Published in collaboration with the University of Bergen and the Institute of Marine Research, Norway

Laonice (Polychaeta, Spionidae) in the Arctic and the North Atlantic

Andrey V. Sikorski

SARSIA

Sikorski AV. 2003. *Laonice* (Polychaeta, Spionidae) in the Arctic and the North Atlantic. *Sarsia* 88:316–345.

Laonice Malmgren, 1867 species from the Arctic and the North Atlantic are revised. Existing types of five species recorded from the area are described. All available material has been used and cited. New approaches to the use of widely varying and size-related numeric characters are put into practice. Eight species of the genus *Laonice* were found: *L. appelloefi, L. bahusiensis, L. blakei, L. cirrata, L. dayianum, L. norgensis* sp. nov., *L. sarsi* and *L. shamrockensis* sp. nov. Descriptive and nomenclatural confusions among existing species are analysed and, where necessary, such species are redescribed on the basis of an appropriate range of common characters. Lectotypes of *L. bahusiensis* and *L. sarsi* are designated. *Spionides foliata, S. sacculata* and *L. pugettensis* are synonymized with *L. cirrata*. A key for all species recorded from the area is provided.

Andrey V. Sikorski, Zoological Museum, Moscow State University, Bolshaja Nikitskaja 6, 103009 Moscow, Russia.
E-mail: Andrey_Sikorski@mail.ru; andrey.sikorski@akvaplan.niva.no

Keywords: *Laonice*; Polychaeta; taxonomy; regional revision; Arctic; North Atlantic.

INTRODUCTION

This article is the result of more than 15 years of work (Sikorski & Sennikov 1985; Sikorski & al. 1988; Sikorski 1997, 1999) on the taxonomy of the genus *Laonice*. It is a regional (the Arctic and the North Atlantic) revision of the genus. The genus *Laonice* was designated by Malmgren (1867) for the species *Nerine cirrata* Sars, 1851. The genus contained only this species until Söderström (1920) described three new species: *L. appelloefi, L. sarsi* and *L. bahusiensis,* from Swedish and Norwegian waters. These descripions were based chiefly on numeric characters, such as the length of the nuchal organ, the number of pairs of branchiae, the ordinal numbers of the setigers where neuropodial hooded hooks, sabre setae and genital pouches first occur. After a short time, Söderström's species were synonymized with *L. cirrata* (Fauvel 1927). He could not differentiate between his material from Roscoff (France) and the material from Spitsbergen. However, Eliason (1962) and Fauchald (1972) disagreed with this. Eliason recognized *L. sarsi* as a distinct species, as did Fauchald with *L. appelloefi*, but neither author examined variation in the numeric characters. Due to wide variations in numeric characters, Foster (1971) combined all species of the genus into *L. cirrata*. However, such problems did not inhibit other authors from describing new species, although such descriptions were sometimes based on a single widely variable numeric character (Banse & Hobson 1968), which is considered a dubious practice. All authors compared widely variable numeric characters by the intervals of variation in pairs of species (normally they overlap). Such a procedure, however, weakens the significance of the numeric characters. Due to the shortage of clearly distinguishable morphological characters, an attempt to use numeric characters more effectively looks sensible. Hitherto there has been no attempt to increase the significance of numeric characters by examining size-related variation and by comparing each character by the intervals of variation within separate size groups or by using arithmetical differences between quantities of the characters as taxonomic characters. Within the present study area, only three papers (Sikorski & al. 1988; Orrhage & Sundberg 1991; Sikorski 1999) have reviewed the taxonomic situation within the genus following the detailed and formative work of Söderström (1920). Sikorski & al. (1988) compared *L. cirrata* and *L. sarsi* and moved *L. annenkovae* into the genus *Marenzelleria*, but these authors still synonymized *L. bahusiensis* with *L. cirrata*. Orrhage & Sundberg (1991) compared *L. sarsi* and *L. bahusiensis*. All known specimens of *L. appelloefi* were examined in Sikorski (1999). Hitherto, definitive published taxonomic descriptions, allowing adequate specific identification of the material collected in recent years, have not been available. One of the problems in previous studies was the geographically limited range of material available. Researchers were not able to see and compare material on several species simultaneously. The main goal of the present work is to prepare suitable and full descriptions that reflect the

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DOI 10.1080/00364820310002551

most taxonomically useful characters for each recorded species.

MATERIAL AND METHODS

All Russian material was examined, together with several Danish, Swedish, Norwegian, American and Spanish collections. The material comprised a total of 611 samples and 1573 specimens.

Five numeric characters normally used in taxonomic descriptions (numbers 1–5) and two not so frequently mentioned (numbers 6 and 7) were used:

1. Setiger with first neuropodial hooded hooks (HH).
2. Last setiger with nuchal organ (NO).
3. Last setiger with branchiae (Br).
4. Setiger with first occurrence of sabre setae (SS) ("genital spines" of Orrhage & Sundberg 1991).
5. Setiger with first occurrence of genital pouches (GP).
6. Number of hooded hooks per neuropodium (QHH).
7. Number of sabre setae per neuropodium (QSS).

Linear correlation tests were carried out to determine any relationships between the above characters and the size of the individual. A size-related character means that its coefficient of linear correlation is reliably different from 0 at a significance of $\leq 1\%$. Nearly all of these characters are size related (only GP sometimes does not show a clear correlation with size) and many of them vary widely. Therefore, it is considered useful to compare certain characters between a pair of species within a certain size group, rather than within the species as a whole. Looking for additional characters brought us to using differences between some pairs of numeric characters, e.g. last setiger with nuchal organ and last setiger with branchiae (NO–Br) or first setiger with hooded hooks and last setiger with nuchal organ (HH–NO) as independent taxonomic characters. The width of the worms was used as a characteristic of size. Following Söderström (1920), we measured the width of the body (minus parapodia) at setiger 7 (the width at the level of setigers 7–12 was measured only in the case of *L. appelloefi*).

All scanning electron microscope (SEM) photographs were made to show the external morphology of the anterior ends of the specimens, the middle parts (ends of nuchal organs and caruncles) with or without dorsal transverse membranes, the pygidium with ventromedial cirrus (first time recorded for the genus) and the hooded hooks. For SEM studies, the specimens were dehydrated in a critical point drier, attached to a stub and sputter coated with gold palladium. SEM observations were made with a Zeiss DSM 960A.

The following acronyms are used in the paper: ZMUM, Zoological Museum, Moscow State University, Russia; ZISP, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia; IORAS, P. P. Shirshov Institute of Oceanology, Russian Academy of Sciences, Moscow, Russia; SMNH, Swedish Museum of Natural History, Stockholm, Sweden; UUZM, Zoological Institution of Uppsala University, Sweden; USNM, National Museum of Natural History, Smithsonian Institution, USA; UBZM, Zoological Museum of the University of Bergen, Norway; ZMUC, Zoological Museum, University of Copenhagen, Denmark; TM, Tromsø Museum, Norway; AKV, Reference collection at Akvaplan-niva AS, Tromsø, Norway; SFGM, private collection of S. F. Garcia-Martín, University of Cadiz, Spain.

SYSTEMATICS

Laonice Malmgren, 1867 (emended)

Prostomium anteriorly rounded or with slight incurvation, T-shaped or sometimes skittle-shaped, often fused with peristomium at anterior angles. Adults with zero to three pairs of eyespots. Occipital tentacle present (absent in *L. brevicristata* Pillai, 1961 and *L. dayianum* Sikorski, 1997). Caruncle well developed, long, extending posteriorly over several setigers. Palps without sheath at base. Nuchal organ following caruncle appearing as four uninterrupted ciliary stripes along several anterior setigers closed posteriorly, thus appearing as a pair of long loops starting from the place of attachment of palps. Peristomium not fused with setiger 1. Setae arranged in two vertical rows on parapodia, sometimes capillaries of most anterior setigers arranged in more than two rows in several species. Parapodia with superior tufts of longer, thinner capillaries in notopodial and inferior tufts situated below and apart from main neuropodial fascicles. Inferior tufts appearing in anterior part of body. Setae in this fascicle, traditionally called "sabre setae" ("Haarborsten" in Söderström 1920), similar to ordinary capillaries but sometimes longer or stouter. Neuropodial hooks with primary hood only, absent in notopodia (notopodial hooded hooks in most posterior setigers in *L. sarsi* only). Hooks in neuropodia without alternating neuropodial capillaries. Branchiae from setiger 2, separated from notopodial post-setal lamellae, present on some anterior segments. Genital pouches present on a various number of anterior setigers. Anus terminal, surrounded by two small ventral papilliform cirri usually closely arranged and with several pairs of comparatively long dorsal anal cirri, sometimes with cirriform ventral-most medial appendage positioned between ventral cirri. Worms usually without pigment.

Type species: *Nerine cirrata* M. Sars, 1851 (by monotypy).

Laonice appelloefi Söderström, 1920

Figs 1A–D, 2A

Laonice appelloefi Söderström, 1920:225–227, figs 131, 132.

Laonice appelloefi – Fauchald 1972:98–99, fig. 3B; Sikorski 1999:1465–1467, figs a–d.

Type locality

Hjeltefjord, 60°32′N 4°34.5′E.

Material examined

HOLOTYPE (cut into two halves in sagittal plane): Hjeltefjord, 60°32′N 4°34.5′E, coll. A. Appellöf, Stn 30. Right half dissected into 27 separate parapodia kept in four slides [UUZM 347a (1–8), 347b (9–16), 347c (17–24), 347d (25–27)]. Left half fixed in ethanol (UBZM 18649). Additional material (Fauchald 1972): Sognefjord S. For Raudberg lokt., 03.05.1966, 1248–1228 m, 61°03′N 5°24′E, Stn S1, coll. T. Brattegard, det. K. Fauchald (1 specimen, UBZM 53367); Sognefjord SW. For Raudberg lokt., 03.05.1966, 1224 m, 61°03′36″N 5°22′36″E, coll. T. Brattegard, det. K. Fauchald (7, UBZM 53368); Sognefjord SW. For Vadheimsfjord, 04.05.1966, 1272 m, 61°08′15″N 5°45′30″E, Stn S3 (6.1), coll. T. Brattegard, det. K. Fauchald (3, UBZM 53369).

Description

HOLOTYPE: anterior fragment with 27 setigers, 1.2 mm wide. HH = 19, QHH = 10, NO = 13; Br = 24; SS = 13; GP = 7 (genital pouches absent after setiger 13). All material examined: up to 2.2 mm wide at setigers 7–12.

Prostomium almost triangular (Fig. 1A). Anterior margin of prostomium truncated or slightly rounded, sometimes slightly incurved, not fused with peristomium at anterior angles. Two pairs of deeply imbedded eyespots, trapeziformly arranged with posterior pair more closely spaced (sometimes only anterior pair visible). Occipital tentacle well developed. Caruncle with nuchal organ extending posteriorly to setigers 8–14. Palps lost in examined material. Anterior 12–15 setigers twice as wide as subsequent segments.

Branchiae as long as notopodial post-setal lamellae at setiger 2; increasing to a maximum length of twice that of the notopodial lamellae over the subsequent three to four segments. Branchiae continuing posteriorly to setigers 23–24 (data for three specimens).

Notopodial post-setal lamellae of anterior seven to eight setigers narrowed dorsally into pointed tips (Fig. 1A). Becoming rounded in subsequent branchial segments, with the pointed tips on the upper lateral margin of lamellae (Fig. 1B, C). Poor condition of material does not allow a description of notopodial lamellae in post-branchial region. Pre-setal lamellae most prominent from setiger 2 to 15; but may present posteriorly up to setiger 30.

Neuropodial post-setal lamellae of seven anterior setigers with pointed tips dorsally; subsequent segments with pointed tips on lateral margins of lamellae. Neuropodial lamellae rounded at the beginning of post-branchial region (Fig. 1B, C). Dorsal transverse membranes connecting bases of notopodial post-setal lamellae inconspicuous. Very low and medially incomplete crests in one specimen at most posterior branchial and on several subsequent segments.

Genital pouches first appearing on setigers 5–7 (normally, on different segments in right and left sides of same worm). Individuals with one to 10 pairs of pouches, continuing to setigers 7–15.

Noto- and neuropodial capillaries arranged in more than two vertical rows per fascicle (up to four to five) varying from setiger 1 to 4; in two rows from setiger 9 to 18. Neuropodial hooded hooks first appearing from setiger 18 to 23, up to seven to 10 per fascicle; hooks tridentate, main fang surmounted by pair of large apical teeth; clearly visible in nearly every slide (Fig. 1D). Sabre setae from setiger 11 to 13, four to six per fascicle at first appearance, reduced to only two after five to six segments. Notopodial hooks not found. Pygidium unknown.

Worms without pigment.

Methylene green

Anterior part of prostomium and lateral lobes of peristomium are the most intensively stained by methylene green.

Distribution (Fig. 2A)

Two W Norwegian fjords at the border between the North Sea and the Norwegian Sea: Hjeltefjord and Sognefjord.

Remarks

This species is very close to *L. nuchala* Blake, 1996 by the presence of genital pouches on several segments (not to the end of body), by having a comparatively short nuchal organ only slightly varying in length and by having the anterior capillaries arranged in more than

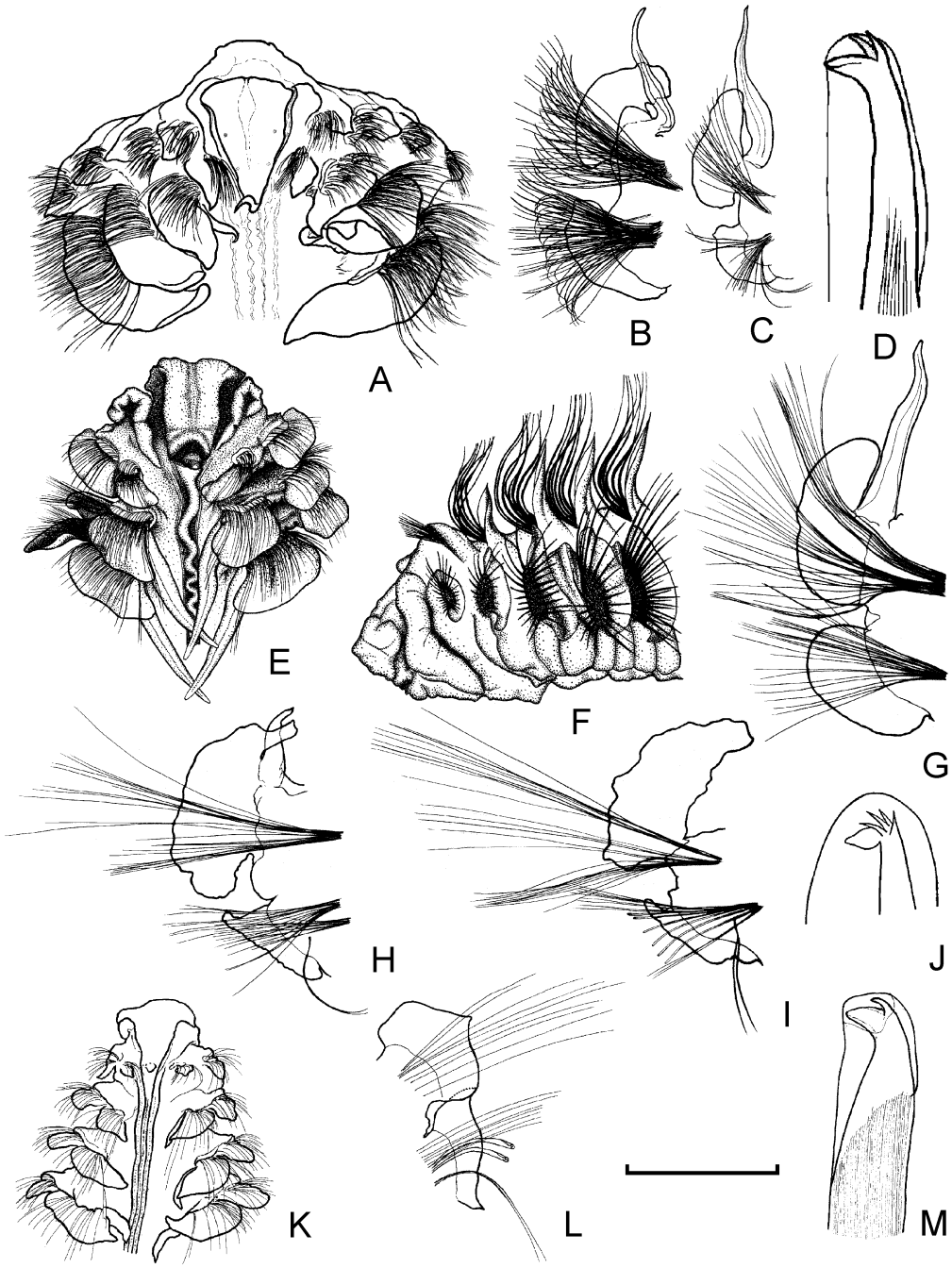

Fig. 1. *Laonice appelloefi* Söderström, 1920. A. Anterior end, dorsal view. B. Right parapodium, setiger 12. C. Right parapodium, setiger 15. D. Hooded hook, setiger 27. *Laonice blakei* Sikorski & al., 1988. E. Anterior end, dorsal view. F. Anterior end, side view (appearance of genital pouches). G–I. Right parapodia, setigers 9, 21 and posterior part of body. J. Top of hooded hook, setiger 26. *Laonice dayianum* Sikorski, 1997. K. Anterior end, dorsal view. L. Left parapodium, setiger 38. M. Hooded hook, setiger 41. Material: A, B. UBZM 53368. C. UUZM 347b-15. D. UUZMd-27. E, F. ZMUM Pl 839. G–I. ZMUM Pl 947. J. ZMUM Pl 746. K–M. USNM 169827. Scales (mm): A = 1.0; B, C = 1.35; D = 0.0027; E, F = 1.5; G–I = 0.6; J = 0.03; K = 1.2; L = 0.5; M = 0.025.

