

Redescription of *Lindia gravitata* with comments on *L. tecusa* (Rotifera: Monogononta: Lindiidae)

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Lindia gravitata, previously considered a synonym of *L. tecusa* by several authors is redescribed. Body shape and trophi structure show that both species are closely related, and unequivocally differentiated by e.g. toe shape, number of sensory papillae, and shape of subunci and epipharynx. Other related, but insufficiently described congeners are listed. The diagnostic features of the subgenus *Halolindia* are discussed.

INTRODUCTION

Lindiidae is a small family of monogonont rotifers, consisting of 15 valid species, mostly freshwater taxa, with only three of them occurring in marine or brackish environments (Segers, 2002; De Smet, in press). Besides these valid species, some nine taxa are considered *species inquirendae* in the recent revision by Segers (2002). Amongst them is *Lindia gravitata* (Lie-Pettersen, 1906), described from two specimens collected in littoral periphyton from a shallow water body on the west coast of Norway. Ever since, there has been only one report by Schulz (1936/1937) from psammon in the upper medio-littoral zone at the Kieler Bucht, Germany. According to the latter, *L. gravitata* might be synonymous with *L. tecusa* Harring & Myers, 1922, the body of *L. gravitata* taking the shape of the ovoviviparous *L. tecusa*, when developing embryos.

Following the rather poor description of *L. gravitata*, Harring & Myers (1922) state that it might be *L. tecusa*, but suggest treating them as two distinct species until more material is studied. Remane (1933), Dehl (1934), Bogoslovsky (1950), Wiszniewski (1954) and Voigt (1957) treat *L. gravitata* as a valid species, but Remane (1929), Kutikova (1970) and Koste (1978) synonymize it with *L. tecusa*.

During a study on psammon rotifers from the Eastern Scheldt (The Netherlands), specimens conforming to the concise description of *L. gravitata* were found. In this paper I redescribe the species, and present additional information on the morphology and the results of the scanning electron microscopy (SEM) of the trophi of *L. tecusa*.

SYSTEMATICS

Phylum ROTIFERA Cuvier, 1812
 Class EUROTATORIA De Ridder, 1957
 Subclass MONOGONONTA Plate, 1889
 Order PLOIMA Hudson & Gosse, 1886
 Family LINDIIDAE Harring & Myers, 1924
 Genus *Lindia* Dujardin, 1841
Lindia gravitata (Lie-Pettersen, 1906)
Notommata gravitata Lie-Pettersen, 1906
Lindia (Halolindia) gravitata (Lie-Pettersen, 1906)
 Remane (1933)
 (Figures 1A–D & 2)

Type material

Neotype: parthenogenetic female in a permanent glycerine glass-slide mount deposited in the Koninklijk Belgisch Instituut voor Natuurwetenschappen (KBIN), Brussels, Belgium, no. IG 30409. Eastern Scheldt,

Table 1. Comparative measurements of trophi elements of *Lindia gravitata* and *L. tecusa* (μm).

	<i>Lindia gravitata</i>			<i>Lindia tecusa</i>		
	Length/length×width	Mean ±SE	N	Length/length×width	Mean ±SE	N
Ramus, left	11.4–16.5	13.6 ±1.54	16	18.0–20.3	19.2 ±0.84	10
Ramus, right	11.2–16.5	13.5 ±1.59	16	18.0–20.0	19.1 ±0.73	10
Fulcrum	7.5–11.3	9.2 ±1.08	15	9.0–11.4	10.1 ±0.83	8
Uncus	8.6–1.1×3.1–3.5	9.7 ±0.85×3.3 ±0.12	8	11.2–14.0×4.3–5.4	12.4 ±1.43×4.9 ±0.49	7
Manubrium, left	15.8–20.9	17.7 ±1.31	20	21.3–24.4	22.6 ±1.25	10
Manubrium, right	16.1–20.5	17.8 ±1.22	20	21.5–24.4	22.8 ±1.09	9
Epipharyngeal plate	29.0–39.1×8.1–12.5	32.1 ±5.53×10.9 ±1.62	8	40.5–47.0×13.3–15.2	44.1 ±2.3×14.5 ±0.68	8
Epipharyngeal platelet	10.7–14.1	10.9 ±1.13	9	–	–	–

