



New sublittoral species of *Laonice* (Annelida: Spionidae) from southern Asian coasts

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Abstract

Four new species of *Laonice* (Annelida: Spionidae) are described from the southern and southeastern coasts of Asia: *L. (Laonice) persica* **sp. nov.**, *L. (Laonice) siamica* **sp. nov.**, *L. (Sarsiana) apicelamella* **sp. nov.** and *L. (Sarsiana) andamanica* **sp. nov.** Materials were collected within the scope of different environmental surveys performed by the consulting company Créocéan, ranging from the Persian Gulf (Indian Ocean) on the west, to the Gulf of Siam (Pacific Ocean) on the east. In addition, specimens found in the Gulf of Siam are tentatively attributed to *L. (Sarsiana) sinica*, and an English translation of the species description is provided for the first time. Different species subgroups within *L. (Sarsiana)* are also recognized based on key morphologic characters, though their phylogenetic relevance requires further confirmation. The scientific value of biological material collected during environmental surveys is emphasized, and contractors are encouraged to deposit reference collections in public natural history collections.

Key words: Polychaete, *Laonice*, *Sarsiana*, new species, morphology, Iran, Myanmar/Burma, Thailand

Introduction

To date, only two species of *Laonice* Malmgren, 1867 (Annelida: Spionidae) have been recorded in the southern and southwestern coasts of Asia, from the Red Sea to the South China Sea: (1) *Laonice brevicristata* Pillai, 1961, described and still known only from Tambalagam Bay, Sri Lanka (Pillai 1961; Sikorski 2011), and (2) *Laonice cirrata* (M. Sars, 1851). The latter was repeatedly cited across the whole region, including the Red Sea (Amoureux *et al.* 1978), the Persian Gulf and Strait of Hormuz (Wesenberg-Lund 1949), the Bay of Bengal (Fauvel 1932), Natuna Islands (Al-Hakim & Glasby 2004, as *Laonice* cf. *cirrata*), Vietnam (Gallardo 1968), and Hong Kong (Shin 1982). Later, it was recorded northwards, extending its distribution from the eastern coast of Asia to the Bering Sea and the Gulf of Alaska (Sikorski 2003a, 2003b). Still, *L. cirrata* was redescribed as having a circumpolar distribution restricted to the Arctic and the northern Atlantic and Pacific oceans (Sikorski 2003a, 2003b), with a southern Asian limit northward the Sea of Japan (V. Radashevsky, personal communication), raising doubts on the identity of the remaining Asian records of the species. However, the short descriptions that normally sustain these records are usually too incomplete to enable adequate comparisons with the recent and more detailed redescriptions, which, combined with the restricted distribution of *L. cirrata*, suggests that most (if not all) records of the species from southern and southeastern Asian waters are misidentifications.

Three additional species of the genus were more recently reported from the Australian Indian waters, namely *Laonice lemniscata* Greaves, Meißner & Wilson, 2011 (type locality: Albany, 35°21.5'S 118°17.4'E, 193 m depth), *Laonice pectinata* Greaves, Meißner & Wilson, 2011 (type locality: west of Perth, 32°51.267'S 114°15.417'E, 1440 m depth), and *Laonice insolita* Greaves, Meißner & Wilson, 2011 (type locality: Shark Bay, 27°57.583'S 112°15.417'E, 393 m depth), although the latter was later recombined as *Aonidella insolita* by Meißner *et al.* (2014).

Overall, this is a very low species richness for the Asian waters, when compared with other similar or even smaller areas, and considering the ongoing new species descriptions from the Arctic, Antarctic, Atlantic, Pacific and Mediterranean waters (Sikorski 2003a, 2003b and 2011; Aguirrezabalaga & Ceberio 2005; Radashevsky & Lana 2009; López 2011; Sikorski & Pavlova 2016; Sikorski *et al.* 2017, 2021a and 2021b; Bogantes *et al.* 2018). Therefore, we suspected that the species diversity currently recorded in southern and southwestern Asian coasts could be an underestimation due to the lack of studies targeting specifically the area.

In this paper, we are confirming the previous assumption after examining the Biological Collections of the Centre d'Estudis Avançats de Blanes (CEAB-CSIC), which include materials from the region collected during several environmental assessment projects carried out in co-operation with the French company Créocéan.

These marine environmental surveys are an important and valuable source of biological material suitable for taxonomic studies. Such material can be collected by consulting companies in localities previously un-investigated, in areas of restricted access, or in regions otherwise unsafe to sample due to political instability, war, piracy, terrorism or health conditions. Biological samples collected by consulting companies can also represent the very last chance to record and study the components of marine habitats subsequently affected or destroyed by large scale works, such as mining, desiccation of salt marshes, mangrove clearing for the expansion of aquaculture facilities and urban development, or coastal landfilling for the enlargement of harbors, airports and other coastal and offshore infrastructures.

The present study clearly proves the relevance of this type of materials for taxonomic studies as, despite the relatively low number of individuals deposited at the CEAB-CSIC, they enabled the formal description of four new species, as well as to report the possible presence of an additional fifth species previously known only from the Yellow and Bohai seas (Pacific Ocean).

Material and methods

The specimens of *Laonice* were obtained from soft sediments sampled with a van Veen grab (35 x 42 x 90 cm, about 0.1 m² per grab) operated from a vessel. The grab contents were first gently mixed in a container and then sieved out on board, by pouring it through a 1 mm mesh sieve. The retained sediment was then transferred to a plastic bag, fixed with a 4% formaldehyde/seawater solution, stained with Rose Bengal and stored until sorting. Sorting was performed under a binocular stereomicroscope and all selected specimens were preserved in 70% ethanol.

Samples were collected in: a) 1998, in the Gulf of Siam (about 180 km east off Songkhla, Thailand); b) 1998, in the east coast of the Persian Gulf (Nakhl Taqi, near Asaluyeh, northern side of Nayband Gulf, 250 km south of Bandar Bushehr, Iran); and c) 2003, in northwestern Andaman Sea (about 90 km off Ayeyarwandy Division, Myanmar/Burma).

Specimens were examined and drawn under a Leica M80 binocular and a Leica DM2000 transmitted light microscopes. As most available specimens were anterior fragments, size is expressed as body width (excluding parapodia) at the level of chaetigers 7–10 (Sikorski 2011). Total body length is provided only when complete specimens are available.

All types together with specimens of *Laonice* cf. *sinica* were deposited in the Museo Nacional de Ciencias Naturales of Madrid, Spain (MNCN). The type material of *Laonice sinica* Sikorski & Wu, 1998 is deposited in the collections of the Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia (ZISP) and Zoological Museum, Moscow State University, Russia (ZMUM).

Results

Taxonomic account

Laonice Malmgren, 1867 (emended)

Type species: *Nerine cirrata* M. Sars, 1851. By monotypy.

Diagnosis. Prostomium anteriorly rounded or slightly concave, either T- or skittle-shaped, clearly fused with

peristomium at anterior angles (subgenus *Laonice*), fused only by a thin membrane normally sunken in a groove between prostomium and peristomium (part of subgenus *Sarsiana*), or not fused at all (part of subgenus *Sarsiana* and subgenus *Appelloefia*). Occipital antenna present (most usual), absent or with variable presence (e.g., in *Laonice bahusiensis* Söderström, 1920). Caruncle well developed, long (except in the deep-sea species *Laonice (Sarsiana) magnacristata* Maciolek, 2000 and *Laonice (Laonice) plumisetosa* Bogantes, Halanych & Meißner, 2018), extending posteriorly over several chaetigers following a pair of nuchal organ loops starting from palp attachments. Nuchal organs long and widely variable in length (subgenus *Laonice*) or short (usually around 10 chaetigers, always less than 20) and less variable in length (subgenera *Sarsiana* and *Appelloefia*). Palps often long, without sheath at base. Peristomium not fused with chaetiger 1. Parapodia biramous; each ramus of anterior chaetigers with three tufts of long, thin capillary chaetae, including anterior and posterior parallel vertical rows of chaetae arranged in single lines (except in subgenus *Appelloefia*, with more than two rows of capillaries in several anteriormost chaetigers), with a third tuft inserted above (notopodia) and below (neuropodia) these rows. Inferior neurochaetae or sabre chaetae [“Haarborsten” in Söderström (1920)] appearing in anterior region, being longer and stouter than ordinary capillaries. Neuropodial hooks with primary hood only, with chaetiger of first appearance varying; notopodial hooks generally absent (may be present in posteriormost chaetigers in some species of subgenus *Sarsiana*). Dorsal branchiae from chaetiger 2, separated from notopodial postchaetal lamellae and on a variable number of anterior chaetigers, rarely up to body end (e.g., in subgenus *Appelloefia*). Lateral inter-neuropodial pouches on a variable number of anterior chaetigers, often up to body end, rarely absent; first chaetiger with pouches varying. Anus terminal, surrounded by two ventral lobes or small papilliform cirri (usually placed close together) and several pairs of comparatively long, thinner dorsal anal cirri. Pigmentation absent.

Laonice (Laonice) Malmgren, 1867

Laonice (Laonice): Sikorski, Gunton & Pavlova 2017: 962.

Diagnosis. Prostomium obviously fused with fronto-lateral peristomial margins. Caruncle long, highly variable in length but extending beyond half of branchiate chaetigers. Capillary chaetae in two vertical rows on anterior chaetigers. Hooded hooks with main fang surmounted by one or two paired apical teeth. Notopodial hooks absent. Continuous dorsal transverse crests in postbranchiate region present or absent.

Laonice (Laonice) persica sp. nov.

Figs 1A–H, 6.

LSID: urn:lsid:zoobank.org:act:B598C9EF-4924-44C0-B42C-403558109C1C

Holotype. MNCN16.01/19125, Persian Gulf, Iran, st. 19, 27°29.156'N, 52°34.003'E, 19 m depth, 34.9% of gravels (0.5–10 mm), 5.8% of silt and clay (<63 µm), 17 June 1998.

Paratypes. MNCN16.01/19126, 2 specimens, Persian Gulf, Iran, st. 8, 27°30.229'N, 52°33.574'E, 19 m depth, 45.1% of gravels (0.5–10 mm), 7.8% of silt and clay (<63 µm), 17 June 1998; MNCN16.01/19127, 1 specimen, Persian Gulf, Iran, st. 24, 27°28.797'N, 52°34.168'E, 18 m depth, 22.4% of gravels (0.5–10 mm), 6.8% of silt and clay (<63 µm), 17 June 1998.