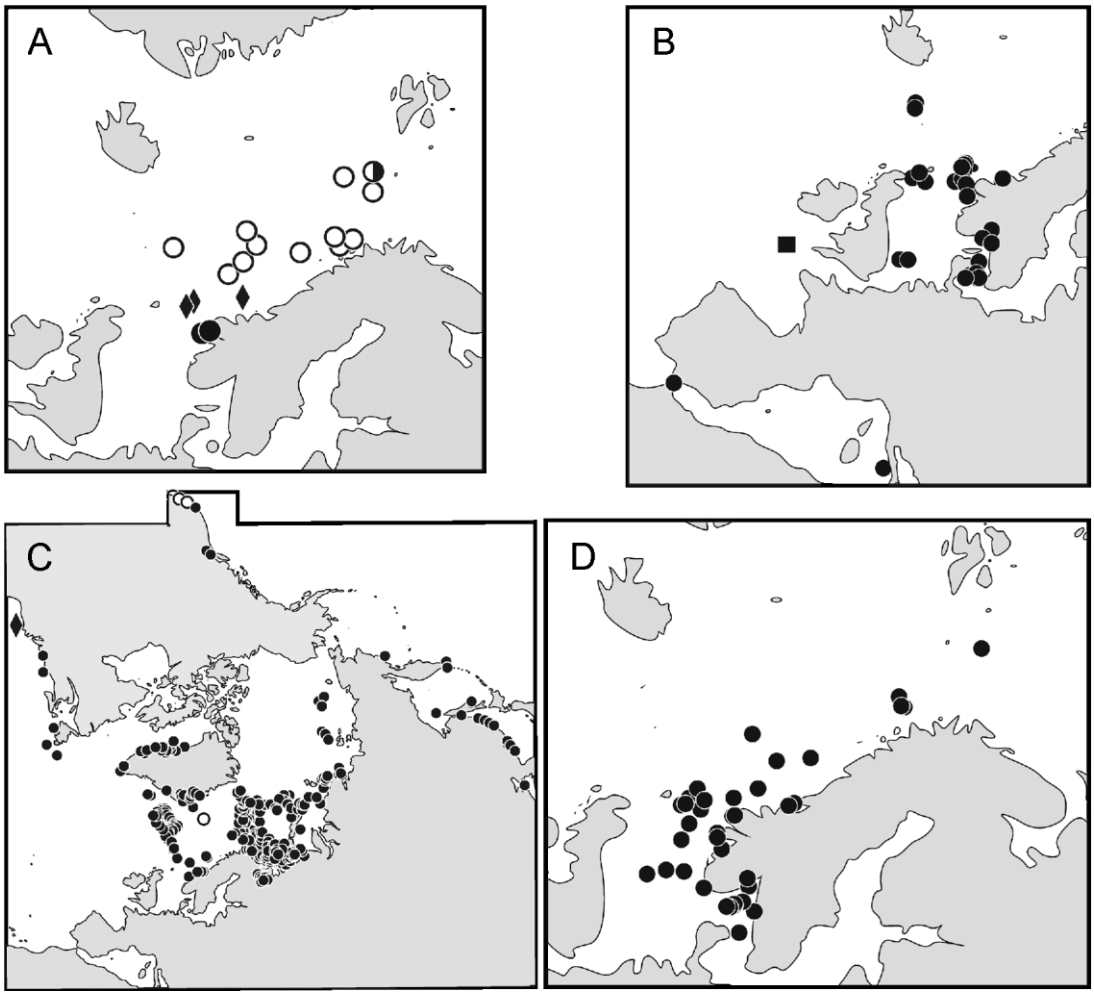

Fig. 2. Maps of samples examined. A. *Laonice appelloefi* Söderström, 1920 (filled circles), *L. blakei* Sikorski & al., 1988 (hollow circles; half-filled circle – literature data), *L. norgensis* sp. nov. (rhombuses). B. *Laonice bahusiensis* Söderström, 1920 (filled circles), *L. shamrockensis* sp. nov. (square). C. *Laonice cirrata* (filled circles – material examined; hollow circles – literature data), *L. dayianum* Sikorski, 1997 (rhombus). D. *Laonice sarsi* Söderström, 1920.

two rows. However, the neuropodial hooks of *L. nuchala* have a completely different shape. *Laonice appelloefi* is also similar to *L. sarsi* in having a limited number of genital pouches and a short nuchal organ. On the other hand, *L. sarsi* has only two rows of anterior capillaries and many more genital pouches. *Laonice blakei, L. norgensis* sp. nov. and *L. weddellia* Hartman, 1978 also have anterior capillaries arranged in more than two rows, but they have a longer nuchal organ. Moreover, *L. appelloefi* has a very characteristic anterior widening of the body.

Laonice bahusiensis Söderström, 1920

Figs 2B, 3A–I, 4A, B, 5A, B, 6F

Laonice bahusiensis Söderström, 1920:4–7, 81–83, 93, 98, 99, 110, 114, 128, 134, 195, 223, figs 78–82.

Scolecolepis cirrata. – ? Möbius 1874:260; ? McIntosh 1915:164 (see Söderström 1920:223).

Spio cirratus – Levinsen 1893:334 (part).

Laonice sarsi Söderström, 1920:223–225, figs 129, 130 (part – see material examined: two specimens in syntypes of *L. sarsi*, UBZM 18645).

Laonice bahusiensis – Orrhage & Sundberg 1991:173–

178, tables 1, 3, 5, figs 1b, c, 2, 4; Sikorski 2002:413–417, fig. 4.
Aonides oxycephala – ? Ditlevsen 1925:328 (non M. Sars 1862).
Laonice cirrata – Ditlevsen 1929:29; Wesenberg-Lund 1951 (part):69, fig. 6; Hannerz 1956:23–26, fig. 6 (part); Boisen-Bennike 1968:4; Kirkegaard 1969:76, fig. 40 (part) (non M. Sars 1851).

Type locality

W Sweden, Bohuslän, Gullmarfjord.

Material examined

Forty samples and 158 specimens.

Type material

LECTOTYPE (newly designated): W Sweden, Bohuslän, Gullmarfjord (approximately 58°15′N 11°00′E), Zool. Stn 1893 (SMNH 4637). PARALECTOTYPES: W Sweden, Bohuslän, Gullmarfjord, Gesö Ränna ("Trekanten"), coll. A. Wirén (4 specimens, UUZM 153c); W Sweden, Bohuslän, Gullmarfjord, Gesö Ränna ("ausserhalb Blebergsholmen"), 1897, coll. A. Wirén, 10% formol. (7, UUZM 153d); W Sweden, Bohuslän, Gullmarfjord, Norra Flatholmsrännan, coll. A. Wirén (23, UUZM 153f); same (2, ZMUM Pl 972, gift from UUZM 153f, through Dr Lars Walin); W Sweden, Bohuslän, Gullmarfjord, Flatholmen, ruttnande botten, chrom. osm. ättiks, coll. A. Wirén 1887 (36, UUZM 153g); W Sweden, Bohuslän, Gullmarfjord, Zool. Stn 1884, ? coll. A. Wirén (10, SMNH 4638); Kosterfjorden (Sneholmen), 150–50 m, Schlamm, fix. $MgSO_4$ and formol., coll. I. Arwidsson 22.08.1901 (1, SMNH 4636).

Additional material

Norwegian Sea: Vågsøy, 62°00′52.4″N 5°09′37″E, 26 m, sandy bottom, 03.09.1996 (3, ZMUM Pl 1035); Faroes: Trangisvaag, RV *Dana*, Stn 2559, 61°33′N 6°45′W, 58 m, coll. R. Spärck, 31.05.1926 (2, ZMUC POL 757). SE corner of Kuno Isl., RV *Dana*, Stn 15, 62°14′N 6°35′W, 10–15 m, very coarse stones (broken), coll. P. Kramp, 21.09.1926 (1, ZMUC POL 756). Border between Norwegian and North Seas, W Norway: Hjeltefjord, 60°27′N 5°02′E, Stn 28, 30–33, 42, 43, coll. A. Appellöf (2, with syntypes of *L. sarsi*, UBZM 18645). North Sea: W Sweden, Gullmarfjord, coll. A. Wirén, summers 1921 and 1922 (2, UUZM 1860 and 1861). Kosterfjord, Styrsö, coll. A. Wirén, 1889 (1, UUZM 4945). Frigg Field, Stn 15, 59°52′58″N 2°04′58″E, 99 m, coll. Akvaplan-niva (Tromsø), 13.05.1992 (1, AKV). Lille Frigg 2 Field, Stn 20, 59°58′03″N 2°24′05″E, 111 m, 09.05.1992 (1, AKV). Oseberg Øst Field, Stn 2, 60°42.22′N 2°56.54′E, 156 m, 17.05.1997 (1, ZMUM Pl 880). Frøy Field, Stn 13, 59°44′N 2°33.24′E, 20 m, 01.06.1997 (1, ZMUM Pl 882). Lille Frigg Field, Stn 11, 59°57.63′N 2°23.22′E, 114 m, 30.05.1997 (1, ZMUM Pl 882). Heimdal Field, Stn 4, 59°34′33″N 2°13′43″E, 114 m, 16.05.1992 (1, ZMUM Pl 288). RV *Dana*, Stn 2889, 57°37.5′N 11°28.5′E, 85 m, mud, 9.5 °C, 34.76 psu, 10.10.1922 (2, ZMUC POL 758); Stn 7480, 54°07.2′N 2°00′E, 60 m, 07.05.1951 (1, ZMUC POL 759); Stn 8022, 54°13′N 3°00′E, 43 m, 16.05.1952 (10, ZMUC POL 760); Stn 8024, 54°15′N 2°20′E, 35 m, coarse sand, stones, 15.05.1952 (2, ZMUC POL 761). W Sweden, Gullmarfjord, Kristineberg Zool. Stn, 50 m, coll. A. Eliason, 03.06.1966 (3, USNM 43286). W Sweden, Bohuslän, Gullmarfjord, Kristineberg Zool. Stn, 19.08.1924 (3, SMNH 7078); 45–50 m, 04.08.1945 (1, SMNH 8718). W Sweden, Gullmarfjord, Rödbergskär, 58°15′44″N 11°27′07″E, 40–42 m, mud, coll. S. Robertsson, 23.08.1969 (3, ZMUC POL 764). Limfjord: Thistedbredning, Biol. Stn, 23.09.1921 (1, ZMUC POL 763). Kattegat: RV *Hauch*, 8 stns (238, 421, 426, 433, 467, 469, 499, 500), 29–73.5 m, sandy and silty, 5.7–14.9°C, coll. Joh. V. Petersen, 21.08.1885, 1–30.07.1886 (13, ZMUC POL 762). Kattegat off Frederikshavn, Denmark: NE of Hirsholm, 28 m, soft bottom, coll. M. E. Petersen, 18.07.1971 (3, ZMUC POL 751); E of Hirtsholmene, 27.5 m, soft bottom, coll. K. Ockelmann & M. E. Petersen, 13.09.1968 (2, ZMUC POL 752); 27 m, coll. J. B. Kirkegaard, 29.06.1971 (3, ZMUC POL 753); beginning of slope off Frederikshavn, 14–15 m, sandy clay with shell fragments, coll. J. Just & M. E. Petersen, 03.09.1974 (3, ZMUC POL 754); 28 m, soft bottom, coll. K. W. Petersen, 06.07.1968 (1, ZMUC POL 755). Gibraltar: SW Spain, Bay of Algeciras, Stn MB6, 17 m, 22.08.1991, coll. S. F. Garcia-Martin, 1 specimen (SFGM). Tyrrhenian Sea: Gulf of Salerno, Stn EU5, 40°39′N 14°42′E, 24 m, grey sandy mud, 12.1981, coll. M. C. Gambi (3, ZMUC POL 765). ? Unknown locality: det. Söderström (2, UUZM 4944, 4946).

Description

LECTOTYPE: the best specimen with regard to preservation and size, although nearly broken into two fragments; 41 mm long, 1.0 mm wide and 107 setigers. HH = 29, QHH = 8, NO = 26, Br = 31, SS = 19, QSS = 2, GP = 17. Pygidium in poor condition, but apparently with eight long dorsal and two short ventral

cirri. Dorsal transverse membranes from setiger 27 to 47. Eyespots not visible. Tips of notopodial post-setal lamellae from setiger 96 to 103 with some dark pigment. Female with oocytes. PARALECTOTYPES: 70 specimens deposited in UUZM; 11 specimens in SMNH; two specimens in ZMUM.

All material examined: largest complete animal 50 mm long, 1.1 mm wide, with 109 setigers (60 mm long, with 120 setigers according to Söderström 1920). Largest animal 1.6 mm wide.

Prostomium triangular, anteriorly wide, truncated or slightly incurved, sometimes broadly rounded, fused with peristomium at anterior angles, clearly visible in dorsal view (Figs 3A, 5A). Occipital tentacle large. Caruncle well developed, extending together with nuchal organ to setigers 6–35. Juveniles (<0.3 mm wide) with two pairs of eyespots: anterior pair larger and more widely separated, crescent-shaped, seemingly deeper under surface but really hidden on lateral surface of prostomium in groove between prostomium and peristomium. Eyespots in posterior pair in juveniles looking like narrow transverse bars. Anterior and posterior pairs separated by considerable distance. Large specimens with only posterior pair, often extremely bright (reddish brown in live specimens, M. E. Petersen, pers. comm.), forming nearly complete transverse stripe (Fig. 3A).

Palps very rarely retained in preserved specimens; rather short, extending posteriorly to setigers 2–4.

Branchiae 11–36 pairs; first pair shorter than or approximately as long as notopodial post-setal lamellae of setiger 2, all other branchiae usually longer than notopodial lamellae. Branchiae twice as long as notopodial post-setal lamellae usually from setiger 6.

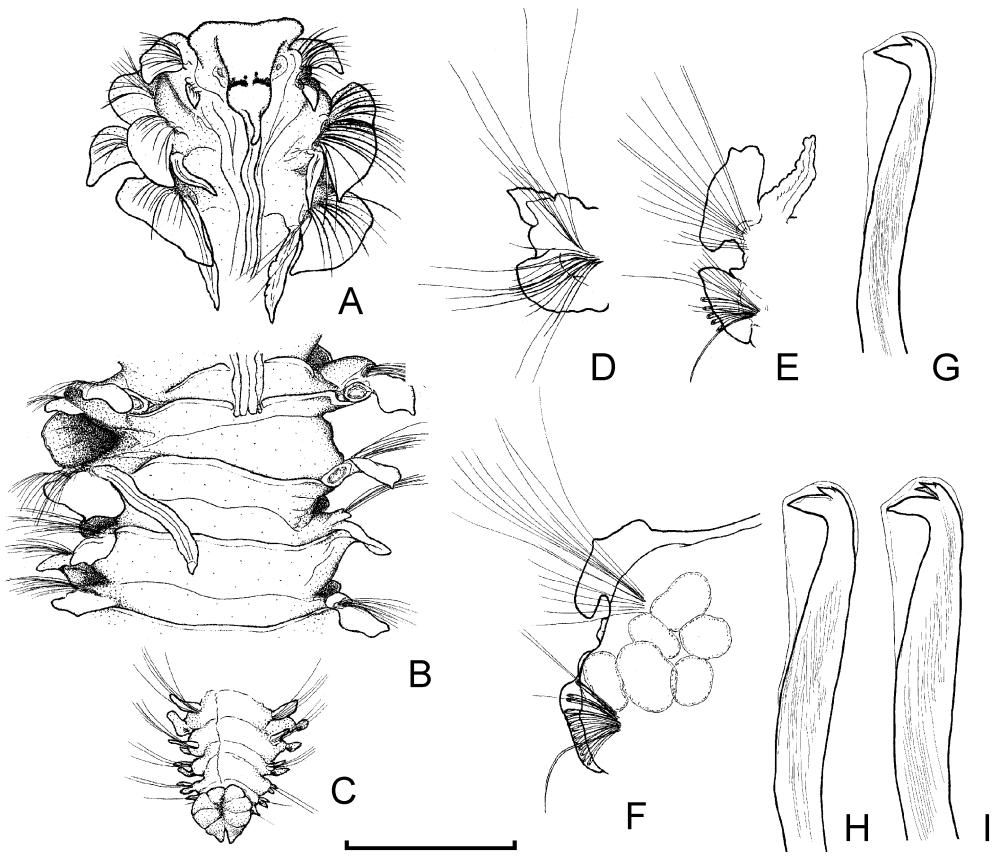

Fig. 3. *Laonice bahusiensis* Söderström, 1920. A. Anterior end, dorsal view. B. Middle setigers at disappearance of branchiae and dorsal sense organ, dorsal view. C. Posterior end, dorsal view (anal cirri absent). D. Right parapodium, setiger 1. E. Right parapodium, setiger 27. F. Right parapodium, setiger 38. G. Inferior hooded hook, setiger 39. H. Middle hooded hook, setiger 39. I. Superior hooded hook, setiger 39. Material: Specimens from the Kattegat (A–G) and North Sea (G–H). A–C, F. ZMUC POL 753. D. ZMUC POL 751. E. ZMUC POL 754. G–I. Specimen from the North Sea (AKV, Frigg Field: Stn 15, 59°52′58″N 02°04′58″E, 99 m, 13 May 1992). Scales (mm): A–C = 1.0; D = 0.33; E–F = 0.8; G–I = 0.068.

