

On a New *Seison* Grube, 1861 from Coastal Waters of Kenya, with a Reappraisal of the Classification of the Seisonida (Rotifera)

Martin V. Sørensen^{1,*}, Hendrik Segers², and Peter Funch³

¹Department of Evolutionary Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark
E-mail: mvsorensen@bi.ku.dk

²Royal Belgian Institute for Natural Sciences, Freshwater Laboratory, Vautierstraat 29, B-1000 Brussels, Belgium
E-mail: hendrik.segers@naturalsciences.be

³Department of Ecology and Genetics, Institute of Biological Sciences, University of Aarhus, Universitetsparken, Building 135, DK-8000 Århus C, Denmark. E-mail: peter.funch@biology.au.dk

(Accepted October 27, 2004)

Martin V. Sørensen, Hendrik Segers, and Peter Funch (2005) On a new *Seison* Grube, 1861 from coastal waters of Kenya, with a reappraisal of the classification of the Seisonida (Rotifera). *Zoological Studies* 44(1): 34-43. On occasion of the discovery of a new species of a marine epizotic rotifer of the enigmatic Seisonidae, from Gazi Bay in Kenya, we reassessed the classification of the group. The taxon was until now known to contain only 2 species, viz. *Seison nebaliae* and *S. annulatus*, both of which live attached to Crustacea of the genus *Nebalia*. The new species, *Seison africanus* sp. nov., was diagnosed by its species-specific trophi morphology and relatively small size. A comparison with the 2 other known seisonid species reveals a sister group relationship between *S. africanus* sp. nov. and *S. nebaliae*, based on similarities in trophi structure and, accordingly, an assumed feeding mode and relationship with their hosts. The fundamental differences between these 2 commensal sister taxa and the ectoparasitic *S. annulatus* prompted a reevaluation of the generic classification of these animals. Accordingly, we propose to reestablish the genus *Paraseison* Plate, 1887 in order to accommodate *P. annulatus* (Claus, 1876) (comb. nov.). <http://www.sinica.edu.tw/zool/zoolstud/44.1/34.pdf>

Key words: Gnathifera, Morphology, Taxonomy, Trophi, Marine rotifers.

With its unique morphology, special biology, and intriguing phylogenetic position, the genus *Seison* is a key taxon in the Rotifera. Only 2 valid congeneric species, *Seison nebaliae* Grube, 1861 and *S. annulatus* Claus, 1876, are presently recognized in the taxon, and both live epizotic on the leptostracan crustacean *Nebalia*. The known geographic range of both species appears to be quite similar: records are from the Mediterranean region, including the Adriatic Sea, and the European part of the Atlantic (Grube 1861, Claus 1876, Plate 1887, Illgen 1916, Koste, 1975, Ricci et al. 1993, Ahlrichs 1997, Ferraguti and Melone 1999). In addition, Markevich (1993) recorded *S. nebaliae* in the Sea of Okhotsk off the Sakhalin Is.,

whereas unidentified *Seison* specimens have been found on *Nebalia* in the Pacific Ocean near California (Menzies and Mohr 1952) and in the Antarctic Ocean (Leung and Mohr 1969). The 2 known *Seison* species may even co-occur on the same host (Ricci et al. 1993), although *S. annulatus* appears to prefer the pereopods and carapace while *S. nebaliae* lives on the pleopods of the host (Illgen 1916, Ricci et al. 1993, Ahlrichs 1995).

Whereas the body morphologies of *S. nebaliae* and *S. annulatus* deviate only in minor points, the 2 species are easily distinguished by their trophi morphology and, consequently, feeding biology (Ricci et al. 1993, Segers and Melone 1998). Several studies have indicated that *S. nebaliae*

* To whom correspondence and reprint requests should be addressed. E-mail: mvsorensen@bi.ku.dk

feeds exclusively on bacteria, while *S. annulatus* appears to be parasitic, feeding on the hemolymph of its host and perhaps also on the contents of the host's eggs (Illgen 1916, Remane 1929-1933, Koste 1975, Ricci et al. 1993, Segers and Melone 1998).

Phylogenetically the Seisonidea plays a key role in the understanding of the Rotifera and related phyla. Its putative relation with the Bdelloidea in the Digononta (Remane 1929-1933, Pennak 1953, Ruttner-Kolisko 1974, Nogrady et al. 1993) has repeatedly been refuted in cladistic analyses. These, to the contrary, suggest a sister-group relationship between the Monogononta and Bdelloidea, as Eurotatoria (Wallace and Colburn 1989, Melone et al. 1998, Sørensen, 2002). The latter hypothesis is further supported by other studies, but these additionally suggest that the Seisonidea and Acanthocephala are sister groups (Ahlrichs 1995 1997), or place Acanthocephala close to Eurotatoria (Sørensen et al. 2000, Mark Welch 2000, Segers 2002). The recent discovery of Micrognathozoa, yet another related taxon of minute worms having a trophi-like jaw apparatus further adds to the confusion (see De Smet 2002, Giribet et al. 2004, Funch et al. in press). Thus, even though little is certain about the phylogenetic position of the seisonids, it is clear that they are pivotal to understanding the evolution of rotifers.

Herein we report on the discovery of an undescribed species of Seisonida in samples from the Kenyan coast of the Indian Ocean, which represents an outstanding opportunity to learn more about this enigmatic taxon; the peculiarities of the specimens are such that a reevaluation of the generic classification of the group was prompted.