Description. Body 0.4–0.5 mm wide (0.4 mm in holotype, one anterior fragment with 51 chaetigers and one short middle fragment with 18). Posterior region not collected.

Prostomium fused with peristomium at fronto-lateral margins (Fig. 1A, G), anteriorly rounded, posteriorly extending to chaetiger 23–26 (26 in holotype) as a low narrow caruncle. Nuchal organs as U-shaped ciliary bands on both sides of caruncle. Occipital antenna large (absent in paratypes, without traces of attachment). Two pairs of eyes in trapezoidal arrangement; median pair large, bean-shaped; lateral pair small, located ahead, set wider apart and often deeply embedded into tissue (Fig. 1A).

Branchiae from chaetiger 2 to 31–34 (32 in holotype), shorter than notopodial postchaetal lamellae at chaetiger 2; 1.5–2 times longer than notopodial postchaetal lamellae on following 15 chaetigers, more than twice longer at midbody (due to decreasing length of notopodial postchaetal lamellae) and shorter than notopodial postchaetal lamellae on last two branchiate chaetigers.

Notopodial postchaetal lamellae ear-like on anterior 25–30 chaetigers (Fig. 1C–E), narrowing upwardly, usually with acute tips on first four chaetigers, then tips becoming slightly rounded. Largest notopodial lamellae from chaetiger 4–10, with tips touching dorsally at chaetiger 4, significantly shortening along postbranchiate region, becoming rounded above and reduced below notochaetal fascicle/notopodium insertion level (Fig. 1F). Neuropodial postchaetal lamellae ear-like, almost triangular (Fig. 1C–E), largest on chaetigers 8–22, shortening afterwards, becoming very short and hardly detectable on postbranchiate chaetigers (Fig. 1F).

Dorsal transverse crests connecting notopodial postchaetal lamellae absent (Fig. 1B).

Lateral inter-neuropodial pouches starting from chaetiger 4–6 (5 in holotype), not visible after chaetiger 32–34.

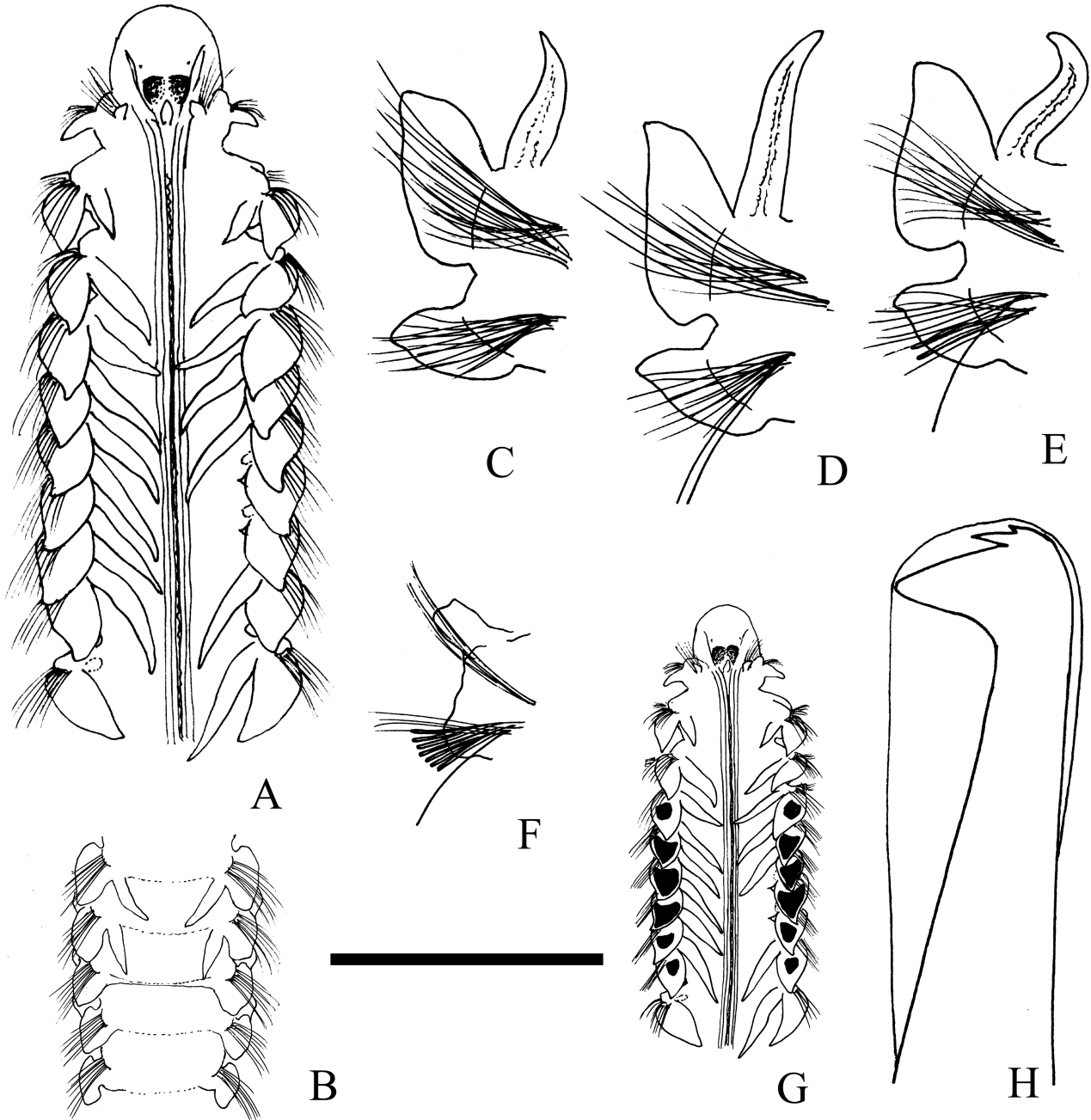


FIGURE 1. *Laonice persica* sp. nov. A: anterior region (10 chaetigers), dorsal view. B: end of branchiate region (chaetigers 31–35), dorsal view. C–F: parapodia of chaetigers 7, 20, 32 and 46, frontal view. G: staining pattern with Methyl Green, anterior region (10 chaetigers), dorsal view. H: neuropodial hooded hook, lateral view. Scale, mm: A–F, 1; G, 1.4; H, 0.05. Material: A–B, G, paratype, Persian Gulf, st. 8 (MNCN16.01/19126); C–F, H, holotype, Persian Gulf, st. 19 (MNCN16.01/19125).

Capillaries of anterior chaetigers arranged in two vertical rows. Neuropodial hooks from chaetiger 29–32, up to seven per neuropodium, with one pair of lateral small apical teeth and a single superior median tooth above main fang, appearing tridentate in lateral view (Fig. 1H). Notopodial hooks not seen. Sabre chaetae from chaetiger 17–22 (20 in holotype), one per fascicle.

Pygidium not seen, missing.

Pigmentation absent.

Methyl Green staining. Strong in upper parts of notopodial postchaetal lamellae from chaetiger 4 to 8–10 (Fig. 1G); very weak and diffuse on ventral surface of chaetigers 24–35, where it fades remarkably sooner than on notopodial postchaetal lamellae.

Type locality. Persian Gulf, Iran, northwest of Naband Gulf (27°29.156'N, 52°34.003'E), 19 m depth.

Etymology. The specific epithet *persica* derives from the toponymic name of the inlet where the types were collected, the Persian Gulf.

Distribution. Persian Gulf (Indian Ocean) (Fig. 6).

Remarks. The existence of specimens having and lacking occipital antenna is not unique to *L. persica* **sp. nov.**, having been also reported in the type-material of *L. bahusiensis* (Sikorski *et al.* 2021b).

Laonice persica **sp. nov.** has the prostomium completely fused with the peristomium, which places the species in *L. (Laonice)* as defined by Sikorski *et al.* (2017). It also lacks entire dorsal transverse crests connecting the notopodial postchaetal lamellae, and so belongs to the *L. cirrata* complex, together with *L. brevicornis* (Kinberg, 1866) [including the junior synonyms *L. aperata* Radashevsky & Lana, 2009 and *L. petersenae* Radashevsky & Lana, 2009], *L. quadridentata* Blake & Kudenov, 1978, *L. bassensis* Blake & Kudenov, 1978 (likely), *L. shamrockensis* Sikorski, 2003, *L. asaccata* Sigvaldadóttir & Desbruyères, 2003, *L. pinnulata* Radashevsky & Lana, 2009, *L. cricketae* Sikorski & Pavlova, 2016, and *L. plumisetosa* Bogantes *et al.*, 2018. However, *L. cirrata* is much larger (adults up to 5 mm wide), with hooks usually appearing bidentate in lateral view (tridentate in *L. persica* **sp. nov.**) and with lateral inter-neuropodial pouches appearing from chaetiger 52 (absent after chaetiger 32–34 in *L. persica* **sp. nov.**). *Laonice brevicornis* has tridentate hooks in lateral view and worms are not large (1.5–2 mm wide), but inter-neuropodial pouches are either absent or present only from chaetigers 3–17. *Laonice cricketae* has nuchal organs reaching chaetiger 20 and lateral inter-neuropodial pouches appearing only from chaetiger 40 (5–6 in *L. persica* **sp. nov.**), while the fusion of prostomium and peristomium is not so evident. Finally, *L. shamrockensis*, *L. asaccata*, *L. pinnulata* and *L. plumisetosa* have nuchal organs reaching chaetiger 5, 4, 7 and 1, respectively (23–26 in *L. persica* **sp. nov.**), while lateral inter-neuropodial pouches appear from chaetiger 3 in *L. shamrockensis*, *L. pinnulata* and *L. plumisetosa* and are absent in *L. asaccata* (5–6 in *L. persica* **sp. nov.**). Nuchal organ are also remarkably shorter in *L. quadridentata* (reaching chaetiger 18) and *L. bassensis* (reaching chaetiger 7).

Laonice (Laonice) siamica **sp. nov.**

Figs 2A–I, 6.