Notopodial post-setal lamellae ear-shaped, those of setiger 1 triangular, with acute tips. Notopodial post-setal lamellae projecting considerably above dorsum in branchial region, becoming approximately level with surface of dorsum in post-branchial region. Notopodial lamellae united across dorsum from posterior-most segment carrying nuchal organ or anterior-most post-branchial segment, forming low crests (dorsal transverse membranes – Figs 3B, F, 5B) through a variable number of segments (up to 21). Number of crests not related to size. Dorsolateral margin of notopodial post-setal lamellae in posterior branchial region and several following post-branchial segments forming pronounced small peak (Fig. 3E, F). Lower part of notopodial post-setal lamellae forming inferior appendage through all branchial segments and through majority of following post-branchial segments. Notopodial post-setal lamellae gradually diminishing in size to setigers 18–20 counting from last segment, then sometimes becoming slightly larger and leaf-shaped. Neuropodial post-setal lamellae of branchial segments triangular with pointed tips (Fig. 3E). Neuropodial post-setal lamellae in post-branchial segments gradually diminishing in size, becoming rounded and lower than hooks; increasing slightly in size in last 10–15 segments, like those of notopodia.

Genital pouches first appearing from setiger 6 to 25. Sabre setae from setiger 10 to 21, up to three per fascicle. Hooded hooks from setiger 14 to 35, three to 14 per fascicle (three to five per fascicle for specimens < 0.4 mm wide). Hooks in lower part of neuropodium usually more close-set than ones in upper part. Number of hooks in neuropodium not increasing perceptibly from middle of body to end. Hooks with five teeth (tridentate in side view) with very small upper apical teeth and sometimes hard to see (better seen with "phase contrast"), especially in hooks from inferior part of parapodium (Figs 3G–I, 6F). Pygidium typically with four to seven pairs of long, dorsally arranged cirri (three pairs in juveniles), together with a pair of short, close-set ventral cirri (or lobes) forming ring around anus. Long cirri commonly absent or lost and only cirrophores visible (Fig. 3C). Ventral cirri of juveniles further apart than those of adults.

Worms without pigment.

Methylene green

Usually provides a distinct staining pattern on tips of notopodial post-setal lamellae from setiger 4–5 up to 6–12. Rest of body has a more or less diffused staining pattern.

Distribution (Fig. 2B)

Known only from the NE Atlantic: from the Mediterranean Sea to the S Norwegian Sea (Vågsøy) and Faroe Islands, 10–200 m; nearly all kinds of sediments, but more frequently from silty sand to silt.

Remarks

HH: 14–35; QHH: 3–14; NO: 6–35; Br: 12–37; SS: 10–21; QSS: 1–3; GP: 6–25; HH–NO: −3 to 9; HH–Br: −6 to 4; HH–SS: − 2 to 24; HH–GP: 5–22; NO–Br: −11 to 2; NO–SS: −8 to 24; NO–GP: 0–22; Br–SS: 2–26; Br–GP: 5–20; SS–GP: −9 to 12.

The following characters show a strong relationship to size (width; Table 1): HH, NO, Br, GP, SS, HH–NO (Fig. 4A), HH–SS, NO–Br (Fig. 4B), NO–SS, NO–GP, Br–SS, plus QHH and QSS. Only the relationship between HH–NO (Table 1; Fig. 4A) and size is negative. The range in variation for all size-related characters for all size groups is given in Sikorski (2002).

A lectotype was established from the syntype series originally labelled by A. Söderström. The complete specimen established as the lectotype was in comparatively good condition demonstrating all taxonomically valuable characters such as: HH, NO, Br, the presence of dorsal transverse crests, and the shape of post-setal lobes along the whole body. Also, several specimens of *L. bahusiensis* contained in the original type material of *L. sarsi* motivated the designation of the lectotype.

Laonice bahusiensis is extremely close to *L. cirrata*

Table 1. *Laonice bahusiensis.* Ranges of variation for size-related characters.

Character	Range of variation	r	n	$r_{1\%}$
HH	14–35	0.794	117	0.240
QHH	3–14	0.589	99	0.258
NO	6–35	0.785	115	0.241
Br	12–37	0.697	114	0.244
SS	10–21	0.592	145	0.213
GP	6–25	0.651	145	0.213
HH–NO	−3 to 9	−0.406	114	0.244
HH–SS	−2 to 24	0.533	117	0.240
NO–Br	−11 to 2	0.622	113	0.244
NO–SS	−8 to 24	0.626	115	0.241
NO–GP	0–22	0.569	115	0.241
Br–SS	2–26	0.486	114	0.244

r, coefficient of correlation; n, size of statistical sample; $r_{1\%}$, critical quantity of r, at significance 1%.
HH – Setiger with first neuropodial hooded hooks; NO – Last setiger with nuchal organ; Br – Last setiger with branchiae; SS – Setiger with first occurrence of sabre setae; GP – Setiger with first occurrence of genital pouches; QHH – Number of hooded hooks per neuropodium.

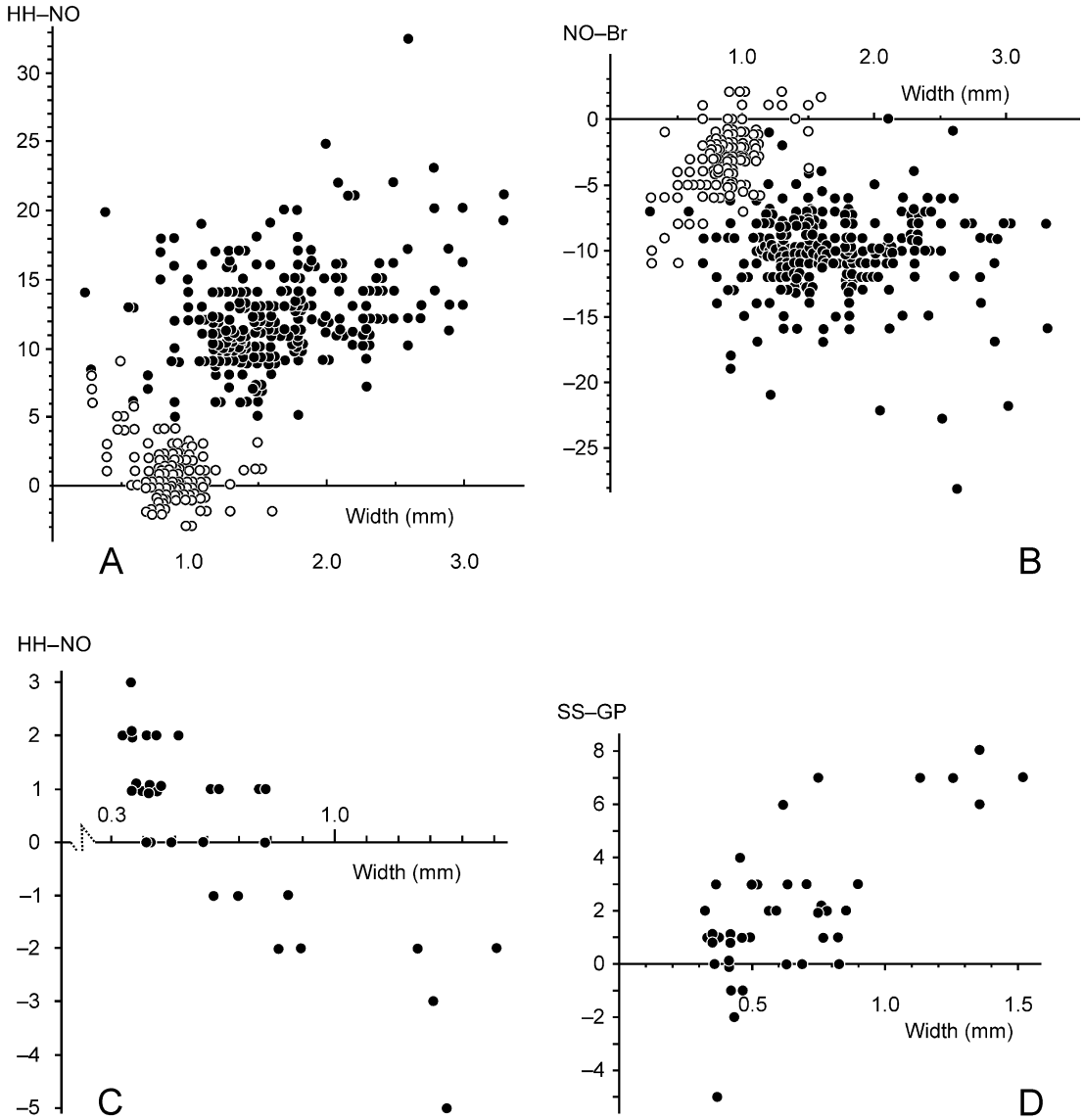

Fig. 4. A. The relationship between HH–NO and width for both *Laonice cirrata* (Sars, 1851) (filled circles) and *L. bahusiensis* Söderström, 1920 (hollow circles). B. The relationship between NO–Br and width for *L. cirrata* (filled circles) and *L. bahusiensis* (hollow circles). C. *Laonice norgensis* sp. nov. The relationship between HH–NO and width. D. *Laonice norgensis* sp. nov. The relationship between SS–GP and width.

morphologically, but differs from *L. cirrata* in the following characters:

1. The presence of complete dorsal transverse membranes joining bases of notopodial post-setal lamellae in the very last branchiate and several following segments.
2. HH–NO: 5–23 in *L. cirrata* and −3 to 9 in *L. bahusiensis* (Fig. 4A).
3. NO–Br: −23 to 0 in *L. cirrata* and −11 to 2 in *L. bahusiensis* (Fig. 4B).
4. Methylene green staining pattern: *L. bahusiensis* has more intensive staining in the tips of notopodial post-setal lamellae from setiger 4–5 to 7–12 in every case;

L. cirrata has more intensive staining in the tips of notopodial post-setal lamellae from setiger 3–4 to 6–11 only in worms < 0.8 mm width (but very rarely in worms > 0.4 mm wide).

5. The shape of neuropodial hooded hooks: usually only *L. bahusiensis* has two pairs of apical teeth (Figs 3G–I, 6F; these are usually easy to see under a light microscope, especially in hooks from the superior part of the neuropodium); but extremely rarely, hooks of *L. cirrata* form a very small second pair of apical teeth. Apical teeth of *L. cirrata* are paired but rather closely arranged (Fig. 6G; see also Sikorski & al. 1988).
6. The last 18–20 notopodial post-setal lamellae and 10–15 neuropodial post-setal lamellae of adults in *L. bahusiensis* sometimes become slightly larger than the preceding ones, and taking the usual leaf-like shape. This is not the case for *L. cirrata*.

Biology

Oocytes oval. Specimens from the middle of the North Sea, collected mid-May 1952 (ZMUC POL 760), had mature oocytes up to 0.27 mm greatest diameter. Other specimens with mature oocytes 0.225–0.250 mm greatest diameter were obtained from Kattegat from July to September in different years (ZMUC POL 752, 762). The smallest specimen (0.28 mm wide) was obtained in the northern part of Kattegat (13.09.1968); slightly larger specimens (0.3 and 0.38 mm wide) from the same area were collected (18.07.1971). Round short-headed type sperm were found in the body cavity in specimens collected in the Gullmar Fjord (23.08.1969). Hannerz (1956) mentioned two spawning periods in the Gullmar Fjord (January to beginning of February and August to September, with occasional specimens spawning in October and November) for the species identified by him as *L. cirrata*, but was unable to find morphological differences between the larvae. There are two species of *Laonice* known from the Gullmar Fjord – *L. bahusiensis* and *L. sarsi* (see Fig. 2B, D).

Laonice blakei Sikorski & Jirkov, 1988 in Sikorski & al. 1988

Figs 1E–J, 2A

Laonice blakei Sikorski & Jirkov, 1988 in Sikorski & al. 1988:830–831, fig. 1; Detinova 1997:121.

Type locality: 72°50′N 14°00′E, 960 m.

Material examined

Fifteen samples, 42 specimens.

Type material

HOLOTYPE: RV *Tunets*, Cruise 105, Stn 16, 72°50′N 14°00′E, 960 m, silt, stones, −0.96 °C, 34.91 psu, 30.06.1978, coll. I. A. Jirkov (ZMUM Pl 746); PARATYPES: RV *Tunets*, Cruise 105, Stn 16 (1 specimen, ZMUM Pl 839), (1, ZMUC POL 945), (1, SMNH 4669); RV *Alaid*, Cruise 30, Stn 5, 72°50′N 10°30′E, 2130–2140 m, −0.9°C, 24.06.1978, coll. I. A. Jirkov (6, ZMUM Pl 939); RV *Sevastopol*, Cruise 5, Stn 1054, 65°43.3′N 4°10′E, 1300 m, clayey silt, −0.9°C, 10.07.1957, coll. L. A. Rittich (1, ZMUM Pl 940); RV *Sevastopol*, Cruise 8, Stn 1351, 69°39.6′N 15°10.7′E, 2198 m, silt, Foraminifera, 23.03.1958, coll. L. A. Rittich (1, ZMUM Pl 941); RV *Sevastopol*, Cruise 8, Stn 1360, 66°57.1′N 4°30′E, 1305 m, clayey silt, Foraminifera, −0.84°C, 34.90 psu, 26.03.1958, coll. L. A. Rittich (1, ZMUM Pl 942); RV *Sevastopol*, Cruise 10, Stn 1705, 67°19.9′N 2°07′E, 1385 m, clayey silt, −0.91°C, 34.88 psu, 27.09.1958, coll. L. A. Rittich (1, ZMUM Pl 943); RV *Sevastopol*, Cruise 10, Stn 1742, 64°34′N 2°50.8′E, 2510 m, clayey silt, −0.94°C, 34.94 psu, 08.10.1958, coll. L. A. Rittich (5, ZMUM Pl 944); RV *Sevastopol*, Cruise 10, Stn 1760, 63°21.4′N 4°35.1′W, 2500 m, −0.94°C, 34.92 psu, 14.10.1958, coll. L. A. Rittich (4, ZMUM Pl 945).

Additional material

RV *Tunets*, Stn 105.6, 68°00′N 10°00′E, 930–1010 m, −0.96°C, 34.91 psu, silty sand, stones, 15.06.1978 (1, ZMUM Pl 946); RV *Johan Ruud*, Stn 1203, 69°30.4′N 14°29′E, 2450 m, 23.08.1982 (14, TM no number), (1, ZMUM Pl 947); RV *Johan Ruud*, Stn 1221, 69°56.5′N 16°00′E, 2100 m, 27.08.1982 (3, TM no number).

Description

Up to 1.2 mm wide (holotype). All worms incomplete. Longest specimen has 40 setigers. Prostomium bell-shaped. Anterior margin broadly rounded, truncated or slightly incurved, not fused with peristomium at anterior angles (Fig. 1E). Occipital tentacle large. Caruncle well developed, extending together with nuchal organ to setigers 10–14. No eyespots. Palps absent in all specimens examined. Branchiae 20–24 pairs. First pair approximately twice as long as notopodial post-setal lamellae of setiger 2. Branchiae on setiger 3 approximately 1.5 times longer than notopodial post-setal lamellae (due to enlarging of lamellae). Anterior branchiae longest (their length equal to body width). Posteriorly they diminish gradually. Last branchiae hardly visible, lower than notopodial lamellae. Branchiae of last five pairs fused

basally to notopodial lamellae (Fig. 1H). Notopodial post-setal lamellae broad; no acute tips. They narrow at top after appearance of sabre setae. Notopodial post-setal lamellae very tall even in posterior part of body (Fig. 1I). Dorsal transverse membranes connecting notopodial post-setal lamellae on last branchial segments, sometimes visible on several post-branchial segments. Upper parts of notopodial post-setal lamellae erect on anterior 12–14 setigers, with rounded tips. Posteriorly they fold downwards. Neuropodial post-setal lamellae broadly rounded anteriorly, narrow with an upper finger-like appendage (Fig. 1H, I) after setigers 12–16. Genital pouches from setiger 3 (Fig. 1F) on each segment to setigers 7–17. These present irregularly or absent afterwards.

Noto- and neuropodial capillaries arranged in three rows per fascicle from setiger 1–3 to 9–12; fascicles not very dense. Appearance of sabre setae from setiger 10 to 13, two per fascicle at first, four to five per fascicle three segments after, usually one after appearance of neuropodial hooks. Sabre setae long with thin tips, but at their base sabre setae two to three times thicker than hooks. Neuropodial hooks from setiger 15 to 23, nine to 22 per fascicle. Hooks with four to six teeth in side view; apical teeth usually paired. Notopodial hooks not found. Long, thin capillary setae in upper part of notopodium occurring with appearance of neuropodial hooks. Pygidium unknown.

Worms unpigmented.

Methylene green

No specific staining in methylene green, only microscopic glands in branchiae stained more intensively. Staining occurs most persistently on outward margins of notopodial post-setal lamellae and branchiae from setiger 10 to 22.

Distribution (Fig. 2A). Norwegian and Greenland Seas; 930–2510 m; soft and mixed bottom; from −0.96 to −0.84 °C.

Remarks

Laonice blakei differs from most *Laonice* taxa in the shape of the hooks that resemble those found in *Prionospio*; it also shows a quite unique absence of variation in GP.

Laonice cirrata (M. Sars, 1851)

Figs 2C, 4A, B, 5C, D, 6G, 7A–G

Nerine cirrata Sars, 1851:207, 208.

Nerine cirrata – Sars 1862:64, 65 (part – "Vadsö sample", rest = *L. sarsi*; see Söderström 1920:221).

Nerine cirrata – Danielssen 1859:118; 1861:52.

Scolecolepis cirrata – Malmgren 1867:91.

Spio cirrata – Ditlevsen 1914:704.