MATERIALS AND METHODS

Locality

Samples were collected in Gazi Bay, Kenya (Fig. 1) for a study on marine meiofauna, by P. Van Avermaet (Ghent Univ., Ghent, Belgium). Gazi Bay covers an area of ~1500 ha, of which 686 ha are mangrove, 300 ha mud and sand flats, and 500 ha seagrass beds. The largest area with seagrass (*Enhalus acoroides* (Linnaeus f.) Royle) is located at the mouth of the River Kidogoweni. Towards the sea side, the bay is sheltered by the Chale Peninsula and large coral reefs. The climate is humid with wet seasons in Apr.~June and Nov.~Dec., and an annual average temperature of

28°C (Fondo and Martens 1998).

Sampling and handling of material

Sampling was carried out 2 Aug. 1989 off the coast of Gazi Bay (4°25'S, 039°50'E). Seagrass standing in patches of 50 x 50 cm on sandy sediment at 500 m from the shore was collected in plastic bags. The sampling was solely qualitative, and data on the precise amount of collected seagrass are unknown. At the time of sampling, the water depth was 1 m, and the current was strong. The tidal amplitude was about 3 m. All collected material was brought to land and exposed to 7% MgCl₂ in seawater to anesthetize the fauna (see Pfannkuche and Thiel 1988). The samples were then washed in fresh water over a 38-µm mesh sieve. The contents of the sieve were fixed in 70°C 4% formalin and sorted using a dissecting microscope. The samples contained 9 specimens of *Seison*, that were subsequently dehydrated and mounted in glycerol, placed between cover slips on aluminum slides, and sealed with paraffin (see Westheide and Purschke 1988). The specimens were examined, photographed, and drawn using Nomarski differential interference contrast with an Olympus BX60 microscope equipped with a drawing tube and an Olympus DP10 digital camera.

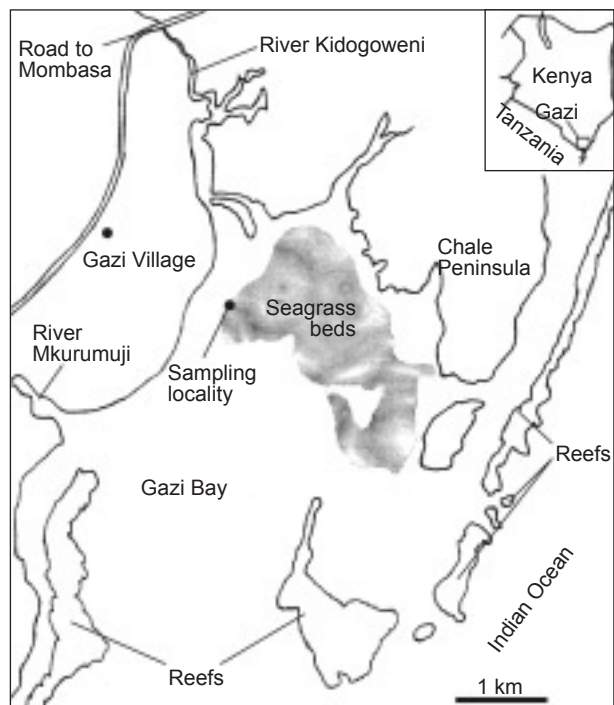


Fig. 1. Map showing the sampling locality in Gazi Bay. Inset: Kenya.

Two specimens were afterwards removed from the whole mount, and their trophi were extracted using dilute sodium hypochlorite and prepared for scanning electron microscopy (SEM) following the procedure given by De Smet (1998). The trophi were examined with a JEOL JSM-840 microscope.

As no specific study on rotifers was intended originally, the handling of the samples was not optimal for this taxon, and was certainly not as suggested as the best procedure in the literature. We therefore tested whether treatment with $MgCl_2$ and 70°C 4% formalin has any influence on trophi morphology as revealed by SEM (Fig. 2). We found no such indication in specimens of *Testudinella patina* (Hermann, 1783).

RESULTS AND DISCUSSION

Seison africanus sp. nov. (Figs. 3-7)

Type locality: Seagrass (*Enhalus acoroides* (Linnaeus f.) Royle) bed off Gazi, Gazi Bay, Kenya (Fig. 1).

Holotype: Adult female (Zoological Museum, Univ. of Copenhagen: ZMUC ROT-253), mounted in glycerol. *Allotype:* Adult male (ZMUC ROT-

254), mounted in glycerol on same slide as holotype.

Paratypes: Five adult females (ZMUC ROT-297 to ROT-301), mounted in glycerol on the same slide as holotype; 2 isolated trophi from an adult female and an adult male (ZMUC ROT-302 and ROT-303), mounted on aluminum stubs for SEM. All types collected on 2 Aug. 1989.

Differential diagnosis

Seison africanus sp. nov. (Figs. 3, 4) is most reliably recognized by its unique trophi morphology (Figs. 5A, B, 6, 7). The species can only be confused with *S. nebaliae*, however, the trophi of the 2 differ in the following aspects (compare with Segers and Melone 1998, compare also Fig. 5A, B with Fig. 5C, D).

1) The rami heads are relatively flat ventrally in *S. africanus* sp. nov., and strongly bulbous in *S. nebaliae*.