LSID: urn:lsid:zoobank.org:act:545BCAEE-01D8-454F-960D-86B54F9025DA

Holotype. MNCN16.01/19128, Gulf of Siam, off Thailand, st. 5, 07°36.018'N, 102°50.543'E, 64 m depth, 92.2% of silt and clay (<63 µm) and 7.6% of fine sand (63–250 µm) with shell fragments, 28 July 1998.

Description. Holotype 0.7 mm wide, 20 mm long for 104 chaetigers (one anterior fragment of 60 chaetigers and one posterior with 44).

Prostomium fused with peristomium at fronto-lateral margin (Fig. 2A, C), anteriorly rounded, extending posteriorly to beginning of chaetiger 41 as a low narrow caruncle, accompanied by nuchal organs as lateral ciliary bands. Occipital antenna thin, erect, half length of notopodial postchaetal lamellae of chaetiger 1. One pair of small, distinct, faded brownish eyespots in front of attachment of occipital antenna.

Branchiae from chaetiger 2; first pair half as long as notopodial postchaetal lamellae, then increasing their length but still shorter until chaetiger 4 (Fig. 2A, E), of equal length on chaetiger 5, and twice longer after chaetiger 10 (Fig. 2F); then branchiae gradually shortening from chaetiger 38 (Fig. 2B, G), being absent after chaetiger 50 (last branchiate chaetiger).

Notopodial postchaetal lamellae leaflike, almost triangular, with narrow acute tips through all body (Fig. 2A–C, E–G), but particularly pronounced on the four anteriormost chaetigers (Fig. 2A, E), gradually shortening to half the length of anterior ones on last branchiate chaetigers, becoming narrow triangles on posteriormost chaetigers (Fig. 2G). Anterior postbranchiate chaetigers with notopodial postchaetal lamella extending slightly dorsally, not

reaching middle dorsum (Fig. 2B). Neuropodial postchaetal lamellae almost trapezoidal anteriorly (Fig. 2E), then triangular, with acute tips through all body (Fig. 2F–G).

Dorsal transverse crests absent.

Lateral inter-neuropodial pouches from chaetiger 5–6, irregularly present from chaetiger 50 to posteriormost chaetigers.

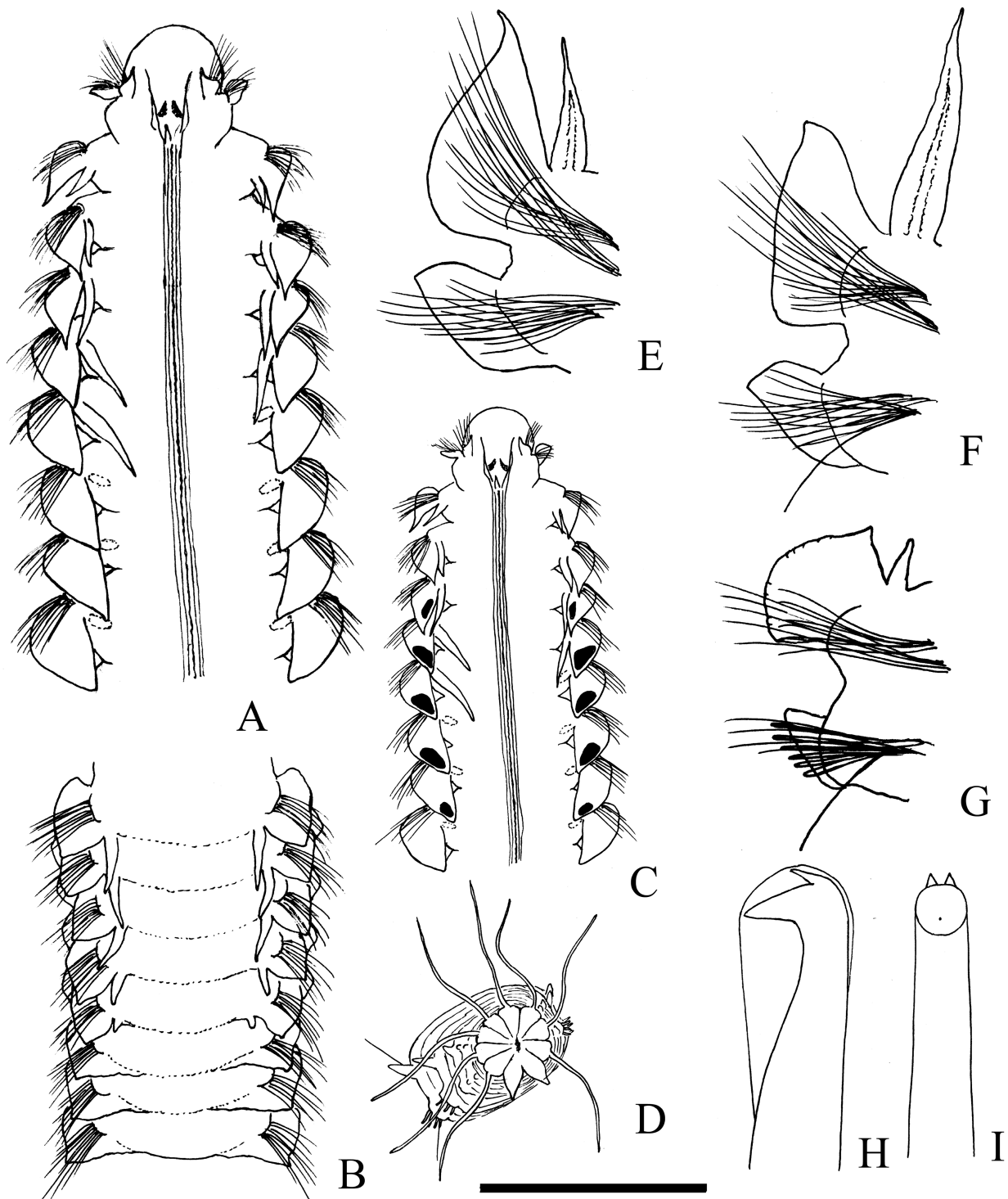


FIGURE 2. *Laonice siamica* sp. nov. A: anterior region (9 chaetigers), dorsal view. B: end of branchiate region (chaetigers 46–53), dorsal view. C: staining pattern with Methyl Green, anterior region (9 chaetigers), dorsal view. D: pygidium, rear view. E–G: parapodia of chaetigers 3, 25 and 49 (chaetiger anterior to last branchiate chaetiger), frontal view. H: neuropodial hooded hook, chaetiger 49, lateral view. I: neuropodial hooded hook, chaetiger 49, frontal view (scheme). Scale, mm: A–B, 1; C–D, 0.7; E–G, 0.5; H–I, 0.05. Material: holotype, Gulf of Siam, st. 5 (MNCN16.01/19128).

Capillaries of anterior chaetigers arranged in two vertical rows. Neuropodial hooks from chaetiger 39, up to 6–8 per fascicle, bidentate in lateral view, tridentate in frontal view, with one pair of small apical teeth side by side above main fang (Fig. 2H–I). Notopodial hooks absent. Sabre chaetae from chaetiger 14, one per fascicle.

Pygidium with ten lobes forming a ring around the anus: four bilaterally symmetrical pairs bearing one thin threadlike anal cirrus, and one ventral pair closely set, pointed and lacking cirri (Fig. 2D).

Pigmentation absent.

Methyl Green staining. As oval spots on upper parts of notopodial postchaetal lamellae of chaetigers 4–8 (Fig. 2C).

Type locality. Gulf of Siam, off Thailand (07°36.018'N, 102°50.543'E), 64 m depth.

Etymology. The specific epithet *siamica* derives from the toponymic name of the inlet where the type was collected, the Gulf of Siam.

Distribution. Gulf of Siam (Pacific Ocean) (Fig. 6).

Remarks. *Laonice siamica* **sp. nov.** can be referred to *L. (Laonice)* as defined by Sikorski *et al.* (2017), as it has the prostomium completely fused with the peristomium. It is closely related to the *L. cirrata* complex [*L. brevicornis* (with both *L. aperata* and *L. petersenae* included), *L. quadridentata*, *L. cricketae* and, probably, *L. bassensis*, *L. shamrockensis*, *L. asaccata*, *L. pinnulata* and *L. plumisetosa*]. However, the gradual reduction of the posterior branchiae is quite unique of *L. siamica* **sp. nov.** While measuring only 0.7 mm wide, the holotype of *L. siamica* **sp. nov.** has nuchal organs extending to chaetiger 41 and up to 50 pairs of branchiae, which only occurs in specimens of *L. cirrata* measuring >2.2 mm wide. Nuchal organs of *L. shamrockensis*, *L. asaccata*, *L. pinnulata* and *L. plumisetosa* are much shorter and do not extend over chaetiger 7 (41 in *L. siamica* **sp. nov.**). In *L. brevicornis* and *L. cricketae* nuchal organs are shorter as well: up to chaetiger 26 in *L. brevicornis* (with last branchiae on chaetiger 36) and up to chaetiger 20 in *L. cricketae* (with last branchiae on chaetiger 39 and lateral inter-neuropodial pouches only from chaetiger 40, instead of chaetiger 7 in *L. siamica* **sp. nov.**). Nuchal organs, as in the case of the species described above, are also remarkably shorter in *L. quadridentata* (up to chaetiger 18) and *L. bassensis* (up to chaetiger 7).

Laonice (Sarsiana) Sikorski, Gunton & Pavlova 2017

Laonice (Sarsiana): Sikorski *et al.* 2017: 962.

Type species: *Laonice sarsi* Söderström, 1920.

Diagnosis. Prostomium not obviously fused or non-fused with fronto-lateral peristomial margin. Anterolateral prostomial corners sometimes fused to peristomium by an inconspicuous (in dorsal view) membrane, often deeply sunken in prostomium/peristomium groove. Nuchal organs generally short (usually extending up to chaetiger 10). Dorsal transverse crests present or absent. Other numerical characters highly variable. Notopodial hooded hooks may be present in posteriormost chaetigers.

Laonice (Sarsiana) apicelamella **sp. nov.**

Figs 3A–L, 6.

LSID: urn:lsid:zoobank.org:act:B915D3EA-1285-49FD-BFD4-A08E7941F968

Holotype. MNCN16.01/19129, Gulf of Siam, off Thailand, st. 14, 07°49.818'N, 102°45.162'E, 73 m, 97.8% of silt and clay (<63 µm) and 2.2% of fine sand (63–250 µm) with shell fragments, 28 July 1998.