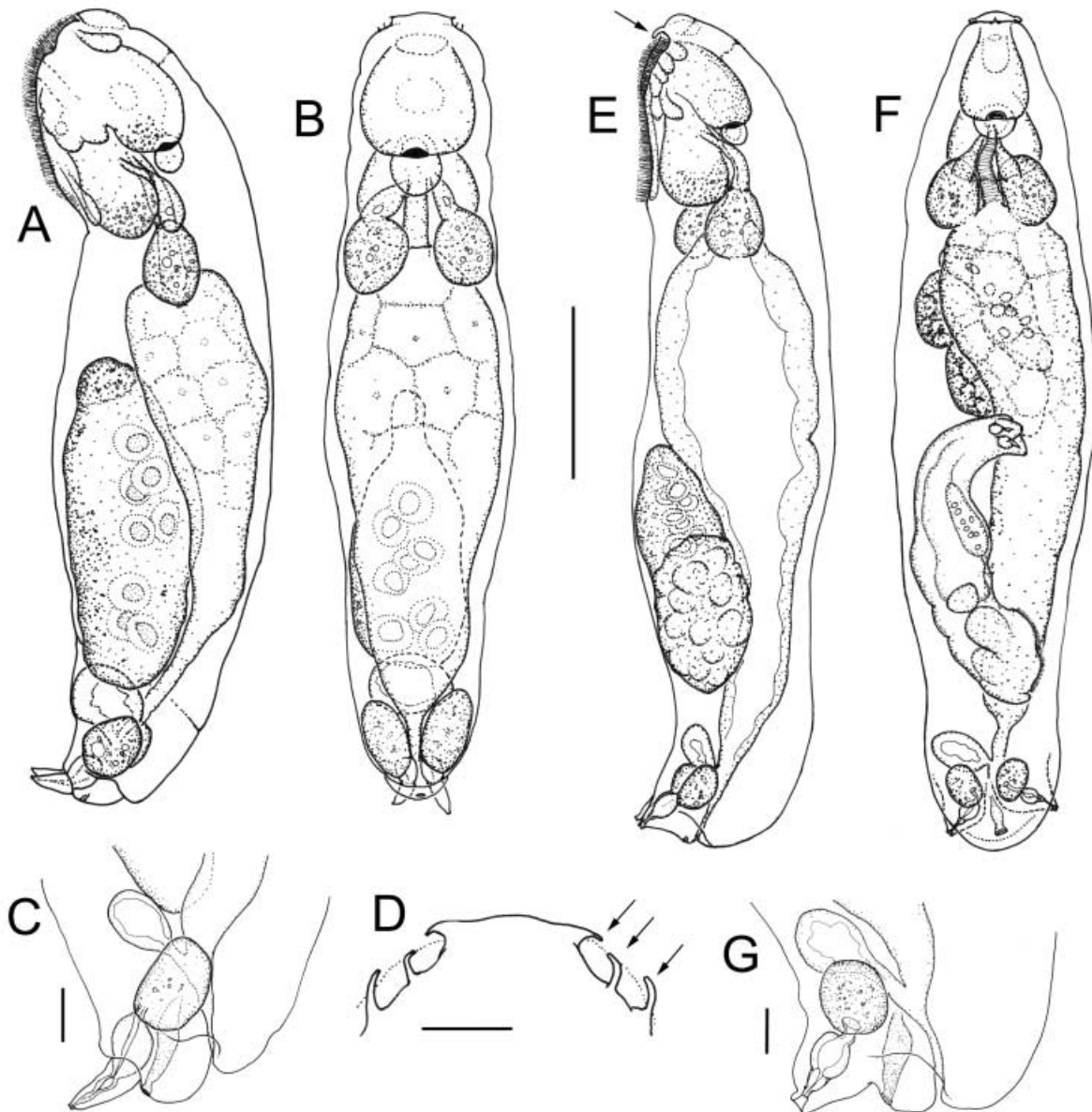


Figure 1. (A–D) *Lindia gravitata*: (A) lateral view; (B) dorsal view; (C) detail of posterior, lateral view (right toe and pedal gland not shown); (D) detail rostrum and sensory papillae (arrows), dorsal view. (E–G) *Lindia tecusa*: (E) lateral view (arrow: sensory papilla); (F) dorsal view; and (G) detail of posterior, lateral view (right toe and pedal gland not shown). Scale bars: A, B, E, F, 100 μ m; C, D, G, 10 μ m.

Yerseke, The Netherlands, in psammon from high medio-littoral. Collected by W.H. De Smet, 22 October 2003.

Additional material: one slide with parthenogenetic female and one with two trophi preparations in KBIN; ten slides containing females, four trophi preparations for light microscopy and 16 stubs each with one trophi preparation for SEM (De Smet, 1998) in the Department of Biology, University of Antwerp, Eastern Scheldt, Yerseke, The Netherlands, in psammon from high medio-littoral, 22 October 2003. Several specimens collected at the same locality throughout 2004. Two specimens, Eastern Scheldt, Zierikzee, The Netherlands, in psammon from high medio-littoral, collected 22 February 1995.

Comparative material examined

Lindia tecusa Haring & Myers, 1922. Parthenogenetic females: whole mounts and trophi preparations in the

Department of Biology, University of Antwerp; collected at Etaples, France, in tide puddle of the estuary of La Canche, 17 September 1998, and at Yerseke, Eastern Scheldt, The Netherlands, in psammon from high medio-littoral, 6 August 2004.

Diagnosis

Lindia with small, thin toes; epipharynx composed of a single plate and two elongate triangular sclerite elements; subuncus composed of loosely bound tuft of long scleropili.

Description of parthenogenetic female

Body elongate (Figure 1A,B), spindle-shaped in dorsal view, in lateral view slightly arched dorsally and gradually tapering distally; shape fairly constant; transversal folds inconspicuous; colour pale olive-green to brown. Head indistinctly offset by neckfold, slightly tilted ventrally,