Laonice cirrata – Söderström 1920:4, 5, 7, 81, 97, 98, 110, 220–223, figs 77, 128. – Ditlevsen 1937:29, table 1. – Spärck 1937:40, 41. – Wesenberg-Lund 1950a:30, chart 40; 1950b:75, 76, chart 21, IX, J; 1951:68, 69 (all material cited; but fig. 6 corresponds to *L. bahusiensis* due to complete dorsal transverse membranes), chart 31; 1953:56, 57, chart 12. – Banse & Hobson 1968:24, 25. – Averincev 1977:155. – Sikorski & al. 1988:831–833, fig. 2a–d; Sikorski 2002:406–413, figs 1, 2.

Laonice pugettensis Banse & Hobson, 1968:25–27, fig. 6a. New synonym.

Laonice pugettensis – Blake 1996:112.

Spionides sacculata Moore, 1923:184, 185. New synonym.

Spionides foliata Moore, 1923:182, 183. New synonym.

Non *Laonice cirrata* – Levinsen 1893 (as *Spio cirratus*):334 (= *L. bahusiensis* + *L. sarsi*). – Ditlevsen 1929:29 (= *L. bahusiensis*). – Wesenberg-Lund 1949:323, 324 (= *Laonice* sp.). – Hannerz 1956:23–26, fig. 6 (= *L. bahusiensis* + *L. sarsi*). – Hartmann-Schröder 1965:204, 205, figs 191, 192 (= *Laonice* sp.). – Boisen-Bennike 1968:4 (= *L. bahusiensis*). – Kirkegaard 1969:76, fig. 40 (= *L. bahusiensis* + *L.sarsi*); 1983:596 (= *Laonice* sp.). – Day 1973:76 (= *Laonice* sp.).

Type locality

Hammerfest (new designation).

Material examined

Four hundred and seven samples with 936 specimens. ATLANTIC OCEAN: NW Atlantic: ZMUM Pl 1694–1696: 3 specimens; SMNH 747: 3; USNM 9634: 7. S Greenland: ZMUC POL 779, 805: 7; SMNH 6978: 2. NE Atlantic, S and W Iceland: ZMUM Pl 1734–1737, 1740, 1744: 11; ZMUC POL 780–782, 804, 807–811: 29. Davis Strait: ZMUC POL 774–778, 783, 812–815: 22. Denmark Strait: ZMUM Pl 1747: 1; ZMUC POL 785, 800–803: 25. North Sea at border with Norwegian Sea: UBZM 18647: 10. ARCTIC OCEAN: Baffin Bay: ZMUC POL 750: 1; SMNH 2008, 2009, 2017, 6415, 6416, 6517: 23. Norwegian Sea: ZMUM Pl 1620, 1656, 1657, 1659, 1731–1733, 1738, 1739, 1743, 1745, 1746, 1748–1751, 1753–1756: 45; ZMUC POL 768, 770, 771: 4; UBZM 2153, 2154, 27377: 13; UUZM 1863, 1875: 3. Greenland Sea: ZMUM Pl 1671–1673, 1675, 1676, 1741, 1742: 9; ZISP 56/25629, 57/25630, 62/25635, 104/7936, 124/41899, 125/41902: 7; ZMUC POL 769, 773, 784, 786–799: 42. Greenland (unknown

locality): SMNH 2024: 6. Spitsbergen: SMNH 2020, 2021, 2023, 2025, 2026–2029, 6418–6430: 113. Barents Sea: ZMUM Pl 950, 951, 1095, 1131, 1154, 1326, 1420, 1538, 1583, 1598–1619, 1621–1627, 1629–1655, 1658, 1660–1670, 1674, 1677–1681, 1691–1693, 1697–1700, 1702, 1703, 1710, 1711, 1725–1730, 1752, 1757–1787: 127–250; ZISP 77/25650, 97/7194, 111/13037–113/13039, 5 samples without numbers: 22; SMNH 2022: 1; UBZM 2155: 3. White Sea: ZMUM Pl 1701, 1704–1707, 1709, 1712–1724: 52; ZISP 2/41962, 110/12081, 105/8048, 123/41963: 24. Frantz Joseph Land: ZMUM Pl 907: 2; ZISP 1/25574, 63/25636, 75/25648, 4 samples without numbers: 7. Kara Sea: ZISP 60/25633, 61/25634, 64/25637, 65/25638, 98/7195, 106/8586, 108/8920, 109/9133, 114/13040: 26; ZMUC POL 766: 7. Laptev Sea: ZISP 91/6440–94/6443, 95/6466, 96/6714, 107/8587, 115/14430, 116/14505: 15. E Siberian Sea: ZMUM Pl 1682: 2; ZISP 76/25649, 90/2349: 2. Chukchee Sea (the border with Central Basin): ZMUM Pl 1683–1687: 6. Central Basin: ZMUM Pl 1688–1690: 4; ZISP 58/25631, 59/25632: 4. PACIFIC OCEAN: Bering Sea: IORAS no number: 1. N Kuril Islands: ZISP 99/7361, 102/7364: 2. Okhotsk Sea: ZISP 43/25616, 44/25617, 50/25623: 4. Tataric Strait: ZMUM Pl 1628: 2; ZISP 24/25597, 30/25603, 34/25607, 39/25612, 84/1207: 9. Japan Sea: ZISP 9/25602, 11/25584–13/25586, 15/25588, 16/25589, 18/25591, 19/25592–23/25596, 26/25599, 30/25603–34/25607, 37/25610, 4025613, 42/25615, 66/25639–73/25646, 79/25652–82/25655, 85/1208, 86/1209, 89/1706, 117/37593–121/37640, 132/46985: 91. Yellow Sea: ZISP 2/10362, 9/10369: 3. NE Pacific: San Juan Islands and Puget Sound: USNM 28874, 28875, 36263 (HOLOTYPE of *L. pugettensis*: "Stn 5, Haul 6, 47°10′48″N 122°50′W, 22 m, 12.02.1963″) and 36262 (4 PARATYPES, of *L. pugettensis*): 9; Monterey Bay: USNM 17100 (HOLOTYPE of *S. foliata*: "RV *Albatross* Stn 4549, 56 fms, 07.06.1904"), 17101 (HOLOTYPE of *S. sacculata*: "RV *Albatross* Stn 4525, 222 fms, 26.05.1904″).

A full list of material is available upon request.

Type material

Syntypes; specimens from Hammerfest were in UBZM (Söderström 1920:221), but could not be traced and may have been lost. Syntypes from Ure in Lofoten and Tromsø were in the Zoological Museum, University of Oslo (Söderström 1920:221) but could not be found there.

Description

According to M. E. Petersen (pers. comm.), the largest complete specimen before transfer from formalin to alcohol (a female with oocytes from setiger *Ca* 43) measured 140 mm long and 5 mm wide (with parapodia, without setae) and had 160 setigers (ZMUC POL 816, Pisigsarfik, W Greenland). The largest examined complete animal had 158 setigers and was 126 mm long and 1.7 mm wide (width measured without parapodia). The broadest animal was a short fragment 3.3 mm wide (measurements of numeric characters impossible, not indicated on Fig. 4A, B). Söderström (1920) indicated a width up to 5 mm with parapodia.

Prostomium broadly rounded, considerably fused with peristomium at anterior angles, well visible in dorsal view (Figs 5C, 7A). Caruncle well developed, extending together with nuchal organ to setigers 4–40 (Figs 5C, D, 7A). Juveniles (*Ca* 0.3 mm wide) with two pairs of black eyespots (preserved specimens); anterior pair of small spots set further apart and hidden on lateral surface of prostomium, in groove between prostomium and peristomium; posterior pair large, elliptical, transversely arranged. Anterior and posterior pairs separated by considerable gap. Large specimens with only posterior pair, sometimes very bright black (Fig. 7A), very rarely forming nearly a complete transverse stripe. Sometimes eyespots lacking. Anterior pair of eyespots very rarely in specimens of *Ca* 1 mm wide and larger.

Palps lost as a rule in preserved specimens; when present usually rather long, extending posteriorly to setigers 11–32; sometimes longitudinal folds along the groove poorly developed.

Branchiae to setigers 16–59 may be absent in smallest specimens (0.25 mm wide). Branchiae in first pair shorter than dorsal post-setal lamellae of setiger 2, shorter than or approximately as long as dorsal post-setal lamellae in second pair. All following branchiae longer than dorsal post-setal lamellae as usual.

Notopodial post-setal lamellae of setiger 1 small, with acute or rounded tips (Fig. 7D). Notopodial post-setal lamellae of branchial region ear-like, longer than wide, distal part wider than basal part. Upper part ("earlobe") considerably higher than surface of dorsum in branchial region, becoming lower (i.e. to approximately level with dorsum) in post-branchial region. Dorsolateral margin of notopodial post-setal lamellae in posterior-most branchial and anterior post-branchial segments forming small peak (Fig. 7F). Lower earlobe lower than base of notopodial post-setal lamellae only from posterior-most branchial segments and nearly up to posterior end (Fig. 7F). Posterior notopodial post-setal lamellae not leaf-shaped, no visible increase in size towards posterior end. Notopodial post-setal lamellae not united by membranes (Figs 5D, 7B, F). Extremely rarely, one to two low dorsal transverse

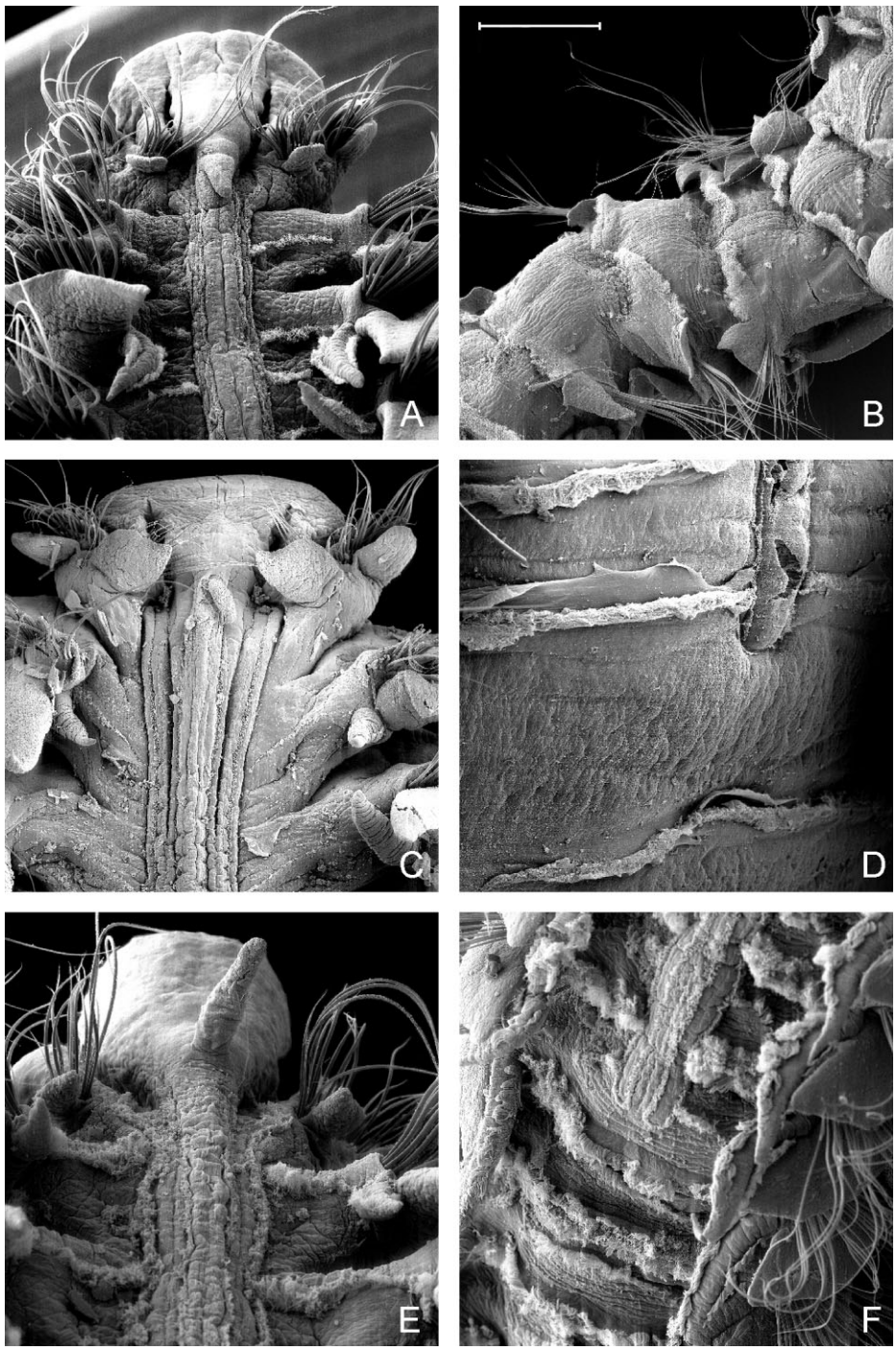

Fig. 5. Scanning electron micrographs. *Laonice bahusiensis* Söderström, 1920. A. Anterior end, dorsal view. B. End of dorsal sense organ; *L. cirrata* (Sars, 1851). C. Anterior end, dorsal view. D. End of dorsal sense organ; *L. norgensis* sp. nov. E. Anterior end, dorsal view. F. End of dorsal sense organ. Material: A, B. S Norwegian Sea. C, D. ZMUM Pl 1131. E, F. S Norwegian Sea. Scales (mm): A, D, F = 0.3; B = 0.4; C = 0.6; E = 0.15.

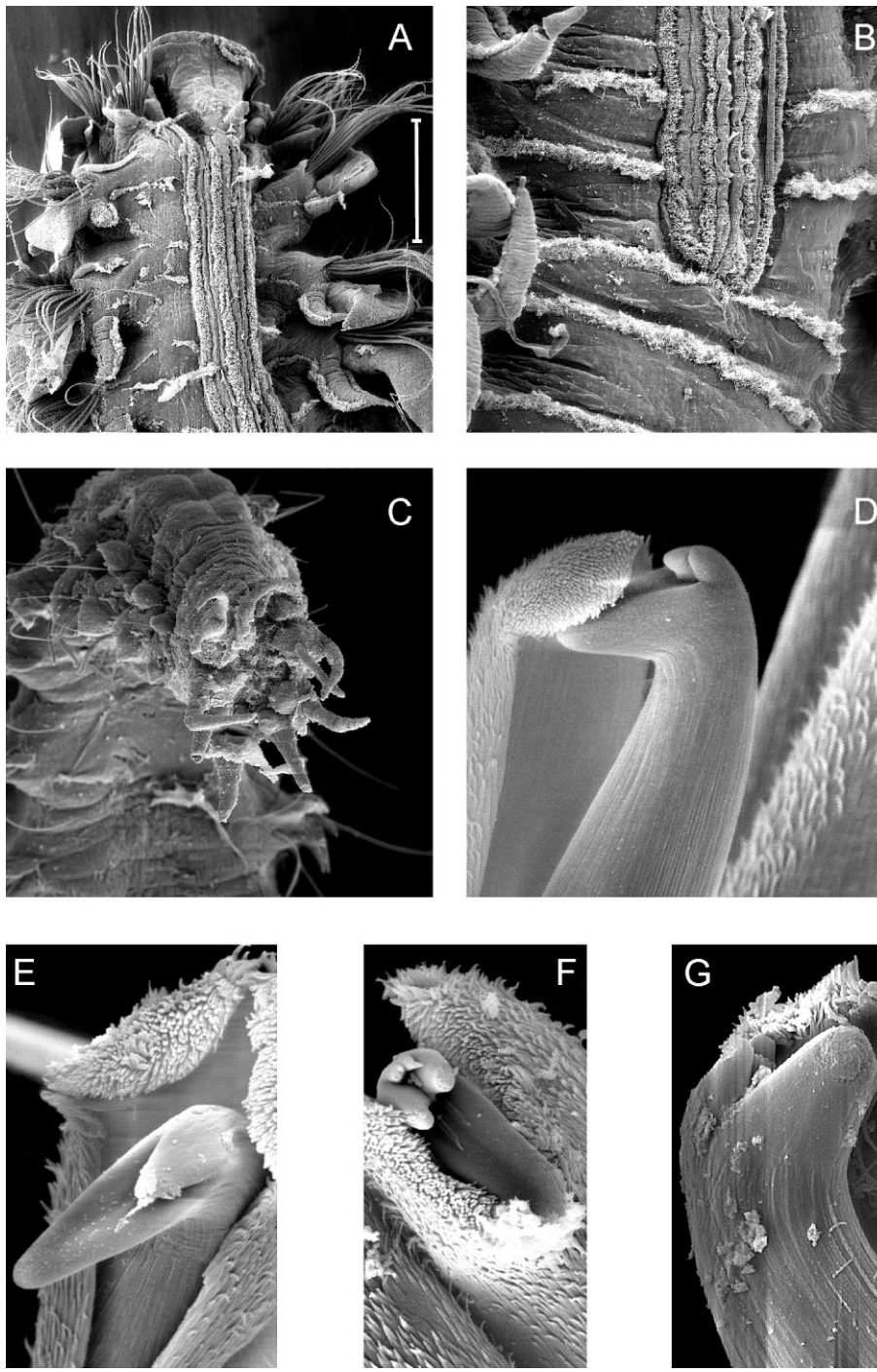

Fig. 6. Scanning electron micrographs. *Laonice sarsi* (Sars, 1851). A. Anterior end, dorsal view. B. End of dorsal sense organ. C. Pygydium. D, E. Neuropodial hooks; *L. bahusiensis* Söderström, 1920. F. Neuropodial hook; *L. cirrata* (Sars, 1851). G. Neuropodial hook. Material: A–F. S Norwegian Sea. G. ZMUM Pl 1131. Scales (mm): A = 0.3; B = 0.17; C = 0.15; D, F = 0.006; E = 0.005; G = 0.0075.

