

Unveiling a hidden wanderer in the NE Atlantic: a new species of *Scalibregma* (Annelida, Scalibregmatidae)

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Abstract

During a biodiversity survey conducted in the Bay of Biscay (Northeast Atlantic Ocean, France) within the framework of offshore wind energy development, a new species of *Scalibregma* was identified. This species is morphologically and genetically (16S rDNA and COI) characterized, and compared with its nearest congeners. A key for *Scalibregma* species with branchiae from chaetigers 3 to 5 and DNA sequences for *S. celticum* Mackie, 1991 and *S. inflatum* Rathke, 1843 occurring in the same area, are provided as well. Based on molecular phylogenetic analysis using the COI gene, *S. celticum* is found as sister species of *S. drouali* sp. nov. Morphologically, the new species is closest to *S. stenocerum* (Bertelsen & Weston, 1980), but it differs by having a distinct mid-ventral row with large (double) epidermal pads and the presence of hirsute capillaries instead of inconspicuous mid-ventral line and only smooth capillaries as observed in *S. stenocerum*. The new species potentially occurs from Atlantic French coast (Bay of Biscay) to Moroccan coast between 55 to 104 m depth.

Key words: Bay of Biscay, DNA, Morphology, New species, Polychaeta, Taxonomy

Introduction

Malmgren (1867) established Scalibregmatidae to accommodate the worms with maggot-shaped body forms: *Polyphysia crassa* (Ørsted, 1843) and *Scalibregma inflatum* Rathke, 1843. The family has been placed as sister-group of Opheliidae within Scolecida clade (Fauchald & Rose 1997). Confusing and sometimes contradictory or erroneous morphological and molecular observations have led to the placement of the genus *Travisia* Johnston, 1840 within Scalibregmatidae (Blake 2025). The new data gathered by this author support the removal of *Travisia* from Scalibregmatidae and its elevation to Travisidae Hartmann-Schröder, 1971 as suggested by Blake and Maciolek (2020). Because phylogenetic analyses including multiple scalibregmatid species based on morphology and/or genetic data are limited (Martínez *et al.* 2013; Wiklund *et al.* 2019), the relationships of Scalibregmatidae with other families and among its genera remain poorly understood (Parapar *et al.* 2021).

Scalibregmatids are not frequently encountered but can occasionally reach extremely high abundances, up to 3,720 or up to 27,222 individuals per m² (Blake & Hilbig 1994; Mackie 1991). Most species show a narrow bathymetric distribution (intertidal-shelf, slope or abyssal, hadal) (Kudenov & Blake 1978; Paterson *et al.* 2009; Blake 2025). They are mostly active burrowers building galleries down to 60 cm depth and feeding on non-selective subsurface deposits (Ashworth 1901; Jumars *et al.* 2015), except for members of *Axiokebuita-Speleobregma* clade which live in crevicular habitats and feed on suspended organic matter (Martínez *et al.* 2013). They are characterized with a T- or Y-shaped prostomium with lateral or anterolateral projecting horns and a rugged appearance with the cuticle having up to six annuli per segment. Scalibregmatidae include 148 species within 15 genera (Read & Fauchald 2025). The most diverse genera are *Asclerocheilus* Ashworth, 1901 and *Oligobregma* Kudenov & Blake, 1978 with 30 species each, followed by *Scalibregma* Rathke, 1843 with 26 species.

Scalibregma inflatum, the type-species of the genus, described from Norway, has been reported worldwide and consequently considered as cosmopolitan in distribution (Furreg 1925; Hartman 1959; Kudenov & Blake 1978; Støp-Bowitz 1945), but this cosmopolitan nature was later questioned (Mackie 1991; Blake 2015; Mendes *et al.*

2023). However, the type-material of *S. inflatum* is not known to exist (Mackie 1991; Bakken *et al.* 2014). Mackie (1991) provided a baseline description and determined a holotype from specimens collected near to the type-locality (i.e., Molde, Norway). He confirmed the synonymy of *Oligobranchus roseus* Sars, 1846 with *S. inflatum* after examining the presumed material used in the original description, and suggested that most of the major descriptions of material from the Northeast Atlantic (Ashworth 1901; Fauvel 1927; Støp-Bowitz 1945) likely refer to the species he redescribed.

Only five new species of *Scalibregma* were described in the following decades (Bakken *et al.* 2014; Blake 2000, 2015; Mendes *et al.* 2023) whereas a total of 14 new species were described in 2025 (Blake 2025). Moreover, this latter work has pointed out important characters that can be used to separate species such as the presence or absence of a prostomial or peristomial dorsal crest, the number and shape of dorsal peristomial rings, the nature of the anterior lip of the mouth, the first chaetiger to have furcate chaetae, the number and arrangement of anal cirri, and the presence and arrangement of pigmented segmental annular rings.

In European waters, the Scalibregmatidae is represented by 18 species with the genus *Scalibregma* being the most diverse: *S. celticum* Mackie, 1991, *S. inflatum*, *S. hansenii* Bakken, Oug & Konsgrud, 2014, *S. robustum* Zachs, 1923 and *S. stenocerum* (Bertelsen & Weston, 1980). During a biodiversity survey conducted in the Bay of Biscay within the framework of offshore wind energy development led by the French government, 3,211 specimens belonging to four scalibregmatid species were collected. Two of them were identified as *S. celticum* and *S. inflatum*, and the two others as unknown species. One of these corresponds to *Scalibregma* sp. nov., apparently awaiting formal description, listed in a previous study (Gil 2011). The other unknown species presented significant differences in relation to its closest congeners, confirming it as new to science. This new species is described based on morphological characters and supplemented by molecular data (16S rDNA and COI genes) and is compared to other species. A morphological key and a table with the main morphological characters for species with branchiae from chaetiger 3 to 5 are included. Moreover, DNA sequences (16S rDNA and COI genes) for *S. celticum* and *S. inflatum* are provided.