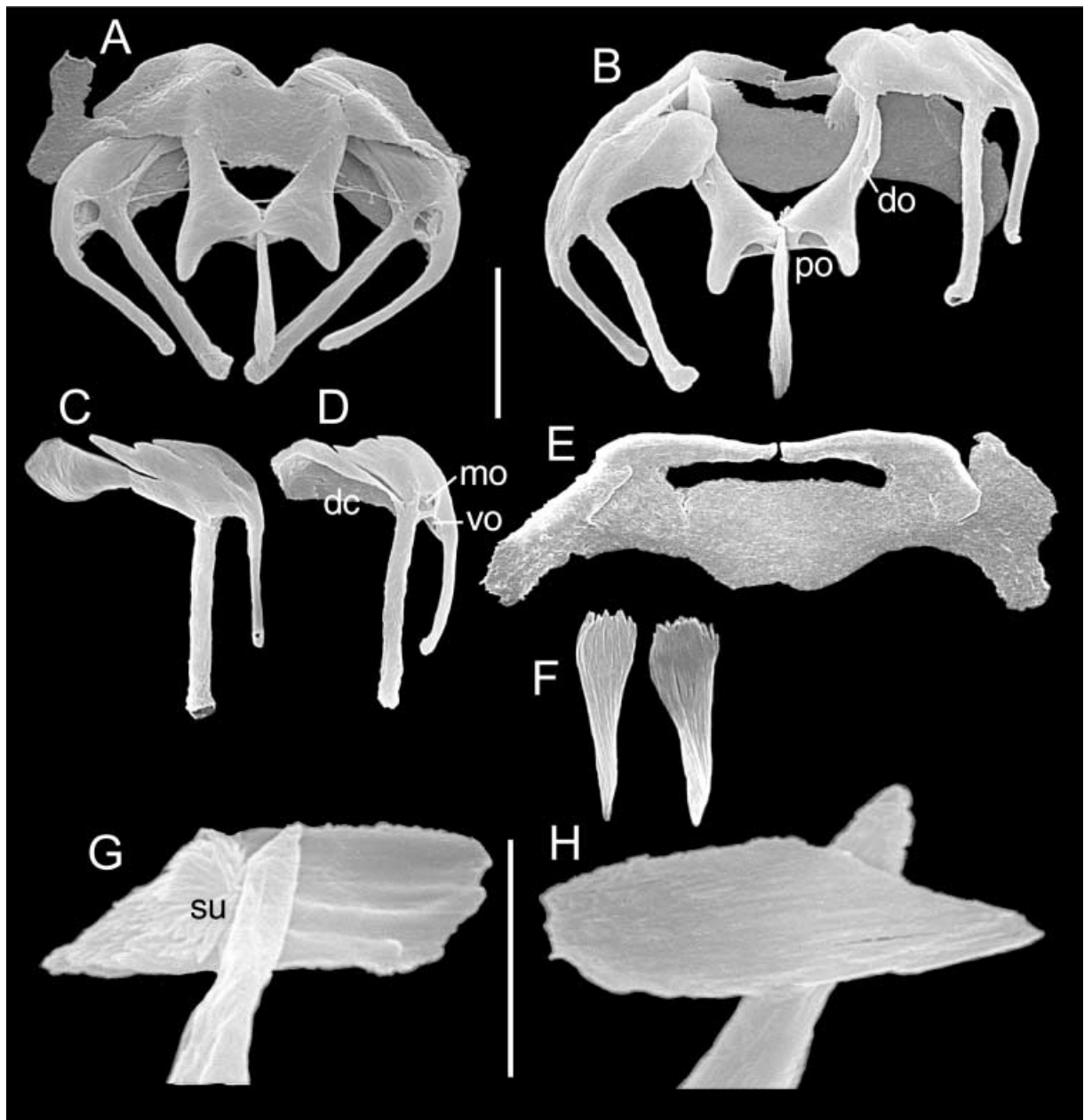


Figure 2. *Lindia gravitata*, SEM photographs of trophi: (A) ventral view with epipharyngeal plate; (B) dorsal view; (C) right manubrium, outer view; (D) left manubrium, inner view; (E) epipharyngeal plate; (F) epipharyngeal platelets; (G) right uncus, inner view; and (H) right uncus, outer view. dc, dorsal chamber; do, distal ramus opening; mo, opening of median chamber; su, subuncus; vo, opening of ventral chamber; po, proximal ramus opening. Scale bars: A–F, 10 μm ; G, H, 5 μm .

broadly rounded anteriorly; chin weak; auricles absent; two very weak antero-lateral depressions; laterally from rostrum three pairs of tiny sensory papillae (Figure 1D); dorsal antenna small, in anterior half of head. Lateral antennae small, the height of the bladder. Tail a weak lobe over cloacal opening. Foot rudimentary, short (Figure 1C). Toes short, small, thin with short tubuli, conical in dorsal view; in lateral view dorsal margin slightly arched and ventral margin more or less straight. Caudal antenna distinct, dorsally near basis of toes. Brain large, obpyriform; eyespot large, dark red; retrocerebral sac hemispherical with few minute pigment granules. Oesophagus relatively long and narrow, annulation apparently absent. Stomach and intestine not separated by constriction. Gastric glands compound, composed of

large, spherical–ovate unstalked basal part attached to the stomach, and tubular anterior part connected proximally to mastax. Bladder small. Pedal glands fairly large, rounded–ovate, with reservoir in foot (Figure 1C). Vitellarium with eight nuclei; oviparous.