2) A single, fused epipharynx with a strong antieriad spiniform projection occurs in *S. africanus* sp. nov., while the epipharynx consists of paired structures both bearing minute and weak, anteriorly pointed projections in *S. nebaliae*.

3) The rami alulae are particularly elongate and medially almost parallel in *S. africanus* sp. nov., while they are elongate and rather homoge-

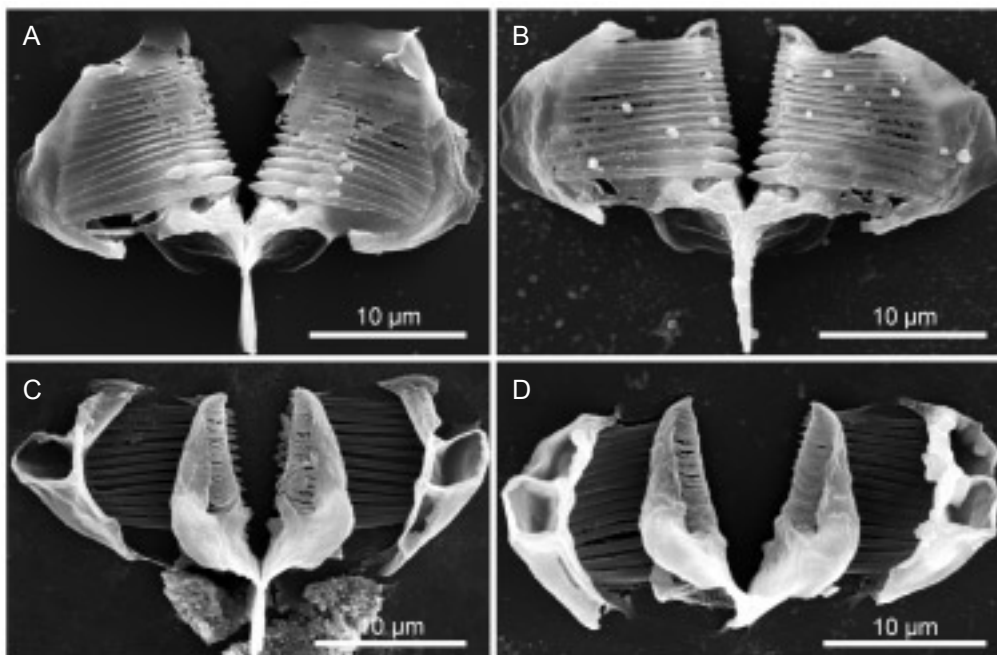


Fig. 2. Scanning electron microscopic photos of *Testudinella patina* trophi. A and C were prepared from specimens fixed in 70°C formalin. B and D are from live specimens. (A, B) Frontal view; (C, D) caudal view.

neously outwardly curved in *S. nebaliae*.

4) Alulae have a terminal recurved medial projection with a single opening in *S. africanus* sp. nov., while this projection is more ventral and with 2 openings in *S. nebaliae*.

5) Finally, the fulcrum has numerous fine striae and no basal plate in *S. africanus* sp. nov. Because of the lack of a basal plate, the caudal ends of the constituent hollow elements of the fulcrum are open in this species. In *S. nebaliae*, the

striae on the fulcrum are less pronounced, and the fulcrum has a well-developed basal plate.

Description

Body divided into 4 distinct regions: head, neck, trunk, and foot (Figs. 3, 4A, C). Head oval (Fig. 4E), distinctly offset at neck. Rostrum small, consisting of 2 lobes. Corona reduced. Mouth subterminal, slightly orientated towards ventral