Material and methods

Study site and sampling. Within the framework of offshore wind energy development financed by the Direction Générale de l'Énergie et du Climat (DGEC, Ministère de la Transition Écologique, France) a survey with four scientific expeditions was conducted in the Bay of Biscay (Northeast Atlantic; Fig. 1A) to study biodiversity, including benthic macrofauna. These campaigns took place on board the ship R/V *Minibex* from "Ship As A Service" society in Autumn (September/October) in 2023 and 2024, and in Spring (April/May) in 2024 and 2025. For each season, benthic macrofauna was sampled at 111 stations distributed within and around the Oléron 1 and Oléron 2 sites (432 km²) at depths of between 53 and 86 m and located 60 km from La Rochelle (France; Fig. 1B). At each station, samples were collected using a Day grab (0.1 m² of surface, 15 L of sediment). Samples were sieved through a 1 mm mesh, and the remaining fraction was immediately fixed and then preserved in 96% ethanol.

Morphological observations. Specimens of *Scalibregma* were examined under a Leica M80 stereomicroscope and a Leica DM2500 optical compound microscope, and photographed with a Leica K5C camera. Leica LAS X software was used to measure the worms' length and their width at chaetiger 5 and at widest segment, without parapodia. Frontal horn length was measured relative to prostomium length, using on available illustrations from the type descriptions and the examined material. Average ratio between tynes was based on 3 measurements.

Type specimens were deposited in the Muséum National d'Histoire Naturelle (MNHN) (Paris, France) and Senckenberg am Meer (Frankfurt, Germany). This article is registered in ZooBank under urn:lsid:zoobank.org:pub:752E2199-BF6D-4D0E-8740-DF20E18011B9 *Scalibregma drouali* sp. nov. is registered in ZooBank under LSID urn:lsid:zoobank.org:act:A2BEF3B7-0E20-432C-9AC8-336C981D7BD8

DNA extraction, gene amplifications and sequencing. Extraction of DNA was performed using an automated DNA/RNA isolation kit (Maxwell® RSC Blood DNA kit; Promega) following the protocol supplied by the manufacturer. Two mitochondrial genes (16S rDNA and cytochrome c oxidase subunit I, COI) were amplified using the primers: Ann16SF and 16SbrH for 16S rDNA (Palumbi 1996; Sjölin *et al.* 2005); and polyLCO, polyHCO, LCO1490 and HCO2198 for COI (Carr *et al.* 2011; Folmer *et al.* 1994).