Trophi (Figure 2). Rami lyrate with distinct alulae and large openings proximally (Figure 2B: po); latero-distally a small, narrow chamber (the so-called external lamella?) with small opening (Figure 2B: do) dorso-caudally; inner margin of rami tips with scleropili. Fulcrum slightly less than ramus length, in lateral view almost parallel-sided, slightly tapering and rounded distally; no basal plate. Unci (Figure 2G,H) a thin striated, more or less rhomboid plate, composed of ± 15 tiny appressed teeth; ventral teeth largest; subuncus (Figure 2G: su) a tuft of loosely bound,

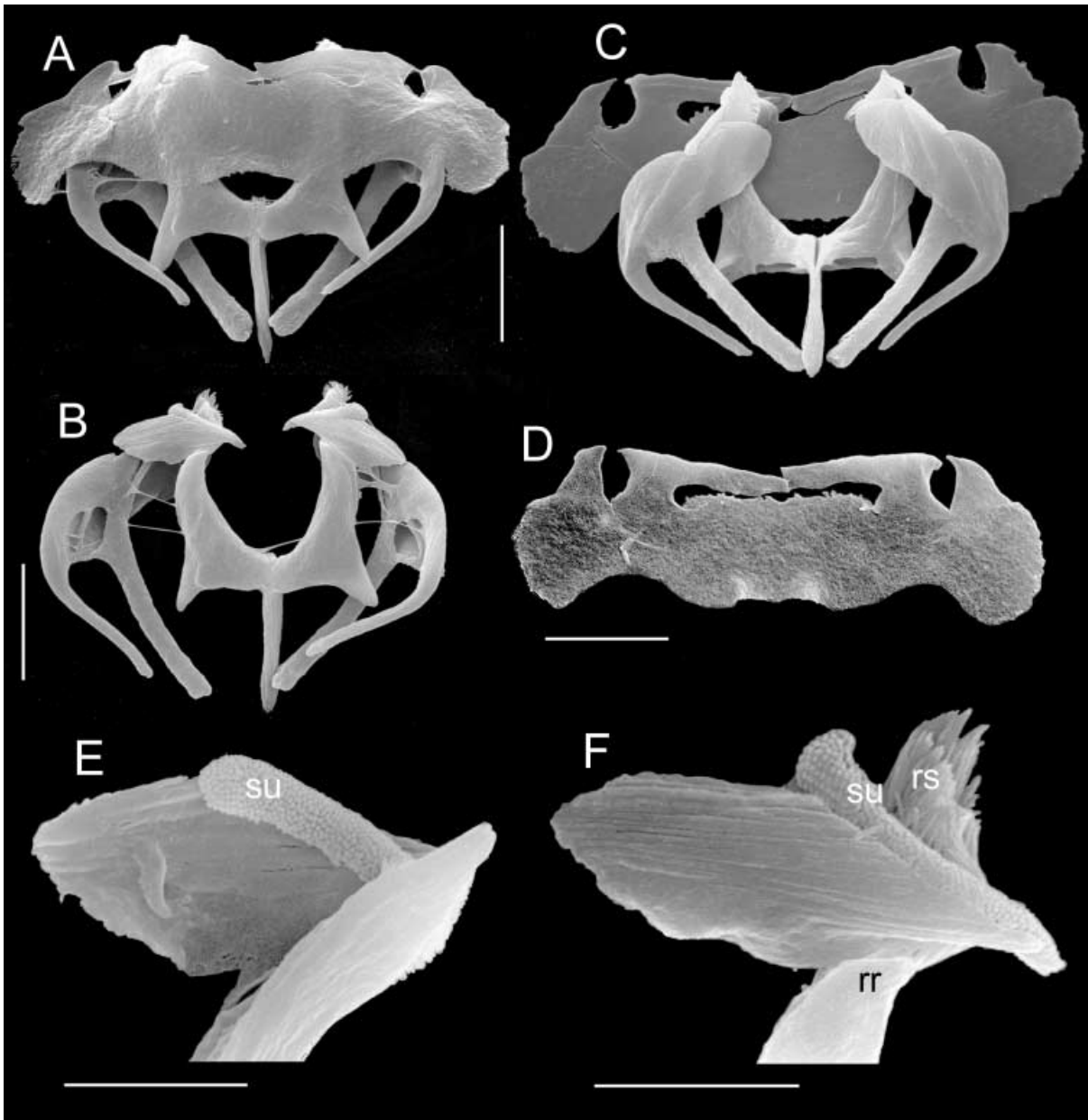


Figure 3. *Lindia tecusa*, SEM photographs of trophi: (A) ventral view with epipharyngeal plate; (B) same as (A) without epipharyngeal plate; (C) dorsal view; (D) epipharyngeal plate; (E) left uncus, inner view; and (F) right uncus, outer view. rs, ramus scleropili; rr, ramus ridge; su, subuncus. Scale bars: A–D, 10 μm ; E, F, 5 μm .

relatively long scleropili. Manubria with characteristic ventral branch; ventral branch rod-shaped, slender, $\sim\frac{3}{4}$ shaft length and nearly parallel to it; head broad, plate-shaped, composed of three manubrial chambers lying next to each other; dorsal chamber with large opening at inner side of head (Figure 2D: dc); median and ventral chamber with small, opening at inner side of head near basis of shaft and ventral branch (Figure 2D: mo, vo). Epipharynx a broad curved plate (Figure 2E), and a pair of elongate-triangular platelets (Figure 2F); epipharyngeal plate with lateral flaps delimited by a broad sinus proximally and a narrower incision distally; distally the central part of epipharyngeal