is univocally distinguished from its known congeners by the characteristic shape of the trophi.

**Distribution and ecology.** The species was found in low numbers in the sublittoral psammon samples from the Côte d'Azur and Tyrrhenian Sea, at distances of 50 m to 3.5 km from the low tide mark and depths between 17 and 40 m. It was present in samples of June and September, at water temperatures of 17–21 °C.

***Encentrum pugiodigitatum* sp. nov.**

(Figs 10, 11)

**Diagnosis.** Female about 165–175  $\mu\text{m}$  long. Integument fairly stiff with faint longitudinal folds; toes dagger-shaped; rami outline elliptical, median rami opening lenticular; long slender unci with very short tooth; unci with bundle of needle-shaped elements; head of manubria with proximal opening, and associated crenate platelet.

**Type locality.** Punta della Madonna, Elba Island, Tyrrhenian Sea, Italy. In psammon collected on 25.09.2006, 50 m from shoreline and depth of 30 m; water temperature 21  $^{\circ}\text{C}$ .

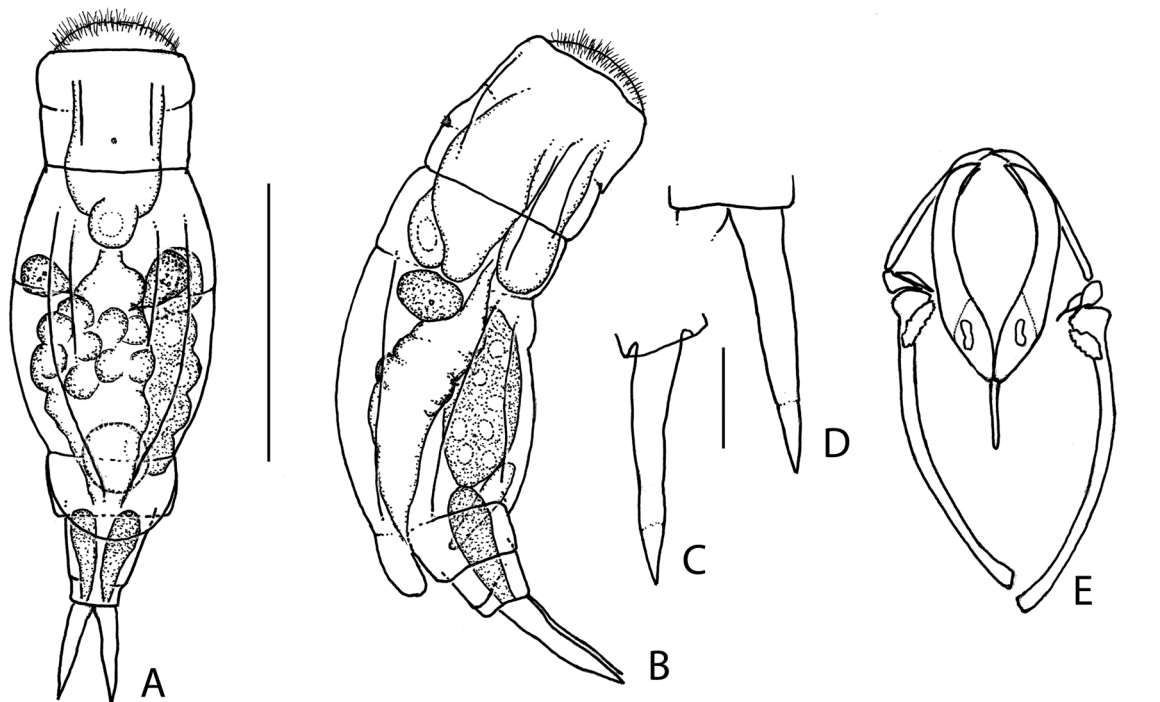
**Holotype.** A female in a permanent, glycerine glass slide mount deposited in the Royal Belgian Institute of Natural Sciences (RBINS), Brussels, Belgium, No. IG 33082, RIR 220.

**Paratypes.** One female from type locality in RBINS, No. IG 33082, RIR 250; 5 mounted paratypes and 5 SEM trophi preparations in Department of Biology, University of Antwerp.

**Additional material.** Several specimens from sublittoral of the Costa Blanca, Balearic Sea, the Côte d'Azur, and Elba Island, Tyrrhenian Sea (see Tab. 2 species list).

**Etymology.** The name of the species is composed of the Latin *pugio* meaning dagger, and the Latin *digitatum*, meaning provided with toes (*digitus*: toe), and refers to the characteristic shape of the toes.

**Description of female.** Body stout fusiform (Fig. 10). Integument fairly stiff with faint longitudinal folds. Head offset by neckfold, with weak transversal fold in distal half. Rostrum broad, shallow, straight to broadly rounded. Corona frontal. Dorsal antenna near posterior 1/3 of head. Trunk with some very weak incomplete transversal folds. Tail large, rounded, partly covering foot. Foot large, conical, 2(3) pseudosegments. Toes (Figs 10C, D) *c.* 1/7 total length, dagger-shaped, almost straight in dorsal and lateral view, margins weakly undulate, terminating in more or less distinctly offset claw. Eyespots not observed, possibly absent. Brain large, saccate; retrocerebral sac present. Gastric glands more or less spherical, stalks short to medium length. Proventriculus small. Pedal glands club-shaped, foot-length. Vitellarium with 8 nuclei.



**FIGURE 10.** *Encentrum pugiodigitatum* sp. nov. A. Female, dorsal; B. female, lateral; C. toe, lateral; D. toe, dorsal; E. trophi, dorsal. Scale bars: A, B: 50  $\mu\text{m}$ ; C–E: 10  $\mu\text{m}$ .

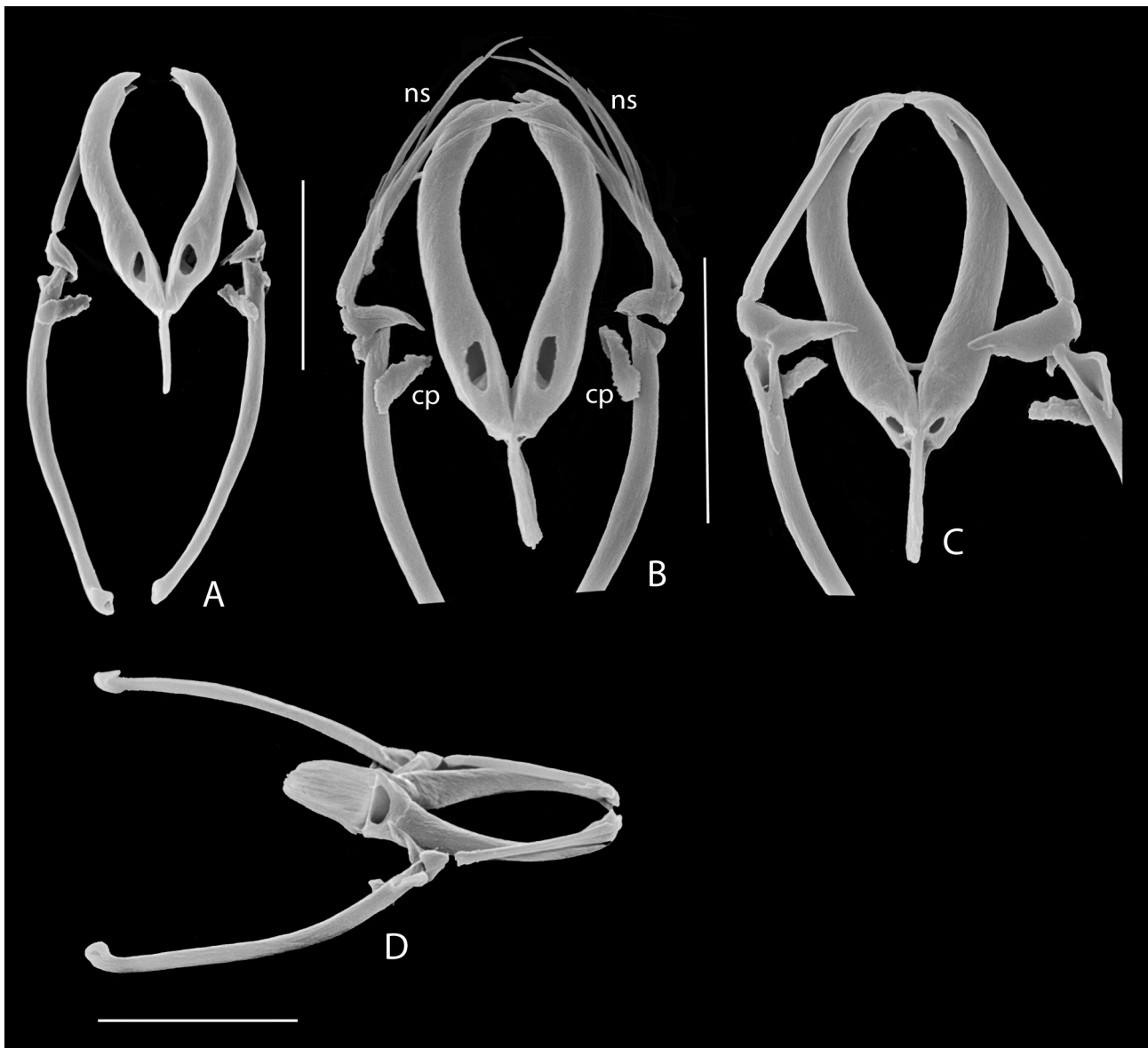
Trophi (Figs 10E, 11) with elliptical rami outline, greatest width in distal half; outer rami margins very weakly indented near proximal 1/3; median rami opening almost lenticular; rami elongate, narrow, widest in proximal half, terminating in very short, weakly offset oblique apical tooth; basifenestrae fairly small, elongate, subbasifenestrae fairly large, rounded. Preuncinal teeth very short, apical, in line with apical rami teeth. Fulcrum short, *c.* 1/3 ramus



length, plank-shaped, in lateral view very slightly narrowing towards rounded distal end. Unci long, *c.* 2/3 ramus length, slender, head very short, weakly offset, bifid, shaft with long dorsal rib. Associated with the unci and running parallel to them are a bundle of about 10 weakly sclerified needle-shaped elements (only shown in Fig. 11B: ns) provided with a seam; they insert somewhere near the intramallei. Intramallei small, elongate triangular, with caudal opening. Supramanubria small, elongate triangular, with caudal opening. Manubria rod-shaped, evenly curved in dorsal view, distal half with weak dorsal torsion in oblique view, slightly crunched distally with small opening and ventral more or less hook-shaped blunt process (only visible by SEM); head simple, distinct dorsal and ventral expansions lacking, with large proximal opening; a small elongate platelet with irregularly crenate margins dorsally from proximal end of manubria (Fig. 11B: cp).

**Measurements.** Body (N=10): total length 165–175  $\mu\text{m}$ , toe 19–27  $\mu\text{m}$ ; trophi (N=5): length 29  $\mu\text{m}$ , ramus 13.1–13.4  $\mu\text{m}$ , fulcrum 4.1–4.5  $\mu\text{m}$ , uncus 9.0–10.0  $\mu\text{m}$ , intramalleus 1.5–1.7  $\times$  2.4–3.1  $\mu\text{m}$ , manubrium 19.0–19.6  $\mu\text{m}$ .

**Comments.** *Encentrum pugiodigitatum* **sp. nov.** can not be confused with any of its congeners, and is neither related to any of the subgenera erected previously on base of the morphology of the trophi (De Smet 1997). Proximally open manubria, the crenate platelet associated with the head of the manubria, and the bundles of weakly sclerified elements paralleling the unci have not been reported before.



**FIGURE 11.** *Encentrum pugiodigitatum* **sp. nov.**, SEM photographs of trophi. A. Complete set, dorsal; B. detail, dorsal; C. detail, ventral; D. complete set, ventro-lateral. cp: crenate platelet; ns: needle-shaped sclerite bodies. Scale bars: 10  $\mu\text{m}$ .

**Distribution and ecology.** The species was usually found in low numbers in sublittoral psammon samples from the Costa Blanca, Côte d'Azur, and Tyrrhenian Sea, at distances of 50 m to 3.5 km from the shoreline, and depths between 15 and 40 m. It was present in samples taken in June, August and September, at water temperatures of 17–25 °C.

**Subgenus *Tricellatum* subgen. nov.**

**Diagnosis.** Rami composed of three longitudinally situated chambers, each with own opening; rami tips twisted around their axis, without apical teeth; preuncinal teeth primarily attached to unci; intramallei large, elongate trapezoid; supramanubria present.

**Type species.** *Encentrum (Tricellatum) uncinatoides* sp. et subgen. nov.

**Etymology.** The name of the subgenus is composed of the Latin *tris*, three, and *cella*, meaning cell, chamber, and refers to the characteristic rami composed of three chambers.

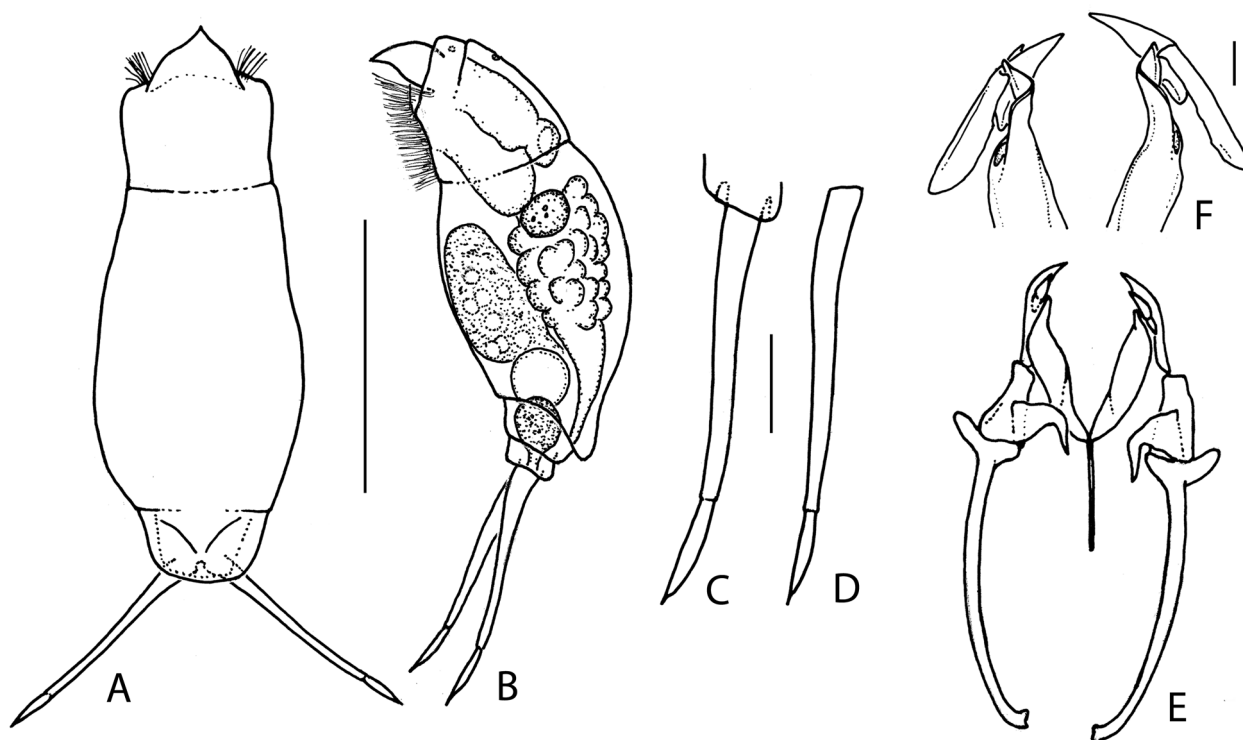
**Comments.** The unique trophi structure of *E. (Tricellatum) uncinatoides* sp. nov. argues for differentiating the taxon from the other taxa in the genus *Encentrum*. The new taxon is proposed as of subgeneric rank, in analogy to the already recognized subgenera in *Encentrum* (De Smet 1997).