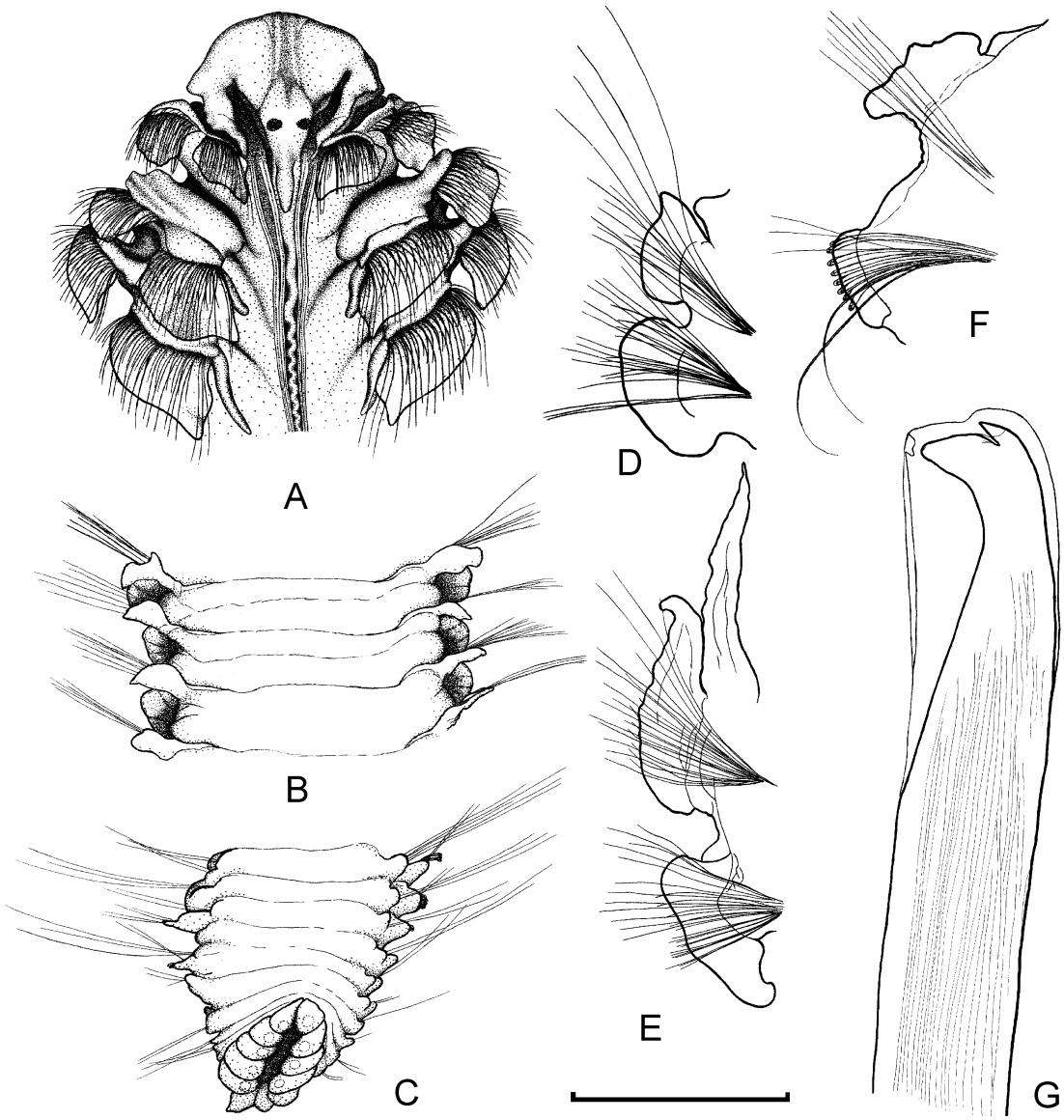

Fig. 7. *Laonice cirrata* (Sars, 1851). A. Anterior end, dorsal view. B. Middle post-branchial setigers, dorsal view. C. Posterior end, dorsal view (no anal cirri). D. Right parapodium, setiger 1. E. Right parapodium, setiger 22. F. Right parapodium, setiger 60. G. Hooded hook, setiger 39. Material: A. ZMUM Pl 1756. B, F. ZMUC POL 783. C. ZISP 123/41963. D, E. ZMUM Pl 1731. G. ZMUC POL 808. Scales (mm): A = 2.0; B = 1.7; C = 1.0; D, F = 0.86; E = 1.75; G = 0.05.

membranes present in post-branchial segments (not immediately after last branchiae) in adults only. Neuropodial post-setal lamellae of setiger 1 small, rounded, becoming three to four times as large by setigers 5–6, with rounded margins here and in branchial region. Neuropodial post-setal lamellae of branchial region usually with considerable part of lower process fused to ventrolateral surface of body, in post-branchial region resembling very low membranes without lower processes (Fig. 7F); neuropodial lamellae not increasing in size in posterior segments.

Genital pouches first appearing from setiger 3 to 52. Setae arranged in two rows in all parapodia. Sabre setae first appearing from setiger 12 to 30, up to five per

fascicle. Hooded hooks appearing in posterior row of neuropodia from setiger 18 to 57, two to 19 per fascicle in middle of body (two to six per fascicle for specimens < 0.6 mm wide). As usual, number of neuropodial hooks increasing slightly in posterior segments, up to 23 in large specimens. Hooded hooks tridentate (Fig. 6G), bidentate in side view (Fig. 7G); exceptionally with two very small extra-apical teeth.

Pygidium typically with three to seven pairs of long, dorsally arranged cirri on cirrophores (or only cirrophores visible if cirri lost, Fig. 7C) and a pair of short, close-set ventral cirri (or lobes), together forming ring around anus. Number of long cirri increasing with size, sometimes odd.

Fixed material usually without detectable pigment. Occasionally diffused blackish pigmentation present on anterior part of dorsum and ventral surface and on palps.

Methylene green

Only specimens < 0.8 mm wide show any distinct staining pattern: tips of notopodial post-setal lamellae from setiger 3–4 to 6–11 stained much stronger than those of adjacent setigers. Specimens >0.4 mm wide show this staining pattern extremely rarely. Worms >0.8 mm wide show no recognizable pattern.

Distribution (Fig. 2C)

Circumpolar: all the Arctic Ocean. Southern points in the Atlantic Ocean: Mofjord (60°42′N 5°14′E) on the Norwegian coast (UBZM 18647), south of Iceland and Greenland, and Long Island, Shinnecock Inlet (40°47′N 72°30′W) on the NE American coast (SMNH 747). In the Pacific Ocean: California, off Point Arguello (Blake 1996), Monterey Bay (examined material, USNM 17100 and 17101) on the NW American coast and Jen-tai (36°45′N 121°20′E) on the Chinese coast (ZISP 9/10369). Depth 0–1412 m, temperature −0.9 to 7.04 °C. Obtained from all types of substrate.

Studies of biomass, population density and frequency of finds in samples from the Barents Sea material show the species to prefer temperatures below 3 °C (especially the interval 0–3 °C), soft bottoms (especially silt and clayey silt) and depths of 150–300 m (Sikorski & Sennikov 1985).

Mofjord on the Norwegian coast is most likely a relict from a colder climatic period, as the fjord is a landlocked "pool" with a narrow sill and permanently cold bottom water.

Remarks

Because types of *L. cirrata* were not found, the original description only was used for identification. The description is quite poor, but it allows, without doubt, the type material to be attributed to the genus *Laonice* and states that *L. cirrata* has up to 40 pairs of branchiae. There are two species of *Laonice* that could be obtained in the type locality of *L. cirrata*: the species described above and *L. sarsi* Söderström, 1920 (*L. sarsi* is considerably rarer in the type locality of *L.cirrata* than the former species). *Laonice sarsi* has less than 33 pairs of branchiae. So, this species has been identified as *L. cirrata*. It seems desirable to designate a neotype for *L. cirrata*. However, I still hope to relocate the missing syntypes; the original description is still adequate for identification. Moreover, a perfectly preserved complete specimen from one of the type localities (Ure in Lofoten Islands, Tromsø and Hammerfest) is now missing. It seems reasonable to narrow down the type locality. Hammerfest suits us better if we follow the logic (quite unclear) of Söderström's (first revised) text.

Some confusion may potentially exist between the morphologically similar species *L. bahusiensis* and *L. cirrata*. Both taxa may be easily distinguished from other members of *Laonice* by having the prostomium markedly fused with the peristomium at the anterior margin (Figs 3A, 5A, C, 7A). The differences between these species are listed in "*Remarks*" on *L. bahusiensis*.

The ranges of values of numeric characters used in this study (branchiae are absent in the smallest specimens) are: HH: 18–57; QHH: 2–19; NO: 4–40; Br: 16–59; SS: 12–30; QSS: 1–5; GP: 3–52; HH–NO: 5–33; HH–Br: −6 to 18; HH–SS: −7 to 32; HH–GP: −11 to 39; NO–Br: −28 to 0; NO–SS: −14 to 18; NO–GP: −22 to 26; Br–SS: −11 to 33; Br–GP: −12 to 36; SS–GP: −27 to 22. HH, QHH, NO, Br, SS, QSS, HH–SS, NO–SS, Br–SS show a strong relationship with size. All these relationships are positive (Table 2). The range in variation for all size-related characters for all size groups is given in Sikorski (2002).

GP shows a rather interesting negative correlation with depth ($r = -0.275$; $n = 254$; $r_{1\%} = -0.162$). This suggests that the bathyal may be an exclusion zone for this species (Sikorski 2002).

The types of *L. pugettensis* have been examined. They appear to be completely identical to *L. cirrata*. The early appearance of genital pouches (setigers 2–3 to 4–5; Blake 1996) was the only character used for the identification of *L. pugettensis*. Examination of the types gave us a different positional range for the pouches – from setiger 3–4 to 6–7. However, this difference is of little consequence, as the character varies extremely widely (thus in the Arctic material GP varies from 6 to 52). It is unsafe to use such a variable character as the only diagnostic one. Moreover, the

Table 2. *Laonice cirrata.* Ranges of variation for size-related characters.

Character	Range of variation	r	n	$r_{1\%}$
HH	18–55	0.806	280	0.150
QHH	2–19	0.694	179	0.200
NO	4–40	0.753	262	0.160
Br*	23–58	0.630	255	0.162
SS	12–30	0.571	364	0.138
QSS	1–5	0.643	184	0.195
GP	3–52	0.395	353	0.140
HH–SS	−7 to 31	0.539	275	0.155
NO–SS	−14 to 18	0.503	260	0.161
Br–SS	−11 to 33	0.524	252	0.163

r, coefficient of correlation; n, size of statistical sample; $r_{1\%}$, critical quantity of r, at significance 1%.
*Branchiae may be absent in the smallest specimens.
HH – Setiger with first neuropodial hooded hooks; NO – Last setiger with nuchal organ; Br – Last setiger with branchiae; SS – Setiger with first occurrence of sabre setae; GP – Setiger with first occurrence of genital pouches; QHH – Number of hooded hooks per neuropodium; QSS – Number of sabre setae per neuropodium.

holotype is a specimen about 1.5 mm wide, so *L. pugettensis* should not be called a small species as was stated in the original description. The results of measurements and the distribution of characters in types of *L. pugettensis* (five specimens) are as follows: width (mm): 0.3–1.5; HH: 17–32; QHH: 3–10; NO: 9–25; Br: 16–32; SS: 12–22; QSS: 1–2; GP: 3–6. All morphological characters are in agreement with those of *L. cirrata*. It allows us to synonymize *L. pugettensis* with *L. cirrata*.

The holotypes of *S. foliata* and *S. sacculata* have been examined. *Spionides foliata*: 2.0 mm wide; HH = 53; QHH = 14; NO = 28; Br = 50; SS = 23; QSS = 3; GP = 36. *Spionides sacculata*: 2.6 mm wide; HH = 57; QHH = 13; NO = 24; Br = 52; SS = 25; GP = 33. Neither *S. foliata* nor *S. sacculata* has complete dorsal transverse membranes. However, *S. sacculata* has quite a short nuchal organ and a rather late appearance of hooded hooks for such a size, compared with all other examined specimens of *L. cirrata*. However, these differences are still not conclusive – the holotype of *S. sacculata* is absolutely identical to *L. cirrata* in all other details. The holotype of *S. foliata* is absolutely identical to *L. cirrata* in all details as well. It suggests that these species should be synonymized with *L. cirrata*. However, in future it would be desirable to compare much more Californian material with the Arctic specimens.

Biology

Oocytes oval, slightly elongate. The maximal size (0.35 mm greatest diameter; M. E. Petersen, pers. comm.) was found in a specimen from off W Greenland (ZMUC POL 816: W Greenland, Pisigsarfik, coll. GFU, Stn 443, 250 m, 28 August 1953). Large oocytes were also found in the central Barents Sea, 11 October 1969, at 320 m depth (0.31 mm greatest diameter); in the Kara Sea in August–September 1884, approximately 100 m, off NW Iceland in the middle of July 1935 (0.3 mm greatest diameter) and at E Greenland (130 m, 25 August 1932, 0.275 mm greatest diameter). A specimen with mature eggs was obtained in October 1970 at Rudolf Island (Averincev 1977). Petrovskaya (1960) reported oocytes in the body cavity in mid-August off E Murman, 193 m, 3 °C, 34.4 psu. The smallest specimen (0.25 mm wide) was obtained at the border between the Chukchi Sea and the central basin of the Arctic Ocean ("North Pole" Drift Stn 22, Stn 101, 250 m, 19–20 February 1977); other small specimens were from the southern part of the Barents Sea (0.4 mm wide, 265 m, 23 April 1986) and from the northeastern part of the Norwegian Sea (0.5 mm wide, 958 m, 13 June 1980). Sperm are round of the short-headed type, found in July (specimens from the Norwegian Sea) and in February (the E Siberian Shelf). Spawning thus appears to take place from the beginning of July to the end of August in the southern part of the area and in autumn in the northern parts.

Laonice dayianum Sikorski, 1997

Figs 1K–M, 2C

Laonice dayianum Sikorski, 1997:501–503.
Laonice cirrata— Day 1973:76.

Material examined

Off Beaufort, NC, 28.06.1965, 34°24′N 75°49′W, 200 m, muddy sand, forams and silt, coll. BST. 120. Y (HOLOTYPE – USNM 169827; PARATYPE – USNM 169828).

Description

Two fragments known, each consisting of 41 setigers. Width 0.5 and 0.8 mm. Prostomium T-shaped with broadly rounded anterior margin. No eyespots. Occipital tentacle rudimentary. Prostomium not fused with peristomium at anterior angles in dorsal view, but anterior angles of prostomium connected to ventral surface of peristomium by thin folders well visible in front view. Branchiae to setigers 25 and 31, as high as notopodial post-setal lamellae on setiger 2. Most long branchiae may overlap dorsally. Both nuchal organ and caruncle extending to setigers 12 and 14. Genital

pouches appearing on setigers 18 and 28. Nine to 10 anterior notopodial post-setal lamellae lancet-like; asymmetrically leaf-shaped, with rounded upper margin and with small peak shifting to upper lateral margin on next 10–16 setigers; symmetrically leaf-shaped from setiger 21 to 27 (Fig. 1L). No dorsal transverse membranes connecting bases of notopodial post-setal lamellae. Neuropodial post-setal lamellae of anterior 27–31 setigers with rounded margins, upper part slightly narrowed with pointed tip; axe-shaped posteriorly (Fig. 1L). Neuropodial hooded hooks from setiger 31 and 37, up to five per fascicle, bidentate in side view (Fig. 1M). Sabre setae from setiger 26, one to two per fascicle. Pygidium unknown.

Worms unpigmented

Remarks

Morphologically, *L. dayianum* is closest to *L. sarsi*. The main differences are: rudimentary occipital tentacle, large apical tooth in hooded hook (cf. *L. sarsi* – Figs 6D, 8H), length of nuchal organ extending to setigers 12–14 and appearance of sabre setae from setiger 26 for 0.5–0.8 mm width of specimens. *Laonice brevicristata* Pillai, 1961, another species without an occipital tentacle, has a shorter nuchal organ (to setigers 7–8) and appearance of sabre setae from setiger 13 to 14.

Laonice norgensis Sikorski sp. nov.
Figs 2A, 4C, D, 5E, F, 9A–F, 10A–G

Material examined

Forty-four specimens from 30 samples collected by Akvaplan-niva AS in May 1998 and June 1999 with a Van-Veen grab (0.1 m^2) plus one sample (ZMUM Pl 963).