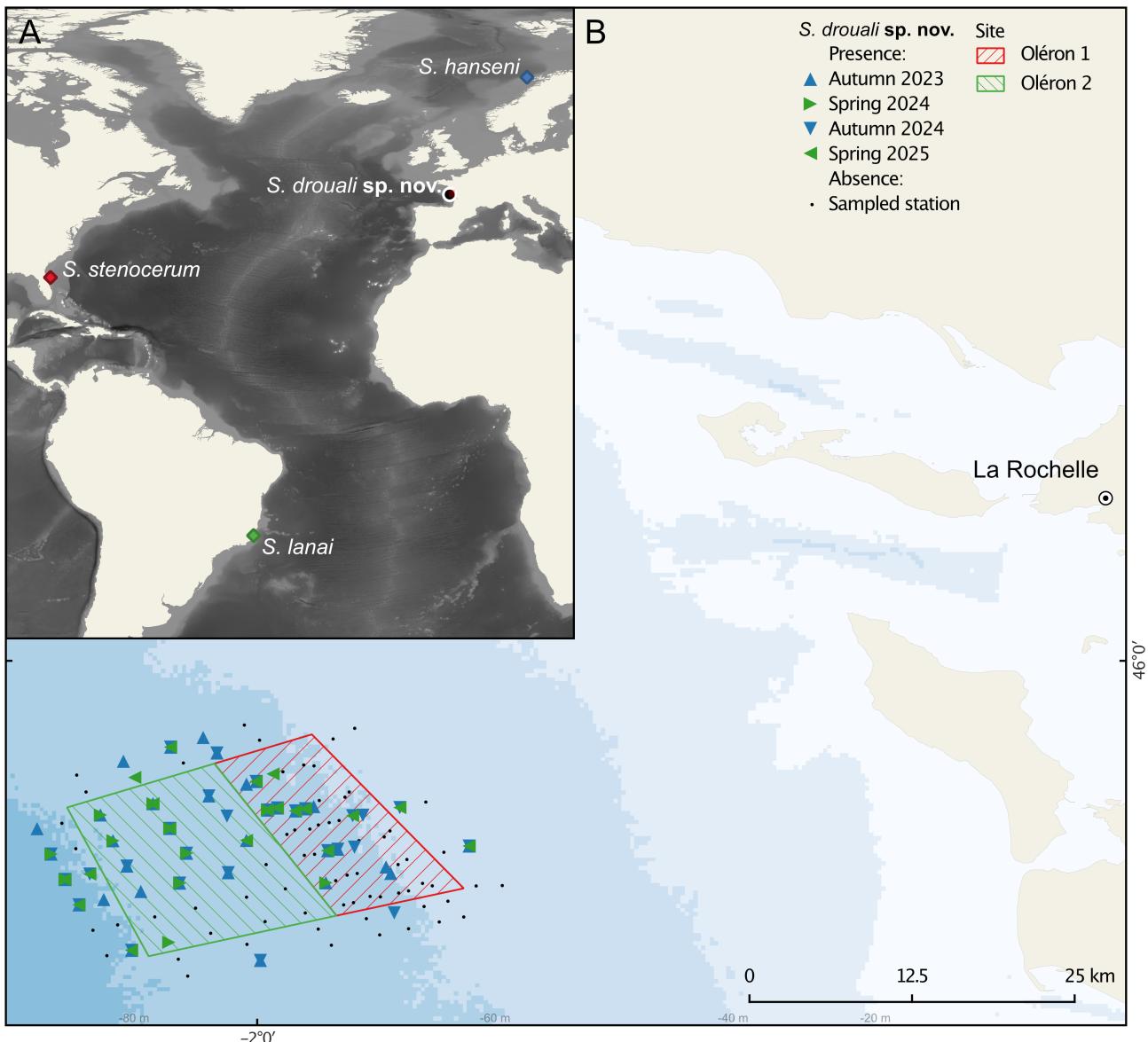


FIGURE 1. A, Map of Atlantic Ocean showing type-localities of *Scalibregma* with branchiae from chaetiger 3 to 5. B, Bay of Biscay (Northeast Atlantic) showing the sampled area (Oléron 1 and Oléron 2 sites) during a biodiversity survey with associated presence and absence of *S. drouali* sp. nov. at each one of the four sampling periods.

The Polymerase Chain Reaction (PCR), with 25 μ L mixtures, contained: 4 μ L of Green GoTaq® Flexi Reaction Buffer (final concentration of 1X), 1.2 μ L of MgCl₂ solution (final concentration of 25 mM), 0.4 μ L of PCR nucleotide mix (final concentration of 0.2 mM each dNTP), 12.9 μ L of nuclease-free water, 0.2 μ L of each primer (final concentration of 1 μ M), 1 μ L template DNA and 0.1 μ L of DNA Polymerase (5U/ μ L). The temperature profile was: 94°C/600s—(94°C/60s—59°C/30s—72°C/90s *40 cycles—72°C/600s—4°C for 16S, and 94°C/600s—(94°C/40s—44°C/40s—72°C/60s *5 cycles—(94°C/40s—51°C/40s—72°C/60s *35 cycles 72°C/300s—4°C for COI. PCR-products, which produced bright bands after electrophoresis on 1% agarose gel, were sent to the MacroGen Europe Laboratory in Amsterdam (Netherlands) to obtain sequences, using the same set of primers as used for the PCR.

Overlapping sequence (forward and reverse) fragments were merged into consensus sequences using Geneious Pro 8.1.7 2005–2015 (Biomatters Ltd). For COI, the sequences were translated into amino acid alignments and checked for stop codons to avoid pseudogenes. The minimum length coverage was 398 bp for 16S rDNA and 619 bp for COI.

Newly assembled sequences were blasted in public databases (see below) to check for contamination. Each set of genes was aligned separately using: MAAFT (Katoh *et al.* 2002) for 16S rDNA and MUSCLE (Edgar 2004) for COI. All sequences obtained in this study have been deposited in GenBank¹ (Clark *et al.* 2016) and BOLD² (Ratnasingham *et al.* 2024).

Phylogenetic analysis and genetic divergence. For the purpose of the present study, sequences of 16S rDNA and COI genes available in GenBank and BOLD from one opheliid (*Ophelina acuminata* Ørsted, 1843) were included as outgroup (Table 1). Sequences of species or taxonomic unities belonging to *Scalibregma* for the same genes were included as ingroup (Table 1). The maximum likelihood phylogenetic tree was built using IQ-TREE multicore version 1.6.12 (Nguyen *et al.* 2015; Trifinopoulos *et al.* 2016) with the best fitting model (TIM2+F+I+G4) selected using ModelFinder (Kalyaanamoorthy *et al.* 2017) and with ultrafast bootstrapping—UFBoot, 1,000 iterations (Hoang *et al.* 2018); associated to a SH-aLRT test (Guindon *et al.* 2010). The support of clades is given as SH-aLRT/UFBoot values. As ultrafast bootstrapping is less conservative than classical bootstrap, only nodes with branch support of SH-aLRT $\geq 80\%$ and UFBoot $\geq 95\%$ should be relied on for high confidence. The tree file was interpreted/edited with FigTree v1.4.4³.

The genetic divergence over sequences pairs was calculated for between closest species (interspecific variation) and between specimens (intraspecific variation) using Kimura 2-parameter—K2P (Kimura 1980) model; in MEGA6 (Tamura *et al.* 2013).

Results and discussion

Scalibregmatidae Malmgren, 1867

Scalibregma Rathke, 1843

Scalibregma drouali sp. nov.

(Figs 2–3, Tables 1–2)

Type material: Holotype, MHNH-2000-2115, complete specimen, ovigerous, length 17.4 mm, width 1.6 mm, widest 2.9 mm, 39 chaetigers with two more achaetous segments and one more without chaetae or cirri, Northeast Atlantic Ocean, France, Bay of Biscay, around Oléron site 2, continental shelf, station 109, replicate b, collected 12 October 2023, Day grab, 45.807666° N, 2.20514884° W, 82 m depth. **Paratype 1, MHNH-2000-2116**, incomplete specimen, length 10 mm, width 1.9 mm, widest 3.0 mm, 27 segments, Northeast Atlantic Ocean, Bay of Biscay, around Oléron site 2, continental shelf, station 104, replicate b, collected 12 October 2023, Day grab, 45.76243293° N, 2.152739676° W, 83 m depth. **Paratype 2, MHNH-2000-2117**, incomplete specimen, length 12.0 mm, width 1.9 mm, widest 3.5 mm, 29 segments, Northeast Atlantic Ocean, Bay of Biscay, around Oléron site 2, continental shelf, station 105, replicate a, collected 30 April 2024, Day grab, 45.75710897° N, 2.177357192° W, 88 m depth, DNA extracted. **Paratype 3, MHNH-2000-2118**, complete specimen, length 15.2 mm, width 1.6 mm, widest 3.0 mm, 39 chaetigers with two more achaetous segments and one more segment without chaetae or cirri, Northeast Atlantic Ocean, Bay of Biscay, within Oléron site 1, continental shelf, station 7, replicate c, collected 10 October 2023, Day grab, 45.85058453° N, 1.96193461° W, 67 m depth. **Paratype 4, SMF 33431**, complete specimen, length 19.5 mm, width 1.7 mm, widest 3.0 mm, 39 chaetigers, posterior end not clear if last segments are with or without chaetae/cirri, Northeast Atlantic Ocean, Bay of Biscay, within Oléron site 1, continental shelf, station 60, replicate b, collected 6 November 2024, Day grab, 45.85144389° N, 1.98979028° W, 69 m depth.