***Encentrum (Tricellatum) uncinatoides* sp. nov. et subgen. nov.**

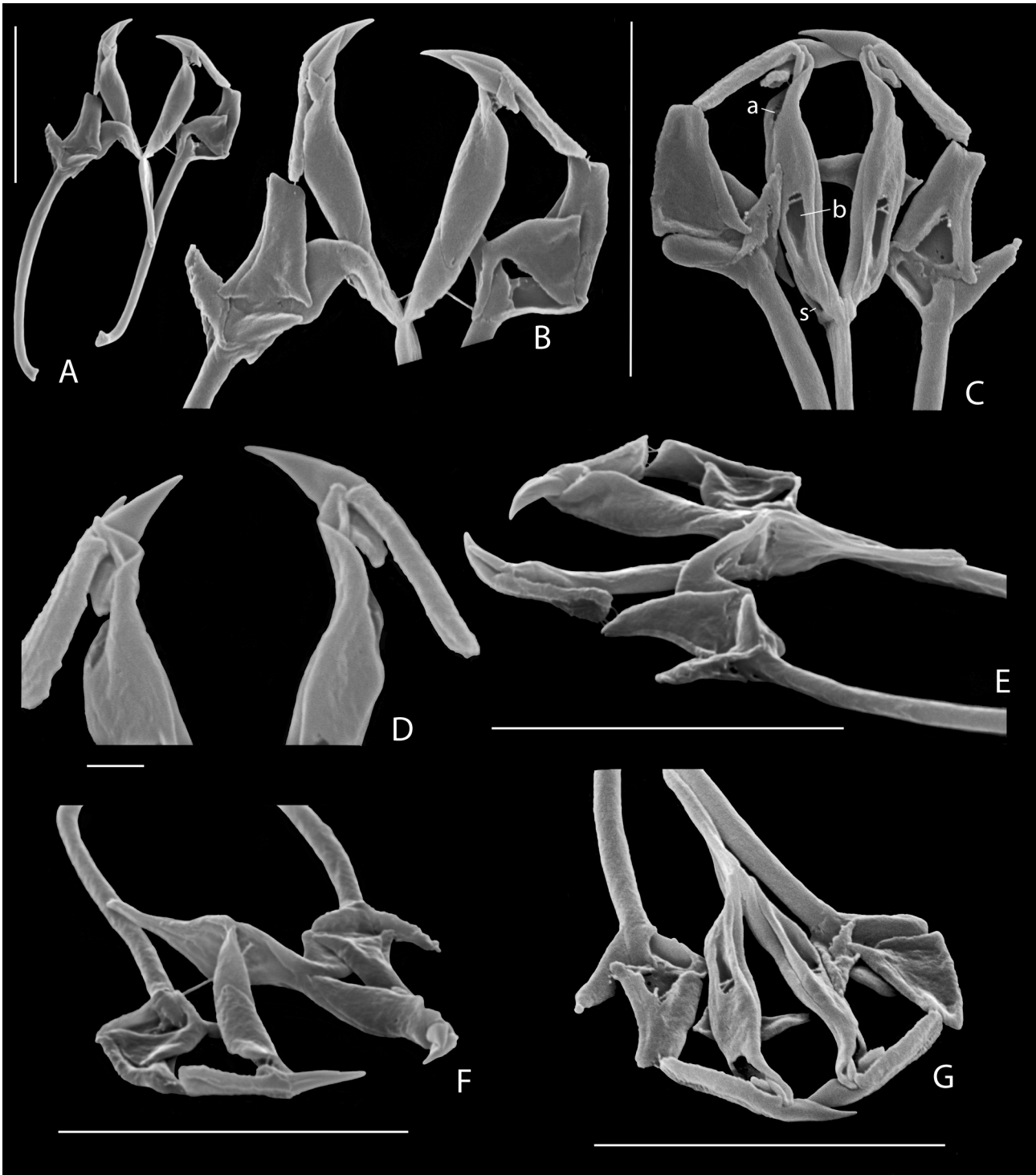
(Figs 12, 13)

**Diagnosis.** Medium-sized species, 135–155 µm long. Toes long, *c.* 1/3 total length, with large claw; corona ventral; rostrum large, triangular, pointed; rami composed of subbasal, basal and apical chamber; rami outline oblong-oval; median rami opening narrow, wedge-shaped; apical rami teeth absent, instead short straight rami tips revolved around their axis; intramallei large, elongate trapezoid; supramanubria hook-shaped, broad basally.

**Type locality.** Cap Bénat, Baie du Lavandou, Côte d'Azur, France. In psammon collected on 01.06.2010, 50 m from shoreline and depth of 20 m; water temperature 17 °C.



**FIGURE 12.** *Encentrum (Tricellatum) uncinatoides* sp. nov. A. Female, dorsal; B. female, lateral; C, D. toes, lateral; E. trophi, ventral; F. rami tips, dorsal. Scale bars: A, B: 50 µm, C–E: 10 µm; F: 1 µm.



**FIGURE 13.** *Encentrum (Tricellatum) uncinatoides* sp. nov., SEM photographs of trophi. A. Complete set, ventral; B. detail, ventral; C. detail, dorsal; D. detail rami tips, dorsal; E. detail, oblique ventro-lateral; F. detail, oblique ventro-frontal; G. detail, oblique dorso-frontal. a: apical ramus chamber, b: basal ramus chamber, s: subbasal ramus chamber. Scale bars: A–C, E–G: 10 µm; D: 1 µm.

**Holotype.** A female in a permanent, glycerine glass slide mount deposited in the Royal Belgian Institute of Natural Sciences (RBINS), Brussels, Belgium, No. IG 33082, RIR 221.

**Paratypes.** One female from type locality in RBINS, No. IG 33082, RIR 251; 5 mounted paratypes and 4 SEM trophi preparations in Department of Biology, University of Antwerp.

**Additional material.** In total 15 specimens from sublittoral of Côte d’Azur and Elba Island, Tyrrhenian Sea (see Tab. 2 species list).

**Etymology.** The specific name *uncinatooides* refers to the great external morphological resemblance of the new species with *Encentrum uncinatum* (Milne, 1886), a wide-spread benthic-periphytic freshwater species.

**Description of female.** Body fusiform (Figs 12A, B). Head weakly offset by shallow neckfold, *c.* 1/3 total length, with faint dorso-lateral transversal fold anteriorly. Rostrum fairly large, triangular, pointed, offset from head by distinct transversal fold, at its base two tufts of long cilia. Corona ventral. Dorsal antenna in posterior third of head. Trunk slightly arched dorsally, almost flat ventrally. Tail extending over most of foot. Foot, short, conical, two indistinct pseudosegments. Toes (Figs 12C, D) long, *c.* 1/3 total length, slender, more or less straight in dorsal view, very weakly S-shaped in lateral view, tapering to fairly long offset lanceolate spur. Brain large, saccate; retrocerebral sac present. Two colourless frontal eyes. Gastric glands spherical, short-stalked. Pedal glands spherical. Vitellarium with 8 nuclei.

Trophi (Figs 12E, 13) with oblong-oval rami outline, widest in distal half; median rami opening very narrow, wedge-shaped. Rami straight, widening distally and narrowing again towards short blunt, more or less gutter-shaped tips revolving around their axis (Figs 12F, 13D), apical teeth absent. Each ramus composed of three chambers with opening: the subbasal chamber with large, rounded-triangular caudal subbasifenestra (Fig. 13C: s), the basal chamber with large, elongate dorsal basifenestra (Fig. 13C: b), and the apical chamber with large oval antero-lateral fenestra (Fig. 13C: a). Preuncinal teeth with very short shaft and lanceolate head; shaft with short dorsal proximal ridge resting on revolved ramus tip; preuncinal teeth firmly connected with unci, and weakly to rami by tiny ligament. Fulcrum less ramus length, narrow in dorsal view, proximal 1/3 triangular, distal 2/3 narrow, parallel-sided. Unci fairly slender, head 1/3 total length, head and shaft making obtuse angle; ventral apophysis of shaft absent, dorsal one resting on rami tip; head expanded in plane of rami. Intramallei long, elongate trapezoid, base with weak lateral projections; inner side with triangular basal opening. Supramanubria hook-shaped with broad triangular base. Manubria long, *c.* twice ramus length, rod-shaped, weakly curved; head fairly large, V-shaped, ventral branch of head parallel-sided, rounded distally with opening at inner side, dorsal branch tapering to more or less offset acute tip, with caudal opening; cauda weakly crutched.

**Measurements.** Body (N=5): total length 135–155  $\mu\text{m}$ , toe 37–47  $\mu\text{m}$ , spur 9–12  $\mu\text{m}$ ; trophi (N=4): length 22–24  $\mu\text{m}$ , ramus 7.4–8.3  $\mu\text{m}$ , fulcrum 5.7–6.0  $\mu\text{m}$ , unci 4.6–5.9  $\mu\text{m}$ , preuncinal tooth 2.6  $\mu\text{m}$ , intramalleus 4.0–4.3 $\times$ 2.6–2.9  $\mu\text{m}$ , supramanubrium 3.1–4.3 $\times$ 2.7  $\mu\text{m}$ , manubrium 15.4–16.1  $\mu\text{m}$ .

**Comments.** The shape of the rami, composed of three well developed chambers, is unique in *Encentrum* species and all other Dicranophoridae of which trophi have been thoroughly studied by SEM. Hitherto, apical chambers were considered to be strongly reduced and lacking a distinct opening in dicranophorids, and it was supposed that they became isolated from the rami or participated in the formation of the apical regions of the rami (Markevich 1989). Another outstanding character of *E. uncinatooides* **sp. nov.** are the revolved gutter-shaped rami tips. Some revolving of the rami tips is only found in the dicranophorid *Albertia vermiculus* Dujardin, 1838, which shows compact drawn out rami tips attached distally near the dorsal uncinal apophysis (De Smet 1997).

**Distribution and ecology.** The species was found on four occasions at very low numbers in psammon from the sublittoral of the Côte d'Azur and Tyrrhenian Sea. Distance from the shore 50 m to 3.5 km, depth 17 to 40 m, June and September, water temperature 17–22 °C.

### ***Paradicranophorus halophilus* sp. nov.**

(Figs 14, 15)

**Diagnosis.** Female 200–240  $\mu\text{m}$ . Trunk with 5–6 conspicuous transversal, and several longitudinal folds; foot almost caudal; lateral antennae fairly long, near posterior 1/3 of trunk; intramallei and supramanubria present; rami outline elliptical-oval; median rami opening more or less oblong-oval; inner margins of rami with tooth prior to apical ramus tooth. Oviparous.

**Type locality.** Scoglietto di Portoferraio, Elba Island, Tyrrhenian Sea, Italy. In psammon collected on 30.09.2006, 1 km off shore and depth of 35 m; water temperature 23 °C.

**Holotype.** A female in a permanent, glycerine glass slide mount deposited in the Royal Belgian Institute of Natural Sciences (RBINS), Brussels, Belgium, No. IG 33082, RIR 222.

**Paratypes.** One female from type locality in RBINS, No. IG 33082, RIR 252; 5 mounted paratypes and 3 SEM trophi preparations in Department of Biology, University of Antwerp.

**Additional material.** Several specimens from sublittoral of Costa Blanca, Costa Brava, Côte d'Azur, and Elba Island (see Tab. 2 species list).

**Etymology.** The name of the species is a Latinization of the Greek *hals*, salt, and *philos*, friend, referring to the environment inhabited by the species.

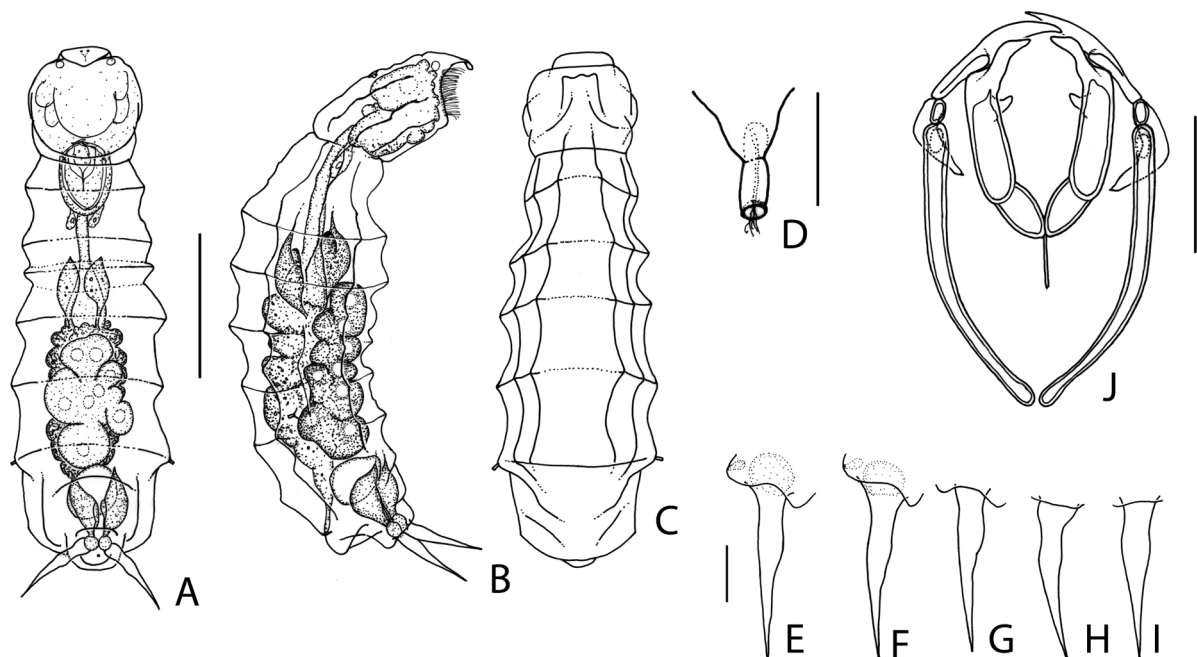
**Description of female.** Body cylindrical (Figs 14A–C); trunk weakly widening towards rounded posterior; head slightly broader than neck, distinctly offset by neckfold; in lateral view trunk almost as high throughout; rostrum narrow, bluntly triangular. Trunk with some 5–6 conspicuous transversal and several longitudinal folds; on contraction usually two deep furrows near mid-length. Tail absent. Foot almost caudal, two pseudosegments; large penultimate segment continuous with trunk, distal pseudosegment small, indistinctly offset. Toes (Figs 14E–I) fairly short, almost straight, slightly indented behind base, tapering to acute points. Dorsal antenna near middle of head. Lateral antennae (Fig. 14D) fairly long, near posterior 1/3 of trunk. Two frontal colourless eyespots at base of rostrum. Gastric glands fusiform, stalked. Pedal glands fusiform with reservoir at base of toes. Vitellarium with 8 nuclei. Oviparous.

Trophi (Figs 14J, 15) elongate. Outline of rami elliptical to oboval; inner margins of rami with tooth prior to robust apical rami teeth; apical rami teeth oblique, tip offset; outer margin of rami with rounded expansion prior to apical tooth whereupon dorsal rib of shaft of unci rest; median rami opening more or less oblong-oval; basifenestrae and subbasifenestrae small, rounded. Fulcrum short, lamelliform, broadly rounded distally. Unci single-toothed; shaft as long as head, with well developed dorsal rib. Each ramus with single stout preuncinal tooth; head somewhat longer than shaft. Intramallei small, with more or less semi-lunar supramanubria. Manubria rod-shaped, weakly curved; head reduced, with latero-ventral opening.

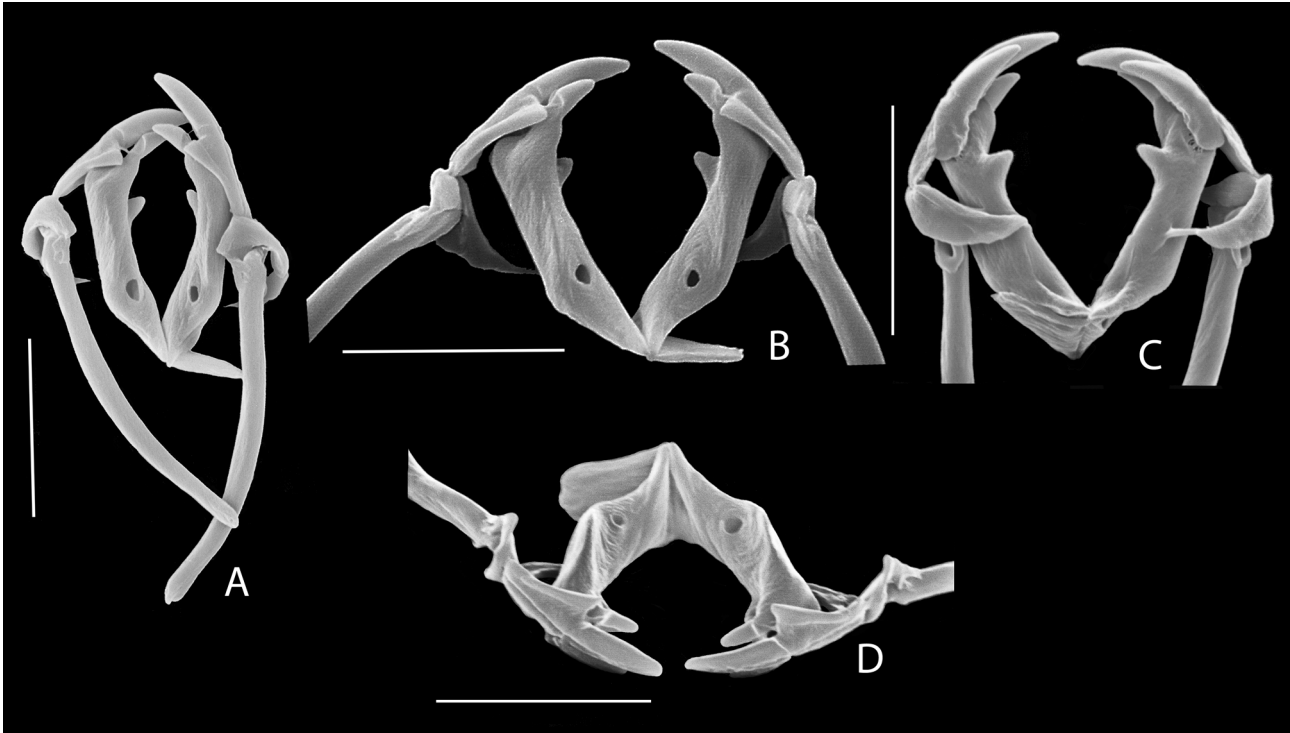
**Measurements.** Body (N=5): total length 200–240  $\mu\text{m}$ , toe 28–33  $\mu\text{m}$ , lateral antenna 4.5–5.0  $\mu\text{m}$ ; trophi (N=3): length 28–29  $\mu\text{m}$ , ramus 12.7–14.1  $\mu\text{m}$ , fulcrum 4.2–4.5  $\mu\text{m}$ , uncus 9.0–9.9  $\mu\text{m}$ , preuncinal tooth 6.1–6.5  $\mu\text{m}$ , intramalleus 1.7  $\times$  1.3  $\mu\text{m}$ , supramanubrium 5.0–6.0  $\mu\text{m}$ , manubrium 19.2–20.8  $\mu\text{m}$ .

**Comments.** *Paradicranophorus halophilus* sp. nov. is easily distinguished from its six described congeners, by the presence of a tooth on the inner margins of the rami. The new species shares the characters presence of intramallei and supramanubria with *P. sordidus* Donner, 1968, *P. wesenberglundi* Sørensen, 2001, and *P. sinus* De Smet, 2003.

**Distribution and ecology.** *Paradicranophorus halophilus* sp. nov. is one of the most frequently encountered species, often occurring in considerable numbers. It was found in the sublittoral psammon samples from the Costa Blanca, Costa Brava, Côte d’Azur, and Elba Island, Tyrrhenian Sea, at distances of 50 m to 3.5 km from the shoreline, and depths between 15 and 40 m. It was present in samples of June, July, August, September, and October, at water temperatures of 16–24 °C.