Paratypes. MNCN16.01/19130, 1 specimen, Andaman Sea, off Myanmar/Burma, st. E7, 15°07.997'N, 94°46.838'E, 46 m depth, 76.3% of silt and clay (<63 µm), 03 December 2003; MNCN16.01/19131, 1 specimen, Andaman Sea, off Myanmar/Burma, st. S4, 15°03.137'N, 94°46.050'E, 51 m depth, 90% of silt and clay (<63 µm), 03 December 2003; MNCN16.01/19132, 1 specimen, Gulf of Siam, off Thailand, st. 8, 07°35.990'N, 102°44.202'E, 66 m depth, 92.7% of silt and clay (<63 µm) and 7.0% of fine sand (63–250 µm) with shell fragments, 27 July 1998; MNCN16.01/19133, 1 specimen, Gulf of Siam, off Thailand, st. 4, 07°32.190'N, 102°47.742'E, 61 m depth, 89.6% of silt and clay (<63 µm) and 10.0% of fine sand (63–250 µm) with shell fragments, 27 July 1998; MNCN16.01/19134, 1 specimen, Gulf of Siam, off Thailand, st. 1, 07°21.293'N, 102°37.073'E, 58 m depth, 81.8% of silt and clay (<63 µm) and 17.8% of fine sand (63–250 µm) with shell fragments, 25 July 1998.

Description. Body 0.6–0.7 mm wide. Holotype in four fragments of 19 (anterior), 5+2 (middle), and 24 (posterior) chaetigers.

Prostomium short, as a nearly equilateral triangle with truncated, slightly concave anterior margin, fused with peristomial ventral surface by a thin fold deeply hidden in prostomium/peristomium groove (Fig. 3A, D). Nuchal organs U-shaped, with two wide loops following caruncle, reaching chaetiger 9–10 (8 in holotype, with a pair of nearly triangular expansions reaching middle of chaetiger 9); distance between loops nearly equivalent to loop width (Fig. 3A, D). Occipital antenna moderately developed. One pair of tear drop-shaped eyespots, with frontal and outer borders more strongly colored, just in front of occipital antenna.

Branchiae from chaetiger 2, probably up to chaetiger 24–29 (uncertainty due to types fragmentary condition); as long as notopodial postchaetal lamellae on chaetigers 2–3 (holotype), 1.2 times longer on chaetiger 4, 1.5 times longer on chaetigers 5–6, twice longer on chaetiger 9 (only after chaetiger 14 in holotype), 2.3 times longer on chaetiger 10 and 2.5 times longer on chaetiger 13 (only up to twice longer in paratypes) (Fig. 3A, C–F); branchiae shortening on the six posteriormost branchiate chaetigers (Fig. 3B), being four and five times longer in last 6–4 chaetigers than in last 3–2 and last one, respectively (Fig. 3G). Branchial margins usually bearing long cilia.

Anterior notopodial postchaetal lamellae leaf-like, with acute pointed tips (Fig. 3E); from chaetiger 6, tips gradually shifting downwards along lateral lamellar margin (Fig. 3F); tips progressively narrowing, becoming elongated upward on posteriormost branchiate chaetigers, and being reduced to small tips (upper one peak-like, lateral one as large, sharply acute peak) on last few branchiate chaetigers (Fig. 3G). Posteriormost notopodial postchaetal lamellae oval, leaf-like (Fig. 3H). Large, sharply acute lateral peaks quite pronounced on several lamellae of postbranchiate chaetigers. Small, tongue-shaped prechaetal notopodial lamellae from chaetiger 2, gradually shortening along branchiate chaetigers, non-visible on postbranchial chaetigers. Neuropodial postchaetal lamellae ear-like, with an acute peak on upper part of lateral margin (Fig. 3E–H).

Dorsal transverse crests connecting notopodial postchaetal lamellae absent, but very pronounced transverse ciliation (nototrochs—Fig. 3B) present in about last four branchiate chaetigers and, at least, on the following 20 postbranchiate chaetigers.

Lateral inter-neuropodial pouches from chaetiger 5–6, up to last chaetiger present in all available anterior fragments.

Capillaries of anterior chaetigers arranged in two vertical rows. Neuropodial hooks probably from chaetiger 28–32 (uncertainty due to types fragmentary condition), up to 10 per fascicle. Notopodial hooks in posterior notopodia (Gulf of Siam, st. 1, MNCN16.01/19134). Neuropodial and notopodial hooks bidentate in lateral view (Fig. 3I, K), tridentate in frontal view, with one pair of small apical teeth side by side above main fang (Fig. 3J, L). Distal region of notopodial hooks smaller than in neuropodial ones, sometimes small, knob-like, with teeth difficult to distinguish. Sabre chaetae from chaetiger 11–20, 1–2 per fascicle.

Pygidium in poor condition, showing a single remaining anal cirrus in only one specimen (Gulf of Siam, st. 1, MNCN16.01/19134).

Pigmentation absent.

Methyl Green staining. Strong on tips and along outer edges of notopodial postchaetal lamellae on chaetigers 2–7 (Fig. 3D) and on upper edges of neuropodial postchaetal lamellae on chaetigers 2–17.

Type locality. Gulf of Siam, off Thailand (07°49.818'N, 102°45.162'E), 73 m depth.

Etymology. The specific epithet *apicelamella* refers to the very pronounced, large, pointed peak on the lateral edge of the notopodial postchaetal lamellae of nearly all branchiate and several postbranchial chaetigers (Fig. 3A–B, D, F–G).

Distribution. Gulf of Siam (Pacific Ocean) and Andaman Sea (Indian Ocean) (Fig. 6).

Remarks. The holotype was assumed as being composed by the four fragments found in st. 14 (Gulf of Siam), but as this may not be the case, the numerical characters of the species must be considered an estimate. All paratypes are short anterior fragments. Also, the single posterior fragment having pygidium was in poor condition, showing only one anal cirrus. However, most likely the species has two short ventral cirri and several paired dorsal cirri surrounding the anus.

Laonice apicelamella sp. nov. belongs to *L. (Sarsiana)* as defined by Sikorski *et al.* (2017), as it has comparatively short nuchal organs, always similar in length in all studied specimens, capillaries of anterior chaetigers arranged in two rows only, prostomium fused to ventral peristomial surface by a thin fold deeply sunken in the prostomium/peristomium groove, and hooks in the posteriormost notopodia.

Dorsal transverse crests connecting notopodial postchaetal lamellae are absent in this species. As in *L. (Laonice)*, this character allows the recognition of various morphological subgroups within *L. (Sarsiana)*, which may or may not have a

phylogenetic significance. In particular, the absence of dorsal transverse crests in *L. (Sarsiana)* is usually combined with the presence of (1) a minute membrane connecting the anterior angles of prostomium and peristomium, usually sunken in the groove between them, and (2) hooded hooks in the most posterior notopodia. This combination of characters is also present in *L. sarsi* Söderström, 1920, *L. antarcticae* Hartman, 1953, *L. dayianum* Sikorski, 1997, *L. rossica* Sikorski, 2003, *L. olgae* Sikorski & Pavlova, 2016, and *L. alberti* Sikorski *et al.*, 2021. Moreover, *L. praecirrata* Hartmann-Schröder, 1965, *L. nuchala* Blake, 1996, *L. junoyi* Aguirrezabalaga & Ceberio, 2005, *L. parvabranchiata* Radashevsky & Lana, 2009, and *L. whittardensis* Sikorski *et al.*, 2017 also resemble morphologically *L. apicelamella* *sp. nov.*