Comparative material. **MHNH-2001-158**, *Scalibregma celticum*, incomplete specimen, 34 chaetigers, Northeast Atlantic Ocean, Bay of Biscay, around Oléron site 2, continental shelf, station 109, replicate b, collected 30 April 2024, Day grab, 45.807666° N, 2.20514884° W, 89 m depth. **MHNH-2001-159**, *Scalibregma inflatum*, incomplete specimen, 25 chaetigers, Northeast Atlantic Ocean, Bay of Biscay, around Oléron site 2, continental shelf, station 103, replicate d, collected 24 May 2024, Day grab, 45.73714882° N, 2.138872225° W, 83 m depth.

1 <https://www.ncbi.nlm.nih.gov/genbank/>

2 <http://www.boldsystems.org>

3 <https://github.com/rambaut/figtree/releases>

Description (based on holotype). Holotype complete specimen, with 39 chaetigers, 17.4 mm long, 2.9 mm in widest section (about chaetiger 10), 1.6 mm wide (chaetiger 4). Paratypes complete specimens measuring 15.2–19.5 mm long for 2.9–3.5 mm at widest section for 39 chaetigers.

Body arenicoliform, expanded from chaetiger 6 to 12; surface covered by annulated secondary rings; anteriorly, each one formed by numerous rectangular pads; posteriorly, individual pads less distinct particularly on dorsal side; giving a complex areolate appearance (Fig. 2A); not pigmented or colored in ethanol, pale white (Fig. 2).

Hexagonal prostomium, T-shaped, anterior margin smooth, with two long lateral horns, about as long as the prostomium length (Fig. 2B–D). Eyes present as two horizontal, red lines (V-shaped; Fig. 2B, C). Nuchal organs not everted in holotype or paratypes, dorso-lateral grooves observed. Peristomium achaetous, biannulate dorsally and ventrally (Fig. 2B–D); second ring composed by a row of 4–5 small pads dorsally (Fig. 2C). Mouth horizontal formed by anterior and posterior lips (Fig. 2D); anterior lip formed by paired triangular lobes with very small central pad; posterior lip formed by a central plicated pad with about 6 lobes. Proboscis not everted.

Ventral groove starting from posterior lip to end of body forming a mid-ventral ridge line; chaetiger 1 with hexagonal, large pad; then two, square to round central pads by segment, longitudinally positioned (Fig. 2D), merged from chaetiger 7. Segmental annulations distinct along body, dorsally and ventrally; chaetiger 1 triannulate, then quadriannulate from chaetiger 2 to the end of body (Fig. 2A–D).

Branchiae present from chaetiger 3 to 5, posterior to notochaetae (Figs 2B–D, 3G). First pair smaller than second and third (Fig. 3G) one, of similar size. Two main stems, pinnated branchiae then bifurcated branches (Figs 2B, 3G).

Parapodia poorly developed on chaetiger 1 (Fig. 3A) and chaetigers 7 to 15; inconspicuous in inflated chaetigers; from chaetiger 17, developed, larger, triangular, distally blunt (Fig. 3I). Ventral cirri present from chaetiger 16, very small; and dorsal cirri present from chaetiger 17, small; both becoming full size by about 3rd to 5th chaetigers. Cirri subtriangular, distally blunt to pointed, of similar size; about same size that parapodia (Fig. 3I). Interramal papilla present from chaetiger 16, very small, following chaetigers small but distinct; knob-like (Fig. 2E). Three additional posteriormost segments with reduced parapodia: two cirrigerous and achaetous, and one without chaetae or cirri; triannulate. Pygidium with crenulate margin around anal aperture (Fig. 2F); with five anal cirri (two short and three 2x longer). Glands absent.

Notopodia and neuropodia with bundle of smooth (some with a hirsute margin, Fig. 3F, but some difficult to see), short and long capillaries (chaetiger 1 with 10–20 observed, chaetiger 2 with 40–50, chaetiger 3 with 50–60, chaetiger 18 with about 10) present in all chaetigers in (Fig. 3A, D, G). Notopodia and neuropodia from chaetiger 1 (5 in noto- and neuropodia) and 2 (9 in noto- and 11 in neuropodia) with short, acicular chaetae, in a row, blunt tip; anterior to capillaries and near their basis (Fig. 3B, C, E, F). Replacing these in notopodia and neuropodia from chaetiger 3 (Fig. 3H) to the end by lyrate chaetae (about 13 anteriorly and posteriorly), in a row, with not equal tynes, spinous in inner tynes (Fig. 3H, J); similar along body, average ratio between tynes in chaetiger 3 1.2 (standard error: 0.01), in chaetiger 18 1.3 (0.04) and chaetiger 24 1.3 (0.09).

Morphological variation. Paratype 3 showed prostomium with frontal horns shorter than prostomium length that seems contracted likely due fixation and pygidium with 6 anal cirri arranged as following: one short (half-length) medially inserted, laterally inserted three more in one side of short, median (three quarters-length) and long lengths, and two in other side of short and long lengths. Additional material (not included here) presented everted branched-like structure as nuchal organs.

Reproduction notes. Holotype is a large and ovigerous specimen.

Staining pattern. Staining with methyl blue (Paratype 4) and shirlastain (Paratype 1), but no specific pattern was observed.