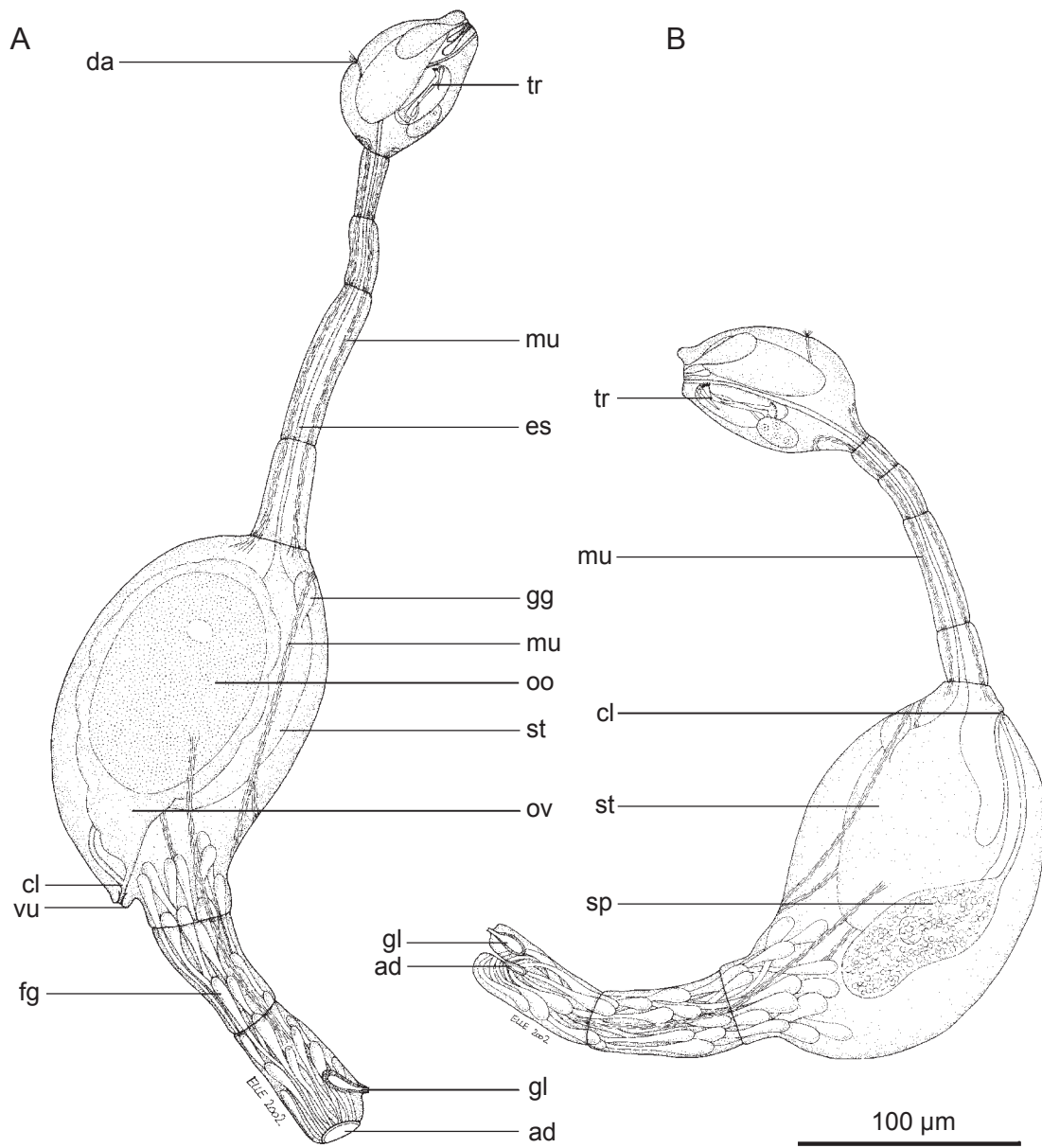


Fig. 3. *Seison africanus* sp. nov. (A) Female habitus, lateral view; (B) male habitus, lateral view. ad, adhesive disc; cl, cloaca; da, dorsal antenna; es, esophagus; fg, foot gland; gl, gland; gg, gastric gland; mu, muscle; oo, oocyte; ov, ovarium; sp, spermatophore-forming organ; st, stomach; tr, trophi; vu, vulva.

side. An unpaired dorsal antenna present, located slightly behind middle of head (Fig. 4E); details of brain and retrocerebral glands not discernible.

Neck consisting of 4 telescopic retractable pseudosegments (Fig. 3); diameter of neck pseudosegments gradually increasing from smallest anteriorly to largest posteriorly, thus anterior thinner ones able to retract into larger posterior ones (Fig. 4C).

Trunk oval, smooth, without annulations. Two or 3 pairs of cutaneous muscles present in trunk; 1 pair of lateral, longitudinal muscles inserted near middle of trunk and running posteriorly through trunk and foot, attaching either in middle of foot or terminally, at adhesive disc. A 2nd pair of prominent ventral longitudinal trunk muscles present; a 3rd pair, probably running from anterior and ventral part of trunk to dorsally near insertion of foot possibly present, but requires confirmation. Protonephridia not observed. Stomach large, with pair of gastric glands located anteriorly on ventral side.

Gut short, located dorsally, opening into cloaca. In females, cloaca opening near foot on dorsal, posterior part of trunk, and surrounded by what appears to be a vulva (Fig. 4B). Male cloaca also located dorsally, but much nearer to point where neck and trunk meet. A cloacal vulva not found in males. Female reproductive organs consisting of paired ovaries with growing oocytes. Lobed nuclei in mature oocytes, reported by Remane (1929-1933), not observed. Ovaries of several females contained 1 large, bean-shaped cell about 100 μm long and 55 μm wide that could be interpreted as a fertilized egg. Oviducts from each ovarium joining and forming common duct that opens at cloaca. Only some details observable regarding male genital apparatus. Male with grayish organ that could be interpreted as spermatophore-forming organ (Fig. 4D), containing approximately 140 loosely organized, round cells with diameter of about 1.5 μm .

Foot consisting of 2 or 3 pseudosegments, with numerous pedal glands of different lengths;