Type material

HOLOTYPE. Oseberg-C Field, Stn 19, grab 3, 60°36.19′N 2°45.64′E, 110 m, fine sand, 05.05.1998 (ZMUM Pl 1818). PARATYPES: Oseberg-FS Field, Stn 12, grab 3, 60°28.46′N 2°52.02′E, 106 m, fine sand, 05.05.1998 (1 specimen, ZMUM Pl 1819); Oseberg-C Field, Stn Ref. 1, grab 9, 60°41.33′N 2°41.91′E, 120 m, fine sand, 06.05.1998 (1, ZMUM Pl 1820); Brage Field, Stn Ref. 1, grab 10, 60°39.55′N 2°54.59′E, 140 m, fine sand, 06.05.1998 (1, ZMUM Pl 1821); Veslefrikk Field, Stn 8, grab 2, 60°46.94′N 2°52.79′E, 172 m, fine sand, 16.05.1998 (1, ZMUM Pl 1822); Nordøstflanken Field, Stn 1, grab 2, 61°20′N 1°57.63′E, 150 m, fine sand, 17.05.1998 (1, ZMUM Pl 1823); grab 3 (1, ZMUM Pl 1824); Nordøstflanken Field, Stn 2, grab 2, 61°21′N 1°56.85′E, 152 m, fine sand, 17.05.1998 (3, ZMUM Pl 1825); grab 3 (3, ZMUM Pl 1826); grab 4 (6, ZMUM Pl 1827); grab 5 (4, ZMUM Pl 1828); Nordøstflanken Field, Stn 3, grab 2, 61°21.52′N 1°56.45′E, 157 m, medium sand, 17.05.1998 (3, ZMUM Pl 1829); grab 3 (1, ZMUM Pl 1830); grab 4 (1, ZMUM Pl 1831); Nordøstflanken Field, Stn 5, grab 5, 61°21.88′N 1°56.15′E, 157 m, fine sand, 17.05.1998 (1, ZMUM Pl 1832); Nordøstflanken Field, Stn 6, grab 2, 61°22.15′N 1°56.53′E, 170 m, medium sand, 17.05.1998 (1, ZMUM Pl 1833); Nordøstflanken Field, Stn 9, grab 5, 61°21.66′N 1°55.20′E, 153 m, fine sand, 18.05.1998 (1, ZMUM Pl 1834); Nordøstflanken Field, Stn 10, grab 3, 61°22.23′N 1°55.72′E, 161 m, fine sand, 18.05.1998 (1, ZMUM Pl 1835); grab 5 (1, ZMUM Pl 1836); Nordøstflanken Field, Stn 11, grab 3, 61°22.44′N 1°55.39′E, 161 m, fine sand, 18.05.1998 (1, ZMUM Pl 1837); Nordøstflanken Field, Stn Ref. 12, grab 10, 61°24.19′N 1°52.75′E, 161 m, fine sand, 18.05.1998 (1, ZMUM Pl 1838); Huldra Field, Stn 12, grab 3, 60°51′51.81″N 02°40′51.72″E, 123 m, sandy bottom, 04.06.1999 (1, ZMUM Pl 2134); Statfjord Field, Stn Ref. 8, grab 6, 61°28′51.68″N 01°51′01.28″E, 266 m, sandy bottom, 08.06.1999 (1, ZMUM Pl 2135); Sygna Field, Stn 2, grab 3, 61°27′51.86″N 01°59′55.18″E, 298 m, silty sand, 09.06.1999 (1, ZMUM Pl 2137); Statfjord C Field, Stn 7, grab 4, 61°17′31.08″N 01°53′46.40″E, 144 m, sandy bottom, 14.06.1999 (1, ZMUM Pl 2140); Gullfaks Field, Stn Ref. 1, grab 3, 61°07′08.31″N 02°07′27.12″E, 135 m, sandy bottom, 17.06.1999 (1, ZMUM Pl 2138); Gullfaks A Field, Stn 6, grab 2, 61°10′51.18″N, 02°12′08.96″E, 135 m, sandy bottom, 19.06.1999 (1, ZMUM Pl 2139); Gullfaks C Field, Stn 10, grab 2, 61°13′04.20″N 02°15′58.27″E, 215 m, sandy bottom, 19.06.1999 (1, ZMUM Pl 2141).

Additional material

RV *Sevastopol*, 10.1747, 63°21′N 6°19′E, 210 m, sand, 7.7 °C, 35.08 psu, 10.10.1958 (1, ZMUM Pl 963); Brage Field, Stn 11, grab 4, 60°30.69′N 3°04.99′E, 140 m, fine sand, 07.05.1998 (1 – middle fragment, ZMUM Pl 1841).

Etymology

The name derives from the Norwegian name of Norway, Norge.

Description (see also Table 3)

Up to 1.5 mm wide, 103 mm long and 142 setigers. The HOLOTYPE is 1.3 mm wide, 60 mm long and with 125 setigers. Prostomium longer than wide, bell-shaped,

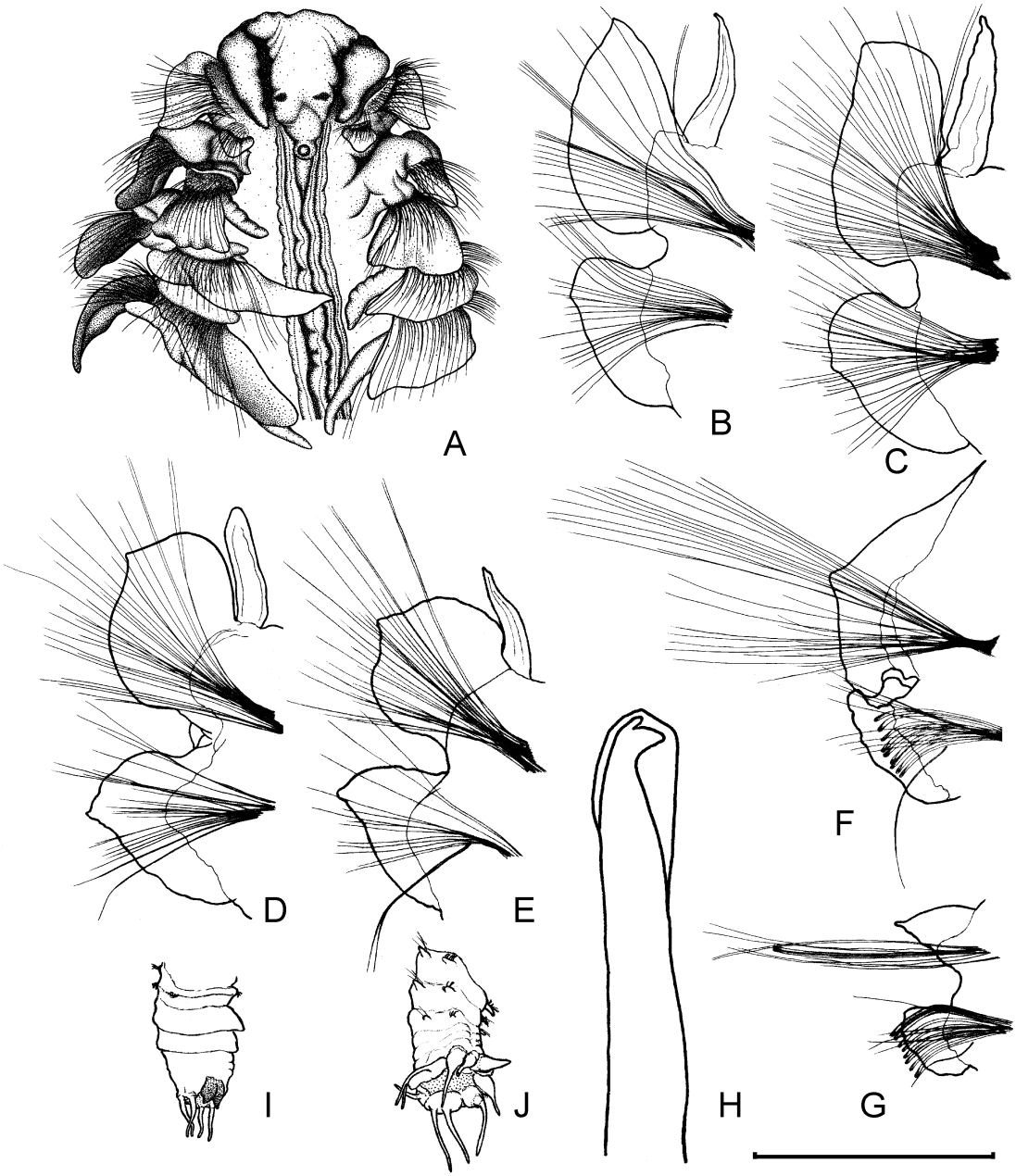

Fig. 8. *Laonice sarsi* Söderström, 1920. A. Anterior end, dorsal view. B–G. Right parapodia, setigers 5, 12, 23, 29, 62 and 111. H. Neuropodial hooded hook, setiger 36. I. Pygidium with paired ventral cirri. J. Pygidium with unpaired ventral cirrus. Material: A. ZMUM Pl 957. B–G. ZMUM Pl 2136. H. ZMUM Pl 961. I. ZMUM Pl 2143. J. ZMUM Pl 2142. Scales (mm): A = 2.0; B–G = 0.8; H = 0.027; I = 0.44; J = 0.58.

broadly rounded on anterior margin (Fig. 9C) or truncated, with small apical incision in some specimens (Fig. 9A). Prostomium not fused with peristomium; narrowing gradually from anterior margin to middle and then abruptly narrowing posteriorly into caruncle (Fig. 9A, C). One or two pairs of brown or reddish eyes. Posterior pair small (Fig. 9A) or rather large (Fig. 9C). Anterior pair small and may be located in front of

Table 3. *Laonice norgensis* sp. nov. Measurements of the main numeric taxonomic characters in type material.

Coll. numb. ZMUM Pl	Setigers	Width (mm)	HH	NO	Br	SS	GP	Coll. numb. ZMUM Pl	Setigers	Width (mm)	HH	NO	Br	SS	GP
1818 holotype	125	1.32	25	28	96	16	8	1828		0.85	23	24		13	11
1819	96	0.62	22	23	64	14	8	1828		0.56	17			11	9
1820		0.51	19	17	32	11	8	1829		0.82	23			11	10
1821	104	0.74	24		79	15	8	1829		0.69	21			13	13
1822		1.12				15	8	1829		0.55	16			11	
1823		0.37	18	16		11	10	1830		0.59	18	18		11	9
1824	105	0.70	21	22	87	14	11	1831	105	0.82	21	23	94	13	13
1825		0.34	17	15		11	10	1832		0.37	20	19	42	12	17
1825	107	0.90	21	23	90	12	9	1833		0.44	17	16		11	10
1825		0.49	17	17		11	8	1834		0.41	17	15	30	10	10
1826		0.37	17			11	11	1835	71	0.41	17	16	51	10	9
1826		0.32	16		36	11	9	1836		0.44	17	15	37	10	11
1826		0.41	17	16		10	11	1837	111	0.78	22	22	82	12	11
1827	70	0.41	17	16	38	10	10	1838		0.42	17	17		10	13
1827		0.41	17	17		10	9	2134	126	1.37	26	31	94	15	15
1827		0.37	17	16		11	10	2135	75	0.45	20	19	41	12	8
1827		0.37	18	16		11	10	2137	95	0.62	22	21	62	14	11
1827		0.62	19	18		12	12	2138	117	1.26	28	30	102	17	10
1827		0.49	18	17		10	9	2139	101	0.77	20	19	86	12	10
1828		0.77	22			14	12	2140	68	0.36	19	16	33	12	9
1828		0.78	22	21		12	10	2141	142	1.51	31	33	115	18	11

HH – Setiger with first neuropodial hooded hooks; NO – Last setiger with nuchal organ; Br – Last setiger with branchiae; SS – Setiger with first occurrence of sabre setae; GP – Setiger with first occurrence of genital pouches.

posterior one (Fig. 9C) or may be moved on to lateral surface of middle part of prostomium, often deeply imbedded within cuticle and not visible in dorsal view. Finger-like erect occipital tentacle as long as setiger 1 located at posterior end of prostomium behind eyespots (Figs 5E, 9A, C). Caruncle long, following nuchal organ up to setigers 15–33 (Figs 5E, F, 9A, B). All palps lost. Most anterior complete intersegmental border visible between setigers 2 and 3 in ventral view. Peristomial lateral wings not rising above prostomium, their length half that of prostomium. Length of nuchal organ correlating with body size. Nuchal organ extending posteriorly to setiger 15 in smallest specimens (0.35–0.45 mm wide); to the border between setigers 28 and 29 in holotype.

Branchiae of setiger 2 lower than the notopodial post-setal lamellae, becoming as high as the lamellae from setiger 3 to 5, then increasing in size and thickness on subsequent setigers (Fig. 9A). Branchiae continuing posteriorly to setigers 30–115 (to setigers 15–36 counting from pigidium). This character is size dependent (Table 3).

The shape of post-setal lamellae is illustrated in Fig. 10A–G. The shape of neuropodial post-setal lamellae is nearly the same throughout body. Their size gradually decreasing towards the end of branchial region and then increasing slightly (Fig. 10F). Notopodial post-setal lamellae retain the same shape from setiger 1 to 7–11 (Fig. 10A); with peaks at tips of notopodial post-setal lamellae from setiger 8 to 12 (Fig. 10B), peaks shifting downwards on to lateral margin of lamellae quickly on subsequent segments (Fig. 10C). Part of notopodial lamellum above peak narrower than rest of lamellum (Fig. 10C–E), more pronounced in segments more posterior to the nuchal organ (Fig. 10D, E). Upper part of notopodial lamellum gradually reduced posteriorly. Notopodial lamellae leaf-shaped at end of branchial region (Figs 3G, 10F). Every setiger with two dorsal transverse membranes: one membrane connecting bases of notopodial lamellae, another following the anterior border of the setiger (Figs 5F, 9B). Normally these membranes visible up to posterior-most setigers. Membranes from bases of notopodial lamellae may be clearly visible (Fig. 9A) from setiger 7, interrupted only by nuchal organ.

Genital pouches appearing from setiger 8 to 17, present regularly on every setiger through two to 65 segments; not found on every setiger afterwards. Genital pouches usually disappearing on setigers 9–21 counting from pygidium, but sometimes within three to eight setigers after appearing regularly.

Noto- and neuropodial capillaries arranged in more than two vertical rows per fascicle (usually in three rows) varying from setiger 1 to 4; in two rows from setiger 8 to 17; sometimes in four rows for several segments (from setigers 4–7 to 9–14) in larger speci-

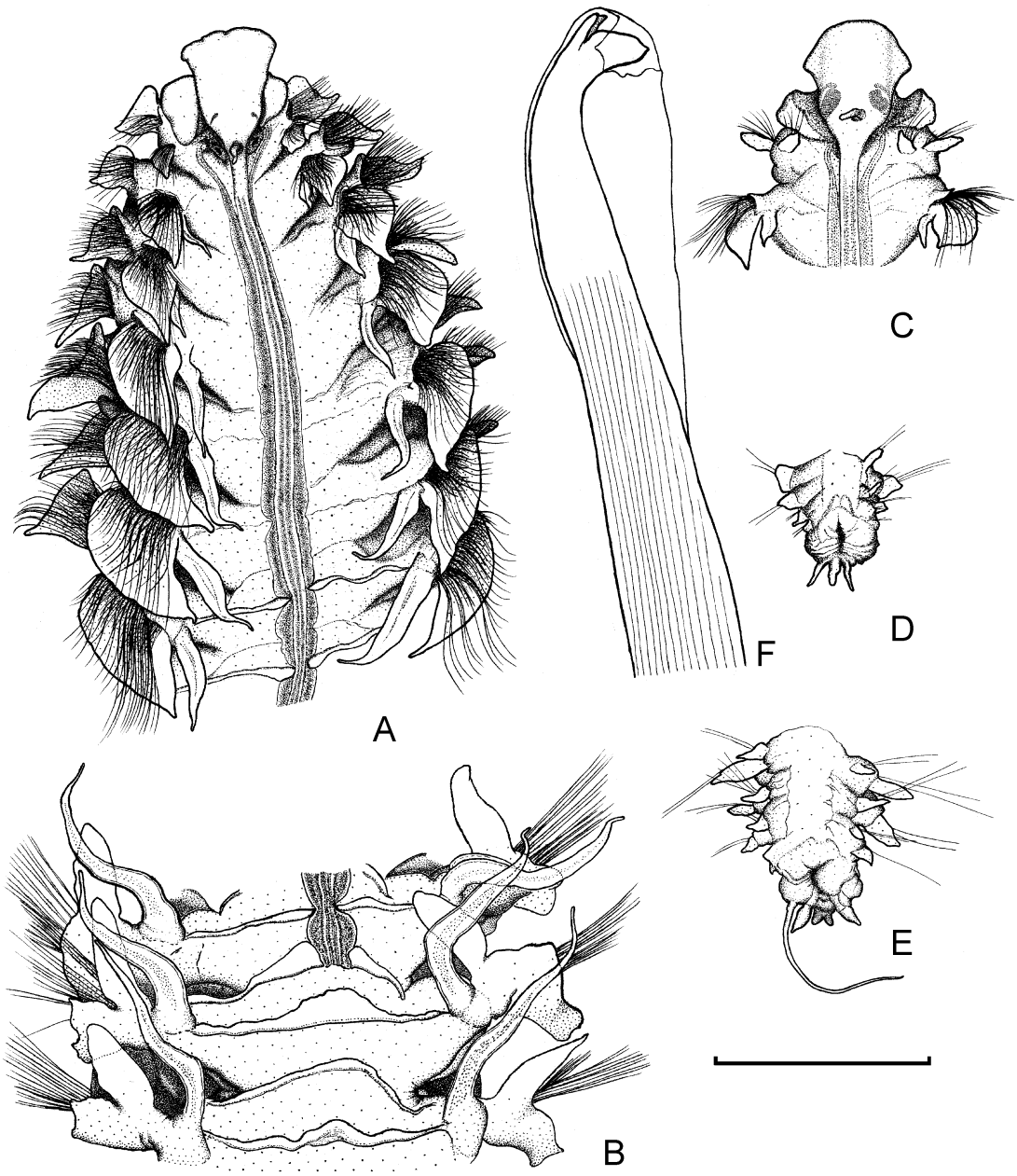

Fig. 9. *Laonice norgensis* sp. nov. A. Anterior end, dorsal view. B. Setigers 28, 29 and 30, dorsal view. C. Anterior end of a smaller specimen, dorsal view. D. Pygidium with mid-ventral cirrus, dorsal view. E. Pygidium with furcated mid-ventral cirrus, dorsal view. F. Hooded hook of setiger 38, side view. Material: A, B. Holotype ZMUM Pl 1818. C. ZMUM Pl 1837. D. ZMUM Pl 1821. E. ZMUM Pl 1822. F. ZMUM Pl 1831. Scale (mm): A, B = 1.1; C–E = 0.64; F = 0.02.