Remarks. Among the 26 described species (Blake 2025) in the genus *Scalibregma* only *S. stenocerum*, *S. hansenii*, *S. lanai* Mendes, Rizzo & De Paiva, 2023 and *S. drouali* sp. nov., show branchiae from chaetigers 3 to 5. *Scalibregma hansenii* described from Norwegian and Greenland seas (Fig. 1A), is the only species lacking eyes and having simpler branchiae with 1–4 filaments (Bakken *et al.* 2014), whereas *S. lanai*, described from Brazilian continental shelf (Fig. 1A), is the unique species showing lyrate chaetae with equal sized tines (Mendes *et al.* 2023). Thus, the new species is closely related to *S. stenocerum*, described for west Atlantic (Fig. 1A), by sharing the presence of eyes, lyrate chaetae with unequal size tines of similar ratio (1.3 from Fig. D in Bertelsen & Weston 1980) and brushy branchiae. However, *S. drouali* sp. nov. differs from *S. stenocerum* by having slightly more acicular chaetae in neuropodia of chaetiger 2 (up to 11 observed), presence of hirsute capillaries, branchiae

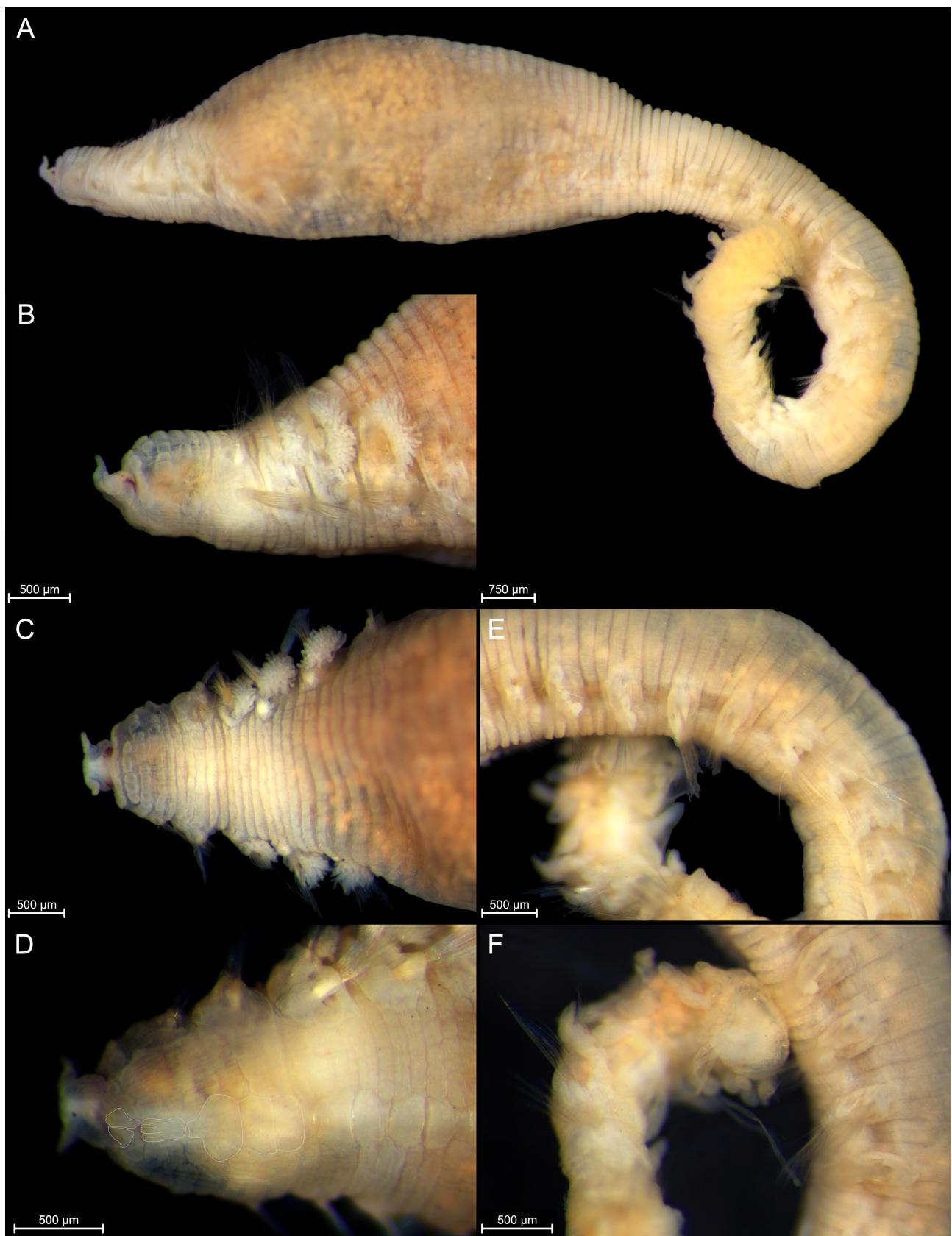


FIGURE 2. *Scalibregma drouali* sp. nov. holotype (MNHN-2000-2115). A, dorsal view of preserved complete specimen. B, anterior end, lateral view. C, anterior end, dorsal view. D, anterior end, ventral view, with anterior lip, posterior lip and anterior mid-ventral pads outlined. E, mid to posterior body, lateral view. F, pygidium, posterior view.