**FIGURE 14.** *Paradicranophorus halophilus* sp. nov. A. Female, ventral; B. female, lateral; C. female, dorsal; D. lateral antenna; E–H. toes, lateral; I. toe, dorsal; J. trophi, dorsal. Scale bars: A–C: 50  $\mu\text{m}$ ; D–J: 10  $\mu\text{m}$ .



**FIGURE 15.** *Paradicranophorus halophilus* sp. nov., SEM photographs of trophi. A. Complete set, dorsal; B. detail, dorsal; C. detail, ventral; D. detail, dorso-frontal. Scale bars: 10 µm.

#### Family LINDIIDAE Harring & Myers, 1924

#### Genus *Lindia* Dujardin, 1841

#### *Lindia aequorea* sp. nov.

(Figs 16, 17)

**Diagnosis.** Foot a single pseudosegment. Manubria with stout hook-shaped cauda; unci composed of single blunt major tooth and acute minor tooth, a strong preuncinal tooth, and chisel-shaped subuncus; epipharynx butterfly-shaped. Oviparous.

**Type locality.** Pomonte, Elba Island, ‘il relitto di Pomonte’ (wreck of Elviscott), Tyrrhenian Sea, Italy. In psammon collected on 26.09.2006, 100 m from shoreline and depth of 10 m; water temperature 23 °C.

**Holotype.** A female in a permanent, glycerine glass slide mount deposited in the Royal Belgian Institute of Natural Sciences (RBINS), Brussels, Belgium, No. IG 33082, RIR 223.

**Paratypes.** One female from type locality in RBINS, No. IG 33082, RIR 253; 1 mounted paratype and 3 SEM trophi preparations in Department of Biology, University of Antwerp.

**Additional material.** Thirty specimens from type locality, and 3 from sublittoral of La Fonza Esterna, Elba Island, Tyrrhenian Sea.

**Etymology.** The species name *aequorea* is a Latin adjective, meaning ‘belonging to the sea, marine’.

**Description of female.** Body (Fig. 16A) elongate fusiform, transversal folds inconspicuous. Head indistinctly offset; auricles not seen. Tail (Figs 16B, C) hemispherical, bulging. Foot a single pseudosegment, short. Toes short, fairly robust, with short tubulus, conical in dorsal view, in lateral view dorsal margin slightly arched and ventral margin straight. Single eyespot, small. Retrocerebral sac hemispherical with few minute pigment granules. Vitellarium with 8 nuclei. Oviparous.

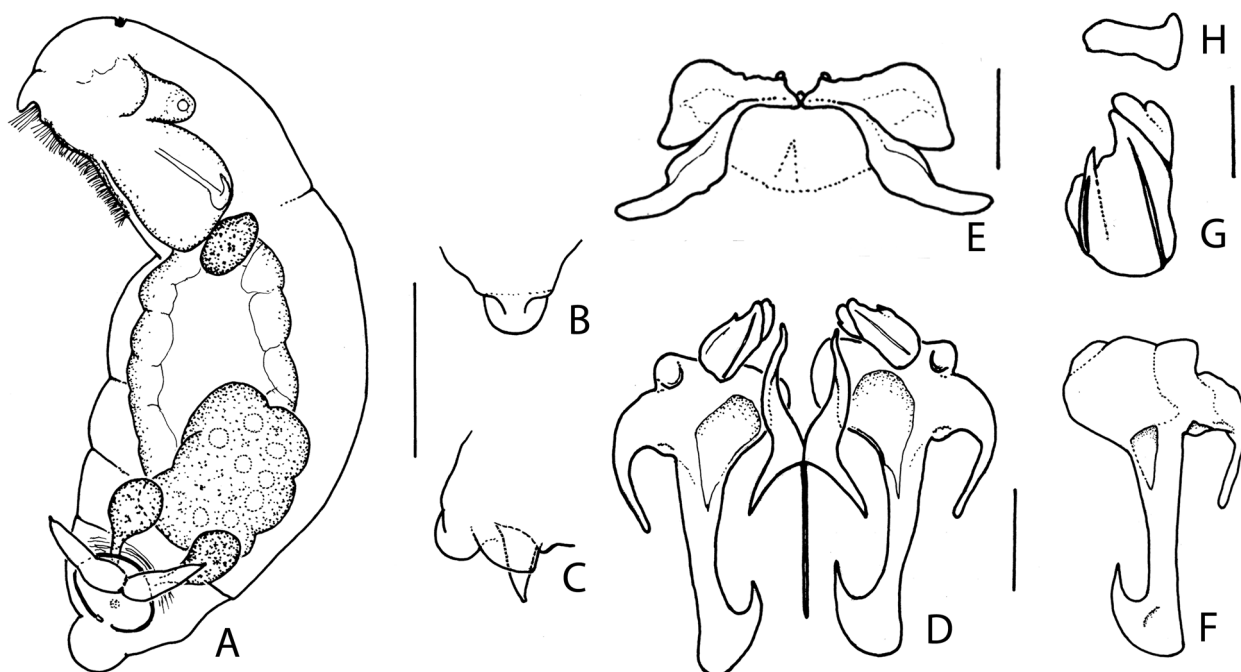
Trophi (Figs 16D–H, 17) with lyrate rami, with slender, long, caudally projecting sharp alulae; rami tips bifid, weakly revolved around axis. Strong broad ligaments connect both rami, and rami and manubria distally. Fulcrum plate-shaped, tapering distally. Ventral branch of manubria rod-shaped, short, *c.* 1/4 length shaft of manubrium;

shaft of manubria stout, with broad hook-shaped caudum; ‘dorsal branch’ (expanded part of dorsal manubrium chamber) short, more or less semi-lunar; opening of dorsal chamber large, at inner side of manubrium; opening of medial and ventral chamber at outer side of manubrium, small and rounded in ventral chamber, somewhat larger and triangular in medial chamber. Unci with single, stout blunt tooth with stout preuncus (Fig. 17G), and lateral expansion with acute toothlet. Subuncus (Fig. 17H) a single, stout chisel-shaped element. Epipharynx (Figs 16E, 17D) thin, butterfly-shaped.

**Measurements.** Body (N=3): total length slightly contracted up to 280  $\mu\text{m}$ , toe 21–22  $\mu\text{m}$ ; trophi (N=3): length  $\sim$ 40  $\mu\text{m}$ , ramus inclusive alula 18.9–19.1  $\mu\text{m}$ , fulcrum 15.7  $\mu\text{m}$ , uncus 8.9–9.3  $\mu\text{m}$ , manubrium 31.7–34.0  $\mu\text{m}$ , subuncus 4.2–4.9, 5.2–5.4  $\mu\text{m}$ , epipharynx 37.5  $\times$  14.4  $\mu\text{m}$ .

**Comments.** *Lindia aequorea* **sp. nov.** is unambiguously differentiated from its congeners (see Segers 2002) by the characteristic shape of the trophi, in particular the strong, terminally hook-shaped manubria and the butterfly-shaped epipharynx. The only other *Lindia* with caudally hook-shaped manubria is *L. euchromatica* Edmondson, 1938, which shows no other affinities with the new species, and inhabits freshwater colonial cyanobacteria and periphyton.

**Distribution and ecology.** To date only known from sublittoral psammon sampled at Elba Island, Tyrrhenian Sea, 50 and 100 m from shoreline, depth 10 and 30 m, September, water temperature 23  $^{\circ}\text{C}$ .



**FIGURE 16.** *Lindia aequorea* **sp. nov.** A. Female, slightly twisted, head lateral, trunk ventral; B. tail, dorsal; C. tail, distal pseudosegment and toe, lateral; D. trophi, complete set, ventral; E. epipharynx; F. left manubrium, outer view; G. uncus with preuncinal tooth; H. subuncus. Scale bars: A–C: 50  $\mu\text{m}$ ; D–H: 10  $\mu\text{m}$ .

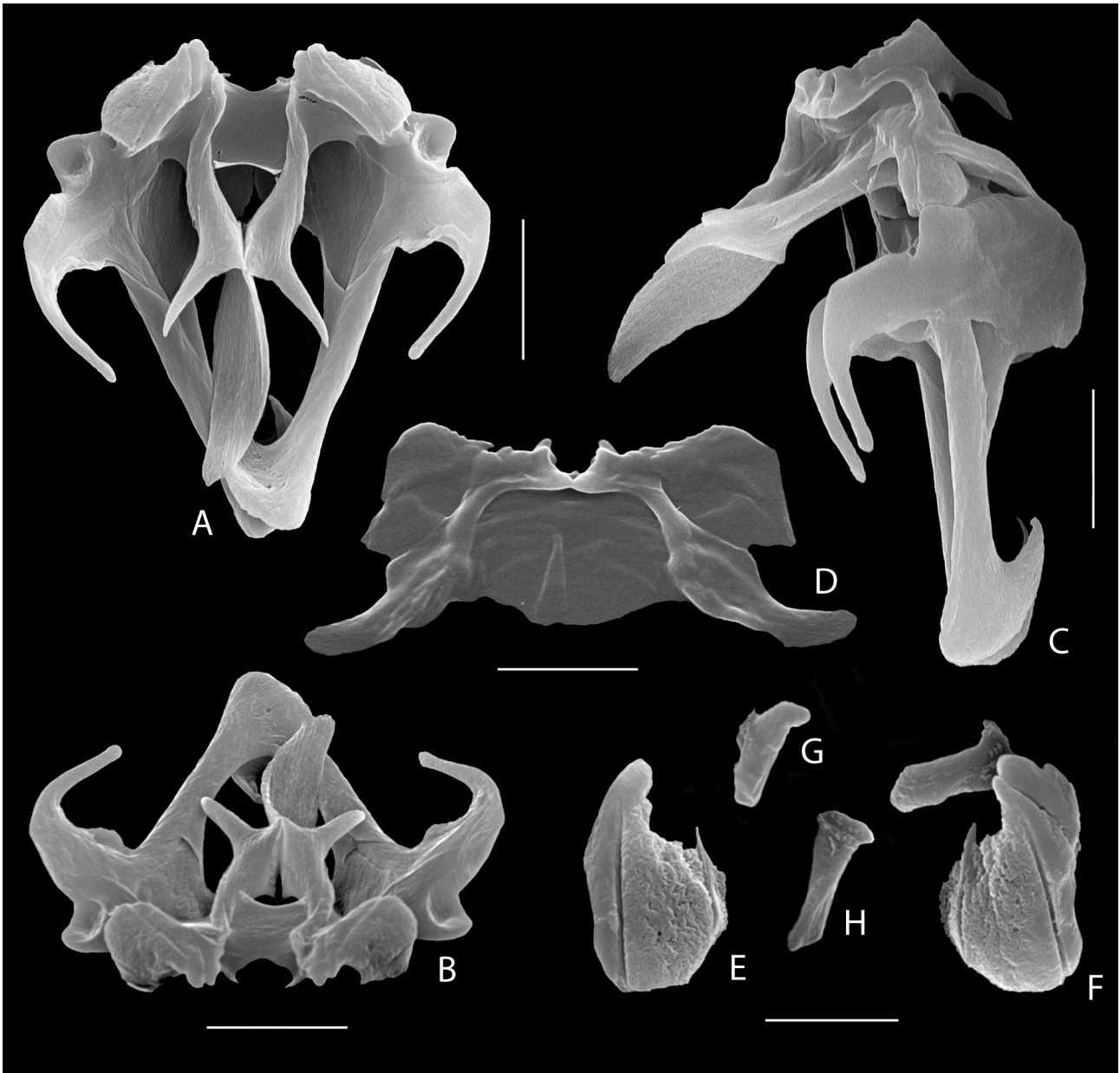
## Family NOTOMMATIDAE Hudson & Gosse, 1886

### Genus *Pleurotrocha* Ehrenberg, 1830

#### *Pleurotrocha fontanetoi* **sp. nov.**

(Figs 18, 19)

**Diagnosis.** Head short, narrower than trunk; foot long, 2–3 pseudosegments; toes conical, with offset distal half; corona slightly oblique; rami with long obtuse alulae; fulcrum with large basal plate; manubria with large head and incurved cauda; a ribbon composed of two bands of short and long sclerite bodies laterally from dorsally recurved part of rami.



**FIGURE 17.** *Lindia aequorea* sp. nov., SEM photographs of trophi. A. Complete set, ventral; B. same as A, frontal; C. complete set, lateral; D. epipharynx; E. left uncus, without preuncinal tooth and subuncus; F. right uncus, with preuncinal tooth and subuncus; G. left preuncinal tooth; H. right subuncus. Scale bars: 10 µm.

**Type locality.** Punta della Madonna di Ponente, Elba Island, Tyrrhenian Sea, Italy. In psammon collected on 28.09.2006, 50 m from shoreline and depth of 40 m; water temperature 22 °C.

**Holotype.** A female in a permanent, glycerine glass slide mount deposited in the Royal Belgian Institute of Natural Sciences (RBINS), Brussels, Belgium, No. IG 33099, RIR 255.

**Paratypes.** One female from type locality in RBINS, No. IG 33099, RIR 256; 5 mounted paratypes and 6 SEM trophi preparations in Department of Biology, University of Antwerp.

**Additional material.** Several specimens from other sampling stations at Elba Island, and Cap Bénat, Côte d'Azur (see Tab. 2 species list).

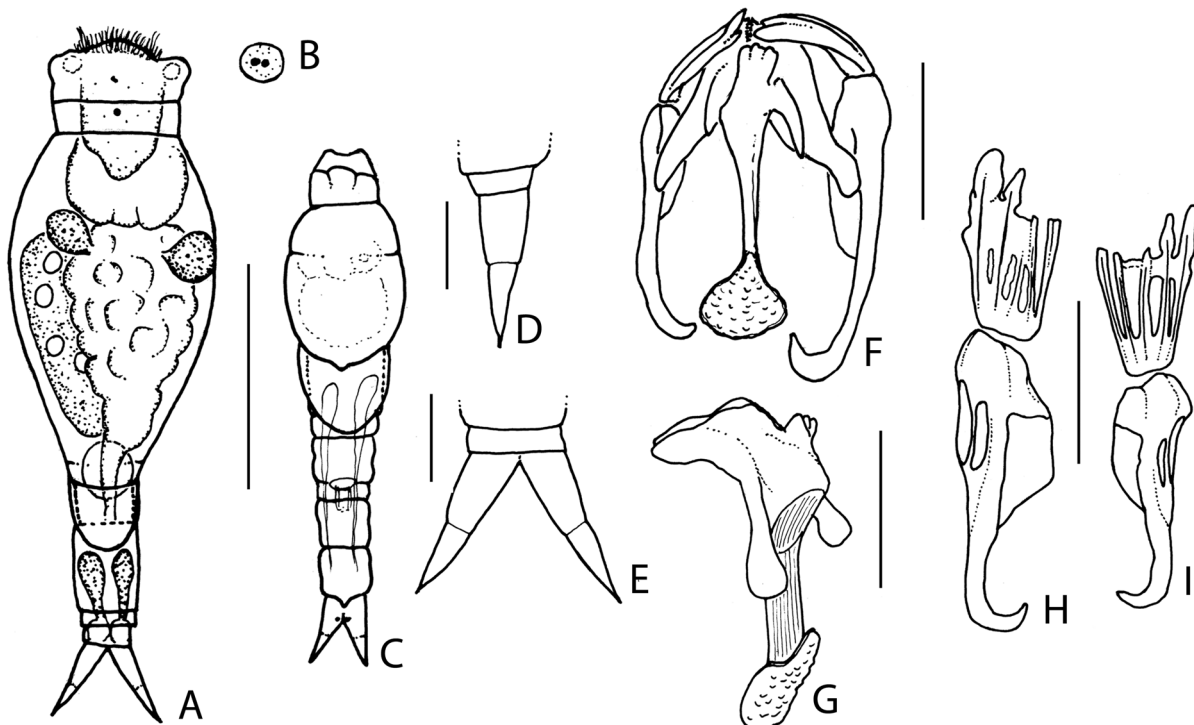
**Etymology.** The species is dedicated to dr. Diego Fontaneto in recognition of his important contributions to our knowledge of the Rotifera.

**Description of female.** Body (Fig. 18A) stout fusiform, somewhat gibbous. Head and foot offset by transversal fold. Head short, narrower than trunk, with transversal fold. Corona slightly oblique, with small lateral tufts of cilia. Dorsal antenna near posterior 1/3 of head. Eyespot on brain, a colourless globule with two minute red-



pigmented granules (Fig. 18B). Trunk elongate-ovate with transversal fold in posterior 1/3. Tail large, rounded. Foot long, cylindrical, 2–3 pseudosegments, occasionally appearing wrinkled proximally. Toes (Figs 18D, E) short, stout conical, tapering to tubular tips, with more or less distinctly offset distal half. Pedal glands club-shaped with reservoirs at base of toes. Stomach separated from intestine by weak constriction. Gastric glands large, rounded.

Trophi (Figs 18F–I, 19) asymmetrical, left more strongly developed than right. Rami with large, elongate blunt alulae pointing latero-caudally, and large dorsally recurved apical branch bearing comb of tiny toothlets at inner margin; basal rami part with irregular knob-shaped teeth on inner margins, and strong, left basal apophysis; basal chambers fairly small, left one with large opening. Fulcrum robust, long, plank-shaped and fairly high, ventral margin reinforced, distal end broadly expanded into oblique oval plate. Unci five incompletely connected teeth of decreasing length, first two teeth with head, the others linear; left uncus more strongly developed, its first tooth with distinct head and prominent medial projection at ventral margin; right uncus more slender, head of teeth weak, projection at ventral margin weak; subuncus composed of few irregular knob-like prominences. Manubria with relatively large elongate head and dorsally recurved cauda, left manubrium largest; openings of ventral and medial chamber narrow, elongate, opening of dorsal chamber broad. A broad ribbon (Figs 19E, I, J: r) composed of two bands of long (frontal) and short (caudal) sclerite bodies inserted laterally from recurved distal part of rami, and partly covered by malleus.