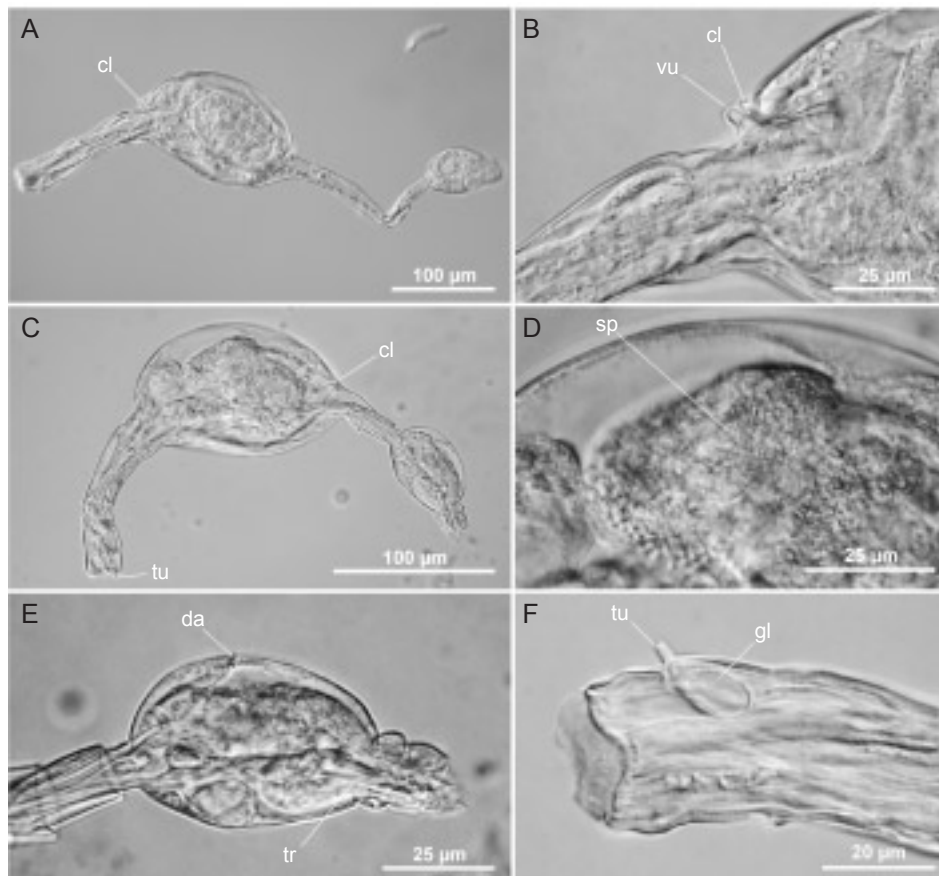


Fig. 4. Light microscopic photos of *Seison africanus* sp. nov. (A) Female holotype, lateral view; (B) cloaca, details from female holotype. (C-E) Allotypic male, lateral view. (C) Overview; (D) spermatophore-forming organ; (E) head, lateral view; (F) Distal foot pseudosegment, lateral view, detail from paratypic female. cl, cloaca; da, dorsal antenna; gl, gland; sp, spermatophore-forming organ; tr, trophi; tu, tubule; vu, vulva.

males with over 20 glands; females apparently with fewer glands. Most glands with long ducts, longest glands extending into trunk. All glands terminating in separate outlets at basal adhesive disc. Unstalked gland, with short, ventrally projecting tubule, present in distal part of foot (Fig. 4F). When basal adhesive disc retracted, tubule of short gland moves to a terminal position (Fig. 4C).

Trophi fulcrate (Figs. 5A, B, 6), identical in both sexes. Rami consisting of anteriorly rounded heads, caudally extending into long alulae. Dorsal sides of rami bulbous, forming an almost symmetrical and weakly reinforced bulla ramus (Fig. 7B). Median opening between rami narrow. Unpaired epipharynx present on ventral side of rami head (Figs. 5A, B, 6B, 7D). Epipharynx slightly asymmetrical, with 2 laterocaudal projections; left projection larger than the right. Anteromedial part of epipharynx with large, projecting tooth. Alulae elongate, showing clear constriction near their connection with rami heads, running parallel along most of their length and outwardly curved distally (Figs. 5B, 6). Pore present laterally near transition of rami into alulae (Figs. 6C, 7C). Distal ends of alulae strongly dilated, forming spatulate terminals. Recurved medial projection present (Figs. 5B, 6C), forming a large opening in each alula (Fig. 7F). Fulcrum elongate triangular, narrow, proximally pointed (Figs. 5B, 6B, C, 7F). Dorsal with median suture (Fig. 7A, B), laterally striated. Fulcrum composed of 7 hollow tubes; these expanding distally, truncated, fully opened (Fig. 7F). No basal plate. Unci elongate rod-shaped; anteromedial ends with weak tooth formation, posterolateral ends pointed (Fig. 7C, E). Unci and rami connected anteriorly and laterally by ligaments.

Measurements

Total length 352~566 μm , head 68~83 μm , neck extended 180 μm , neck retracted 43 μm , neck diameter at narrowest point 8~10 μm ; neck diameter at widest point 17~18 μm ; trunk 125~180 μm , foot 108~169 μm long, distal foot pseudosegment extended 110 μm , same retracted 10 μm , trophi 32 μm , unci 11 μm , fulcrum 27 μm .

Etymology

The species name *africanus* is an adjectival toponym, after the Latin name for the African continent.

Taxonomy and ecology

Seison africanus sp. nov. is a relatively small species, when compared to its relatives. Although records show strong variations, the males and females of *S. africanus* sp. nov., measuring only 352~566 μm (males 352~536 μm , females 447~566 μm), are consistently smaller than *S. nebaliae* (males 1.1 mm, females 0.8 mm according to Ricci et al. 1993; up to 2.5 mm according to Remane 1929-1933) and *S. annulatus* (males 0.4~0.7 mm, females ca. 1 mm according to Plate 1887). Its general morphology, however, is similar to these other 2 species. One difference appears to be the presence of a vulva around the cloaca in