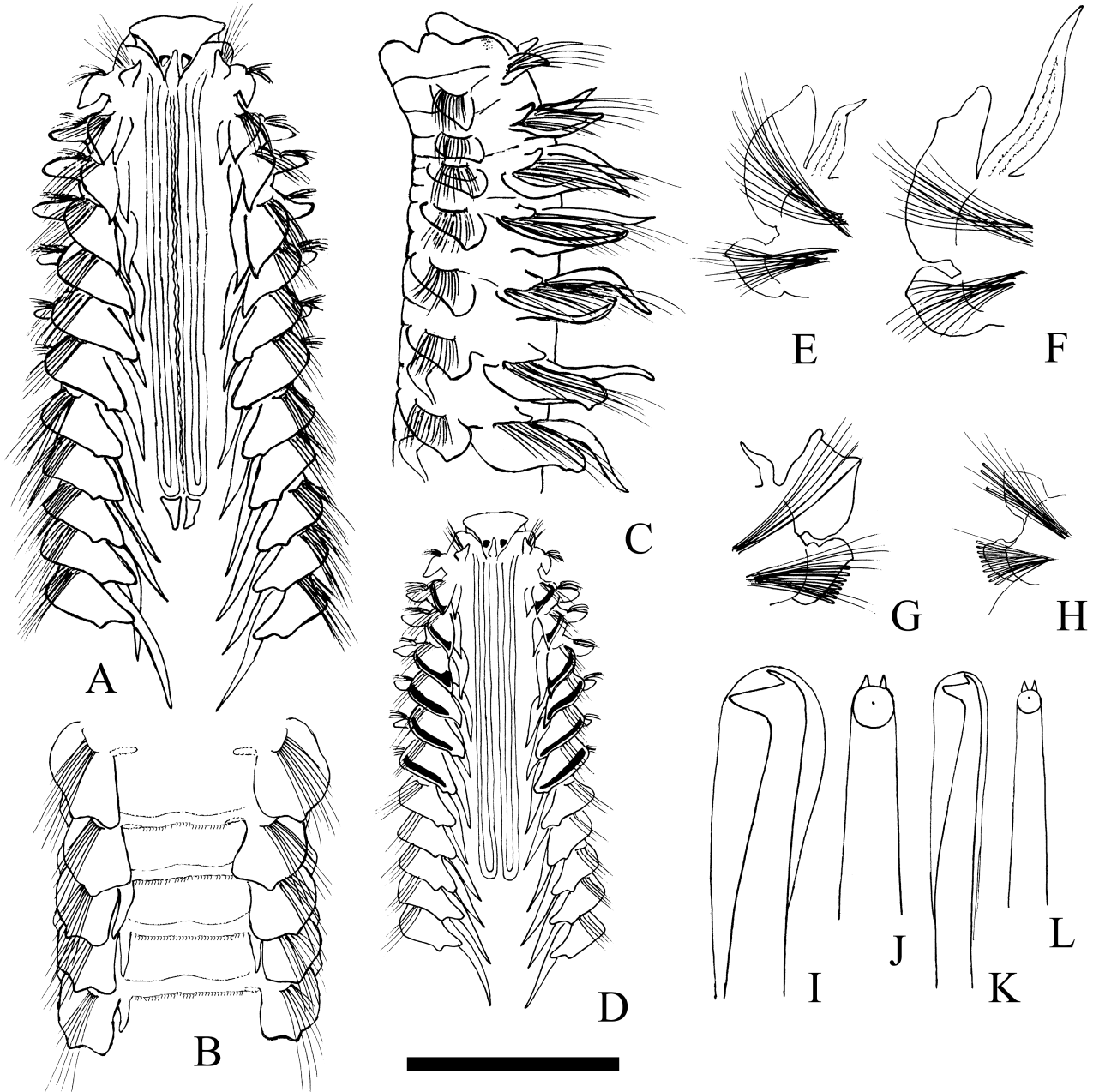


FIGURE 3. *Laonice apicelamella* *sp. nov.* A: anterior region (12 chaetigers), dorsal view. B: end of branchiate region (chaetigers 44–48), dorsal view. C: anterior region (7 chaetigers), lateral view. D: staining pattern with Methyl Green, anterior region (12 chaetigers), dorsal view. E–H: parapodia of chaetigers 4, 13, 29? (last branchiate chaetiger) and 19 before pygidium, frontal view. I: neuropodial hooded hook, chaetiger 19 before pygidium, lateral view. J: neuropodial hooded hook, chaetiger 19 before pygidium, frontal view (scheme). K, notopodial hooded hook, chaetiger 19 before pygidium, lateral view. L: notopodial hooded hook, chaetiger 19 before pygidium, frontal view (scheme). Scale, mm: A–C, 1; D, 1.4; E–H, 2.1; I–L, 0.05. Material: A–C, E–G, paratype, Andaman Sea, st. E7 (MNCN16.01/19130); D, paratype, Gulf of Siam, st. 8 (MNCN16.01/19132); H–L, paratype, Gulf of Siam, st. 1 (MNCN16.01/19134).

In *L. apicelamella* **sp. nov.** the lateral inter-neuropodial pouches appear from chaetiger 5–6, while in *L. sarsi* they start from 4–33, with only the specimens measuring less than 0.4 mm wide having lateral pouches starting before chaetiger 8 (Sikorski 2003a). In *L. rossica* they range from 2–50, and only specimens less than 0.4 mm wide may have lateral inter-neuropodial pouches starting before chaetiger 8 (Sikorski 2003b). *Laonice antarcticae* has lateral inter-neuropodial pouches from chaetiger 3–4 and nuchal organs extending to chaetiger 12–13 (Sikorski, 2011) (9–10 in *L. apicelamella* **sp. nov.**); *L. olgae* has lateral inter-neuropodial pouches starting at chaetigers 32–33 and *L. alberti* at chaetiger 21–34, but also nuchal organs reaching chaetiger 5–7 and neuropodial hooks starting at chaetiger 35–38 (28–32 in *L. apicelamella* **sp. nov.**), and branchiae absent from chaetiger 31–39 (24–29 in *L. apicelamella* **sp. nov.**). *Laonice dayianum* has longer nuchal organs reaching chaetiger 12–14, lateral inter-neuropodial pouches starting from chaetiger 18–28, and sabre chaetae from chaetiger 26 (11–20 in *L. apicelamella* **sp. nov.**) (Sikorski 2011). *Laonice parvabranchiata* has lateral inter-neuropodial pouches starting from chaetiger 14–16, sabre chaetae from chaetiger 27–29, neuropodial hooks after chaetiger 42, and branchiae absent from chaetiger 35 onwards. *Laonice junoyi* has shorter nuchal organs extending for 6–7 chaetigers and lateral inter-neuropodial pouches starting at chaetiger 8–9. *Laonice nuchala* and *L. praecirrata* have longer nuchal organs reaching chaetiger 13 and 15–21, respectively, lateral inter-neuropodial pouches starting at chaetigers 7–8 and 9–24, and more numerous branchiae (>47 and 59, respectively). The deep-sea species *L. whittardensis* measures less than 0.4 mm wide and can be distinguished from *L. apicelamella* **sp. nov.** by the majority of morphological characters discussed above (Sikorski *et al.* 2017). Finally, the characteristic presence of nototrochs on several postbranchiate chaetigers in *L. apicelamella* **sp. nov.** is rarely present in the other morphologically similar species.

***Laonice (Sarsiana) andamanica* sp. nov.**

Figs 4A–L, 6.

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Holotype. MNCN16.01/19135, Andaman Sea, off Myanmar/Burma, st. E14, 15°07.334'N, 94°46.852'E, 47.4 m depth, 77% of silt and clay (<63 µm), 03 December 2003.

Paratype. MNCN16.01/19136, Andaman Sea, off Myanmar/Burma, st. E13B, 15°07.537'N, 94°46.854'E, 47 m depth, 85% of silt and clay (<63 µm), 03 December 2003.

Description. Holotype incomplete, 0.7 mm wide, in three fragments with 37 (anterior) and 6 plus 2 (middle) chaetigers. Paratype incomplete, 0.7 mm wide, with 22 anterior chaetigers.

Prostomium T-shaped, with rounded anterior margin, joined to peristomium, with junction clearly outlined, but completely lacking a space between prostomium and peristomium (Fig. 4A). Caruncle visible, extending to posterior border of chaetiger 7–9. Nuchal organs extending to end of chaetiger 9–11, as U-shaped ciliary bands on sides of caruncle. Palps not seen.

Long, acute occipital antenna on posterior prostomial region, as long as notopodial postchaetal lamellae of chaetiger 1. One pair of eyespots in front of occipital antenna (Fig. 4A).

Branchiae from chaetiger 2 (Fig. 4A, C), narrowing into thread-like tips (Fig. 4F–G), shorter than notopodial postchaetal lamellae until chaetiger 4 (those on chaetigers 2–3 being half long), as long as on chaetigers 5–8, and slightly longer (approx. 1.2 times—Fig. 4A, G) until chaetiger 27–28; last pair visible on chaetiger 35 (Fig. 4B, H).

Notopodial postchaetal lamellae much longer than branchiae on posteriormost branchiate region (Fig. 4B, H), up to four times longer than last pair of branchiae. Notopodial postchaetal lamellae narrowing to acute tips until chaetiger 42 (Fig. 4I), gradually lengthening to end of branchiate region (Fig. 4B), then considerably longer from chaetiger 29–35, being twice as long on chaetiger 35 than on chaetigers 5–8 (Fig. 4F, H) and three times longer than on chaetiger 2, and sharply decreasing on the postbranchiate chaetigers (Fig. 4J). Tips of lamellae acute, gradually extending to increasingly narrow, long, sharply pointed processes from chaetigers 18–29 (Fig. 4H), lacking acute tips backwards (Fig. 4J). Tips of lamellae reaching opposite chaetal tuft (Fig. 4B). Notopodial postchaetal lamellae ear-like, with rounded upper edges from chaetiger 42 (Fig. 4J). Inferior regions of notopodial postchaetal lamellae (below neuropodial chaetal tuft) becoming visible from chaetiger 31 (Fig. 4H–J). Neuropodial postchaetal lamellae axe-shaped, with upper lateral angle forming an acute tip anteriorly, progressively becoming more rounded on posterior chaetigers (Fig. 4F–J). Noto- and neuropodial prechaetal lamellae short, not easily distinguishable.

Continuous dorsal transverse crests connecting notopodial postchaetal lamellae first appearing three chaetigers before last branchiate one; maximum height at chaetigers 35–37 (Fig. 4B); present up to the last chaetiger of holotype. Transverse nototrochs quite pronounced anteriorly on several branchiate chaetigers.