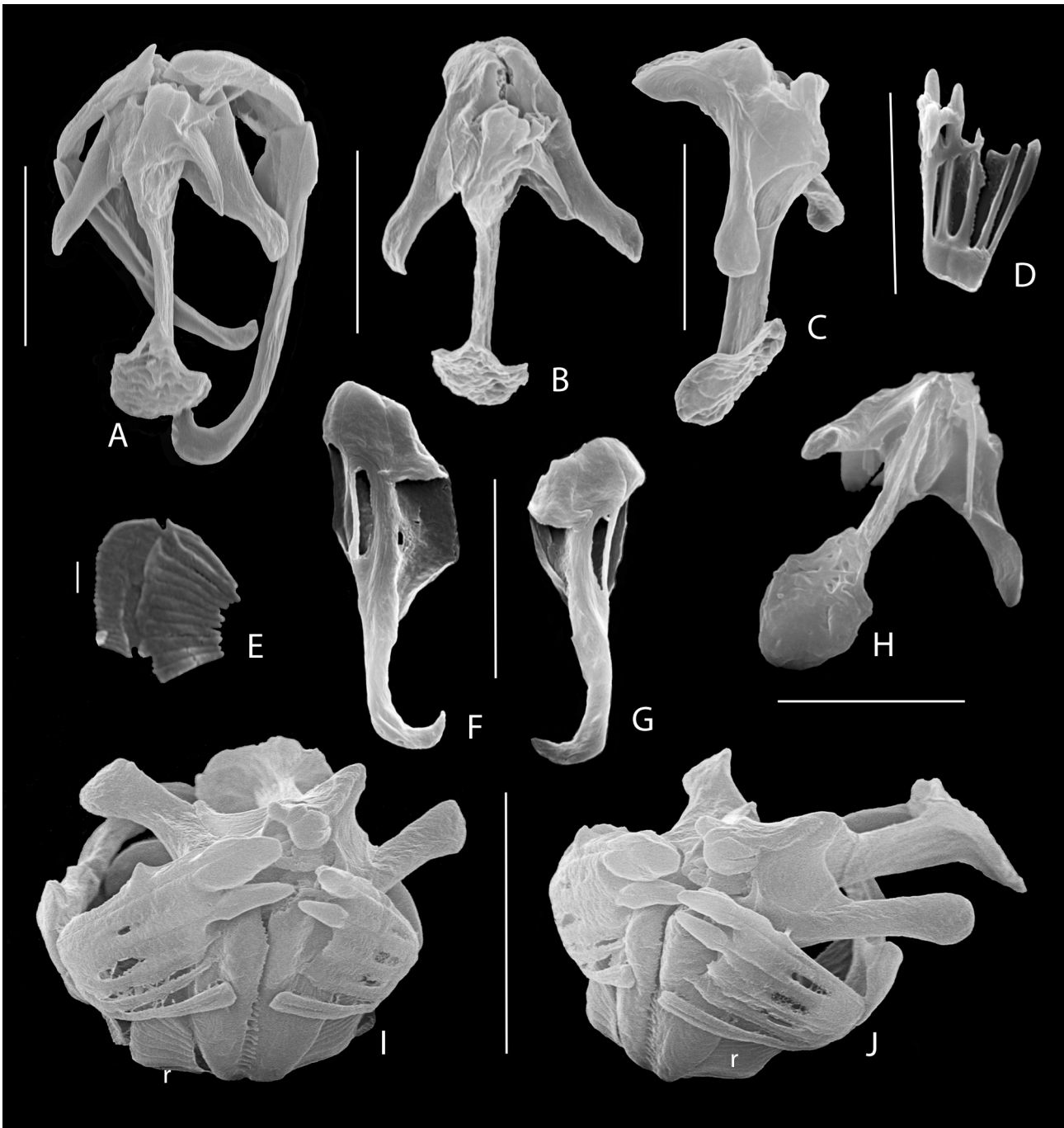
**FIGURE 18.** *Pleurotrocha fontanetoi* sp. nov. A. Female, dorsal; B. eye, female; C. male, dorsal; D. toe, female, lateral; E. toes, female, dorsal; F. trophi, complete set, ventral; G. incus, lateral; H. left malleus, outer view; I. right malleus, outer view. Scale bars: A, C: 50  $\mu$ m; D–I: 10  $\mu$ m.

**Description of male.** Male more or less similar in habitus to female, with small head, oval trunk, and long foot composed of *c.* 5 pseudosegments; toes conical with more or less distinctly offset distal part.

**Measurements.** Female, body (N=5): total length 150–180  $\mu$ m, toe 17–28  $\mu$ m; trophi (N=5): length 21.8–23.3  $\mu$ m, ramus with alulae  $\sim$ 13  $\mu$ m, fulcrum 9.9–13.3  $\mu$ m, left uncus 9.1–12.8  $\mu$ m, right uncus 8.1–9.0  $\mu$ m, left manubrium 18.7–20.9  $\mu$ m, right uncus 11.1–15.6  $\mu$ m, ribbon of sclerite bodies (length  $\times$  height)  $\sim$ 10  $\times$  4.8  $\mu$ m. Male (N=4): total length  $\sim$ 120  $\mu$ m, toe 18–20  $\mu$ m.

**Comments.** The species is allocated to the genus *Pleurotrocha* Ehrenberg, 1830 on basis of the stout body with well-separated head and trunk, the long cylindrical foot with two short toes, the slightly oblique corona with lateral tufts of cilia, auricles absent, a single cerebral eyespot, and fairly large pedal glands with reservoir; the trophi are virgate, with long fulcrum and dorsally recurved rami (Koste 1978; Nogrady *et al.* 1995). In fixed material, *P. fontanetoi* sp. nov. can be mistaken for *Proales similis* Beauchamp, 1907 but is unambiguously differentiated from the latter and all other Notommatidae by its characteristic trophi.

**Distribution and ecology.** The species was found in psammon from the Côte d'Azur and Elba Island, Tyrrhenian Sea, 50 m and 1 km off shore, depth 20–40 m, June, September, water temperature 17–23 °C.



**FIGURE 19.** *Pleurotrocha fontanetoi* sp. nov., SEM photographs of trophi. A. Complete set, ventral; B. incus, ventral; C. incus, lateral right; D. right uncus, inner view; E. distal part of ribbon of short and long sclerite bodies; F. left manubrium, outer view; G. right manubrium, outer view; H. incus, oblique ventro-caudal; I, J. complete set, oblique ventro-frontal. R: ribbon of sclerite bodies. Scale bars: A–D, F–J: 10 µm; E: 1 µm.

**Family PROALIDAE** Harring & Myers, 1924

**Genus *Proales*** Gosse, 1886

***Proales francescae* sp. nov.**

(Figs 20, 21)

**Diagnosis.** Female 125–135  $\mu\text{m}$  long; outline trunk broad-oval in dorsal view, with prominent tail overlying basal foot pseudosegment, and small indentations near base of tail; head narrower than trunk, with transversal fold near mid-length; foot with 4 pseudosegments, usually a narrow joint between distal and penultimate pseudosegment; toes with long drawn out points; rami with 2 alulae each; cauda of manubria incurved at right angle, and slightly enlarged at angle.

**Type locality.** Cap Bénat, Baie du Lavandou, Côte d'Azur, France. In psammon collected on 01.06.2010, 50 m from shoreline and depth of 20 m; water temperature 17 °C.

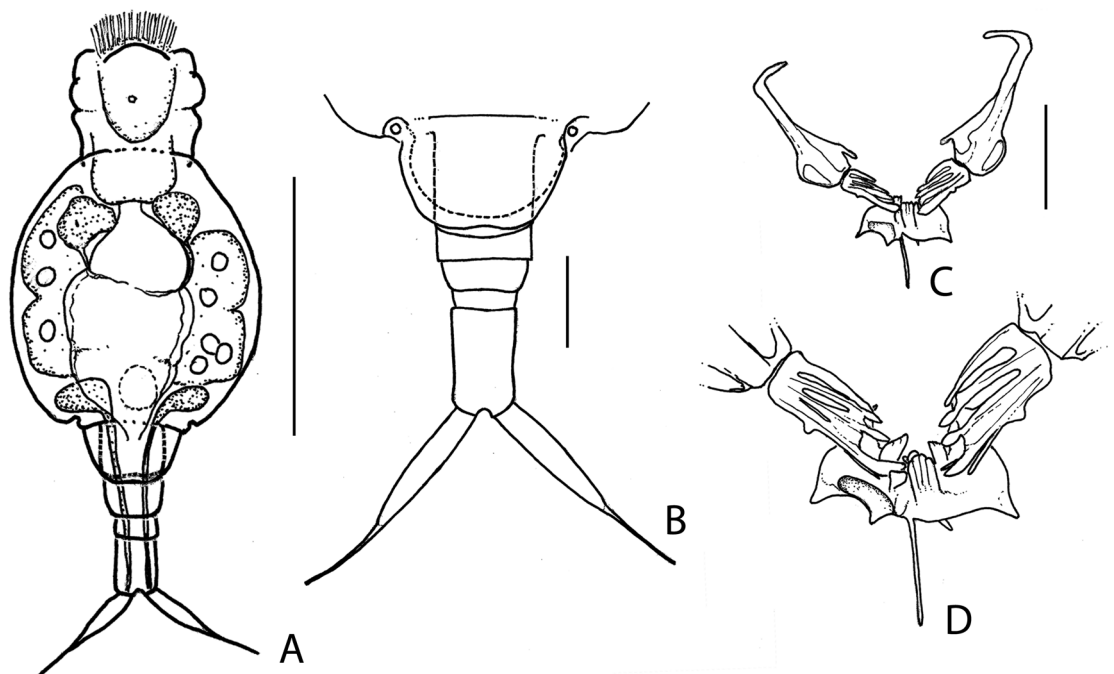
**Holotype.** A female in a permanent, glycerine glass slide mount deposited in the Royal Belgian Institute of Natural Sciences (RBINS), Brussels, Belgium, No. IG 33082, RIR 224.

**Paratypes.** One female from type locality in RBINS, No. IG 33082, RIR 254; 5 mounted paratypes and 7 SEM trophi preparations in Department of Biology, University of Antwerp.

**Additional material.** Several specimens from most of the study area (see Tab. 2 species list).

**Etymology.** The species is named for dr. Francesca Leasi, in recognition of her interesting contributions to our knowledge of the Rotifera.

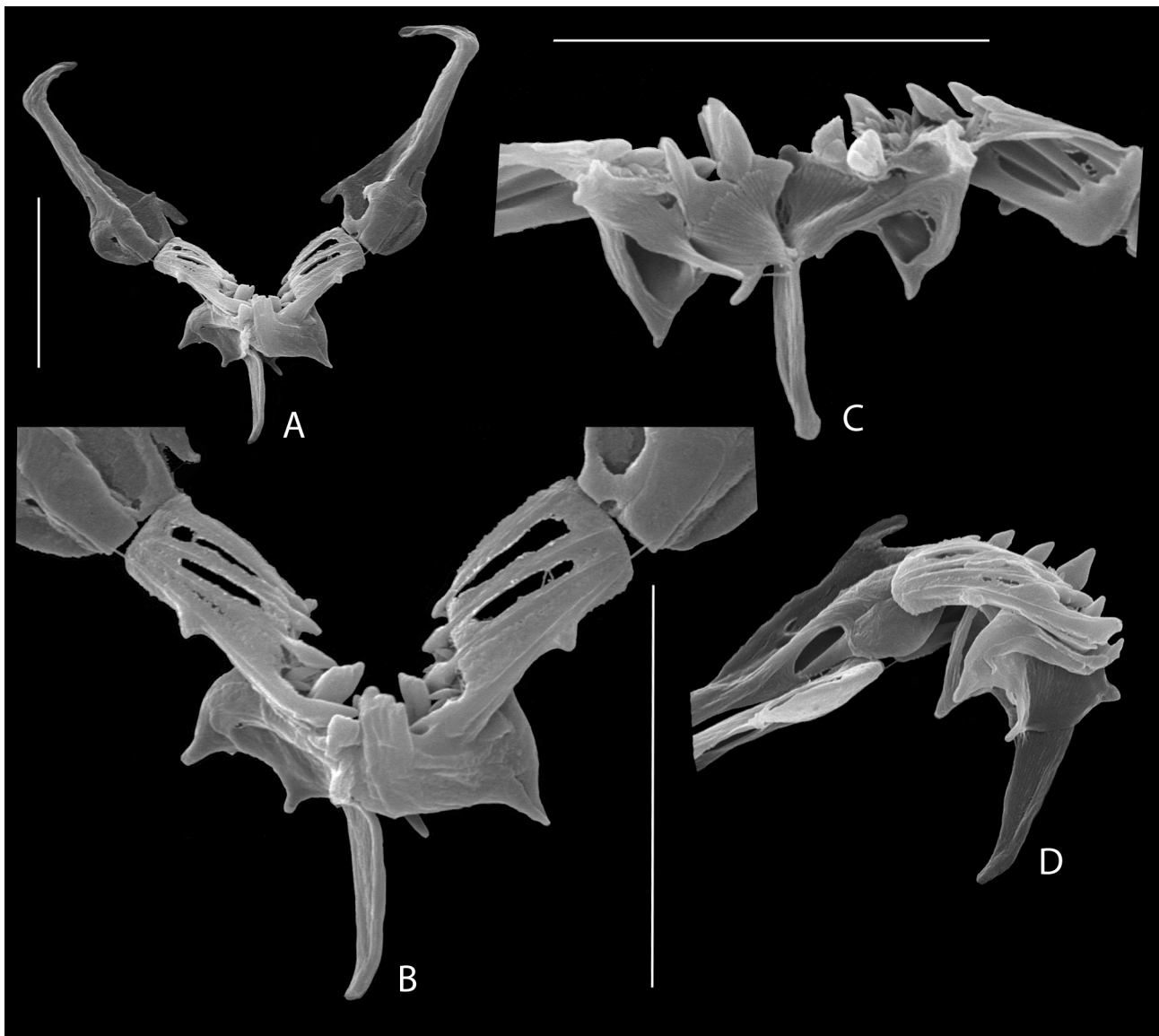
**Description of female.** Semi-loricated. Trunk (Fig. 20) broad ovate in dorsal view, with prominent small lateral indentations prior to tail; tail (Fig. 20B) distinctly offset from trunk, covering basal foot pseudosegment, distal margin straight-cut, mostly with broad, very shallow indentation; ventral to the tail a similar, rounded lobe. Head offset by neckfold, quadratic, dorsally with delicate transverse folds medially and at anterior 1/4, laterally slightly bulging near transversal folds. Corona almost frontal, lateral ciliary tufts absent. Foot (Fig. 20B) long, *c.* 1/3 total length; four pseudosegments, distal longest, penultimate shortest, usually with distinct narrow joint between. Toes long, slender, inner margins straight, outer margins weakly curved, tapering to long drawn-out and slightly offset points. Brain large, saccate; Y-shaped retrocerebral duct. Dorsal antenna near midlength of head; lateral antennae at lateral indentations. Eyespots absent. Proventriculus present. A shallow constriction between stomach and intestine. Gastric glands spherical, stalked. Pedal glands clubbed, extending into trunk, ducts very long.



**FIGURE 20.** *Proales francescae* sp. nov. A. Female, dorsal; B. foot and toes, dorsal; C. trophi, complete set, ventral; D. detail incus and unci. Scale bars: A: 50  $\mu\text{m}$ ; B–D: 10  $\mu\text{m}$ .

Trophi (Figs 20C, D, 21) malleo-virgate. Rami asymmetrical, each with triangular basal part, and anterior dorsally recurved part narrowing into broad tip with about three shallow knobs; alulae acute, right an additional

projection between fulcrum and alula at caudal ramus margin, left near base of fulcrum an additional caudal projection inserted dorsally; right subbasal chamber and subbasifenestra large, ventral, left subbasal chamber and subbasifenestra dorsal; basifenestrae large, dorsal; each ramus ventrally with two broad crenate crests at inner margin, more or less transverse to the trophi axis and pointing antero-ventral; left: a huge basal crest composed of at least 5 fused sclerite elements, and a smaller distal one composed of at least 4 fused sclerite elements; right: a smaller basal and a large distal crest composed of at least 4 fused sclerites; right near base of fulcrum an additional blunt prominence pointing caudally. Fulcrum rod-shaped in ventral view; in lateral view less high, more or less tapering to oblique end. Uncus with 4(5) clubbed teeth, gradually decreasing in size, and 1–2 small, less differentiated minor teeth; teeth connected by membrane; principal teeth with prominence on free margin and distinct preuncinal tooth; subuncus a bundle of fusiform sclerite bodies; the second rami crests fit in the space between the head of the first two uncinal teeth. Manubria long, left somewhat longer, posterior end fairly abruptly incurved at a right angle, and enlarged at the height of the angle; head with short dorsal and longer ventral chamber.



**FIGURE 21.** *Proales francescae* sp. nov., SEM photographs of trophi. A. Complete set, ventral; B. detail, ventral; C. detail, dorsal; E. detail, lateral. Scale bars: 10  $\mu$ m.

**Measurements.** Body (N=5): total length 125–135  $\mu$ m, toe 25–26  $\mu$ m; trophi (N=5) ~20  $\mu$ m, ramus ~6  $\mu$ m, fulcrum 5  $\mu$ m, uncus 7.2 & 8.0  $\mu$ m, manubrium 12.6 & 14  $\mu$ m.

**Comments.** *Proales francescae* sp. nov. belongs to the *Proales reinhardti* (Ehrenberg, 1834) group. It can be confused with *P. halophila* Remane, 1929, which shows a more vase-shaped trunk, narrower head, less drawn out

toes, and lacks the indentations near the base of the tail. It may safely be distinguished by the trophi which in *P. halophila* (see De Smet 1996a) show only two alulae, and a single crenate crest of fused elements on the left ramus, and three on the right ramus. The caudae are smoothly incurved and gradually tapering in *P. halophila*, instead of incurved at a right and slightly enlarged angle in the new species. *Proales francescae* **sp. nov.** bears some resemblance with the species described as *P. halophila* by Tzschaschel (1979), but can not be compared seeing the poor and unreliable trophi description not based on SEM, imperative for the small *Proales* species.