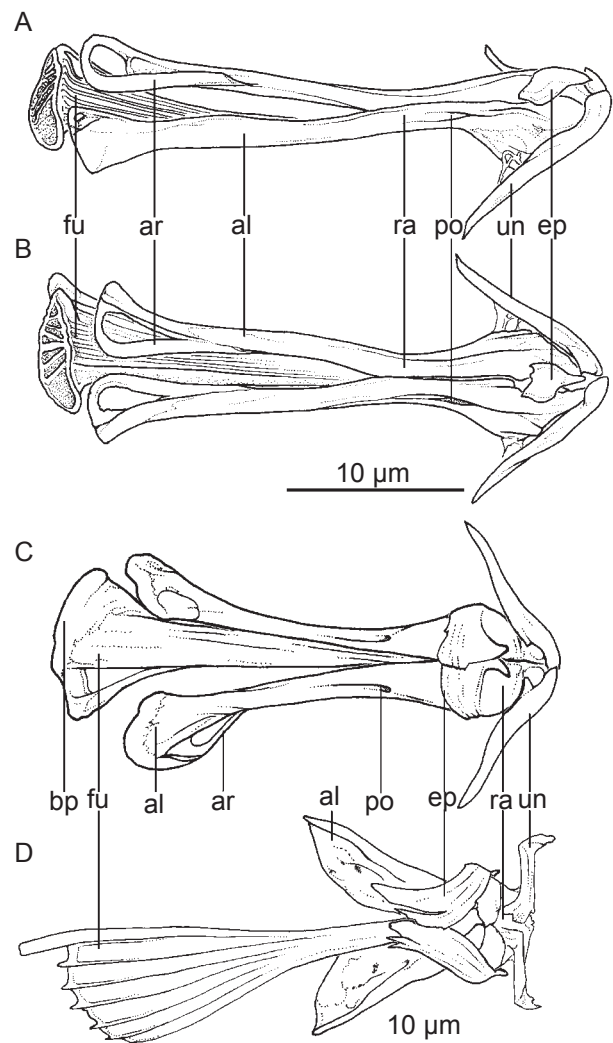


Fig. 5. Line drawings of trophi. (A) *Seison africanus* sp. nov., ventrolateral view; (B) *Seison africanus* sp. nov., ventral view; (C) *Seison nebaliae*, dorsal view; (D) *Seison annulatus*, dorsal view. al, alula; ar, alula rim; bp, basal plate; ep, epipharynx; fu, fulcrum; po, pore; ra, ramus; un, unci.

the female (Fig. 4B), but it should be noted that the reliability of structures of the relatively soft tegument is uncertain, especially considering the unusual and strong fixation technique applied to the present specimens. On the other hand, male specimens of *S. africanus* sp. nov. were treated and fixed as the females and lacked a cloacal vulva. So the female cloacal vulvae are probably genuine structures. Differences in trophi morphology are important and reliable, and apparently not influenced by the treatment: a test using *Testudinella patina* revealed no sign of an effect of the technique on trophi morphology (Fig.1).

Both *S. annulatus* and *S. nebaliae* are known to live exclusively as epibionts on species of the genus *Nebalia* (Crustacea). Our specimens of *S. africanus* sp. nov. were not attached to any host organism, and although *Nebalia* has been recorded from shallow waters of East Africa (Olesen 1999), the samples taken at the type locality of *S. africanus* sp. nov. did not contain any specimens of *Nebalia*. Nevertheless, we consider it a likely hypothesis that *S. africanus* sp. nov. does live associated with a host, with *Nebalia* as the most-probable candidate for this. The presence of a similarly large number of well-developed foot



Fig. 6. Scanning electron microscopic photos of trophi of *Seison africanus* sp. nov. (A) Dorsolateral view; (B) ventral view; (C) ventrolateral view. al, alula; br, bulla ramus; ep, epipharynx; fl, fulcral lamella; fu, fulcrum; li, ligament; po, pore; ra, ramus; un, uncus.

glands in *S. africanus* sp. nov. as in the other 2 species also points in this direction.

So, admittedly, our material of *S. africanus* sp. nov. consists of a limited number of isolated specimens, and the material was fixed following a technique that is unusual for rotifers. On the other hand, we are confident that the present material actually does represent a hitherto unknown species in view of its clear and unequivocal diagnosis when compared to all available reports on the trophi morphology of *S. nebaliae* (see Koste 1975, Markevich 1993, Melone and Segers 1998). Differences in trophi morphology between the 2 as reported herein are consistent with a species-level diagnosis in other groups of rotifer, as, for exam-

ple, *Scaridium* (see Segers 1995 1996) or Dicranophoridae (see De Smet and Pourriot 1997). Similarly, it is equally plausible that further detailed morphological analysis using SEM will uncover additional extant representatives of the taxon.