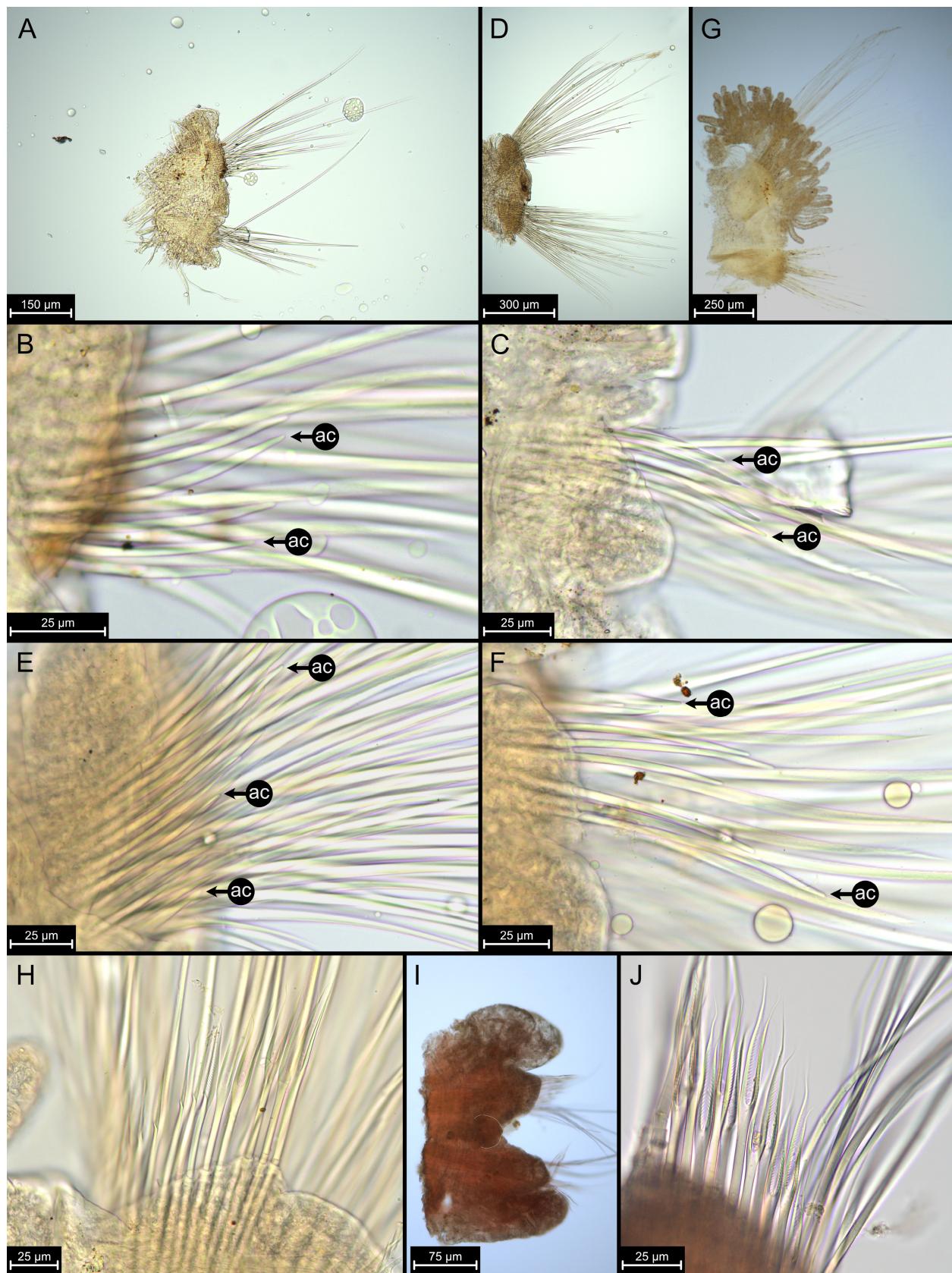


FIGURE 3. *Scalibregma drouali* sp. nov. paratype 1 (MNHN-2000-2116). A, parapodia, chaetiger 1, anterior view. B, notopodia, same chaetiger. C, neuropodia, same chaetiger. D, parapodia, chaetiger 2, anterior view. E, notopodia, same chaetiger. F, neuropodia, same chaetiger. G, parapodia with branchiae, chaetiger 3. H, neuropodia with lyrate chaetae, same chaetiger. I, parapodia with dorsal and ventral cirri, chaetiger 24, interramal papilla outlined. J, neuropodia with lyrate chaetae, same chaetiger. Abbreviation: ac, acicular chaetae.

with 2 stems pinnated with bifurcations that appear larger, 3 last segments achaetous instead up to six acicular in first two chaetigers, smooth capillaries, branchiae pinnate each pinna with bifurcations that appear smaller, and no achaetous segments (at least not mentioned) as found in *S. stenocerum*. Interestingly, the ventral annulation in *S. drouali sp. nov.* is much more similar to *S. celticum* with distinct mid-ventral row of large (double) epidermal pads (Mackie 1991) instead of indistinct mid-ventral row as observed in *S. stenocerum* (Bertelsen & Weston 1980). Morphologically, *S. drouali sp. nov.* seems to have much more in common with *S. celticum* because high similarities in external annulation in anterior (biannulated peristomium) and posterior end (cirrigerous and achaetous), and by showing the presence of hirsute capillaries (difficult to see if all of them or just some). Among the undescribed species, *S. drouali sp. nov.* is close of *Scalibregma sp. nov.* (Gil 2011) by sharing the presence of branchiae in segments 3 to 5, but differs by having eyes.

Few DNA sequences are currently available (i.e., two species and four MOTUs in GenBank; one species in BOLD), yet the newly sequenced specimens found a perfect match (1–1.3% of genetic divergence) with specimens identified as Scalibregmatidae from Moroccan coast (two specimens at 102 m depth sampled in 2011; Table 1).

TABLE 1. List of taxa included in the Maximum Likelihood analysis with corresponding GenBank accession number or BOLD Process-ID (indicated by *).