**Distribution and ecology.** *Proales francescae* **sp. nov.** was collected in sublittoral psammon from the Costa Brava, Golfe du Lion, Côte d'Azur and Elba Island, from 20 m up to 8 km off shore, depth 15–50 m, June, July, September, October, 17–22 °C. The species was previously reported sub *Proales* sp. from Aufwuchs of a stand of brown algae in the sublittoral fringe of Grande Anse, Réunion Island, Indian Ocean (De Smet 2006).

## Notes on selected taxa

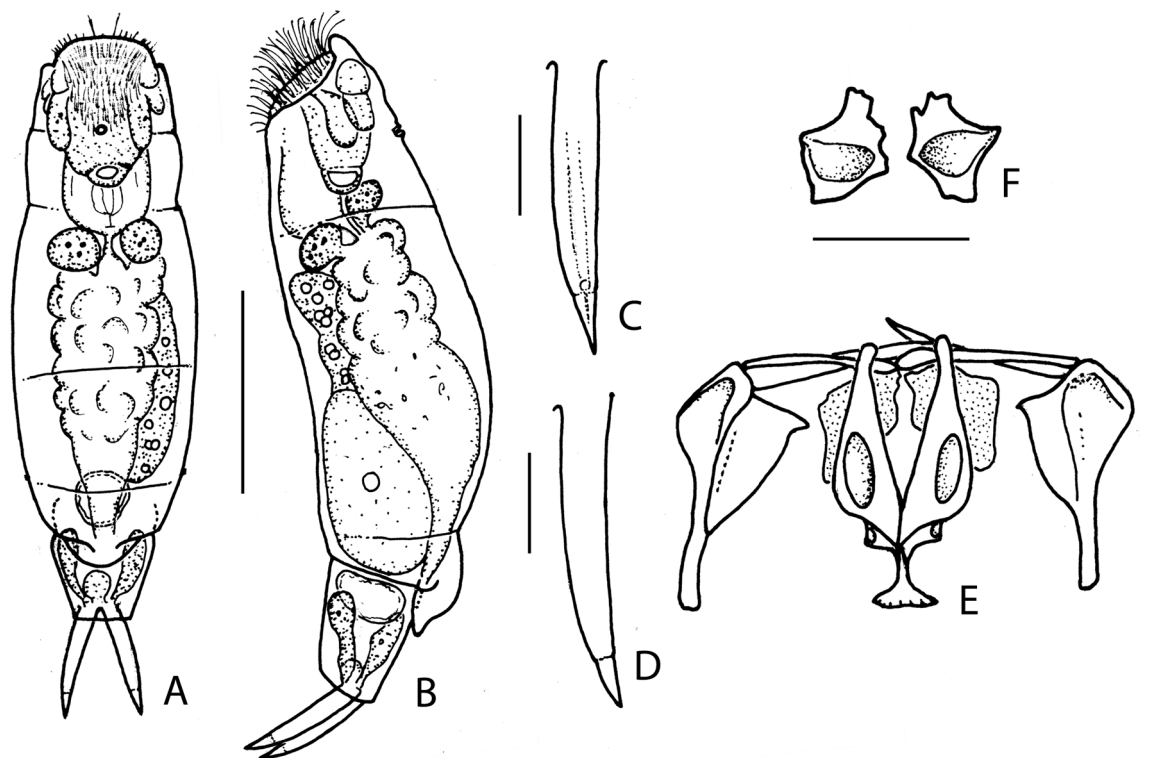
### Genus *Allodicranophorus* gen. nov.

(Figs 22, 23)

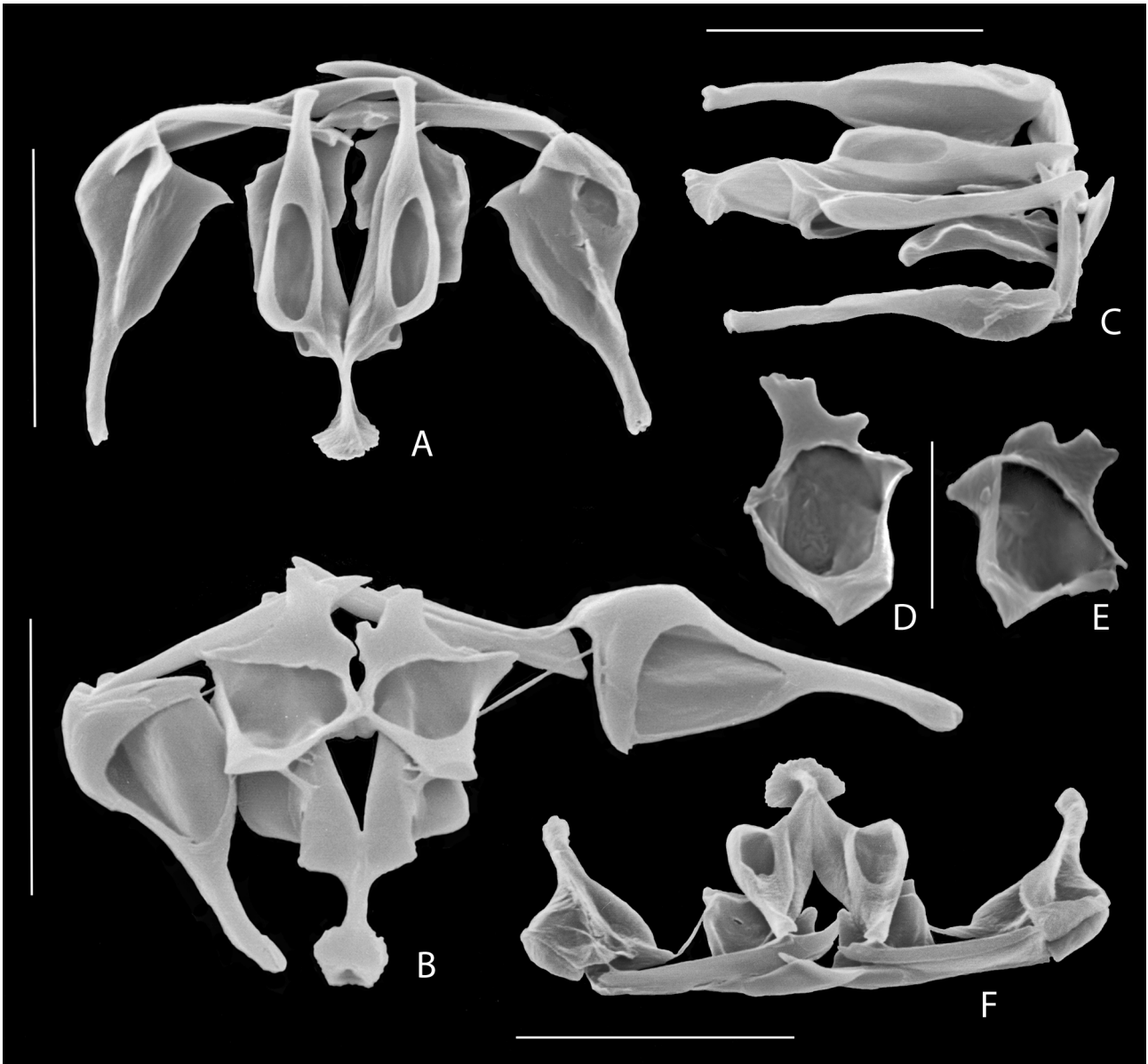
**Diagnosis.** Trophi symmetrical. Incus flat. Rami elongate; opening of subbasal chambers lateral, opening of basal chambers dorsal; rami tips blunt with minute medially directed blunt toothlet; inner margins without teeth; alulae absent. Fulcrum short, strongly expanded distally. Unci each with two equally long teeth composed of head and shaft. Manubria ramus length, with large head and rod-shaped cauda. Epipharynx two more or less trapezoid and slightly asymmetrical robust plates with large ventral opening.

**Type species.** *Allodicranophorus bulgaricus* (Althaus, 1957) **nov. comb.** for *Dicranophorus bulgaricus* Althaus, 1957.

**Etymology.** The name *Allodicranophorus* combines the Greek *allos*, meaning different, and *Dicranophorus*, alluding to the differences in trophi structure with the latter.



**FIGURE 22.** *Allodicranophorus bulgaricus* (Althaus). A. Female, dorsal; B. female, lateral; C. toe, dorsal; D. toe, lateral; E. trophi, dorsal; F. epipharynx, ventral. Scale bars: A, B: 50 µm; C–F: 10 µm.



**FIGURE 23.** *Allodicranophorus bulgaricus* (Althaus), SEM photographs of trophi. A. Complete set, dorsal; B. complete set, ventral; C. complete set, dorso-lateral; D, E. epipharyngeal elements, ventral; F. complete set, dorso-frontal. Scale bars: 10  $\mu$ m.

**Material.** Several specimens from most of the study area (see Tab. 2 species list). A female in a permanent, glycerine glass slide mount deposited in the Royal Belgian Institute of Natural Sciences (RBINS), Brussels, Belgium, No. IG 33082, RIR 225.

**Comments.** The external morphology of the species is typically dicranophorid-like, but the morphology of the trophi, which is the most important character state in the establishment of genera in Dicranophoridae (De Smet 1997), is completely aberrant. The unique combination of characters arguing for the establishment of a new genus of Dicranophoridae are: (1) the short distally enlarged fulcrum, (2) the manubria with large head of peculiar shape, (3) the two irregularly shaped hollow epipharyngeal plates, (4) the subbasifenestrae opening laterally, (5) the absence of distinct and medially projecting apical rami teeth, resulting in a wedge-shaped, distally open median rami opening.

**Description of female.** Body fusiform (Fig. 22), sub-cylindrical, in lateral view weakly arched dorsally, almost straight ventrally. Head, trunk and foot distinctly offset by transversal folds; trunk with two additional transversal and two latero-dorsal folds. Rostrum small, rounded. Corona small, oblique frontal. Dorsal antenna near middle of head. Tail prominent, keeled, projecting beyond basal 1/3 of foot pseudosegment. Foot fairly long, conical-cylindrical, a single pseudosegment. Toes (Fig. 22C, D) fairly short, slender, almost cylindrical with short

acute end; distal end in lateral view slightly decurving ventrally. Eyespots absent. Brain saccate, large. Retrocerebral organ present; cerebral sac large, hemispherical, posteriorly on brain; subcerebral glands present. Proventriculus, stomach and intestine very weakly demarcated. Gastric glands globular, weakly lobate, stalked, ventral. Pedal glands weakly stalked, foot length. Vitellarium with twelve nuclei. Oviparous.

Trophi (Fig. 22E, 23) modified forcipate, symmetrical. Incus flat. Rami elongate, alulae absent; basal chambers larger than subbasal ones, proximal margin broadly rounded; subbasal chambers somewhat projecting beyond basal ones caudally, proximal margin more or less angular laterally; ending distally in shallow blunt projection whereupon unci rest; subbasifenestrae lateral, small, rounded-triangular, basifenestrae dorsal, large, ellipsoid; median rami opening wedge-shaped, distally open; inner margins of rami without teeth, distinct apical rami teeth absent, basal chambers apically with very short blunt, medially directed knob. Fulcrum short, in dorsal/ventral view narrow proximally, strongly expanded distally, in lateral view slightly narrowing towards expanded distal end. Unci each with two equally long teeth composed of head and shaft; head dorsal tooth *c.* ¼ tooth length, head of ventral tooth *c.* ½ tooth length. Manubria ramus length, with large head and rod-shaped cauda; outer side with large opening of median (?) chamber, other chambers reduced. Epipharynx (Figs 22F, 23D, E) two more or less trapezoid and slightly asymmetrical robust plates, with marginal extensions and large ventral opening.

**Measurements.** Body (N=5): total length 190–260 µm, toe 28–32 µm; trophi (N=5) length 14.3–16.0 µm, incus 13.3–14.7 µm, ramus 9.6–10.9 µm, fulcrum 3.1–4.9 µm, uncus 8.7–11.6 µm, manubrium 11.0–14.6 µm, epipharynx 7.3–9.0 × 5.3–6.4 µm; amictic egg 63–88 × 41–53 µm.

**Distribution and ecology.** *Allodicanophorus bulgaricus* was to date only reported from the sublittoral (mesopsammon from 0.5 and 1 m) of its type locality, Varna, Sosopol, Bulgaria, Black Sea (Althaus 1957) and the sublittoral of Elba Island (De Smet 2007). In the present study it proved a rather common species of sublittoral psammon from the Costa Blanca, Golfe du Lion, Côte d'Azur, and Elba Island. It was found from 50 m to 5 km off shore, depth 15–50 m, June, August, September, October, water temperature 16–25 °C.

### Genus *Halolepadella* gen. nov.

(Figs 24, 25)

**Diagnosis.** Lorica outline oval, compressed dorso-ventrally, closed laterally, with dorsal and ventral indentations for head and foot. Retractable head shield present. Foot with four pseudosegments; foot and toes completely retractable in trunk. Two slender, moderately long toes with acutely pointed claw. Trophi malleo-virgate. Rami reduced, triangular with lateral alulae. Fulcrum fairly short, thin, straight and less high, without distal expansion. Unci a thin plate with five slender teeth of decreasing length; head of teeth free, tiny additional linear teeth present. Manubria long, straight, head reduced; cauda strongly expanded.

**Type species.** *Halolepadella pontica* (Althaus, 1957) **nov. comb.** for *Lepadella pontica* Althaus, 1957; junior synonym *Lepadella psammophila* Tzschaschel, 1978.

**Etymology.** The prefix *halo* is derived from the Greek *hals*, salt, and refers to the saline environment the species lives in.

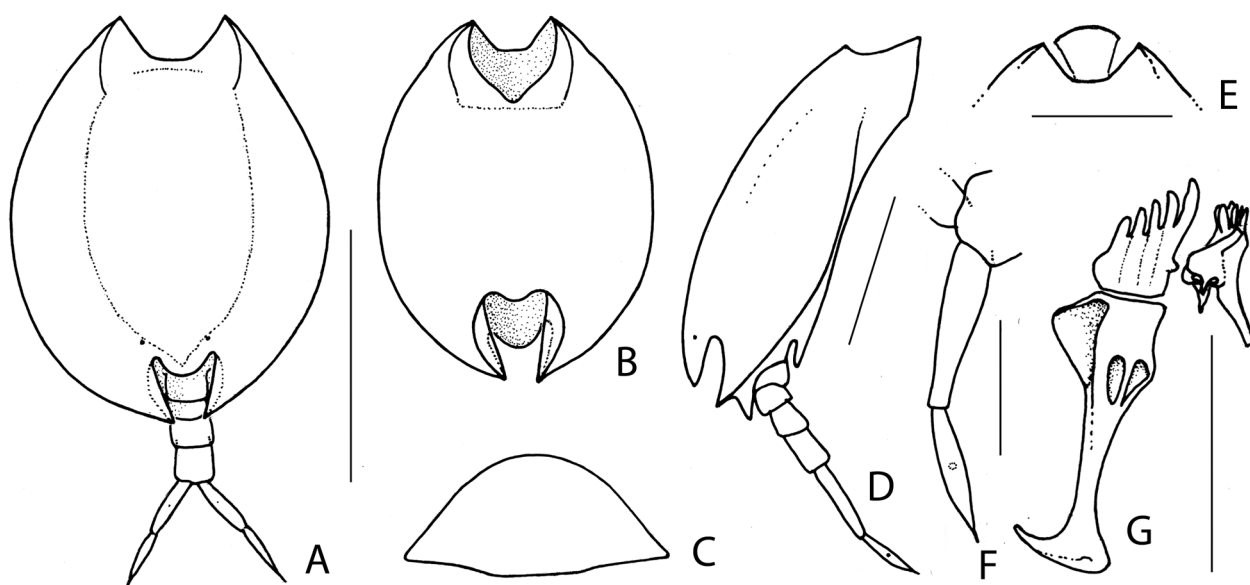
**Material.** Several specimens from most of the study area (see Tab. 2 species list). A female in a permanent, glycerine glass slide mount deposited in the Royal Belgian Institute of Natural Sciences (RBINS), Brussels, Belgium, No. IG 33082, RIR 226.

**Comments.** The main features differentiating the species from the genus *Lepadella* Bory de St. Vincent, 1826, and considered here as significant enough to justify the erection of a new genus are: (1) the foot and toes which are retractable in the lorica, but not retractable in *Lepadella*, and (2) the trophi morphology which is malleo-virgate, instead of malleate in *Lepadella*. The assignment to Lepadellidae is questionable and the trophi rather conform to the *Proales reinhardti* species group of Proalidae, characterized by reduced rami with strong apophyses and rami teeth fused into few stout projections, long distally incurved manubria with small head, plate-shaped unci with 4–5 larger teeth with free head, and foot opening delimited by a ventral and dorsal lobe of the lorica. The species is provisionally kept in family Lepadellidae awaiting molecular analyses to evaluate its exact phylogenetic position.

Althaus (1957) erroneously interpreted the dorsal surface as being flat instead of arched, and described the toes as long and weakly incurved without mentioning the characteristic claws which, however, are clearly distinct in her microphotograph 13. The present author therefore opines that supposed differences between *Lepadella pontica* and

*L. psammophila* result from inaccuracies in the original description, and the latter is here considered as subjective junior synonym. Koste (1978) synonymises *L. pontica* and *L. psammophila* with reserve, giving incorrectly priority to the second name.