CONCLUSIONS

Phylogeny and classification of Seisonidae

The trophi morphologies of *S. nebaliae* and *S. africanus* sp. nov. are remarkably similar (Fig. 5A-C), and this undoubtedly translates into a similar function of their mastax, and, hence, similarities in



Fig. 7. Scanning electron microscopic photos of details of the trophi of *Seison africanus* sp. nov. (A-E) Apical rami parts and unci; (F) distal parts of alulae and fulcrum. (A) Dorsoapical view; (B) dorsocaudal view; (C) ventrocaudal view; (D) ventral view; (E) ventro-frontal view; (F) lateral view. al, alula; ar, alula rim; br, bulla ramus; ep, epipharynx; fl, fulcral lamella; fs, furcal suture; po, pore; ra, ramus; un, uncus.

their ecology and feeding habits. Like *S. nebaliae*, we assume that *S. africanus* sp. nov. is a food specialist, possibly feeding on bacteria ingested by suction resulting from a pumping action of the mastax. Consequently, these 2 should be regarded as commensals rather than parasites (see Markevich 1993). The numerous similarities in trophi morphology between *S. nebaliae* and *S. africanus* sp. nov. strongly support a sister-group relationship between these 2 species. Contrarily, *S. annulatus* now occupies a fairly isolated position in the Seisonidae. The latter species is an ectoparasite, which uses its unique mastax and trophi (Fig. 5D) to pierce the tegument of its host by protruding the sharp tip of its fulcrum through the mouth, and sucking out hemolymph of its host (see Remane 1929-1933, Ahlrichs 1995, Melone and Segers 1998).

The present phylogenetic scheme of the Seisonidae, with 2 closely related sister taxa and a 3rd more remotely related species fundamentally differs from the previous one, in which only 2 sister taxa were known. This new scheme is based on significant differences in feeding in conjunction with mastax functioning. Accordingly, we suggest a classification that adequately reflects this phylogeny, and propose to allocate *S. annulatus* to a different supra-specific taxon than *S. nebaliae* and *S. africanus* sp. nov. This can conveniently be done by reestablishing the genus *Paraseison* Plate, 1887, of which the type, *Paraseison asplanchnus* Plate, 1887, is a junior synonym of *S. annulatus* Claus, 1876 according to Illgen (1916). The resulting classification and nomenclature are given here.

Family Seisonidae Wesenberg-Lund, 1899
Genus Seison Grube, 1861

Diagnosis (emended): Pumping mastax with non-protrusible fulcrum; microphageous epizootic symbionts on *Nebalia*.

Synonym: *Saccobdella* Van Beneden and Hesse, 1864 (monotype: *S. nebaliae* van Beneden and Hesse, 1864 non Grube 1861¹)

***Seison africanus* sp. nov.**
***Seison nebaliae* Grube, 1861 (Genotype)**
Synonyms (after Illgen 1916)

Seison grubei Claus, 1876

Saccobdella nebaliae Van Beneden and Hesse, 1864 non Grube 1861¹. Genus *Paraseison* Plate, 1887

Diagnosis (emended): Pumping mastax with protrusible, piercing fulcrum; blood-sucking epizootic ectoparasite of *Nebalia*.

***Paraseison annulatus* (Claus, 1876) comb. nov.**
***Seison annulatus* Claus, 1876**
Synonym (after Illgen 1916)

P. asplanchnus Plate, 1887 (Genotype, designation by Haring 1913)

Nomina inquirendae: *P. ciliatus* Plate, 1887, *P. nudus* Plate, 1887, *P. proboscideus* Plate, 1887

Acknowledgments: We are grateful to A. Coomans, M. Vincx, R. Huys, and G. De Smet for their hospitality and help during P. Funch's visit to the State Univ. of Ghent in Belgium. We thank M. E. Petersen for correcting the language and S. Elle for her line drawings of the animals. Funding was provided by ERASMUS (ICP-E-0073), the Danish NSRC (51-00-0278 and 21-02-0455), and the Carlsberg Foundation (ANS-0178/20 and ANS 0724/20).

REFERENCES

- Ahlrichs WH. 1995. Ultrastruktur und Phylogenie von *Seison nebaliae* (Grube 1859) und *Seison annulatus* (Claus 1876), and a comparison of epidermal structures within the Gnathifera. Dissertation, Georg-August-Univ. zu Göttingen, Germany
- Ahlrichs WH. 1997. Epidermal ultrastructure of *Seison nebaliae* and *Seison annulatus*, and a comparison of epidermal structures within the Gnathifera. *Zoomorphology* **117**: 41-48.
- Claus C. 1876. Über die Organisation und systematische Stellung der Gattung *Seison* Gr. Festschrift zur Feier des Funfundzwanzigjährigen Bestehens der K.K. Zoologisch-Botanische Gesellschaft in Wien. *Veinna*: K.K. Zoologisch-Botanische Gesellschaft, pp. 77-88.
- De Smet WH. 1998. Preparation of rotifer trophi for light and scanning electron microscopy. *Hydrobiologia* **387/388**: 117-121.
- De Smet WH. 2002. A new record of *Limnognathia maerski Kristensen* and Funch, 2000 (Micrognathozoa) from the Subantarctic Crozet Islands, with redescription of the trophi. *J. Zool. (Lond.)* **258**: 381-393.
- De Smet WH, R Pourriot. 1997. Rotifera: the Dicranophoridae (Monogononta) and the Ituridae (Monogononta). In T Nogrady, HJF Dumont, eds. *Guides to the identification of the microinvertebrates of the continental waters of the world 12*, Vol. 5. Amsterdam: SPB Academic Publishing, 344 pp.
- Ferraguti M, G. Melone. 1999. Spermiogenesis in *Seison*

¹ Van Beneden and Hesse (1864) described *Saccobdella nebaliae* while apparently being unaware of Grube's (1859) *Seison nebaliae*. That the 2 species names are identical is a mere coincidence.