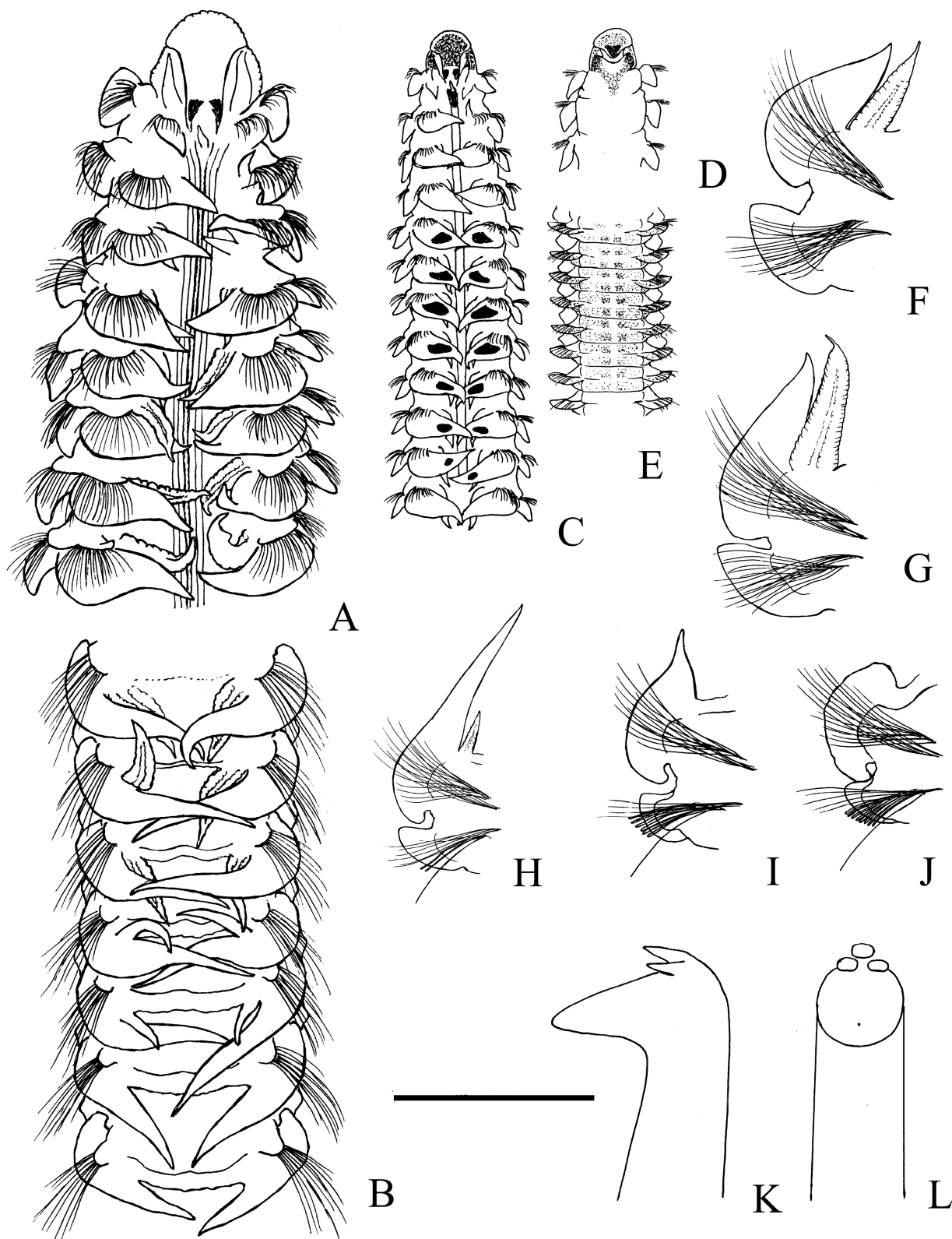


FIGURE 4. *Laonice andamanica* sp. nov. A: anterior region (8 chaetigers), dorsal view. B: end of branchiate region (chaetigers 31–37), dorsal view. C: staining pattern with Methyl Green, anterior region (12 chaetigers), dorsal view. D: staining pattern with Methyl Green, prostomium and peristomium, ventral view. E: staining pattern with Methyl Green, middle region (chaetigers 26–33), ventral view. F–J: parapodia of chaetigers 8, 21, 35 (last branchiate chaetiger), 38 and 46, frontal view. K: neuropodial hooded hook, chaetiger 46, lateral view. L: neuropodial hooded hook, chaetiger 46, frontal view (scheme). Scale, mm: A–B, 1; C–E, 2; F–J, 0.7; K–L, 0.025. Material: holotype, Andaman Sea, st. E14 (MNCN16.01/19135).

Lateral inter-neuropodial pouches from chaetiger 26, up to at least chaetiger 37 in holotype anterior fragment.

Capillaries of anterior chaetigers arranged in two vertical rows. Neuropodial hooks from chaetiger 34, up to eight per fascicle, tridentate in lateral view (Fig. 4K), quadridentate in frontal view, with one pair of small apical teeth side by side and a single superior median tooth above main fang (Fig. 4L). Notopodial hooks absent in holotype. Sabre chaetae from chaetiger 27.

Pygidium not seen, missing.

Pigmentation absent.

Methyl Green staining. Strong on inner upper parts of notopodial postchaetal lamellae from chaetiger 5–10, on dorsal and ventral side of peristomium, on prostomium below eyespots and behind occipital antenna, and ventrally in front of mouth (Fig. 4C–D). Very weak, diffuse staining ventrally and on neuropodial postchaetal lamellae of chaetigers 25–32 (Fig. 4E), fading remarkably sooner than on notopodial postchaetal lamellae, prostomium and peristomium.

Type locality. Andaman Sea, off Myanmar/Burma (15°07.334'N, 94°46.852'E), 47.4 m depth.

Etymology. The specific epithet *andamanica* derives from the toponymic name of the sea where the types were collected, the Andaman Sea.

Distribution. Andaman Sea (Indian Ocean) (Fig. 6).

Remarks. The holotype was the single specimen having enough chaetigers to determine the main numerical characters. *Laonice andamanica* sp. nov. belongs to *L. (Sarsiana)* as defined by Sikorski *et al.* (2017), as it has comparatively short nuchal organs (similar in length in all studied specimens) and capillaries of the anterior chaetigers arranged in two vertical rows only. Moreover, it has dorsal transverse crests, but apparently lacks the membrane connecting the anterior angles of prostomium and peristomium, as well as hooks in most posterior notopodia. Thus, it most closely resembles *L. japonica* (Moore, 1907), *L. sinica* Sikorski & Wu, 1998, *L. praecirrata*, *L. branchiata* Nonato, Bolívar & Lana, 1986 and *L. magnacristata*. *Laonice andamanica* sp. nov. can be easily distinguished from these species in having several notopodial postchaetal lamellae of posterior branchiate chaetigers with pointed tips elongated into narrow long lanceolate processes with length equal to the body width on the last branchiate chaetigers (Fig. 4B, H). Besides, *L. japonica* has nuchal organs reaching chaetiger 18 (9–11 in *L. andamanica* sp. nov.) and lateral inter-neuropodial pouches appearing from chaetiger 4 (26 in *L. andamanica* sp. nov.); *L. sinica* has lateral inter-neuropodial pouches from chaetiger 5–9 and a different shape of dorsal transverse crests; *L. magnacristata* is 0.4 mm wide, has nuchal organs reaching chaetiger 2, 4–7 pairs of branchiae (34 pairs in *L. andamanica* sp. nov.), sabre chaetae from chaetiger 6 (27 in *L. andamanica* sp. nov.), and lateral inter-neuropodial pouches from chaetiger 7–8; and *L. praecirrata* has nuchal organs extending until chaetiger 15–21 and the membrane connecting prostomium with peristomium at the anterior angles is sunken in the groove between them. Finally, the lateral inter-neuropodial pouches in *L. branchiata* [species mistakenly placed in *L. (Laonice)* by Sikorski *et al.* (2017)] start from chaetiger 4–10 (instead of 26 in *L. andamanica* sp. nov.).

Laonice andamanica sp. nov. has the prostomium joined to the peristomium, but the junction still clearly outlined. This unique feature is shared with *L. branchiata* (see Sikorski 2011) and, probably, is also present in *L. japonica* (see Sikorski 2003b), which allows us to suggest that these species form a distinctive morphological group within the genus. However, the relevance of this group requires further confirmation.

Laonice (Sarsiana) sinica Sikorski & Wu, 1998

Laonice sinica Sikorski & Wu 1998: 1243–1247, Figs 1–3, Tabs 1–3 [in Russian].

Material examined. Translated and adapted from Sikorski & Wu (1998).

Holotype. ZISP 1/10363, Kiao Chou Bay, Qingdao, China, st. 43, 17–37 m, silt with shells, 20 June 1957.

Paratypes. ZISP 9/10369, 1 specimen, Chefoo Bay, Yantai, China, st. 52, 10 m, silt, 03 July 1957. Kiao Chou Bay, Qingdao, China, 5–37 m, silt with shells: ZISP 1/10361 and 12/10372, 2 specimens, st. 3, 37 m, 03 June 1957; ZISP 13/10373, 1 specimen, st. 18, 17 m, silt, 07 June 1957; ZISP 5/10365, 8 specimens, ZMUM 1789, 2 specimens, st. 20, 08 June 1957; ZISP 7/10367, 1 specimen, st. 23, 08 June 1957; ZISP 15/10375, 1 specimen, st. 24, 17 m, silt, 08 June 1957; ZISP 4/10364, 2 specimens, st. 41, 5 m, 20 June 1957; ZISP 6/10366, 1 specimen, st. 42, 27 m, 20 June 1957; ZISP 2/50406, 5 specimens, ZMUM 1788, 1 specimen, st. 43, 25 m, 20 June 1957. Bohai Sea, China,

10–32 m, silt: ZISP 16/10376, 1 specimen, st. 110, 18 July 1957; ZISP 8/10368, 5 specimens, st. 206, 14–26 m, silt, 13 July 1957; ZISP 10/10370, 2 specimens, st. 209, 23 September 1957. ZISP 14/10374, 1 specimen, Bohai Strait, China, R/V “Venus”, st. 5, 05 July 1958. ZISP 11/10371, 4 specimens, Yellow Sea, off China, R/V “Venus”, st. 201, 20–60 m, sandy silt with stones and broken shells, 27 July 1957.

Description of Chinese specimens (translation of the original description). Up to 77 mm long and 1.3 mm wide for 144 chaetigers (re-examination of type material showed size-related data being slightly different from original description); largest incomplete specimen 1.4 mm wide.

Prostomium T-shaped with rounded anterior margin, not fused with peristomium at antero-lateral angles. Nuchal organs reaching chaetiger 8–11, as U-shaped ciliary bands on sides of caruncle. Palps reaching chaetiger 19. Short erect occipital antenna. Large bright bean-shaped eyespots in front of occipital antenna, sometimes with additional small pale spots in front.

Branchiae from chaetiger 2, short, very gradually lengthening from 1.5 times shorter on chaetiger 2 to nearly as long as notopodial postchaetal lamellae at chaetiger 7–8. Last pair of branchiae on chaetiger 26–42.

Notopodial postchaetal lamellae leaf-like, narrowing into sharply acute tips in all branchiate chaetigers, losing acute tips to become round on first 3–4 post-branchial chaetigers, becoming small rounded dorso-laterally shifted protrusions on posterior chaetigers, and finally becoming lanceolate on posteriormost chaetigers. Neuropodial postchaetal lamellae triangular, with acute upper tips becoming round on posterior post-branchial chaetigers.

Dorsal transverse crests first appearing on last 4–6 branchial chaetigers, then continuing up to chaetiger 25; first 2–3 as large oval (tongue-shaped) mid-dorsal membranes non-connecting with notopodial postchaetal lamellae; of equal height without any mid elevation from mid postbranchiate region to reach maximum size on last 1–2 branchial chaetigers.

Lateral inter-neuropodial pouches from chaetiger 5–9, sometimes larger than parapodia in most posterior chaetigers; usually not visible on posteriormost 12–17 chaetigers.

Capillaries of anterior chaetigers arranged in two vertical rows. Neuropodial hooks from chaetiger 27–41, up to 7–13 per fascicle, bidentate in lateral view, tridentate in frontal view, with one pair of small apical teeth very close to each other, side by side above main fang. Notopodial hooks absent. Sabre chaetae from chaetiger 20–36, at first two per fascicle (one in juveniles less than 0.5 mm wide), only one after 6–12 chaetigers.