Taxa	16S rDNA	COI	Location of sequences
<i>Ophelina acuminata</i>	KF511813	MN138411	San Juan Islands (NW Pacific); type-locality: Sweden
<i>Scalibregma</i> sp. MB1	KX867349	KX867454	Deep-sea Antarctic
<i>Scalibregma</i> sp. MB2	KX867363	KX867455	Deep-sea Antarctic
<i>Scalibregma</i> sp. MB3	KX867365	KX867458	Deep-sea Antarctic
<i>Scalibregma</i> sp. voucher SIO:BIC:A1391	-	PQ449279	Costa Rica (E Pacific)
<i>Scalibregma</i> sp. 11BIOAK-1363	-	MF121534	Alaska (N Pacific)
<i>Scalibregma inflatum</i> CMC01	-	HQ023912	Canada (NW Atlantic)
<i>Scalibregma californicum</i>	-	*BBPS1089-19	USA (E Pacific); type-locality: same
<i>Scalibregma inflatum</i> voucher MT08947	-	PQ738807	North Sea (NE Atlantic)
<i>Scalibregma inflatum</i> CMC03	-	GU672593	Russia (Barents Sea, NE Atlantic)
<i>Scalibregma inflatum</i> CMC02	-	HM473802	Alaska (Bering Sea, NE Pacific)
Scalibregmatidae	-	*MIWAP413-14	Morocco (E Atlantic)
Scalibregmatidae	-	*MIWAP414-14	Morocco (E Atlantic)
<i>Scalibregma inflatum</i> (present study)	PX634566	PX634563	France (NE Atlantic); type-locality: Norway
	*SETEC012-25	*SETEC012-25	
<i>Scalibregma celticum</i> (present study)	PX634565	PX634562	France (NE Atlantic); type-locality: Wales, Scotland and France
	*SETEC003-25	*SETEC003-25	
<i>Scalibregma drouali</i> sp. nov. (present study)	PX634564	PX634561	France (NE Atlantic); type-locality: same
	*SETEC004-25	*SETEC004-25	

Scalibregma stenocerum (type-locality: West Atlantic) has been recorded in European waters: Northern United Kingdom, around the Shetland Islands in 20 to 130 m depth (R. Barnich pers. comm.); Irish sea in 53 m depth (Mackie *et al.* 1995); east coast of England, Humber and Outer Wash Region (Pears & Worsfold 2011); Northern Ireland, Outer Ards peninsula (Agri-Food and Biosciences Institute 2019); and eastern of English Channel (Hawes *et al.* 2019). The wide distribution of the *S. drouali* sp. nov. suggest that the European records of *S. stenocerum* could belong to *S. drouali* sp. nov.

The genetic sequences obtained during the present study characterize the following species for 16S rDNA and COI genes: *S. celticum*, *S. inflatum* and *S. drouali* sp. nov. *Scalibregma inflatum* has been recorded from numerous sites distant to the type-locality which is Molde (Norway) resulting in few sequences that seem likely to represent different genetic lineages (Fig. 4) or undescribed species. Because only 6 out of 15 species included in the phylogenetic analysis had 16S rDNA gene available, the phylogenetic analysis presented is limited to COI gene, as the genetic divergence. After more than three decades (Mackie 1991), *S. celticum* is here genetically characterized

for 16S rDNA and COI genes. It shows high genetic divergence when comparing the COI gene in relation to *S. inflatum* (31.5%) and *S. drouali* sp. nov. (26.3%), all sampled in the Bay of Biscay. Genetic divergence between *S. inflatum* and *S. drouali* sp. nov. was slightly lower (27.1%). As suggested above and based on morphological analysis, *S. celticum* was found as sister-group of *S. drouali* sp. nov. with marginal high support. High confidence support was observed only for the clade composed of *S. drouali* sp. nov. specimens which showed an intra genetic divergence between 0.3 to 1.3%.

Etymology. This species is named for Gabin Droual (Ifremer) in recognition of his valued friendship and our shared passion for polychaete worms.

Genetic data. DNA sequencing for this species was successful for 16S rDNA (423 bp length) and COI (669 bp length; Table 1). Intraspecific variation for COI divergence was in average 0.89% (standard error: 0.29%).

Distribution. Most of the examined material comes from the Bay of Biscay (Northeast Atlantic), collected during a survey (178 specimens sampled during four sampling time between 55 and 88 m depth; Fig. 1B). The genetic match between specimens from the Bay of Biscay and those from the Moroccan coast (104 m depth) suggests that *S. drouali* sp. nov. may have gone hidden because of misidentifications with *S. celticum*, with its range potentially extending from France to Morocco.

Ecological notes. Temporal variability in abundance was marked by high values in autumn (82 and 53 individuals in 2023 and 2024, respectively) and low values in spring (15 and 28 individuals in 2024 and 2025, respectively). Most species occurrences (69%) were associated with gravelly sand sediments, followed by 17% in slightly gravelly sand (Folk 1954). Sediment composition averaged 12.9% gravel (standard error: 1%), 84.9% sand (1.1%), and 2.2% mud (0.4%).