- nebaliae* (Rotifera, Seisonidea): further evidence of a rotifer-acanthocephalan relationship. *Tissue and Cell* **31**: 428-440.
- Fondo EN, EE Martens. 1998. Effects of mangrove deforestation on macrofaunal densities, Gazi Bay, Kenya. *Mangroves Salt Marshes* **2**: 75-83.
- Funch P, MV Sørensen, M Obst. 2005. On the phylogenetic position of Rotifera – Have we come any further? *Hydrobiologia* (in press)
- Giribet G, MV Sørensen, P Funch, R M Kristensen, W Sterrer. 2004. Investigations into the phylogenetic position of Micrognathozoa using four molecular loci. *Cladistics* **20**: 1-13.
- Grube AE. 1861. Ein ausflug nach Triest und dem Quarnero. Berlin: Nicolaische Verlagsbuchhandlung, pp. 109-115.
- Illgen H. 1916. Zur Kenntnis der Biologie und Anatomie der parasitischen Rotatorien-Familie der Seisoniden. *Zool. Anz.* **47**: 1-9.
- Koste W. 1975. Das Rädertier-Porträt. *Seison annulatus*, ein ectoparasit des marinen Krebses *Nebalia*. *Mikrokosmos* **75**: 341-347.
- Leung YM, JL Mohr. 1969. On the chonotrich ciliates, the rotifer *Seison* and other animals living on *Nebalia* in far southern waters. Symposium on Antarctic Oceanography, 1966. Cambridge, UK: W Heffer and Sons, pp. 72-73.
- Mark Welch DB. 2000. Evidence from a protein-coding gene that acanthocephalans are rotifers. *Invertebr. Biol.* **119**: 17-26.
- Markevich GI. 1993. SEM observations on *Seison* and phylogenetic relationships of the Seisonidea (Rotifera). *Hydrobiologia* **255/256**: 513-520.
- Melone G, C Ricci, H Segers, RL Wallace. 1998. Phylogenetic relationships of phylum Rotifera with emphasis on the families of Bdelloidea. *Hydrobiologia* **387/388**: 101-107.
- Menzies RJ, JL Mohr. 1952. The occurrence of the wood-boring crustacean *Limnoria* and of Nebaliacea in Morro Bay, California. *Wasmann J. Biol.* **10**: 81-86.
- Nogrady T, RL Wallace, TW Snell. 1993. Rotifera: biology, ecology and systematics. In HJF Dumont, ed. *Guides to the identification of the microinvertebrates of the continental waters of the world*, Vol. 4. Amsterdam: SPB Academic Publishing, 142 pp.
- Olesen J. 1999. A new species of *Nebalia* (Crustacea, Leptostraca) from Unguja Island (Zanzibar), Tanzania, East Africa, with a phylogenetic analysis of leptostracan genera. *J. Nat. Hist.* **33**: 1789-1809.
- Pennak RW. 1953. Fresh-water invertebrates of the United States. New York. The Ronald Press, pp. 159-213.
- Pfannkuche O, H Thiel. 1988. Sample processing. In RP Higgins, H Thiel, eds. *Introduction to the study of meiofauna*. Washington, DC: Smithsonian Institution Press, pp. 134-145.
- Plate L. 1887. Über einige ectoparasitische Rotatorien des Golfes von Neapel. *Mitteilungen Zool. Station Neapel* **7**: 234-262.
- Remane A. 1929-1933. Aschelminthes: Rotatoria. In H. G. Bronn, ed. *Klassen und Ordnungen des Tier-Reichs*. Leipzig: Akademische Verlagsgesellschaft, 576 pp.
- Ricci C, G Melone, C Sotgia. 1993. Old and new data on Seisonidea (Rotifera). *Hydrobiologia* **255/256**: 495-511.
- Ruttner-Kolisko A. 1974. Plankton rotifers. *Biology and taxonomy. Binnengewässer* **26(Supplement)**: 1-146.
- Segers H. 1995. A reappraisal of the Scaridiidae (Rotifera, Monogononta). *Zool. Scr.* **24**: 91-100.
- Segers H. 1996. *Scaridium elongatum* n. sp., a new monogonont rotifer from Brazil. *Belg. J. Zool.* **126**: 57-63.
- Segers H. 2002. The nomenclature of the Rotifera: annotated checklist of valid family- and genus-group names. *J. Nat. Hist.* **36**: 631-640.
- Segers H, G Melone. 1998. A comparative study of the trophi morphology in Seisonidea (Rotifera). *J. Zool. (Lond.)* **244**: 201-207.
- Sørensen MV. 2002. On the evolution and morphology of the rotiferan trophi, with a cladistic analysis of Rotifera. *J. Zool. Syst. Evol. Res.* **40**: 129-154.
- Sørensen MV, P Funch, E Willerslev, AJ Hansen, J Olesen. 2000. On the phylogeny of the Metazoa in light of Cyclophora and Micrognathozoa. *Zool. Anz.* **239**: 297-318.
- Van Beneden PJ, CE Hesse. 1864. Recherches sur les Bdellodes (Hirudinées) et les Trématods marins. *Mém. Acad. Royale Belgique* **34**: 1-149, 15 pls.
- Wallace RL, RA Colburn. 1989. Phylogenetic relationships within phylum Rotifera: orders and genus *Notholca*. *Hydrobiologia* **186/187**: 311-318.
- Westheide W, G Purschke. 1988. Organism processing. In RP Higgins, H Thiel, eds. *Introduction to the study of meiofauna*. Washington, DC: Smithsonian Institution Press, pp. 146-160.