**Description of female.** Loricata. Lorica outline oval (Fig. 24A, B); in cross-sectional view fairly convex and evenly arched dorsally, ventral margin flat to slightly concave; antero-dorsal sinus semi-hexangular, fairly narrow and shallow, with collar; antero-ventral sinus larger, semi-circular with small median indentation and slightly thickened border; head shield present (Fig. 24E), median margin rounded, slightly strengthened, lateral margins weakly concave; lorica dorsally often with two more or less pronounced shallow longitudinal ridges extending from the lateral margins of the collar of the dorsal sinus till the corners of the foot opening, or continuing on the medio-dorsal lobe. Foot opening heart-shaped ventrally, dorsally elongate, narrowing distally, ventral and dorsal proximal margins a semi-circular lobe. Lateral antennae dorsal, close set, near corners of foot opening. Foot with four pseudosegments, distal segment longest, others almost equally long. Toes (Figs 24D, F) slender, with long more or less cylindrical and distally tapering proximal part, and large, *c.* 3/4 of proximal part, lanceolate and movable distal spur; proximal part and spur with opening. Foot and toes completely retractable in trunk. Four pedal glands. Two distinct pear-shaped, often dark-coloured salivary glands on mastax.



**FIGURE 24.** *Halolepadella pontica* (Althaus). A. Female, dorsal; B. female, trunk, ventral; C. trunk, cross-sectional view; D. female, lateral view; E. detail head shield and dorsal sinus; F. toe, dorsal; G. trophi, lateral. Scale bars: A–D: 50  $\mu$ m; F–G: 10  $\mu$ m.

Trophi malleo-virgate (Figs 24G, 25). Rami strongly reduced, triangular, distal part recurved dorsally, very small; proximal part larger, with prominent distally rounded alulae and large dorsal opening; left ramus with strong basal apophysis, right ramus with at least three smaller sclerite elements, placed more apically; a fairly long cylindrical projection pointing antero-laterally (Figs 25B, F, G: cp), left inserted on basal apophysis, right inserted on margin of ramus; subbasifenestrae small, rounded. Two long strings of sclerite bodies connected distally to rami; proximal sclerite bodies cylindrical and rounded terminally, distal ones becoming spherical. Fulcrum slightly longer than rami, thin, straight and less high, proximal extremity only slightly higher than distal one. Unci a thin plate with 5 slender knobbed teeth of decreasing length, and 1–2 tiny, linear additional teeth; free margin of major teeth with prominence at *c.* 2/3 from tip; subuncus a bundle of slender, fusiform sclerite bodies; preuncinal tooth lanceolate. Manubria long, straight, head reduced, cauda strong, bird's head in appearance: ventrally curved and pointed, dorsally with rounded expansion; dorsal chamber a very thin triangular lamella, ventral chamber small, elongate triangular with small opening; median chamber with small elongate opening.

**Measurements.** Body (N=10): lorica length 61–80  $\mu$ m, width 48–60  $\mu$ m, foot 18–20  $\mu$ m, toe 21–28  $\mu$ m, spur 10–11  $\mu$ m; trophi (N=5): length ~17–19  $\mu$ m, ramus 2.6  $\mu$ m, fulcrum 3.4  $\mu$ m, unci 5.2–5.5  $\mu$ m, manubrium 11.2–11.4  $\mu$ m.

**Distribution and ecology.** The species was described from sublittoral psammon at 2 m depth from Spatnite



pjasatzi near Varna, Bulgaria, Black Sea (Althaus 1957), and reported from the intertidal of a sandy beach at the island of Sylt, Germany, North Sea (Tzschaschel 1979, 1980, 1983) and sublittoral of Elba Island, Tyrrhenian Sea (De Smet 2007). The present observations extend its distribution to the sublittoral of the Costa Blanca and Côte d'Azur, at distances of 50 m to 8 km off shore and depth of 10–50 m; June, August, September, October, water temperature 15–23 °C.

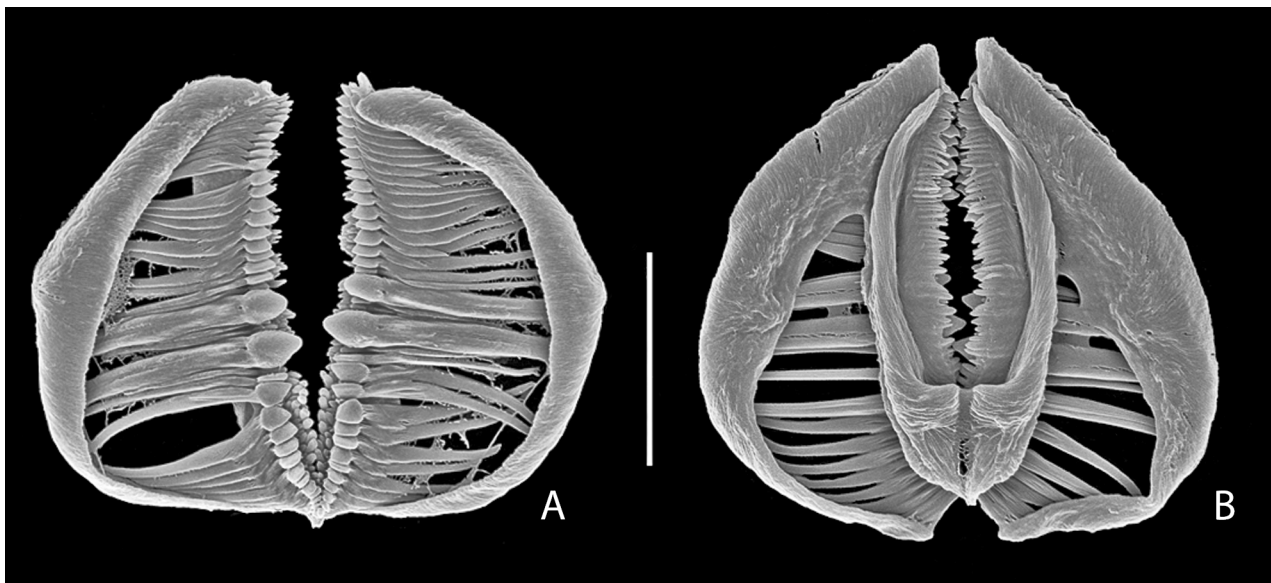


**FIGURE 25.** *Halolepadella pontica* (Althaus), SEM photographs of trophi. A. Complete set, ventral; B. complete set, lateral. C. complete set, mallei outer view, incus inner view; D. detail, oblique dorsal; E. detail, ventral; F. detail, oblique dorso-frontal left; G. detail, dorso-lateral right. cp: cylindrical projection; f: fulcrum; pt: preuncinal tooth. Scale bars: A–C, E: 10 µm; D, F, G: 1 µm.

### ***Rotaria laticeps* Wulfert, 1942**

*Rotaria laticeps* is to date only known with certainty from the Mediterranean Sea. This strictly saline species was originally described from algae in a canal connecting a salt marsh (salinity 27.6–77.2 ‰) with the Adriatic Sea (Wulfert 1942). It occurred in almost all present areas studied, and was formerly reported for the Adriatic, Tyrrhenian and Ionian Sea by Fontaneto *et al.* (2008b, c), the Costa Blanca, Hyères Archipelago and Tyrrhenian Sea (De Smet 2009), and a retrodunal pond (salinity 8 ‰, algae at –0.5 m) at the Costa Paradiso, Strait of Bonifacio, Sardinia, W. Mediterranean Sea by Curini-Galletti *et al.* (2012). It is often one of the numerically dominant rotifers in periphyton, psammon, and benthic sandy detritus up to 8 km off shore and a depth of 45 m. A record, perhaps doubtful, is from inland saline Neusiedler See, by Donner (1972). A species differing from the nominate species, and requiring further study, was reported as *R. ? laticeps* from sediments and mosses of the alpine freshwater Slippery Rock Creek, Victoria, Australia by Ricci *et al.* (2003).

The ramate trophi (Fig. 26) show two pairs of major unci teeth, 16–17 pairs of minor unci teeth in the proximal, and 9–12 pairs in the distal group.



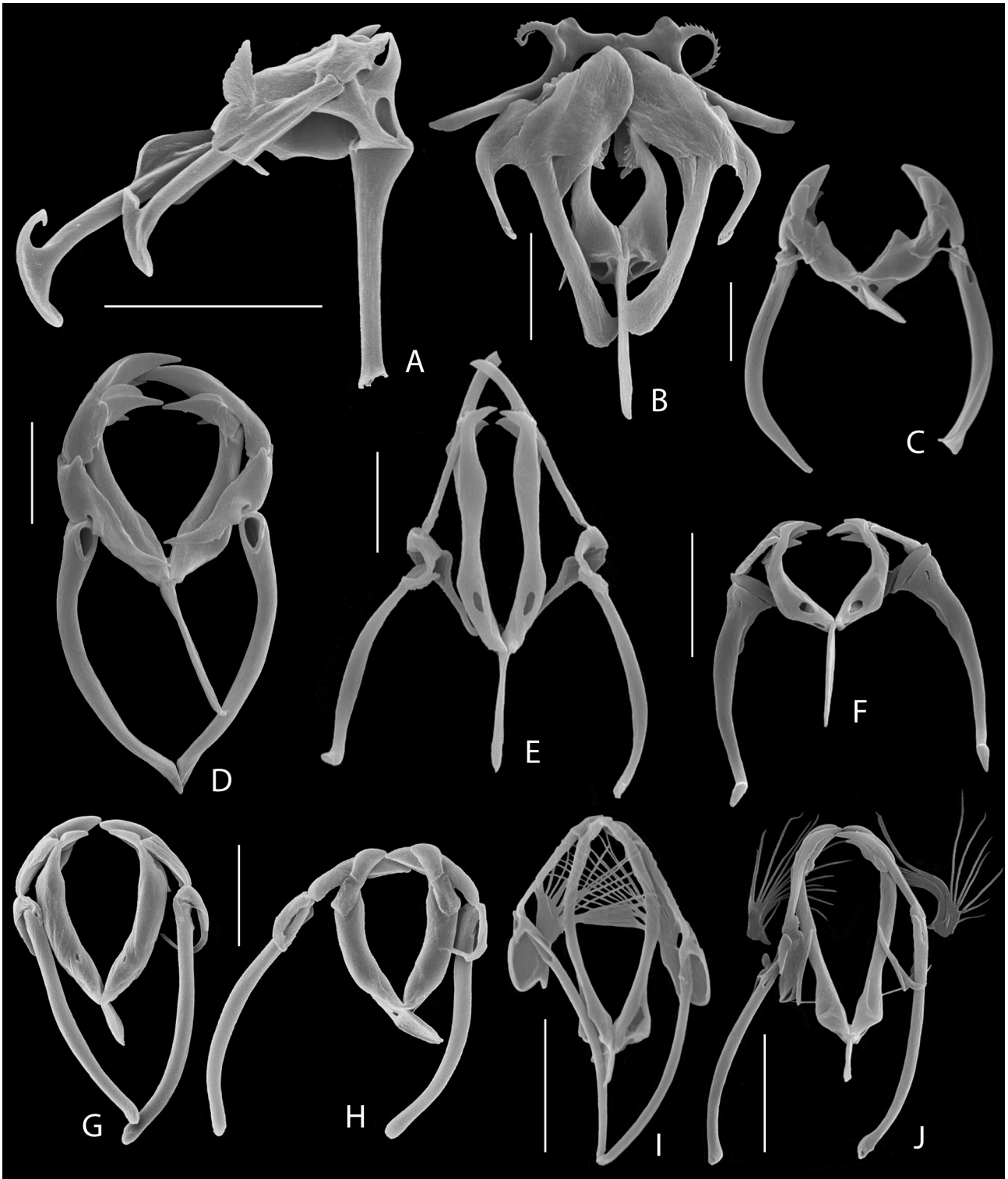
**FIGURE 26.** *Rotaria laticeps* Wulfert, SEM photographs of trophi. A. Frontal view; B. caudal view. Scale bar: 10  $\mu\text{m}$ .

### ***Cephalodella* sp.**

A single specimen of a small (~125  $\mu\text{m}$ ) and apparently new species was found on two occasions in sublittoral psammon of the Côte d'Azur and Tyrrhenian Sea; 50 m to 3.5 km off shore, depth 17–30 m. Habitus and trophi (Fig. 27A) suggest identity with the *Cephalodella* sp. reported from sandy detritus of the Northern Adriatic Sea (Fontaneto *et al.* 2008; D. Fontaneto pers. comm.).

### ***Encentrum astridae* Sørensen, 2001**

This species with large characteristic trophi (Fig. 27E) was found in sublittoral psammon from Elba Island, Tyrrhenian Sea, 50 m from shoreline, 40 m deep, September, water temperature 22 °C. It was originally described from subtidal coral sand at Gibbon Bay, Bermuda, NW Atlantic, and intertidal sand at Præstebugten, Hirsholmene, Denmark in the northern Kattegat, Baltic Sea (Sørensen 2001a).



**FIGURE 27.** SEM photographs of trophi, complete sets. A. *Cephalodella* sp., lateral; B. *Lindia elsaе* De Smet, dorsal; C. *Encentrum* sp. 1, ventral; D. *Encentrum striatum* Althaus, ventral; E. *Encentrum astridae* Sørensen, dorsal; F. *Encentrum* sp. 2, dorsal; G. *Paradicranophorus* sp. 1, dorsal; H. *Paradicranophorus* sp. 1, ventral; I. *Paradicranophorus* sp. 2, dorsal; *Paradicranophorus* sp. 3, ventral. Scale bars: 10 µm.

***Encentrum kutikovae* De Smet & Chernyshev, 2006**

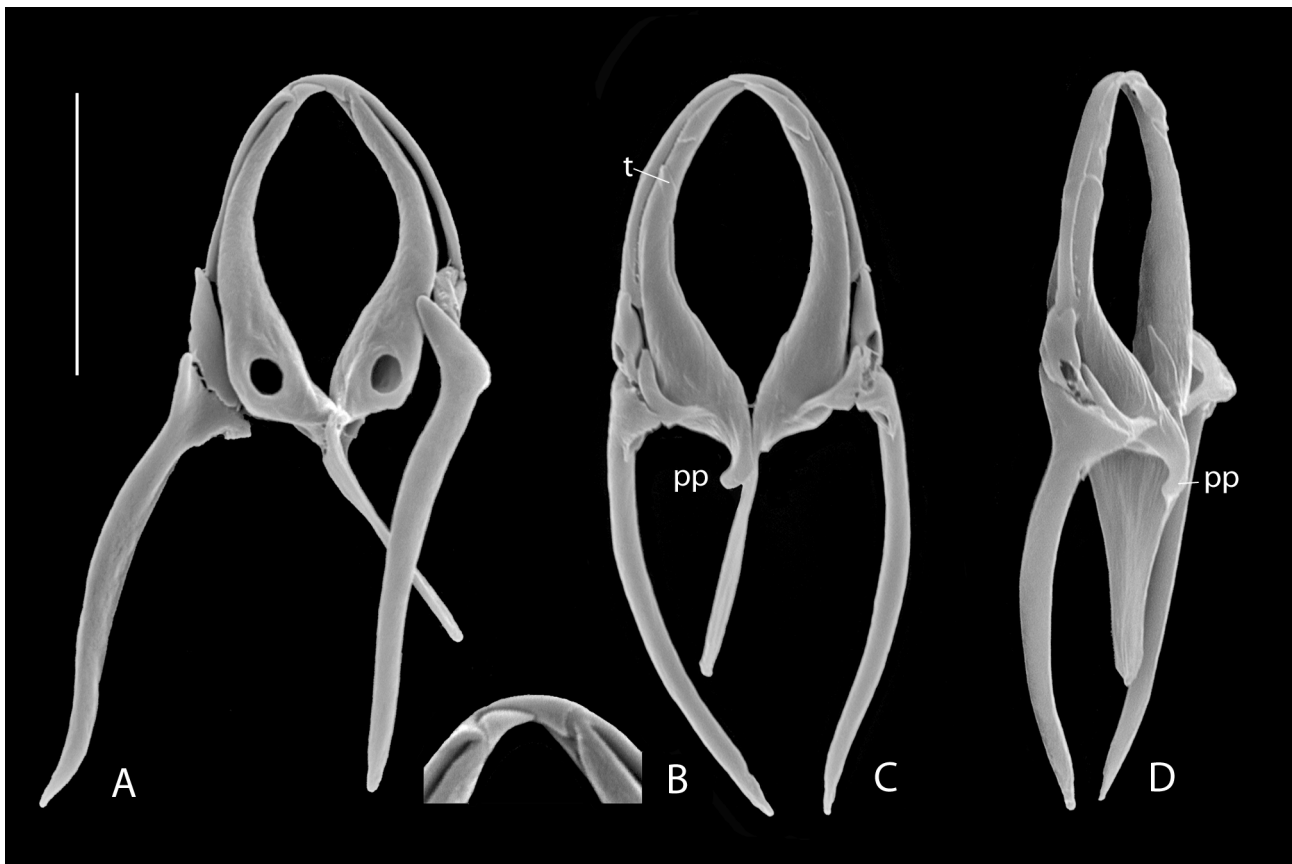
The distribution of this benthic-periphytic species now comprises the Ussuriyskiy Bay, Peter the Great Bay, Sea of

Japan, Russia (De Smet & Chernyshev 2006), the Grande Anse, Réunion Island, Indian Ocean (De Smet 2006 sub *Encentrum* sp.) and the Côte d'Azur, Îlot de la Fourmigue, France. It was found once in psammon, 3.5 km off shore, depth 15 m, June, water temperature 16 °C.

### *Encentrum longirostrum* Tzschaschel, 1978

The general morphology of the Mediterranean specimens conforms to the description of *E. longirostrum*. A minor difference concerns the toes which show a minute terminal acute point distally from the ventral opening of the pedal glands, not mentioned by Tzschaschel (1979).

The species was found in sublittoral psammon from the Côte d'Azur and Elba island, from 50 m to 3.5 km off shore and 15 to 20 m deep; June, September; water temperature 16–23 °C. *Encentrum longirostrum* was to date only known from its type locality, a semilotic sandy beach of Uthörn Island, North Sea, Germany (Tzschaschel 1979, 1980, 1983).