plate bears two incurved branches, with smooth or slightly notched outer margin at the incurvation; the lateral flaps show a blunt apex distally; both incurved branches and apices are slightly more reinforced than the rest of the epipharyngeal plate,

that shows the individual sclerite bodies it is built of; the exact position of the thin, elongate-triangular epipharyngeal platelets, composed of long sclerite bodies, could not be determined by light microscopy nor SEM.

Measurements

Total length 375–475 μm , mean=427 μm , N=15, (1260 μm after Lie-Pettersen, 1906), toe 13–22 μm , mean=15 μm , N=15.

Trophi see Table 1.

Distribution and ecology

Norway, North Sea, Bergen (Lie-Pettersen, 1906), Germany, Baltic Sea, Kieler Bucht (Schulz, 1936/1937), The Netherlands, Eastern Scheldt (this paper). Living in periphyton and psammon from high medio-littoral. Perennial. The average salinity of the Eastern Scheldt at the

sampling locality is 31.0 ppt (values for 2003–2004: 29.1–33.0 ppt). In the psammon of the sampling locality *L. gravitata* was accompanied by an unidentified bdelloid, *Cephalodella megalcephala* (Glascott, 1893), *Colurella marina* Althaus, 1957, *Encentrum marinum* (Dujardin, 1841), *Encentrum (Isoencentrum) sp.*, *Encentrum (Pseudoencentrum) sp.*, *Lecane inermis* (Bryce, 1892), *Lepadella patella* (Müller, 1773) and *Lindia tecusa*. It is feeding on Cyanobacteria, viz *Merismopedia*.

DISCUSSION

The data on *Lindia tecusa* (Figures 1E–G & 3) used in the comparison following, are based on my own observations and on the only descriptions supplemented with illustrations by Harring & Myers (1922), Dehl (1934) and Koste (1970, 1978).