mens. Sabre setae first appearing between setigers 10 and 18; from setiger 10 only in smallest specimens (0.42–0.50 mm wide); up to four per fascicle, decreasing to one in posterior part of body (Fig. 10F, G). Hooded hooks appearing from setiger 16 to 31; from setiger 16 to 20 only in small specimens (0.3–0.6 mm wide). Starting from four to 12 hooded hooks per fascicle it reaches six to 17 hooded hooks per fascicle (a

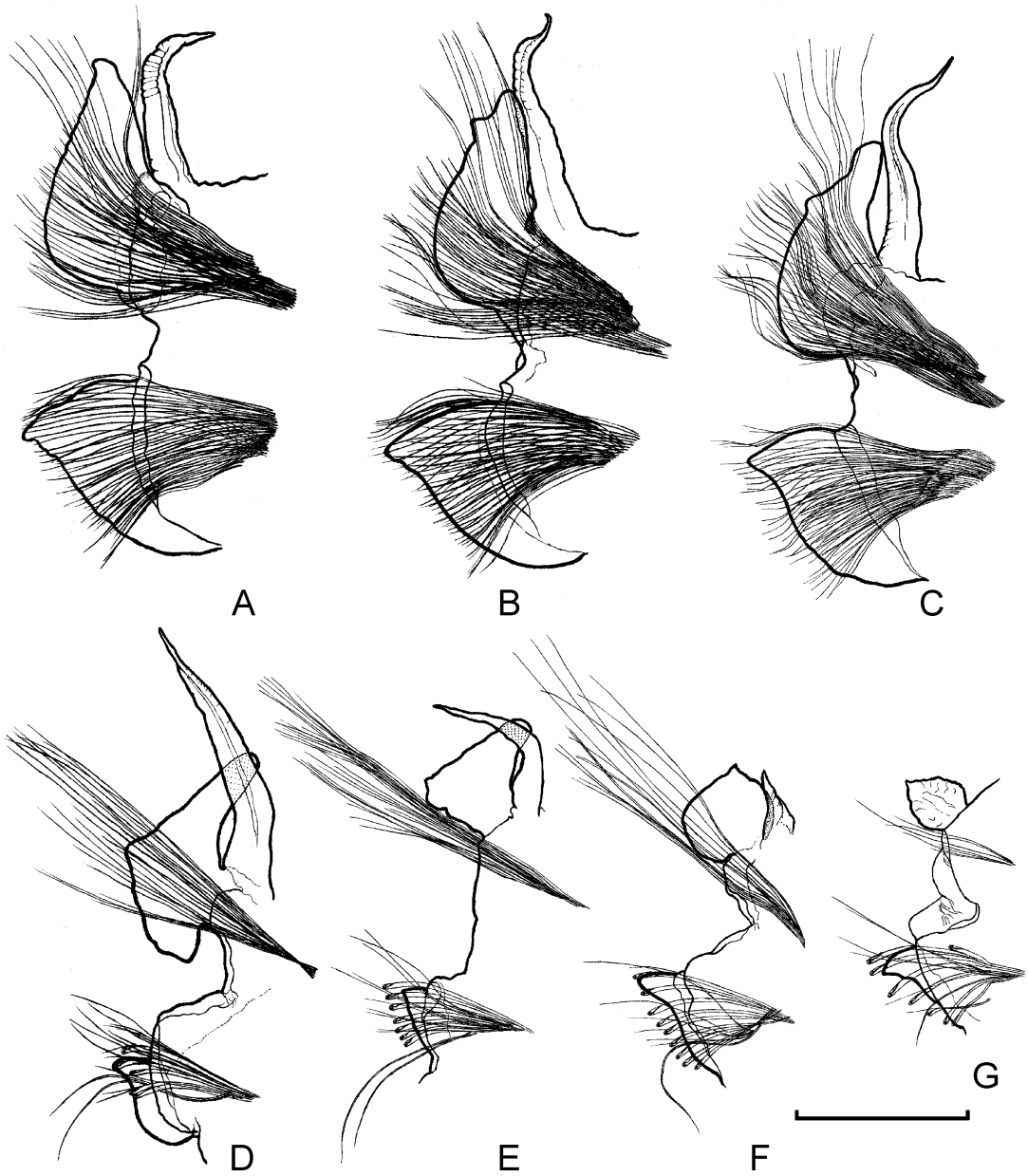

Fig. 10 *Laonice norgensis* sp. nov. Right parapodia. A. Setiger 9. B. Setiger 11. C. Setiger 12. D. Setiger 25. E. Setiger 44. F. Setiger 64. G. Setiger 86. Material: A–G. ZMUM Pl 1819. Scale (mm): 0.5.

maximum number) in central neuropodia. Hooded hook bidentate in side view; but main fang surmounted by paired apical teeth (best seen using phase contrast).

Pygidium bearing a pair of short and thick ventral cirri placed rather far apart; characteristic for all species of *Laonice* (Fig. 9D, E). Pygidium also with up to six pairs of thread-like long dorsal cirri; they may all be absent or lost (Fig. 9D) or partially present (Fig. 9E). Cirriform ventral-most medial appendage positioned between ventral cirri. Tip of appendage may be forked (Fig. 9E) or entire, resembling single ventromedial cirrus (Fig. 9D). Holotype with ventromedial cirrus and one of the dorsal cirri only.

Body of worms normally unpigmented but ventro-

medial appendage of the pygidium sometimes darkly pigmented.

Methylene green

Anterior part of prostomium (approximately two thirds of length), base of occipital tentacle, post-setal lamellae, anteroventral surface of body (approximately length of nuchal organ) visibly stained stronger than adjacent parts of body.

Distribution (Fig. 2A)

Northern North Sea and Norwegian Shelf north to 63°30′N; 106–298 m, sandy bottom and sometimes mixed bottom.

Differential diagnosis

Laonice norgensis most resembles *L. appelloefi, L. weddellia* Blake 1983, *L. blakei* and *L. nuchala* Blake, 1996, given the arrangement of capillary setae in more than two rows in the anterior parapodia. The new species differs from *L. appelloefi* mainly by the absence of visible widening of the 12–15 anterior setigers (Sikorski 1999), a longer nuchal organ (to setigers 15–28 instead of setigers 8–14 in *L. appelloefi*), genital pouches starting from setiger 8 to 17 (from setiger 5 to 7 in *L. appelloefi*) and by the absence of complete dorsal transverse membranes in *L. appelloefi*. I have not examined any entire specimen of *L. appelloefi*, such that the pygidia of these species cannot be compared. Differences from *L. weddellia*, which also has a mid-ventral cirrus, are as follows: two to three pairs of eyes in *L. weddellia* (one to two in *L. norgensis*); the shape of hooded hooks (in *L. weddellia* the second apical tooth is not located side by side as in *L. norgensis* "in tandem with the first" – *sensu* Blake 1983); the shape of the anterior-most notopodial post-setal lamellae (see Blake 1983: figs 5A, 9B) – the notopodial post-setal lamellae of *L. weddellia* has inferior extensions. Moreover, the branchiae in *L. weddellia* (maximum number of setigers = 130) continue posteriorly for 20–50 setigers (Hartman 1978; Blake 1983) as in *L. norgensis* – for 30–115 setigers (maximum number of setigers = 142). There is a discrepancy in Blake's description: the left parapodium of setiger 100 depicted on (Blake 1983) fig. 9C has a branchium and does not have a neuropodial post-setal lamellum. This runs counter to the text description. There is no information about dorsal transverse membranes in *L. weddellia. Laonice norgensis* differs from *L. blakei* in that the latter taxon has genital pouches only from setiger 3 and a completely different shape of hooded hooks and notopodial post-setal lamellae. The main differences between *L. norgensis* and *L. nuchala* are that *L. nuchala* has a much shorter nuchal organ (to setiger 13) and differently shaped hooded hooks.

Remarks

Ranges of values of numeric characters: HH: 16–31; NO: 15–33; Br: 30–115; SS: 10–18; GP: 8–17; HH–NO: −5 to 3; HH–SS: 5–13; HH–GP: 3–20; NO–SS: 4–16; NO–GP: 2–20; Br–HH: 13–84; Br–NO: 15–82; Br–SS: 20–97; Br–GP: 20–104; SS–GP: −5 to 8. It is clear from Table 3, showing the results of measurements of the main numeric characters, that only GP does not correlate with size and only the correlation between HH–NO and size is negative (Fig. 4C). The correlation between HH–SS, HH–GP, NO–SS, NO–GP, Br–HH, Br–NO, Br–SS, Br–GP and size seems to be not so interesting as a special taxonomic character. All of these values are differences between comparatively widely varying characters strongly correlated with size and another less variable character sometimes with little relationship to size (GP). Figure 4D illustrates the correlation of SS–GP with width that might be more useful as a taxonomic character.

Laonice sarsi Söderström, 1920

Figs 2B, 6A–E, 8A–J

Laonice sarsi Söderström, 1920:223–225, figs 129, 130 (part).

Laonice sarsi – Eliason 1962:263; Sikorski & al. 1988:833–835, fig. 2e–f; Orrhage & Sundberg 1991:173–178.

Type locality

W Sweden, Gullmaren, N Flatholmsrännan.

Material examined

One hundred and fourteen samples, 379 specimens.

Type material

LECTOTYPE: Gullmaren, N. Flatholmsrännan, coll. A. Wirén (UUZM 154h); PARALECTOTYPES: Trondhjemsfjord, Röberg, 70 m, silt, stones, rocks, coll. I. Arwidsson (1 specimen, SMNH 4639); Trondhjemsfjord, Röberg, 180–150 m, 15.06.1901, coll. I. Arwidsson (1, SMNH 4640); Trondhjemsfjord, Röberg, 195–140 m, coll. I. Arwidsson (1, SMNH 4641); Trondhjemsfjord, Röberg, 70–35 m, silt, stones, 08.06.1901, coll. I. Arwidsson (3, SMNH 4642); Trondhjemsfjord, Röberg, 140–90 m, 10.06.1901 (1, SMNH 4643);

Österfjord, Stn 19, 20, 20.08.1892, coll. A. Appellöf (6, UBZM 18646); Hjeltefjord, Stn 28, 30–33, 42–43, coll. A. Appellöf (16, UBZM 18645 – 2 specimens of *L. bahusiensis* excluded); Verrafjord: Svean, 20–30 m, lerbund, 19.08.1906, coll. Nördgärd (1, UBZM 27376); Kristianiafjord: "? ved. Drøbak i Hallandspollen, 25 F., og pe Ellmedet, 40–50 F." coll. Sars (1, UBZM 4556); Kattegat, Sweden, Kosterfjorden, Styrsö-Sneholmarna, coll. A. Wirén (1, UUZM 1874); Bohuslän, Kosterfjorden, Vattholmen, coll. A. Wirén (8, UUZM 154a), (2, ZMUM Pl 974); Gullmaren, coll. A. Wirén (4, UUZM 154j); Gullmaren, Flatholmen, coll. A. Wirén (5, UUZM 154i); several unexamined paralectotypes should be in the collections of Oslo and Göteborg museums.

Additional material

RV *Hauchs*, Skagerak, Stn 25, Skagens Fyrskib i S.S.V., 12–15 Kvml., 110 Fv., Fed Slik, 8.5 ° C, 06.08.1884 (1, ZMUC); RV *Dana*, Stn 7749, 57°43′N 8°42′E, 165 m, 04.07.1951 (1, ZMUC); RV *Dana*, Stn 7848, 57°51′N 4°47′E, 100 m, 1951 (1, ZMUC); RV *Dana*, Stn 8088, 57°00′N 1°40′E, 96 m, 1952 (3, ZMUC); Bohuslän, Grisbädarna, 60 m, 10.06.1909, coll. Bock, Oldevig (1, UUZM 1864); Uppsala Exp.-33, Stn 34 (1, UUZM 1865); Uppsala Exp.-33, Stn 10, 57°57.5′N 9°38′E, 141 m, 6.91 °C, 35.19 psu, grey silt, 30.06.1933 (1, UUZM 1866); Uppsala Exp.-33, Stn 24, 57°41′N 8°35′E, 191 m, 7.07 °C, 35.17 psu, grey silt, 06.07.1933 (1, UUZM 1867); Uppsala Exp.-33, Stn 35, 58°30′N 10°26′E, 300 m, 6.7 °C, 35.21 psu, grey silt, 15.07.1933 (1, UUZM 1868; 1, UUZM 1872); Uppsala Exp.-33, Stn 33, 57°18′N 10°49.5′E, 140 m, 7 °C, 35.08 psu, grey silt, 14.07.1933 (1, UUZM 1869; 2, UUZM 1873); Uppsala Exp.-33, Stn 16, 59°22′N 8°49.5′E, 131 m, 6.72 °C, 34.97 psu, grey silt, 03.07.1933 (1, UUZM 1870); Uppsala Exp.-33, Stn 32, 57°56′N 6°54.5′E, 321 m, 6.50 °C, 35.16 psu, grey silt, 12.07.1933 (1, UUZM 1871); RV *Atlantida*, 9.8/1373, 71°00′N 18°00′E, 240 m, clay, stones, shells 28.04.1972 (1, ZMUM Pl 954); RV *Otto Schmidt*, 26.2901, 74°30′N 20°10′E, 90 m, coarse sand, stones, broken shells, 05.08.1986 (1, ZMUM Pl 955); RV *Tunets*, 105.13, 70°32′N 18°52′E, 220–240 m, 6.09 °C, 28.06.1978 (1, ZMUM Pl 956); RV *Tunets*, 105.14, 70°41′N 18°38′E, 326–330 m, silt, 5.05 °C, 34.99 psu, 28.06.1978 (1, ZMUM Pl 957); RV *Sevastopol*, 5.1049, 65°40′N 8°30′E, 405 m, clayey silt, 6.76 °C, 35.16 psu, 09.07.1957 (1, ZMUM Pl 958); RV *Sevastopol*, 5.1104, 60°35′N 0°45′E, 130 m, silty sand, 8.16 °C, 35.37 psu, 18.07.1957 (1, ZMUM Pl 959); RV *Sevastopol*, 5.1106, 65°35′N 2°01′E, 100 m, silty sand, pebbles, broken shells, 7.52 °C, 35.34 psu, 19.07.1957 (1, ZMUM Pl 960); RV *Sevastopol*, 8.1406, 62°10′N 4°45′E, 145 m, silty sand, broken shells, 4.45 °C, 05.04.1958 (2, ZMUM Pl 961); RV *Sevastopol*, 8.1467, 60°35′N 1°23′E, 140 m, broken shells, 5.95 °C, 35.23 psu, 18.04.1958 (2, ZMUM Pl 962); RV *Sevastopol*, 10.1754, 61°33′N 1°07′E, 138 m, 9.48 °C, 35.37 psu, 13.10.1958 (2, ZMUM Pl 964); several fields at the border between the Norwegian and the North Seas: from 59°34′ to 61°28′N and from 1°59′ to 2°27′E, 104–297 m, silt–sand (296, ZMUM Pl 471, 909, 937, 952, 953, 965–969, 972, 974–1033, 2136, 2142, 2143, 2244, 2245).

Description

LECTOTYPE: 1.6 mm wide, 57 mm long, 109 setigers. HH = 39, QHH = 13, NO = 10, Br = 32, SS = 25, QSS = 3, GP = 31; notopodial hooks first appearing on setiger 84, up to four per fascicle. Genital pouches disappearing on setiger 81. Pygidium with three pairs of dorsal and one pair of small ventral cirri. Occipital tentacle not complete, but its base well visible. Branchiae of setiger 2 slightly above notopodial post-setal lamellae. Anterior six pairs of notopodial post-setal lamellae clearly pointed. They have dorsally rounded margins with a small peak visible on the upper margin from setiger 7; peak starts shifting laterally from setiger 13. Notopodial lamellae rounded with lateral peak at disappearance of branchiae; narrow, asymmetrical, with lower appendage in post-branchial region; becoming triangular in most posterior segments. Neuropodial post-setal lamellae with a small peak on upper lateral margin from setiger 8. Ten segments after branchiae disappear the neuropodial lamellae lose the peak but have a superior appendage. Neuropodial lamellae asymmetrically rounded in the most posterior segments.

All material examined: size up to 1.6 mm wide, 75 mm long and 129 setigers.

Prostomium broadly rounded anteriorly, not fused with peristomium at anterior angles in dorsal view (Fig. 8A), but the anterior angles of the prostomium connected to the ventral surface of peristomium by a thin fold clearly visible in face view. Prostomium T- or bell-shaped. Occipital tentacle comparatively short, erect. One pair of eyes visible on dorsal and lateral surface of prostomium. Caruncle extending together with nuchal organ to setigers 2–14. Usually branchiae from setiger 2 to 4 (sometimes 5) slightly lower than notopodial post-setal lamellae, but may be higher (see description of lectotype). Branchiae to setigers 6–33, but in smallest specimens (<0.3 mm wide) they may be

completely absent. Genital pouches from setigers 4–33 to 15–91, disappearing 19–52 segments from pygidium. Number of segments with genital pouches varying from nine to 60 depending on size.