**FIGURE 28.** *Encentrum longirostrum* Tzschaschel, SEM photographs of trophi. A. Complete set, dorsal; B. detail tips of rami and unci, dorsal; C. complete set, ventral; D. same as B, lateral. pp: posteriorly pointing projection on right ramus; t: toothlet. Scale bar: 10  $\mu$ m.

**Redescription of trophi by SEM.** (Fig. 28) Rami outline oboval with blunt postero-lateral corners; median rami opening lenticular. Rami curved, broad at base, tapering to offset short oblique acute apical tooth (left) or simple tip (right); right ramus ventrally with small blunt toothlet at outer margin *c.* 1/4 from tip pointing to anterior (Fig. 28C: t), and short, blunt outcurved posterior projection near junction with left ramus (Fig. 28C, D: pp). Preuncinal teeth in line with curved rami, slender, with short shaft and acute head. Fulcrum long, *c.* 2/3 ramus length, narrow and parallel-sided in dorsal/ventral view; in lateral view broad at base, gradually tapering to narrow tip. Unci long, *c.* 2/3 ramus length, slender; shaft very long, head short *c.* 1/5 uncus length, very weakly offset from shaft; the left head grasps with a dorsal apophysis behind the offset left apical ramus tooth, the right head rests with its shallow apophysis on the blunt tip of the ramus (Fig. 28 B). Intramallei blunt conical with latero-ventral

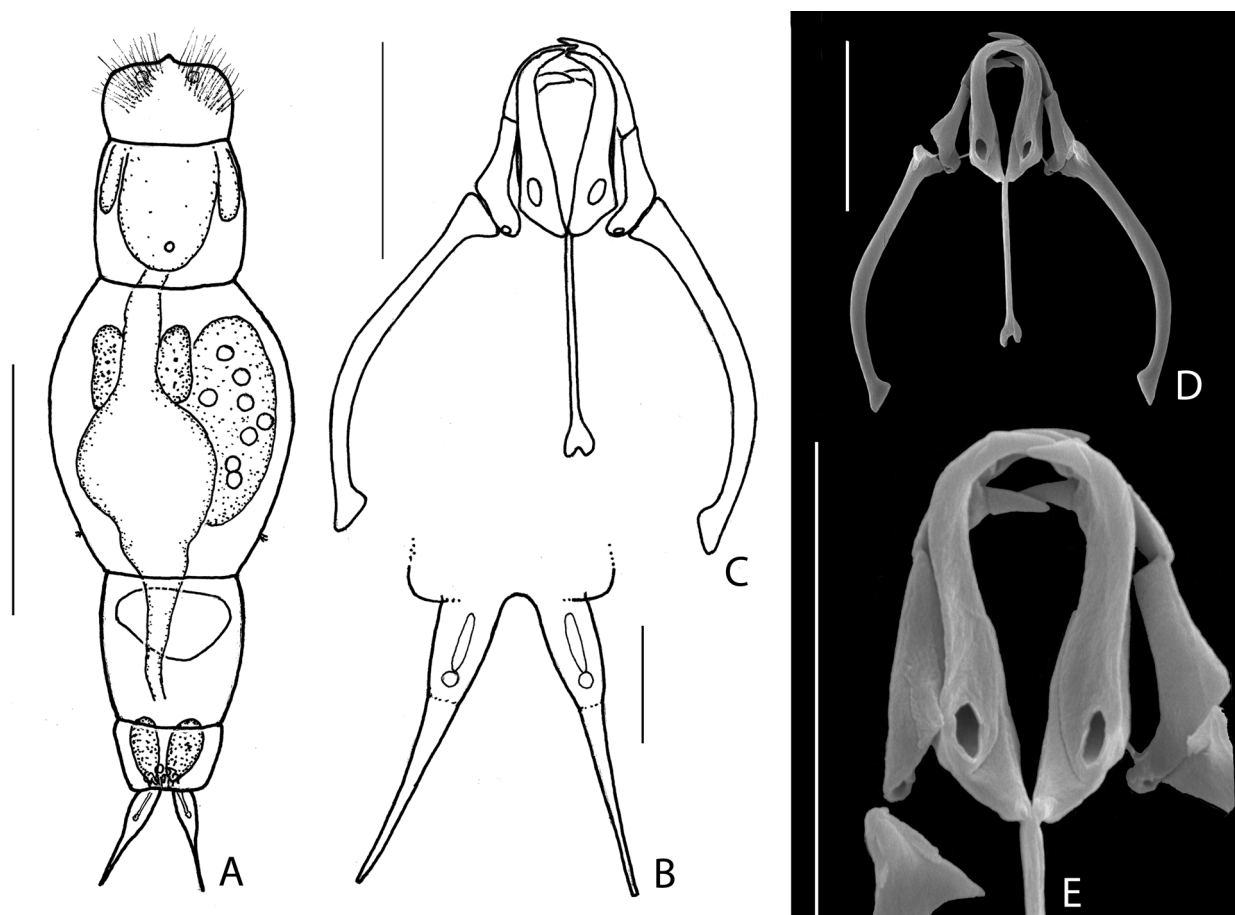
opening. Supramanubria triangular with drawn-out extension pointing towards trophi axis. Manubria *c.* 3/5 incus length, rod-shaped, evenly curved with acute cauda in dorsal/ventral view, in lateral view curved with broad triangular head and slightly dorsally recurved end.

**Measurements.** Body (N=8): total length 170–210  $\mu\text{m}$ , toe 9–16  $\mu\text{m}$ ; trophi (N=4): length 25–27  $\mu\text{m}$ , ramus 12.0–13.3  $\mu\text{m}$ , fulcrum 7.8–9.0  $\mu\text{m}$ , uncus 8.6–9.3  $\mu\text{m}$ , preuncinal tooth 3.1–3.3  $\mu\text{m}$ , intramalleus 3.4–4.1  $\mu\text{m}$ , supramanubrium 3.7  $\mu\text{m}$ , manubrium 16.2–18.1  $\mu\text{m}$ .

**Comment.** The species can not be attributed with certainty to the recognized subgenera.

### *Encentrum psammophilum* Althaus, 1957

The specimens seen (Fig. 29A) largely conform to the original description, and only differ in minor aspects. The basal third of the toes is weakly swollen, and slightly offset from the tapering distal 2/3 part; the swelling of the toes is slightly unequal all around; two colourless frontal eyespots are present, not mentioned by Althaus (1957). The outer margin of the right toe is reported to be undulate ('wellenförmig geschwungen') in the original description, but this comes about when the basally, all around unequally swollen toes are not positioned in the same way. The vitellarium contains 8 nuclei instead of 4.



**FIGURE 29.** *Encentrum psammophilum* Althaus. A. Female, dorsal; B. toes, dorsal; C. trophi, complete set, dorsal; D. SEM photograph, complete set of trophi, dorsal; E. SEM, detail, dorsal. Scale bars: A: 50  $\mu\text{m}$ ; B–E: 10  $\mu\text{m}$ .

*Encentrum psammophilum* was a rather rare inhabitant of sublittoral psammon from the Costa Brava, Côte d'Azur and Tyrrhenian Sea, 20 m to 3.5 km off shore, depth 15–40 m, June, July, September, water temperature 17–22 °C. The species was to date only known from sublittoral mesopsammon (depth 2 m) of its type locality, the Central bath of Varna, Black Sea, Bulgaria (Althaus 1957). The species reported sub *E. psammophilum* from the North Sea (island Sylt, Germany) is considered as a different species on basis of the morphology of the body and trophi (De Smet 1997).

**Redescription of trophi by SEM.** Trophi (Fig. 29C–E) of subgenus *Encentrum* type; large, elongate, fairly slender. Rami outline longer than wide, ratio length:width of closed rami 1.7–1.9; outer margin of rami weakly concave dorso-laterally, rounded-angular posteriorly; outer ventral margin with carina rami near 3/7 from apical ramus tip; median rami opening elongate drop-shaped. Each ramus with single, slightly offset apical tooth set at right angle to trophi axis; cardal apophyses very small. Prior to apical teeth a preuncinal tooth set at a right angle to trophi axis; preuncinal teeth with elongate triangular head and short shaft forming obtuse angle; head with small cardal apophysis. Fulcrum longer than ramus, in dorsal/ventral view distal end slightly widening and indented dorsally; in lateral view with broad base, quickly tapering, continuing parallel-sided. Unci medium long, slightly curved, head slightly shorter than shaft, with dorsal and ventral apophyses. Intramallei long, sock-shaped, with relatively long, rounded medio-lateral basal expansion bearing medio-caudal opening; inner side expanded, fitting lateral concavity of rami. Supramanubria absent. Manubria slightly less incus length, stout, rod-shaped, proximal half straight, distal half incurving with crutched cauda, head short, rounded-triangular.

**Measurements.** Body (N=5): total length 175  $\mu\text{m}$ , toe 25–28  $\mu\text{m}$ ; trophi (N=3): length 25  $\mu\text{m}$ , ramus 8.9  $\mu\text{m}$ , fulcrum 10.4  $\mu\text{m}$ , uncus 5.0  $\mu\text{m}$ , intramalleus 5.0  $\mu\text{m}$ , manubrium 16.0–16.6  $\mu\text{m}$ .

### *Encentrum* spp.

Two species belonging to the genus *Encentrum* concern undescribed species judging from their trophi (Figs 27C, F), but could not be described due to their contracted state and the too low number of specimens.

### *Encentrum striatum* Althaus, 1957

A single specimen of *E. striatum* was found in psammon from the Côte d'Azur at Îlot de la Fourmigue, 3.5 km off shore, depth 15 m, June, water temperature 16 °C. The species was originally described from psammon of the sea water aquarium at Varna, Black Sea, Bulgaria (Althaus 1957), and reported from psammon of sandy beaches from the North Sea, island Sylt, Germany (Tzschaschel 1979), and from hygropsammon of a saline backwater-pool in the Santa Rosa Sound, Gulf of Mexico, Florida, U.S.A. (Turner 1990).

The trophi need redescription as SEM (Fig. 27D) shows a more complicated morphology with differences in number of apical rami teeth and preuncinal teeth, and shape of intramallei and supramanubria, that could not be observed by light microscopy (Althaus 1957; Tzschaschel 1979). Such a redescription awaits discovery of additional specimens.

### *Encentrum valkanovi* Althaus, 1957

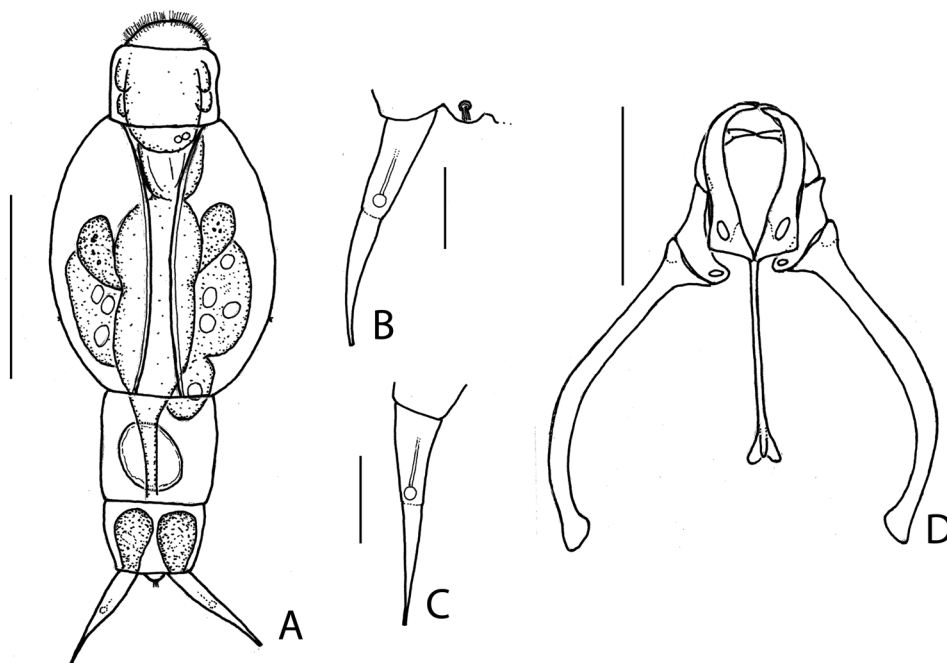
This typical species (Fig. 30) is characterized by its dorso-ventrally flattened body with large and broad anterior pseudosegment showing longitudinal folds, the wide apart-set toes, and the 2 close-set light-refracting globules displaced to the right at the posterior of the brain. The specimens seen fit the original description, except for some details: the toes are more drawn-out and more or less distinctly offset near mid-length; the 'ovate structure' in the toes consists of a light-refracting spherical reservoir and part of its supply canal; the 4 dorsal longitudinal folds on the anterior trunk segment are 2 double-folds; the 'spine' between the toes is a rounded caudal papilla with projecting cilia.

*Encentrum valkanovi* was not uncommon in the sublittoral of all areas studied, from 50 m up to 8 km off shore, and depths of 15–40 m, June, July, August, September, water temperature 17–25 °C. To date the species was only known from sublittoral psammon of the Black Sea, Varna, Bulgaria (Althaus 1957).

**Redescription of trophi by SEM.** Trophi (Figs 30D, 31) of subgenus *Encentrum* type. Trophi large, elongate, fairly slender. Rami outline longer than wide, ratio length:width of closed rami 1.8–1.9; dorsal outer margin of rami weakly concave laterally, angular posteriorly; ventral outer margins with shallow carina rami (Figs 31C, E: cr) near 3/7 from apical ramus tip; median rami opening elongate drop-shaped; subbasal chambers dorsally with small depression medio-caudally from basifenestrae; basifenestrae dorsal, small, ellipsoid; subbasifenestrae caudal,

small, rounded. Each ramus with single, slightly offset apical tooth set at right angle to trophi axis; cardal apophyses very small. Prior to apical teeth a preuncinal tooth set at a right angle to trophi axis; preuncinal teeth with elongate triangular head and short shaft forming obtuse angle; head with small cardal apophysis. Fulcrum longer than ramus, in dorsal/ventral view distal end slightly widening; distal widening indented dorsally, with median prominence ventrally; in lateral view with broad base, quickly tapering, continuing parallel-sided. Unci medium long, slightly curved, head shorter than shaft, with dorsal and ventral apophyses; dorsal and ventral ribs fairly broad. Intramallei long, sock-shaped, with relatively long, rounded medio-lateral basal expansion bearing opening medio-caudally; inner side expanded, fitting lateral concavity of rami. Supramanubria absent. Manubria slightly less incus length, stout, rod-shaped, proximal half straight, distal half incurved with crutched cauda, head short, triangular.

**Measurements.** Body (N=5): total length 180–210  $\mu\text{m}$ , toe 28–35  $\mu\text{m}$ ; trophi (N=5): length 24–26  $\mu\text{m}$ , ramus 8.5–9.8  $\mu\text{m}$ , fulcrum 11.6–11.7  $\mu\text{m}$ , uncus 5.6  $\mu\text{m}$ , preuncinal tooth 2.4  $\mu\text{m}$ , intramalleus 4.8 $\times$ 3.7  $\mu\text{m}$ , manubrium 18.2–18.7  $\mu\text{m}$ .



**FIGURE 30.** *Encentrum valkanovi* Althaus. A. Female, dorsal; B. toe and caudal antenna, dorsal; C. toe, lateral. Scale bars: A: 50  $\mu\text{m}$ ; B–D: 10  $\mu\text{m}$ .

### ***Lindia elsae* De Smet, 2006**

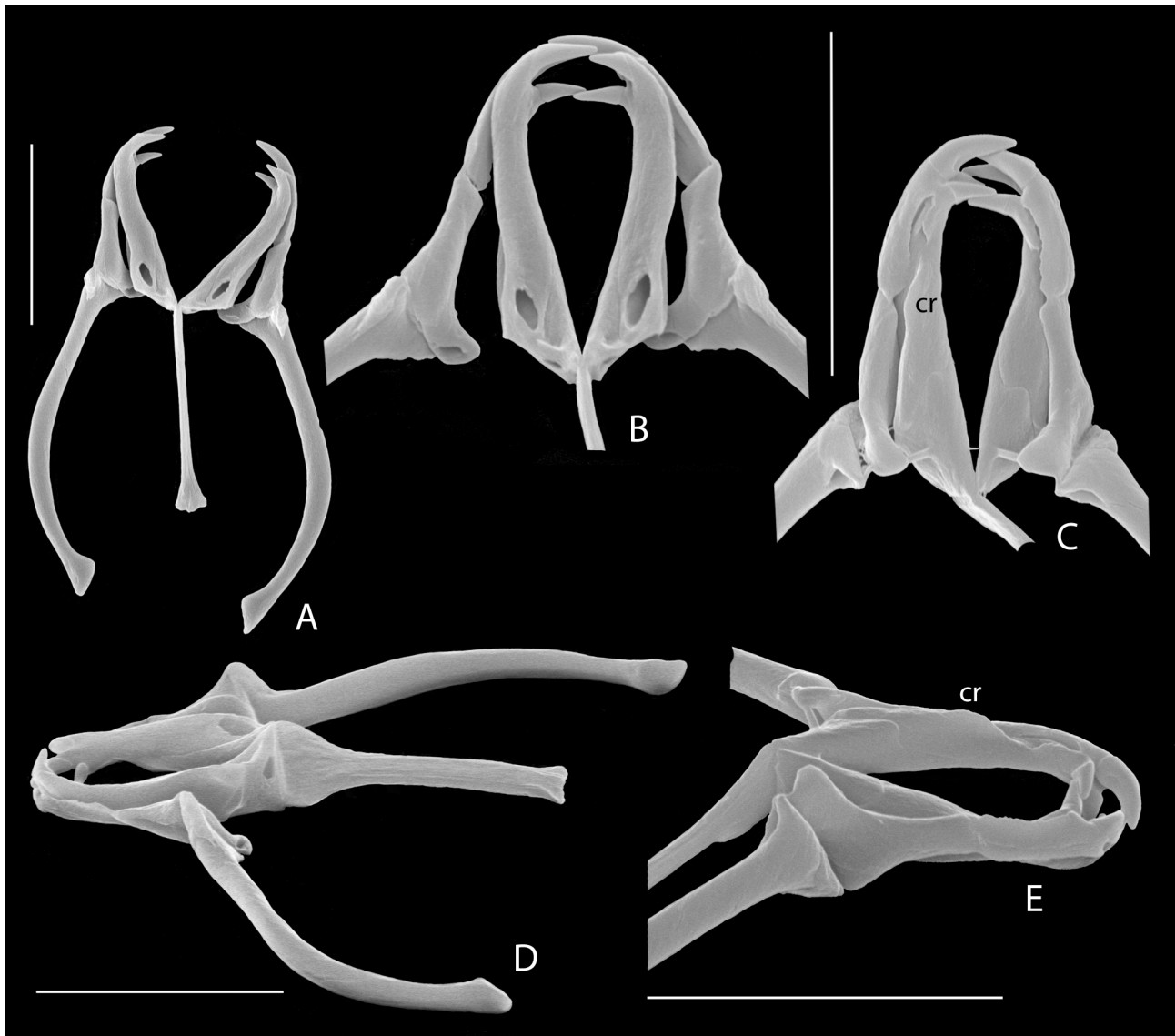
Two specimens of *L. elsae* (trophi Fig. 27B) hitherto known only from its type locality, *i.e.* Aufwuchs among a stand of macro-algae in the sublittoral fringe of the Grande Anse, Réunion Island, Indian Ocean (De Smet 2006), now found in psammon at –10 m, 100 m off Elba, Tyrrhenian Sea; September, water temperature 23 °C.