Pygidium with one pair of closely set ventral lobes resembling small tubercles, and up to six bilaterally symmetrical pairs of thin threadlike dorsal anal cirri around anus.

Yellow-brown *in vivo*, non-pigmented when preserved.

Methyl Green staining. Lacking a distinct pattern.

Biology. Sexually mature females having oocytes 0.13–0.15 mm in diameter found on the 3rd and 20th of June of 1957 at Kiao Chou Bay (Yellow Sea). Mature specimens (with oocytes and sperm) found on the 26–27th of July 1957 at the Yellow Sea, and on the 17th of August 1957 at the Bohai Sea.

Type locality. Kiao Chou (= Jiaozhou) Bay (Yellow Sea), 17–37 m depth.

Distribution. *Laonice (S.) sinica* is known from the Yellow and Bohai seas (Pacific Ocean), where it can be dominant in sublittoral communities (Fig. 6).

Remarks. The original description of *Laonice sinica* was published only in Russian by Sikorski & Wu (1998). Here we are presenting the first English translation. The comparison with the specimens collected in the Gulf of Siam can be found in the Remarks for *Laonice (Sarsiana) cf. sinica*.

***Laonice (Sarsiana) cf. sinica* Sikorski & Wu, 1998**

Figs 5A–F, 6.

Material examined. MNCN16.01/19137, 2 specimens, Gulf of Siam, off Thailand, st. 4, 07°32.190'N, 102°47.742'E, 61 m depth, 89.6% of silt and clay (<63 µm) and 10.0% of fine sand (63–250 µm) with shell fragments, 27 July 1998.

Description of specimens from the Gulf of Siam. Two anterior fragments, one very short, longest one 0.8 mm wide with 44 chaetigers (used for numerical characters).

Prostomium T-shaped, with rounded anterior margin, not fused with peristomium by anterolateral angles (Fig. 5A). Caruncle accompanied by nuchal organs, extending to posterior end of chaetiger 12. Occipital antenna quite

large, erected, slightly longer than branchiae of chaetiger 2 (Fig. 5A). One pair of bright elongate eyespots along lateral margins of prostomium, in front of occipital antenna.

Branchiae from chaetiger 2, short, one third of length of notopodial postchaetal lamellae of same chaetiger, half longer on chaetiger 4, 1.5 times shorter on chaetiger 5, very gradually lengthening to become nearly as long as notopodial postchaetal lamellae at chaetiger 25, then becoming shorter again, half the size of the last pair of branchiae, on chaetiger 34 (Fig. 5A–B).

Notopodial postchaetal lamellae leaf-like, narrowing into sharply acute tips on first three chaetigers (Fig. 5A), slightly rounded from chaetiger 4 (Fig. 5A), becoming acute again at posterior branchiate chaetigers (Fig. 5B). Notopodial postchaetal lamellae gradually shortening on four last branchiate chaetigers, without erect terminal peak on postbranchiate chaetigers (Fig. 5B). Neuropodial postchaetal lamellae as leaf-like triangles with dorsolateral tips; tips acute on four anteriormost chaetigers (Fig. 5A) and rounded from chaetiger 5. Neuropodial postchaetal lamellae gradually becoming shorter from posterior branchiate chaetigers, and then much shorter from chaetiger 42 onwards.

Dorsal transverse crests first appearing on chaetiger 31, as square tongue-shaped membranes on middle of dorsal surface of chaetigers 31–32 (Fig. 5B). Continuous crests connecting notopodial postchaetal lamellae from last branchial chaetiger to at least the 14th post-branchial chaetiger, first two with strongly elevated middle region (Fig. 5B). Ventral borders between chaetigers bearing dorsal transverse crests with two parallel transverse short strips (Fig. 5C).

Lateral inter-neuropodial pouches from chaetiger 7 (right side) and 8 (left side), until last chaetiger present.

Capillaries of anterior chaetigers arranged in two vertical rows. Neuropodial hooks from chaetiger 37, up to five per neuropodium, bidentate in lateral view (Fig. 5D), tridentate in frontal view (Fig. 5E). Notopodial hooks not seen. Sabre chaetae from chaetiger 31, one per fascicle.

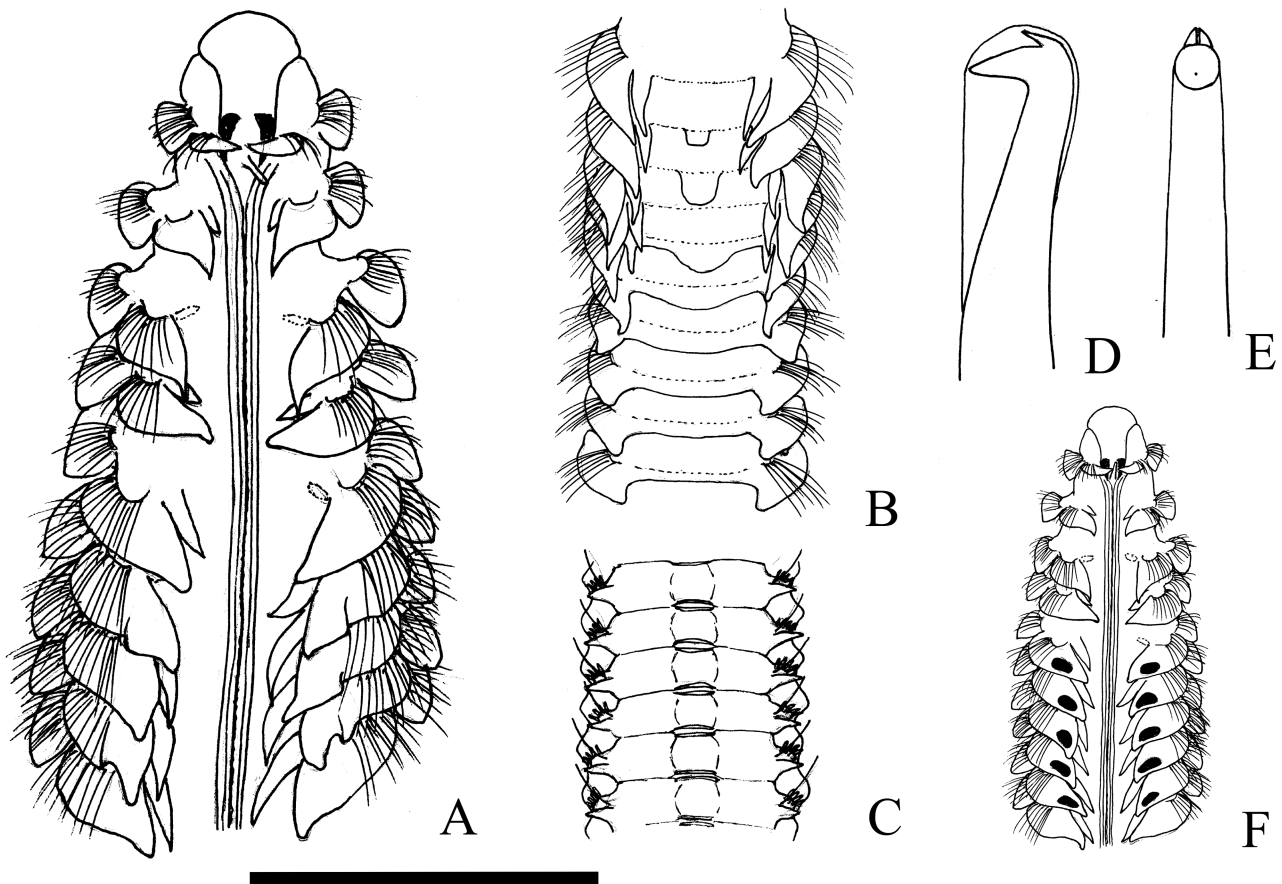


FIGURE 5. *Laonice cf. sinica* Sikorski & Wu, 1998. A: anterior region (9 chaetigers), dorsal view. B: end of branchiate region (chaetigers 30–39), dorsal view. C: postbranchiate region, ventral view. D: neuropodial hooded hook, chaetiger 44 (lateral view). E: neuropodial hooded hook, chaetiger 44 (frontal view, scheme). F: staining pattern with Methyl Green, anterior region (10 chaetigers), dorsal view. Scale, mm: A–C, 1; D–E, 0.01; F, 2. Material: two specimens, Gulf of Siam, st. 4 (MNCN16.01/19137).

Pygidium not seen, missing.

Pigmentation absent.

Methyl Green staining. Strong on inner upper parts of notopodial postchaetal lamellae from chaetiger 5–9 (Fig. 5F).

Distribution. Gulf of Siam (Pacific Ocean) (Fig. 6).