Anterior four to six pairs of notopodial post-setal lamellae clearly pointed (Fig. 8B); having dorsally rounded margins with small peak visible on upper margin from setiger 7 (Fig. 8C); the peak shifting laterally from setiger 11 to 13 (Fig. 8D). Notopodial lamellae rounded with lateral peak on three to five last branchial segments (Fig. 8E); narrow, asymmetrical, with inferior appendage in post-branchial region (Fig. 8F); becoming triangular in most posterior segments (Fig. 8G). No complete dorsal transverse membranes connecting bases of notopodial post-setal lamellae. Length of incomplete membranes (on both sides) not more than two fifths body width. Neuropodial post-setal lamellae of anterior three to four setigers narrowing dorsally; rounded with a small, not so obvious, smoothed peak on upper lateral margin posteriorly (Fig. 8B, C). Peak clearly pointed after disappearance of nuchal organ (Fig. 8D, E). In post-branchial region, peak not visible and neuropodial lamellae having upper appendage (Fig. 8F). Upper appendages in neuropodial post-setal lamellae disappearing 10–12 segments earlier than genital pouches. Neuropodial lamellae asymmetrically rounded in most posterior segments (Fig. 8G).

Neuropodial hooded hooks bidentate in side view (Fig. 8H); but main fang may be surmounted by one apical tooth or by a pair of apical teeth (Fig. 6D, E). Neuropodial hooks from setiger 16 to 39, four to 13 per fascicle. Notopodial hooks from setiger 33 to 96, one to five per fascicle. Number of setigers with notopodial hooks from 11 to 37 [six to 34 according to Söderström (1920), but I have not seen specimens having less than 11 segments with notopodial hooded hooks; this disparity might be because of the difficulty in determining where the notopodial hooks first appear]. Sabre setae from setiger 10 to 26, up to four per fascicle. Pygidium bearing a pair of short and thick ventral cirri, characteristic for all species of *Laonice* (Fig. 8I). Pygidium also bearing up to seven pairs of longer and thinner dorsal cirri (Figs 6C, 8I, J). A cirriform ventral-most medial appendage positioned between ventral cirri may also be present (Figs 6C, 8J).

Tube very thin, mucous, easily removed.

Epitoke region after setigers 25–33.

Worms unpigmented. Occasionally diffused blackish pigmentation is present on anterior part of dorsum.

Distribution (Fig. 2B)

From Skagerak and the central North Sea (56–57°N) to the W Barents Sea (75°N) along all Norwegian coasts. Shetland Islands, NE Scotland; 25–405 m, 3.10–9.48 °C, sandy and mixed bottom.

Remarks

Designating a lectotype for the species is mandatory to stabilize its taxonomic status as the original type material of *L. sarsi* contains several specimens belonging to *L. bahusiensis*. It was established from syntype series originally labelled by A. Söderström.

Laonice sarsi is the only species known in the genus to have notopodial hooded hooks. The presence of a cirriform ventral-most medial appendage positioned between ventral cirri in the pygidium is noted for the first time for *L. sarsi*. Ranges of values of numeric characters: HH: 17–39; NO: 3–13; Br: 9–33; SS: 10–26; GP: 4–33; HH–NO: 13–30; HH–Br: −1 to 10; HH–SS: 3–16; HH–GP: 2–20; NO–Br: −25 to −5; NO–SS: −15 to −5; NO–GP: −23 to 1; Br–SS: −5 to 13; Br–GP: −1 to 12; SS–GP: −11 to 10. Table 4 shows the values of strongly size-related numeric characters for distinct intervals of width. All relationships are positive.

This is the first time a cirriform ventral-most medial appendage positioned between ventral cirri in the pygidium is mentioned for the species.

Biology

Oocytes oval elongated, up to 0.13 mm long, 0.08 mm wide. Hannerz (1956) recorded planktonic larvae of *Laonice* in Gulmar Fjord from January to the beginning of February. The data probably concern *L. sarsi* (see "*Remarks*" for *L. bahusiensis*).

Laonice shamrockensis Sikorski sp. nov.
Figs 2B, 11A–D

Material examined

One specimen (HOLOTYPE) from Shamrock Canyon, RV *Shackleton*, Stn 1885/3, 47°47.7′N 8°11.5′W, 1700 m, 20.04.1977 (ZMUC 646); slide of parapodia (setigers 18 and 27) and neuropodium only (setiger 26) and slide of entire parapodium (setiger 26) – both slides with the number ZMUC 646.

Etymology

The name derives from Shamrock Canyon where the species was collected.

Description

Two fragments in tube: anterior fragment (0.8 mm

Table 4. *Laonice sarsi.* Values of strongly size-related characters for distinct intervals of width. Numbers of specimens in parentheses.

	Width (mm)						
	<0.4	0.5–0.6	0.7–0.8	0.9–1.0	1.1–1.2	1.3–1.4	>1.5
HH	16–22 (10)	24–33 (10)	27–31 (10)	23–36 (22)	32–39 (21)	31–36 (10)	30–39 (5)
QHH	4 (6)	6–8 (5)	6–8 (8)	6–12 (18)	6–12 (16)	7–12 (7)	9–13 (4)
NO	2–6 (11)	6–10 (9)	8–11 (11)	7–13 (26)	8–13 (32)	8–13 (11)	8–10 (5)
Br	0*–16 (10)	18–28 (10)	26–28 (8)	21–32 (19)	28–32 (22)	30–33 (9)	30–32 (5)
SS	10–14 (11)	16–21 (9)	17–21 (10)	18–26 (24)	20–26 (30)	20–26 (10)	22–25 (5)
GP	4–9 (10)	8–29 (9)	15–23 (8)	21–32 (22)	23–31 (27)	24–33 (9)	26–31 (5)

*Branchiae absent.
HH – Setiger with first neuropodial hooded hooks; NO – Last setiger with nuchal organ; Br – Last setiger with branchiae; SS – Setiger with first occurrence of sabre setae; GP – Setiger with first occurrence of genital pouches; QHH – Number of hooded hooks per neuropodium.

wide) consisting of 17 setigers and another fragment (from setiger 18 to 26). Prostomium longer than wide, with anterior margin broadly rounded. Prostomium fused with peristomium at anterior margin (Fig. 11A). Two pairs of eyes. Posterior pair larger and appear as transversally oriented stripes. Anterior pair small rounded dots. Occipital tentacle absent (may be lost). Caruncle following nuchal organ extending to setiger 5. Palps lost.

The only remaining branchium on setiger 3 *Ca* 2–2.5 times shorter than notopodial post-setal lamellum. Traces of branchiae clearly visible on setigers 2 and 4, but nothing clearly visible posteriorly. Post-setal lamellae of setiger 1 with pointed tips oriented upwards; notopodial lamellae lancet-shaped. Notopodial post-setal lamellae on setigers 2 and 3 standing out by size and being stretched towards one another (their tips nearly meet at mid-dorsum). Notopodial post-setal lamellae having rounded margins with small peak visible dorsally up to setiger 12; peak shifting on lateral margin of lamellum further back. Neuropodial post-setal lamellae with acute upper lateral margins up to setiger 20; rounded further back; with superior appendage after appearance of hooks. Lower parts of notopodial post-setal lamellae overlapping with upper parts of neuropodial post-setal lamellae (Fig. 11B, C). No membranous crests across dorsum. Body cylindrical in section backwards from setiger 12. Insertion of posterior parapodia gradually moving ventrally.

Genital pouches appearing after setiger 3, visible on all setigers. In every genital pouch membrane attaching to neuropodia at notably lower level anteriorly than posteriorly.

Sabre setae from setiger 12; two per fascicle. Neuropodial hooded hooks from setiger 23; up to seven per fascicle. Hooded hook bidentate in side view; but main fang surmounted by paired apical teeth (best seen using phase contrast; Fig. 11D).

Pygidium unknown.
Worms unpigmented.

Methylene green

Usually a distinct staining pattern on the tips of notopodial post-setal lamellae from setiger 4 up to 8 (tips of notopodial post-setal lamellae on setigers 2, 3 and 9 less stained). The rest of the body has a more or less diffused staining pattern.

Differential diagnosis

It is clear that the specimen belongs to a new, undescribed species. It has a short nuchal organ, and only a few short branchiae. Moreover, the occipital tentacle appears to be absent altogether and not merely lost. The specimen also has particularly well-developed notopodial post-setal lamellae on setigers 3 and 4. All listed characters are also typical for *Prionospio*, although *Prionospio* does not have such a long nuchal organ. This specimen has hooded hooks of a similar shape to those of most *Laonice*. Its prostomium fused with the peristomium at the anterior margin similar to prostomia of *L. cirrata, L. bahusiensis, L. quadridentata* Blake & Kudenov, 1978, *L. bassensis* Blake & Kudenov, 1978 and *L. brevicornis* (Kinberg, 1866). *Laonice cirrata, L. bahusiensis* and *L. quadridentata* have an occipital tentacle, a much longer nuchal organ, more branchiae, a different size of anterior branchiae, a different shape of post-setal lamellae and the hooded hooks. *Laonice brevicornis* has more branchiae and HH–Br = 2 (HH–Br = 17 in *L. shamrockensis*). It most resembles *L. bassensis* by the short nuchal organ and the appearance of genital pouches so close to the prostomium. But *L. bassensis* has branchiae after setiger 5 (from the original description it is not clear how many branchiae it has), an occipital tentacle, a

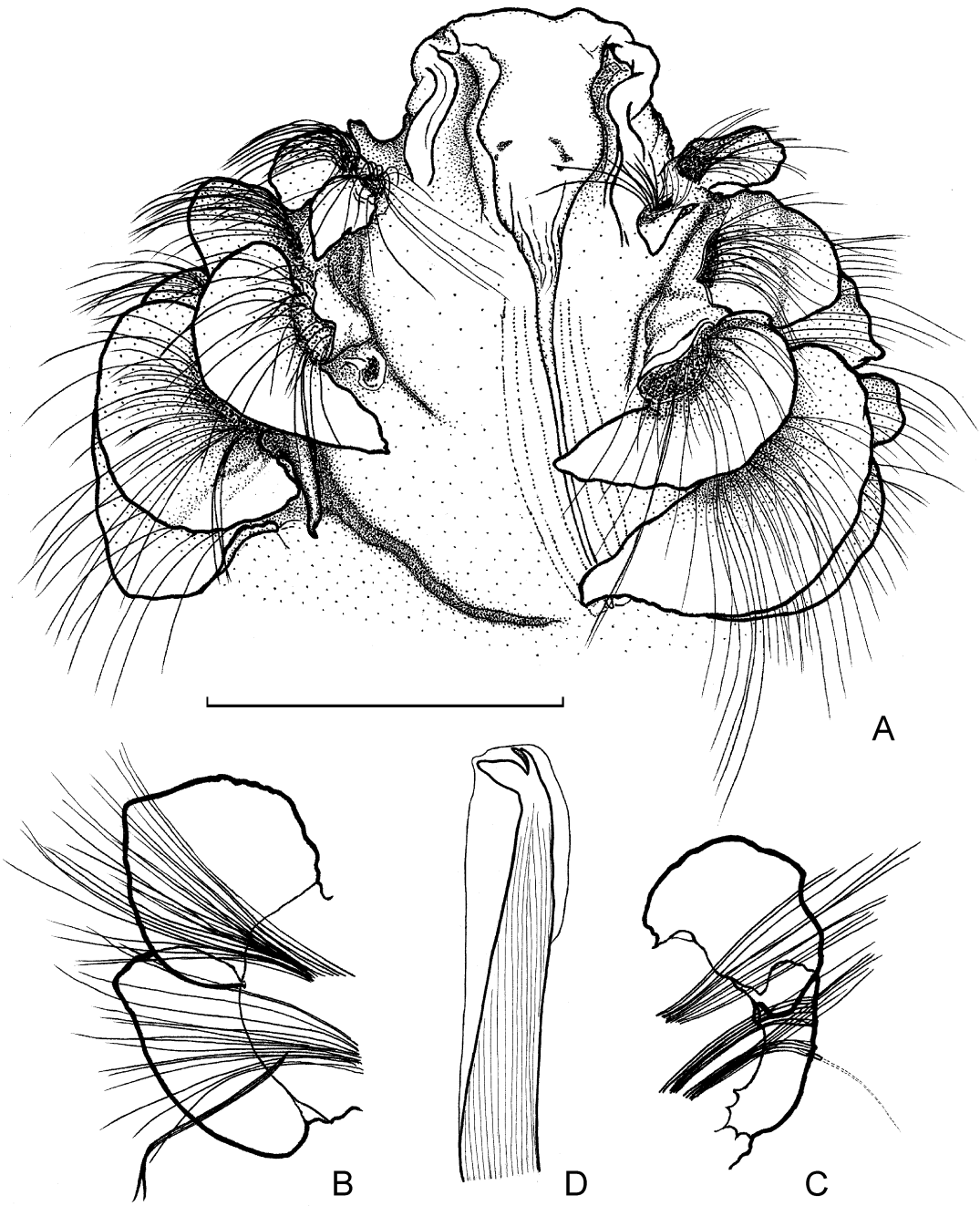

Fig. 11 *Laonice shamrockensis* sp. nov. A. Anterior end, dorsal view. B. Right parapodium, setiger 18. C. Left parapodium, setiger 27 (dotted line – broken sabre seta). D. Neuropodial hooded hook, setiger 26. Scales (mm): A–C = 0.7; D = 0.05.

longer nuchal organ, a different shape of post-setal lamellae, no eyes and only one apical tooth above the main fang in hooks.

Remarks

It was decided to describe a new species based on a single specimen, as today there is little probability of obtaining supplementary material on this group from the Shamrock Canyon.

CONCLUSIONS

Eight species of the genus *Laonice* were found in the material examined from the Arctic and North Atlantic, these being *L. appelloefi, L. bahusiensis, L. blakei, L. cirrata, L. dayianum, L. norgensis, L. sarsi* and *L. shamrockensis*.

Laonice norgensis and *L. shamrockensis* are new to science.

Lectotypes of *L. bahusiensis* and *L. sarsi* are designated. *Spionides foliata, S. sacculata* and *L. pugettensis* are synonymized with *L. cirrata*.

For size-related characters, it seems useful to show the values of size-dependent characters for distinct width intervals of specimens. This gives more information for comparing species (see the comparison of *L. dayianum* and *L. sarsi* above) and makes the use of that character more reliable. However, a large amount of material representing different size classes is required. We only possess such information for four species (see "*Remarks*" for *L. bahusiensis, L. cirrata, L. sarsi* and *L. norgensis*). I have given all the measurements (the amount of material was not great) and conclusions for *L. norgensis* as this seems to be the most useful way. Values of size-dependent characters for distinct intervals of width for *L. sarsi* are given in Table 2. Similar information for *L. bahusiensis* and *L. cirrata* is available in Sikorski (2002).

Arithmetic differences between some pairs of numeric characters may often be used as independent taxonomic characters.

KEY TO THE NORTH ATLANTIC AND ARCTIC SPECIES OF *LAONICE*

1 Prostomium fused with peristomium at anterior margin, clearly visible in dorsal view **6**
– Prostomium not fused with peristomium at anterior margin or it is not visible in dorsal view **2**
2 Genital pouches always start between setigers 3 and 4 . . . . . ***Laonice blakei***
– Genital pouches start after setiger 4. . . . . **3**
3 Large complete dorsal transverse membranes connecting bases of notopodial post-setal lamellae exist in post-branchial region ***Laonice norgensis* sp. nov.**
– No complete dorsal transverse membranes connecting bases of notopodial post-setal lamellae **4**
4 Occipital tentacle rudimentary. . ***Laonice dayianum***
– Occipital tentacle well developed **5**
5 Body widened anteriorly on 12–15 setigers; capillary setae arranged in three to four rows on several of most anterior 15–17 setigers . . . . . ***Laonice appelloefi***
– Body not widened anteriorly; capillary setae arranged in two rows on anterior setigers ***Laonice sarsi***
6 Branchiae on setiger 3 twice as short as notopodial post-setal lamellae or even shorter. . . . . . ***Laonice shamrockensis* sp. nov.**
– Branchiae on setiger 3 longer (more or less similar to notopodial post-setal lamellae in length) **7**
7 Complete dorsal transverse membranes connecting bases of notopodial post-setal lamellae in last branchiate and several following segments. Hooded hook with two apical teeth in lateral view . . . . . ***Laonice bahusiensis***
– No complete dorsal transverse membranes connecting bases of notopodial post-setal lamellae in very last branchiate and several following segments. Hooded hook with one apical tooth in lateral view . . . . . ***Laonice cirrata***

ACKNOWLEDGEMENTS

I am grateful to Akvaplan-niva for financial support while compiling this paper, for access to material and to Tom Pearson for advice during that process and for linguistic assistance. Examination of the types of *Laonice bahusiensis* in Swedish collections was made possible through grant no. 1A-276998 from the Lerner Gray Fund for Marine Research (American Museum of Natural History) and Dr Brenda G. Williams personally. I am also very grateful to the oil companies Elf Aquitaine Norge AS, Norsk Hydro (5020 Bergen) and Statoil (4035 Stavanger) for letting me work with the material. I would like to thank Dr Mary E. Petersen (ZMUC) for practical help and support during my stay in Copenhagen and for discussions of the manuscript. It would have been much more difficult to do this work without the aid of Dr G. N. Buzhinskaja and V. V. Potin (ZISP), Dr A. N. Mironov (IORAS), Dr L. Wallin (UUZM), Dr A. Warén and K. Sindemark (SMNH), Dr F. Pleijel (Tjärnö Marine Biological Laboratory), Dr A. Bick (University of Rostock), Dr K. Fauchald and L. Ward (USNM), Dr E. Willassen and G. Vasstrand (UBZM), Mr S. F. Garcia-Martín (University of Cadiz, Spain). I am very much obliged also to all collectors of examined material. I am grateful for the support of the Electron Microscopic Centre of the Medical Faculty of the University of Rostock and of Gerd Fulda personally.

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Accepted 14 June 2002 – Printed 5 November 2003
Editorial responsibility: Tore Høisæter