### ***Lindia gravitata* (Lie-Pettersen, 1905)**

The specimens seen showed a bit more distinct pseudosegmentation of the body than those used in its redescription (De Smet 2005); habitus and trophi otherwise identical. Males present, similar in habitus to females, but smaller (~150  $\mu\text{m}$ ), and without trophi.

The species was found in psammon from the Costa Brava, Côte d'Azur, and Tyrrhenian Sea, at 50 m to 3.5 km off shore, and depths varying from 15 up to 30 m; June, July, September, October; water temperature 16–21 °C. Previous records are from the Norwegian Sea at Bergen, Norway (Lie-Pettersen 1905), the North Sea: Kieler

Bucht, Germany (Schulz 1936/37), Eastern Scheldt, The Netherlands (De Smet 2005), Tyrrhenian Sea, Elba Island (De Smet 2007), and Skagerrak, Sweden (Willems *et al.* 2009).



**FIGURE 31.** *Encentrum valkanovi* Althaus, SEM photographs of trophi. A. Complete set, dorsal; B. detail, dorsal; C. detail, ventral; D. complete set, dorso-lateral; E. detail, ventro-lateral. cr: crina rami. Scale bars: 10  $\mu$ m.

### *Paradicranophorus* spp.

*Paradicranophorus* sp. 1 is very similar in habitus to *P. halophilus* **sp. nov.** and occasionally co-occurring, but can not be described for lack of specimens. However, the trophi (Fig. 27G, H) allow for an unambiguous distinction: main differences concern shape of rami, unci, apical rami teeth and preuncinal teeth, and the absence of a stout tooth on the inner ramus margin in *Paradicranophorus* sp. 1.

It was found in psammon from the Costa Blanca and Tyrrhenian Sea, 50 m to 1 km off shore, depth 30–40 m, water temperature 22–24 °C.

Two more species with affinities to *Paradicranophorus wesenbergi* Sørensen, 2001 could not be described due to the small number of specimens available. Trophi of *Paradicranophorus* sp. 2 (Fig. 27I) and 3 (Fig. 27J) differ from those of *P. wesenbergi* (see Sørensen 2001b) by, amongst others, shape of unci and apical rami teeth; main differences distinguishing sp. 2 and sp. 3 are the shape of the median rami opening (lenticular in sp. 2 vs. elongate drop-shaped in sp. 3), and the manubria (evenly curved in sp. 2 vs. weakly incurved distally in sp. 3).



Both species were found once at the Côte d'Azur: sp. 2 in the Hyères Archipelago at 4 km off shore and depth of 45 m; sp. 3 at Cap Bénat, 50 m from shoreline and depth of 20 m.

### *Proales litoralis* De Smet, 1996

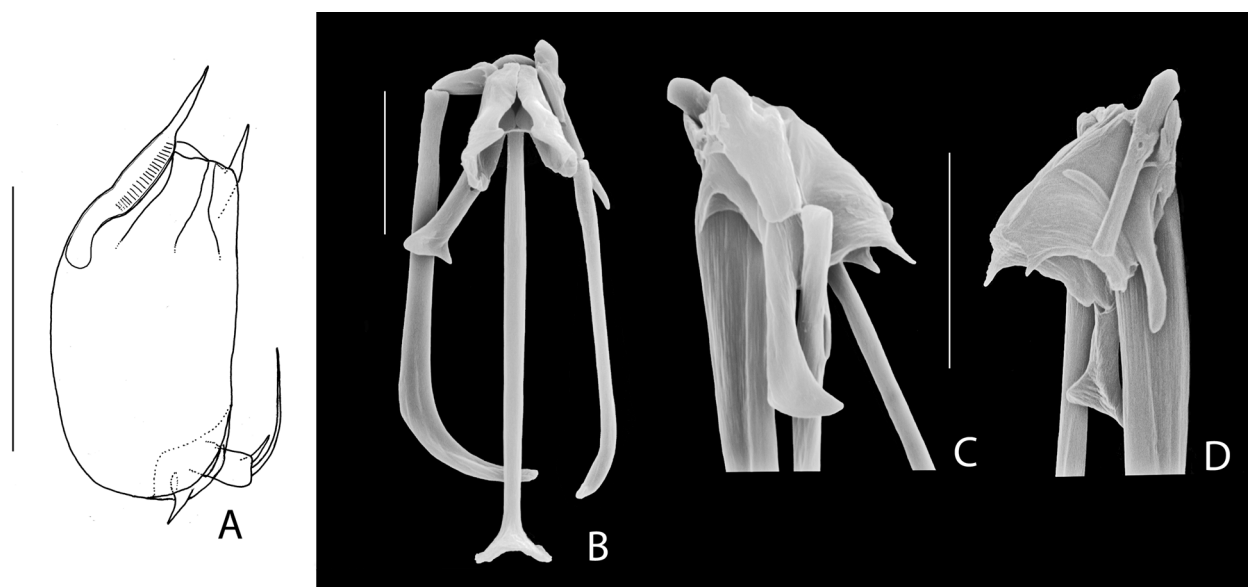
The species was once found among *Enteromorpha* sp. from the low-eulittoral at the Costa Blanca. It was previously known only from vegetation and psammon from the eulittoral zone and sublittoral fringe of the type locality, the English Channel, Boulogne, France, and one locality from the Eastern Scheldt, the Netherlands, North Sea (De Smet 1996b).

### *Proales syltensis* Tzschaschel, 1978

Two specimens of this species were found in sublittoral psammon from both the Costa Blanca and the Côte d'Azur, at 250 and 50 m from the shoreline, 20 and 22 m deep; June, August; water temperature 17 and 25 °C. *Proales syltensis* was so far only recorded from its type locality, the eulittoral of a semi lotic beach at the island of Sylt, Germany, North Sea (Tzschaschel 1979, 1980, 1983).

### *Trichocerca pediculus* Remane, 1949

The species (Fig. 32A) has not been reported since its description by Remane (1949) from movable fine sand in the *Bathyporeia*-zone at the Kieler Bucht, Baltic Sea, and Amrum Island, North Sea (Germany). In my samples it occurred twice in psammon, 50 and 100 m from the shoreline of Elba Island, at -10 and -40 m; September; water temperature 21 and 23 °C.



**FIGURE 32.** *Trichocerca pediculus* Remane. A. Female, lateral; B. SEM photographs of trophi, complete set, dorsal; C. detail left incus and uncus, lateral; D. detail right ramus and uncus, lateral. Scale bars: A: 50 µm; B–D: 10 µm.

In contrast with the original description by Remane (1949) the Mediterranean specimens showed a very weakly striated field right-dorsally in the anterior third of the trunk, delimited by two longitudinal ridges uniting posteriorly in a rounded rim. The species has a rather flexible integument as shown by the Figs 16 and 17 in Remane *l.c.*, but the fully contracted specimens in my material displayed the 'typical' *Trichocerca* shape.

Study of the trophi by SEM (Figs 32B–C) shows some more minor details: the thin rod-shaped right manubrium is weakly incurved distally; the slender right uncus is accompanied by a thin, slender cylindrical tooth;

the right uncus has a small porus at the distal end of the uncinal shaft, to date only reported in the major teeth of Bdelloidea (Melone *et al.* 1998; see also Fig. 26A); the massive head of the left tooth bears three small fused preuncinal teeth; suprarami with distinct sharp alula.

Measurements. Body (N=5): total length 115–120  $\mu\text{m}$ , left toe 28–32  $\mu\text{m}$ ; trophi (N=4): length 35–38  $\mu\text{m}$ , left ramus 8.1– 9.0  $\mu\text{m}$ , right ramus 8.0  $\mu\text{m}$ , fulcrum 30.0–32.0  $\mu\text{m}$ , left uncus 7.4–12.0  $\mu\text{m}$ , right uncus major tooth 6.0–9.0  $\mu\text{m}$ , right uncus minor tooth 4.6–5.2  $\mu\text{m}$ , left preuncinal teeth 2.0  $\mu\text{m}$ , right preuncinal teeth 3.0  $\mu\text{m}$ , left manubrium 28.0–30.0  $\mu\text{m}$ , right manubrium 24.0–27.0  $\mu\text{m}$ .

### Notes on ecology and distribution

In the present study one rotifer species was found in the eulittoral zone, two species in the sublittoral fringe, and 42 taxa in the sublittoral zone up to 8 km off shore and depths up to 66 m. Taxon richness for each sample ranged from 1 to 2 (mean 1.8) in the eulittoral and sublittoral fringe, respectively, and from 1 to 23 (mean 8.8, s.d. 5.9), with most of the samples between 4 and 11 taxa, in the sublittoral zone. Combining the taxon numbers obtained for each of the similar sampling distances seaward from the strandline resulted in 2 taxa for the sublittoral fringe, and 6 to 35 (mean 13.5) taxa for the different sampling distances of the sublittoral zone. Within the sublittoral zone, comprising samples from 20 m to 8 km off shore, no tendency was apparent, the overall taxon richness of the nearby samples (20–500 m, 6 samples) being similar (mean 13.0 *vs.* 12.6) to the one of the more distant samples (1–8 km, 5 samples). The occurrence of the taxa with depth, and their cumulative frequency, *i.e.* the sum of the frequencies at which the different taxa were observed for a specific depth (grouped into classes of 10 m in the sublittoral; single sample –66 m included in last class), is summarized in Table 3. It shows that a single species occurred in the eulittoral at low frequency; in the sublittoral fringe the number of taxa is low (2 species) but cumulative frequency of their occurrence is high (64% of total potential occurrences, *i.e.* number of samples  $\times$  number of species per depth class); and the number of taxa is high (10–30 taxa) and cumulative frequency of occurrence is rather low to moderate (25–53% of total potential occurrences) in the sublittoral. This indicates that the different species do not occur at constant frequency over the whole sublittoral as a result of patchiness of their distribution pattern.

**TABLE 3.** Number of samples and taxa, and cumulative frequency of taxa pe littoral zone.

Littoral zone	Eulittoral	Sublittoral fringe	Sublittoral				
Depth (m)	-	0-5	6-15	16-25	26-35	36-45	46-66
Number of samples	6	7	5	6	11	9	3
Number of taxa	1	2	28	30	24	30	10
Cumulative frequency of taxa	1	9	40	60	65	66	16

Of all species fully identified, four only, *Colurella adriatica*, *C. colurus*, *Encentrum algente*, and *E. marinum* are not strictly thalassic (for a review of ecology and distribution of the latter and following species see Jersabek & Leitner (2013)). Both *Colurella* species are apparently eurionic, euryhaline and eurythermic ubiquitous species reported from lentic and lotic fresh waters, and thalassic and athalassic saline waters. *Encentrum algente* appears strictly thalassic, known from the sea and brackish environments. *Encentrum marinum* has been reported from thalassic, both sea and brackish habitats, and athalassic waters, as well as from alkaline fresh waters. Of the other species, only *Proales halophila* and *P. similis* are known to occur in both sea and brackish water, and the remainder may be considered strictly marine.

Within the Mediterranean ten distinct biogeographic sectors can be recognized on basis of the occurrence, origin and biogeographic category of composing marine biota (Bianchi & Morri 2000). The present sampling stations are located in the Balearic Sea to Tyrrhenian Sea sector (24 samples from Costa Blanca, Costa Brava, Tyrrhenian Sea) and the Golfe du Lion – Ligurian Sea sector (23 samples from Golfe du Lion, Hyères archipelago, Côte d’Azur). Both sectors had 31 rotifer taxa in common, and six taxa were restricted to each of the Golfe du

Lion–Ligurian Sea sector and the Balearic–Tyrrhenian Sea sector. The latter taxa were found only in a single (10 taxa) or two samples (2 taxa) and thus can not be used at this stage to characterize both sectors.

Little is known on the large-scale biogeographical distribution of marine rotifers. The present observations of *Encentrum longirostrum*, *E. psammophilum*, *E. valkanovi*, *Lindia elsaе*, *Proales syltensis*, and *Trichocerca pediculus* are but the first report since their description, and for *Allodicranophorus bulgaricus*, *Encentrum astridae*, *E. kutikovae*, *E. striatum*, and *Proales litoralis* it is only the third observation. For several species, e.g. *Encentrum astridae*, *E. kutikovae*, *Lindia elsaе*, the occurrence in the Mediterranean also represents a huge extension of their distribution range.

## Discussion

The Mediterranean Sea is known as a marine biodiversity hotspot hosting approximately 17,000 species or *c.* 8 % of the global marine biodiversity (Bianchi & Morri 2000; Myers *et al.* 2000; Coll *et al.* 2010) and an extremely high percentage of endemic species for various taxonomic groups (Boudouresque 2004). However, notwithstanding that most of the marine biodiversity may reside in meiofauna, diversity for the latter is substantially underestimated, even in the Western Mediterranean which is considered as one of the best-studied seas of the world. For example, Curini-Galetti *et al.* (2012) studying soft-bodied meiofauna from Northern Sardinia, recognized at least 76 or about 37 % of the total of the 203 morphospecies found to be undescribed species. Information on the rotifer diversity of the Mediterranean meiofauna is virtually lacking, but the recent description of five previously unknown species (De Smet 2007, 2009; Fontaneto *et al.* 2008b) and the present report of 43 taxa among which ten new species to science, five undescribed ones and ten previously known ones new for the area, merely as the result of an anecdotal sampling, illustrates that rotifers may constitute a diverse component of Mediterranean meiofauna. Moreover, in their study on meiofauna from Northern Sardinia Curini-Galetti *et al.* (2012), using amplification and sequencing of a fragment of the cytochrome c oxidase subunit I, also found strong indications for the presence of cryptic rotifer taxa.

The present results increase the number of rotifers on record for the whole Mediterranean Sea to 116 fully described taxa, of which 41 can be considered strictly marine. This illustrates once more that the common idea of poor rotifer species richness in marine habitats is a misconception due to a lack of interest or study. The preponderance of Dicranophoridae, with *Encentrum* as most species-rich genus, and to a lesser extent Proalidae, represented by strictly marine species of genus *Proales*, confirms the general observation that these taxa are the most common of the benthic-periphytic marine rotifer fauna (Fontaneto *et al.* 2006, 2008c).

The data presented here show, for the first time, that rotifers form a constant component of the meiofauna, from the eulittoral to at least 8 km off shore and a depth of 66 m. An apparent zonation was found, with rotifer diversity lowest and similar in the eulittoral zone (one species) and sublittoral fringe (2 species), and highest in the sublittoral zone (42 taxa). Although the total number of samples and habitats studied is low, and neither physical nor chemical variables were measured systematically, it seems reasonable to explain these differences in rotifer occurrence between the different zones primarily by environmental stress (e.g. Pinet 2003; Harley 2007). The eulittoral is undoubtedly the most stress-rich zone, highly influenced by the tides inducing great daily changes. Especially during low tide the zone will be under temperature stress, variations in salt concentration due to evaporation or dilution by rain, water pressure and ultraviolet radiation. In the sublittoral fringe changes of physical and chemical variables will be less, although we may still expect an unstable temperature regime due to its shallow depth, dilution effects by run-off of rain water, and a less stabilized bottom by the wave action inducing turbulent water. In the sublittoral zone the physical and chemical variables are known to be more or less stable compared to the uppermost zones, probably allowing for the establishment of the more diversified rotifer populations observed. The high biodiversity of the Mediterranean Sea can be explained by the long and complex geological history (e.g. Bianchi & Morri 2000; Taviani 2002) and present-day variety of peculiar environmental features and immense diversity of habitats (UNEP 2006). Especially geological processes through the Tertiary, in particular the re-opening of the Strait of Gibraltar at the start of the Pliocene (5 Ma) creating a diversity pump from the Atlantic influencing immigration and extinction of species, have led to important environmental changes and species occurrence (e.g. Bianchi & Morri 2000; Taviani 2002). Among the environmental drives of the high biodiversity likely are the variety of climatic and hydrological situations, e.g. differences in salinity between the western and

eastern basin, the presence of gradients in temperature (e.g. Pinarđi *et al.* 2006) and production (e.g. Danovaro *et al.* 1999), and the Mediterranean-specific biotopes. In the light of the above remarks on general Mediterranean biodiversity and our results of a limited sampling effort on benthic-periphytic material, it is justified to expect that a more extensive sampling extended to the different biotopes and their habitats will be most rewarding for marine rotifer taxonomy, ecology and zoogeography.

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