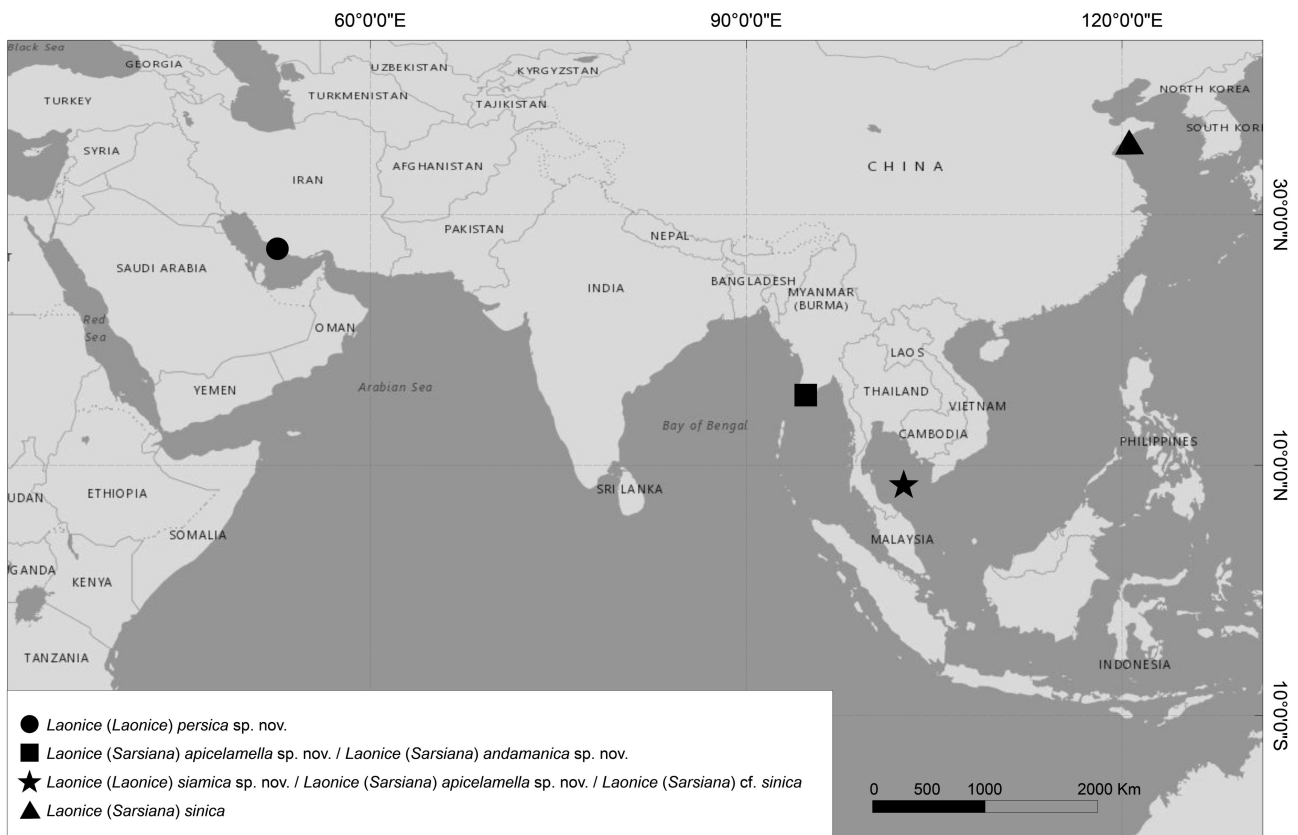


FIGURE 6. Location of the different species of *Laonice* discussed in the study: Persian Gulf (dot), Andaman Sea (square), Gulf of Siam (star), and Yellow Sea (triangle).

Remarks. The examined specimens were consistent with the original description of *L. sinica* in nearly all characters, except in nuchal organs length, which reach chaetiger 12 in Siamese specimens instead of 8–11 as in Chinese specimens. Moreover, the Chinese specimens did not show a distinct Methyl Green staining pattern. The populations from the Bohai and Yellow seas and from the Gulf of Siam may represent opposite clines at the extremes of the species distribution area, but assessing conspecificity will not only require molecular methods, but also finding additional populations between the two extremes. Therefore, we are proposing a tentative attribution of the Siamese specimens to the species, as *L. (S.) cf. sinica*.

Identification key for all described Asian Indo-Pacific species of *Laonice*

- 1 Anterior margin of prostomium fused with fronto-lateral peristomial margins. Caruncle long, extending beyond half of branchiate chaetigers (length of caruncle highly variable) 2
- Anterior margin of prostomium not fused (in dorsal view) with fronto-lateral peristomial margins. 5
- 2(1) Hooks tridentate (in lateral view). Occipital antenna often absent 3
- Hooks bidentate (in lateral view). Occipital antenna always present. 4
- 3(2) Caruncle not extending behind chaetiger 10. Lateral inter-neuropodial pouches starting before chaetiger 10 *L. brevicristata* [Sri Lanka]
- Caruncle extending to chaetiger 23–26. Lateral inter-neuropodial pouches starting from chaetiger 4–6 *L. persica* sp. nov. [Persian Gulf]
- 4(2) Posterior branchiae gradually shortening along large number of chaetigers from chaetiger 38 and then absent. Worms 0.7 mm wide with nuchal organs extending to chaetiger 40 and branchiae disappearing after chaetiger 50 *L. siamica* sp. nov. [Gulf of Siam]

- Gradual shortening of posterior branchiae along large number of chaetigers absent. Only worms 2 mm wide or more have nuchal organs extending to chaetiger 40 and branchiae absent after chaetiger 50. *L. cf. cirrata** [Sea of Japan]
- 5(1)** Nuchal organs not extending beyond chaetiger 13. Notopodial postchaetal lamellae of chaetigers 4–5 not significantly different in length to subsequent ones **6**
- Nuchal organs extending to chaetiger 18. Notopodial postchaetal lamellae of chaetigers 4–5 significantly larger than subsequent ones *L. japonica* [Sendai Bay]
- 6(5)** Continuous dorsal transverse crests connecting notopodial postchaetal lamellae present in anterior postbranchiate chaetigers **7**
- Continuous dorsal transverse crests connecting notopodial postchaetal lamellae absent **8**
- 7(6)** Prostomium and peristomium clearly separated. Last branchiate chaetigers with large and very distinctive tongue-shaped membranes in middle of dorsal surface. Notopodial postchaetal lamellae of posterior branchiate chaetigers without narrow long, pointed tips *L. sinica* [Yellow Sea; Bohai Sea; ?Gulf of Siam]
- Prostomium and peristomium appearing as fused along their ventral margins. Tongue-shaped middle membranes absent. Notopodial postchaetal lamellae of posterior branchiate chaetigers with upper part forming narrow long, sharply pointed processes *L. andamanica* **sp. nov.** [Andaman Sea]
- 8(6)** Branchiae of chaetigers 3–4 longer than notopodial postchaetal lamellae. *L. apicelamella* **sp. nov.** [Andaman Sea; Gulf of Siam]
- Branchiae of chaetigers 4–5 shorter than notopodial postchaetal lamellae *L. rossica* [Northern Pacific, from Sea of Japan to Gulf of Alaska]

* *Laonice cf. cirrata* used here instead of *L. cirrata* due to evidence that materials from the Norwegian Sea and the Sea of Japan may belong to different species (V. Radashkevsky, personal communication).

Discussion

Four new species of *Laonice* are herein described based on materials originally collected by Créocéan. Additionally, we have tentatively identified two specimens from the Gulf of Siam as belonging to *L. sinica*, a species formerly described from Kiao Chou (= Jiaozhou) Bay, Yellow Sea (China, Pacific Ocean). Two of the new species belong to the *L. cirrata* complex within the subgenus *L. (Laonice)*, while the other two belong to subgenus *L. (Sarsiana)*, together with the formerly described *L. sinica*.

In *L. (Laonice)*, the combination of the presence/absence of dorsal transverse crests in the postbranchiate region with the simultaneous occurrence of other morphological features allows the recognition of at least two subgroups (Sikorski *et al.* 2021b). In *L. (Sarsiana)*, we have observed that the absence of dorsal transverse crests in the postbranchiate region is usually combined with the presence of a membrane joining the prostomium and peristomium and of hooded hooks in posteriormost notopodia (see the Remarks for *L. (S.) apicelamella* **sp. nov.**). However, the association with the hooks requires further validation due to the difficulties of collecting complete specimens. *Laonice (S.) japonica*, *L. (S.) branchiata*, *L. (S.) sinica*, *L. (S.) magnacristata* and *L. (S.) andamanica* **sp. nov.** have midbody dorsal transverse crests and form one subgroup, while *L. (S.) sarsi*, *L. (S.) antarcticae*, *L. (S.) dayianum*, *L. (S.) rossica*, *L. (S.) olgae*, *L. (S.) alberti*, *L. (S.) parvabbranchiata* and *L. (S.) apicelamella* **sp. nov.** lack these crests and form another subgroup. Moreover, the character having the prostomium closely attached to the peristomium, but showing a distinctly outlined junction, suggests the presence of a third subgroup, including *L. (S.) branchiata*, *L. (S.) andamanica* **sp. nov.** and, probably, *L. (S.) japonica*. Nevertheless, the phylogenetic relevance of these subgroups within *L. (Sarsiana)* requires further analyses.

Though, the affiliation of some species within *L. (Sarsiana)* is not clear yet. For example, *L. praecirrata*, which has the prostomium connected with the peristomium by an inconspicuous membrane and continuous dorsal transverse crests, also has a long caruncle (up to chaetiger 15–21). Also, the small size of *Laonice papillibranchiae* Ward, 1981 and *L. whittardensis*, and the poor condition of the type-material of *L. junoyi*, prevents some key characters being observed. Collecting new material and using molecular analyses would probably be key in providing additional information to determine their systematic position.

As a result, the genus *Laonice* today contains 49 valid species.

All specimens here analyzed, including those belonging to the four new taxa, were originally collected during the implementation of different projects performed by the environmental consulting company Créocéan and deposited at the CEAB-CSIC. Such data is a key contribution that consulting companies can play in the discovery and description of the world's biodiversity, when their samples are deposited in collections accessible to the scientific community.

Biological specimens collected during such environmental survey programs are usually fixed in formalin, which renders them unsuitable for molecular analyses, and probably this is the reason why they are frequently neglected and

ignored by taxonomists. Still, they have a considerable scientific value, as they may include undescribed taxa that can be formally described using non-molecular techniques that are well established and which have been successfully applied for decades. Moreover, these samples can also (1) provide additional knowledge on the distribution and habitats of already known taxa, (2) supply valuable materials to train future generations of taxonomists, (3) keep a temporal record on how and when the structure of different communities changed due to natural and anthropogenic causes, (4) document the first local occurrence of presumably alien and invasive species, or (5) help refining future surveys aimed at collecting specifically targeted taxa to complement their knowledge through new analyses, such as tracing their molecular profiles.

The value of marine specimens collected during environmental survey programs and the reasons why they should be preserved and made available for the scientific community were well summarized by Mackie (2001). The author supplied a proposal encouraging clients of environmental surveys to allow their contractors to deposit the resulting specimens in public collections that guarantee their safe-keeping, cataloguing and availability for future scientific study. The present work shows clearly the benefits of adopting and supporting such proposal, and conforms a new contribution to the long history of taxonomic highlights derived from the ongoing collaboration between Créocéan and scientific circles (e.g., Bhaud *et al.* 2003; Britayev & Martin 2006; Corbera *et al.* 2005; Cosel & Salas 2001; Fiege & Barnich 2020; Martin *et al.* 2022; Mortimer *et al.* 2012; Sikorski *et al.* 2021b).

Thus, considering the good results derived from this particular partnership, we embolden other contractors to deposit reference collections of the performed environmental surveys in public natural history institutions that accomplish the three conditions of (1) preserving, (2) cataloguing and (3) granting access to the interested scientific community.

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