In spite of the strong resemblances between *Lindia gravitata* and *L. tecusa* in external morphology, anatomy, and all but the similar body length (*L. gravitata* 375–1260 µm, *L. tecusa* 350–1500 µm), both morphospecies are unmistakably differentiated by morphological features, and the structure of the trophi. The most striking character is the shape of the toes, which are small, fairly thin and offset from the trunk by a fold in *L. gravitata* (Figure 1C), and very broad conical, without fold separating them from the trunk in *L. tecusa* (Figure 1G). The reservoirs of the pedal glands are located in the foot in *L. gravitata*, whereas in *L. tecusa* they lie almost completely inside the toes. The tail is less pronounced in lateral view in *L. gravitata*, but bulging over the cloaca in *L. tecusa*. Laterally from the rostrum *L. gravitata* bears three pairs of tiny sensory papillae (Figure 1D), whereas *L. tecusa* shows a single pair of sensory palps apically from the antero-lateral depressions (Figure 1E). A further difference between both species might be their method of reproduction. *Lindia tecusa* is ovoviviparous, and up to five developed embryos (Dehl, 1934; personal observation) can be seen in the body cavity (only a single embryo according to Harring & Myers (1922), Koste (1970) and Segers (2002); up to three in different stages of development following Thane-Fenchel (1968)). As concerns *L. gravitata*, I never observed any developing embryo, and neither did Lie-Petersen (1906) or Schulz (1936/1937), so it is most probably oviparous. The suggestion by Schulz (l.c.) that *L. gravitata* might take the shape of *L. tecusa* when developing embryos inside the body, and thus should be synonymous, is falsified by the embryos of the latter already showing the characteristic toes (Figure 1F). According to Koste (1970), *L. tecusa* shows a strong annulation of the oesophagus. This feature was neither mentioned by Harring & Myers (1922) or Dehl (1934), and very weak or absent also in the specimens I studied, as it was in *L. gravitata*, proving that oesophageal annulation has no discriminating value. The anterior tubular part of the gastric glands found in *L. gravitata* is present in *L. tecusa* as well (Figure 1E,F), contrary to the descriptions and figures of the latter in Harring & Myers (1922), Dehl (1934) and Koste (1970, 1978).

The trophi of both species are very similar (*L. gravitata*: Figure 2, *L. tecusa*: Figure 3), indicating a very close relationship. The most striking differences in trophi morphology concern the subunci that are rod-shaped and

armed, the full length and all around, with close-set short protuberances in *L. tecusa* (Figure 3E,F: su), and composed of a tuft of scleropili in *L. gravitata* (Figure 2G: su). Elongate–triangular epipharyngeal platelets (Figure 2F) are present in *L. gravitata* only. The outer margin of the incurved distal branches of the epipharyngeal plate is smooth or slightly notched laterally in *L. gravitata* (Figure 2E), whereas in *L. tecusa* (Figure 3D) it bears a pronounced, acute projection. The lateral flaps of the epipharyngeal plate are more broadly rounded in *L. tecusa*. Other, less pronounced differences characteristic for *L. gravitata* are the weaker sclerification, the on average smaller dimensions of the trophi (Table 1), the more slender rami, and the less developed ramus ridges whereupon the unci rest (Figure 3F: rr). The descriptions and figures of the trophi of *L. tecusa* presented in Harring & Myers (1922), Dehl (1934) and Segers (2002), and obtained by light microscopy are highly accurate. On the contrary, those shown in Koste (1970), and reproduced in his classical identification work (1978) are incorrect: the epipharyngeal plate was reported as an unpaired ring-shaped structure, the fulcrum is not expanded distally, the rod-shaped subunci were interpreted as oval platelets and the associated oval platelets are non-existent.

The geographic distribution of both species is insufficiently known, due to the taxonomic confusion and the few records substantiated by illustrations. As for *L. gravitata*, *L. tecusa* was reported from Scandinavian coastal waters, and the Baltic and North Sea as well, and moreover from the Black Sea, and the Atlantic coasts of Brittany, France, and Cape Breton Island, Nova Scotia, Canada (De Ridder & Segers, 1997). The report of *L. tecusa* from garden ponds in Tokyo, Japan, by Sudzuki (1975) is a misidentification, judging from the accompanying microphotograph, and the record from plankton of an eutrophic freshwater pond in Korea (Turner, 1986) is unverifiable.

A third marine *Lindia* species, *L. brotzkayae*, has been described from the Kandalakcha Bay, White Sea, Russia, by Bogoslovsky (1950), who considered it related to *L. tecusa* and *L. gravitata* on the basis of the general morphology and the trophi. According to Koste (1978), *L. brotzkayae* is probably identical with *L. tecusa*, and Segers (2002) qualified it as unrecognizable. The description is poor indeed, and mainly based on unreliable features. Some of its characters of interest in the comparison with *L. tecusa* and *L. gravitata* are the slender toes (cf. *L. gravitata*), the ovoviviparous way of reproduction (cf. *L. tecusa*), and the great number of trunk pseudosegments (absent or indistinct in *L. gravitata* and *L. tecusa*). Tzschaschel (1979) describes and figures sub *L. tecusa* a species from the littoral of the Island Sylt, North Sea, Germany, that shows characteristics of *L. gravitata*, i.e. small conical toes and three pairs of sensory bristles, and *L. tecusa*, i.e. ovoviviparity, but moreover displays a great number of well pronounced pseudosegments as mentioned in *L. brotzkayae*. It follows that, if Schulz's (1936/1937) and my observation that *L. gravitata* is oviparous proves correct, *L. brotzkayae* may be a valid species as well. The report of an embryo-bearing *L. annecta* Harring & Myers, 1922 from the Baltic Sea by Schwarz (1962) is undoubtedly a misidentification, and then might concern *L. brotzkayae* likewise.

Another *species inquirenda* that should be mentioned here is *L. anebodica* Bērziņš, 1949, found in moors among *Utricularia* and *Sphagnum* in Sweden. The description of this taxon is too poor to permit identification (Segers, 2002). However, the illustration of the trophi (Bērziņš, 1949: pl. 4, figure 15) clearly shows an epipharynx which is very similar to the plate-shaped one found in *L. tecusa* and *L. gravitata*, suggesting that if correct, *L. anebodica* might be a related taxon inhabiting freshwater.

Remane (1933) recognized the subgenera *Lindia* and *Halolindia* (accommodating *L. tecusa* and *L. gravitata*), on the basis of differences in the shape of the body, corona, reproduction and habitat. A third subgenus *Neolindia* was erected by Segers (2002), based on the peculiar and unique trophi structure, to separate *L. deridderae* Koste, 1980 from the otherwise fairly homogenous group of taxa in the subgenus *Lindia*. The relevant diagnostic characters of *Halolindia* introduced by Remane (1933), and accepted till now are: auricles absent, foot rudimentary, unci plate-shaped without pronounced teeth, epipharynx a single dome-shaped plate, subunci with fine spinulation, ovoviviparous, marine and brackish waters. The present study shows that, in view of the oviparity and the differently shaped subunci in *L. gravitata*, reproduction and subuncus shape can no longer be used as diagnostic features. Furthermore, the description (De Smet, in press) of the oviparous, auricle-bearing *Lindia elsae* from the marine littoral of Réunion Island (Indian Ocean), is evidence that ecology is not a valid discriminating character of the subgenus. It follows that only the characters auricles absent, foot rudimentary, unci plate-shaped without pronounced teeth, and epipharynx plate-shaped (whether or not with accessory platelets cf. *L. gravitata*) should be retained as diagnostic. Another feature that could be useful concerns the manubria. In *L. gravitata* and *L. tecusa* the manubrial chambers are lying next to each other, the dorsal chamber occupying approximately half the width of the head and opening at the inner side. In the few representatives of the subgenus *Lindia* studied to date by SEM, i.e. *L. torulosa* Dujardin, 1841, *L. janickii* Wiszniewski, 1934, *L. elsae* De Smet, in press (De Smet, 2002, in press, unpublished; Segers, 2002), the dorsal chamber is largely superimposed on the other chambers, its opening occupying almost the whole width of the manubrial head and opening at the inner side as well.

Present confusion in rotifer taxonomy is often due to the casual nature of many early species descriptions, the high intraspecific morphological variability leading to disproportionate lumping or splitting, the synonymization of good species with the recognized taxon they resemble most closely, and neglect of taxonomic education (for reviews see e.g. Koste & Shiel, 1989; Nogrady et al., 1993; Segers, 1998; Jersabek, 2002). The case of *Lindia gravitata-tecusa* outlined above, in combination with the *species inquirendae* that might be related to them, is a typical example of such taxonomic uncertainties that, nevertheless, can be resolved for the greater part by simple light microscopy and application of SEM for the morphological study of trophi.

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