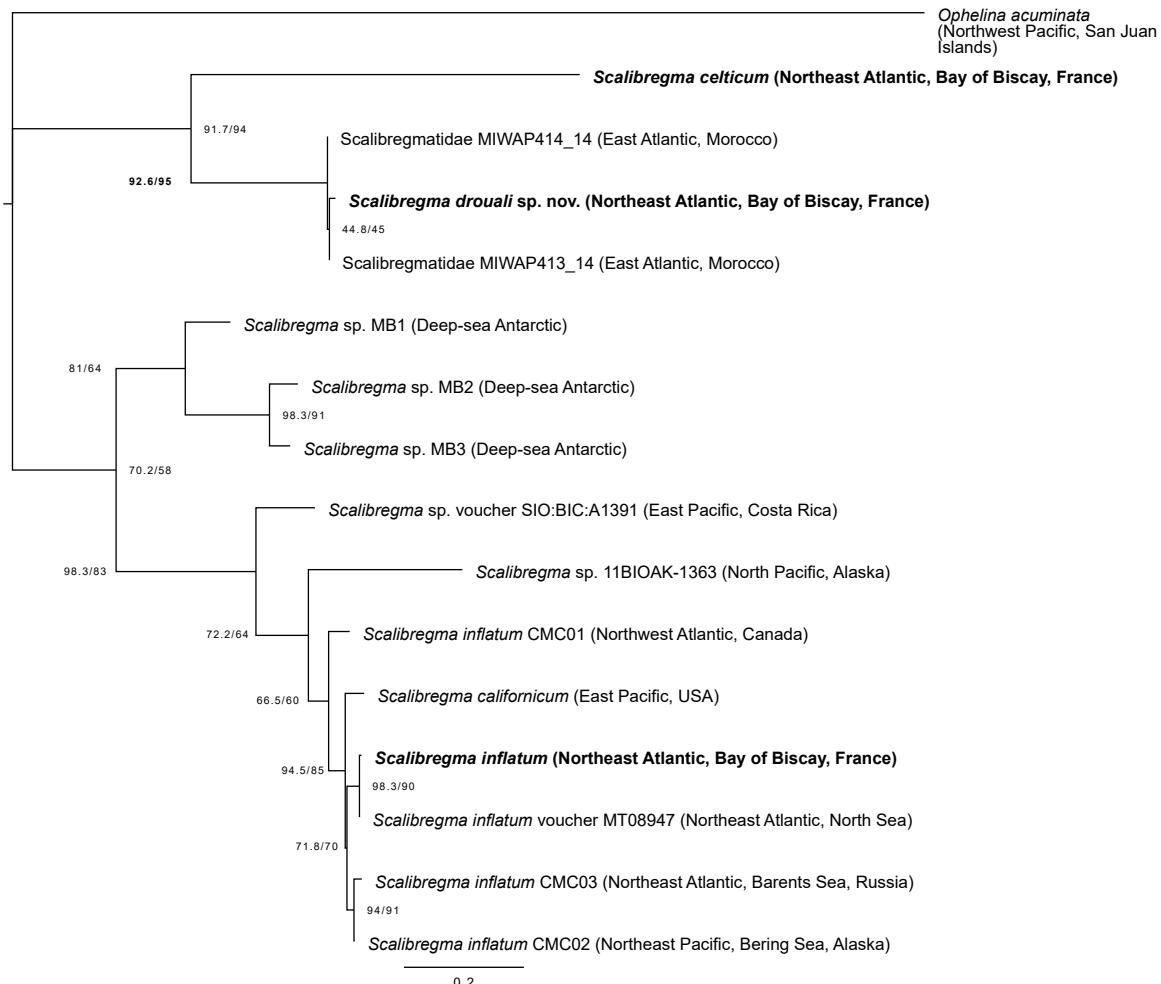


FIGURE 4. Molecular phylogenetic relationship within *Scalibregma* based on available COI gene sequences. Branch support from Maximum Likelihood analysis with SH-aLRT/UFBoot values (high confidence support for SH-aLRT $\geq 80\%$ and UFBoot $\geq 95\%$ in bold). Species sequenced during the present study (Bay of Biscay) in bold. The geographical location of each sequence is provided between parentheses.

TABLE 2. Morphological characters (based on Blake 2025) for all valid species in *Scalibregma* with branchiate segment from 3 to 5 and *S. celticum* (4 pairs of branchiae). “?” indicates uncertain information. Abbreviations: aLmo, anterior lobe of mouth; ant, anterior(ly); dors, dorsal(ly); elong, elongate; gls, glands; int, internal; lat, lateral(ly); perist, peristomium; pigm, pigment(ed); pLmo, posterior lobe of mouth; post, posterior(ly); prost, prostomium; ch(s), chaetiger(s); seg(s), segment(s); ventr, ventral(ly). Present study observations indicated with “**”.

	<i>S. stenocerum</i>	<i>S. hansenii</i>	<i>S. lanai</i>	<i>S. drouali</i> sp. nov.	<i>S. celticum</i>
Prostomium	Narrow ant end; horns close projected ant	T-shaped; horns projected lat	T-shaped; horns projected ca. 45 degrees	T-shaped; horns projected lat or ant-lat	T-shape; horns projected lat or ant-lat
Eyes	2 eyes, each V-shaped	Eyes absent	2 eyes, as patches	2 eyes, each V-shaped	2 eyes, each V-shaped
Frontal horns	Elong, slender; longer than prost length*	Elong, slender; about as long as prost length*	Elong, slender; about as long as prost length*	Elong, slender; about as long as prost length*	Elong, slender; slightly longer than prost length*
Peristomium	Smooth, 2 rings apparent dors and ventr; ventr encompassing mouth	With 2 dors rings, partially covering post prost	With 2 dors rings, partially covering post prost	With 2 multilobed dors rings encircling prost, covering eyes and post prost; ventr bordering mouth	With 2 multilobed dors rings encircling prost, covering eyes and post prost; ventr bordering mouth
Oral morphology	Not described; Fig. 6 of Bertelsen and Weston (1980) show mouth with vertical slit bordered lat by perist	Mouth ventr, oval with broad ant and post lips	Mouth a short transversal slit; with aLmo post to first perist ring as row of 6–8 short lobes; pLmo with 1 row short lobes attached to large ant lobed pad	aLmo formed by a paired triangular lobes with very small central pad; pLmo formed by a central plicated pad with about 6 lobes	Mouth a short transversal slit between perist and ch 1; aLmo with long medial fold; pLmo with long lobes on venter of ch 1
Segmental annulations	4 annuli in Figs 2B, C of Bertelsen and Weston (1980)	Ant chs with 4 annuli; following with 5–6 annuli	Ch 1–2 with 3 annuli, then 4 annuli with some 5 annuli far post	Ch 1 with 3 annuli, following 4 annuli; post 5 annuli; last 3 annuli	Ch 1 with 3 annuli, following 4 annuli; far post 5 annuli
Branchia	Chs 3 to 5, dense; pinnate, each pinna with additional bifurcations	Chs 3 to 5, simple; few branches	Chs 3 to 5, dense;	Chs 3 to 5, dense; pinnate, each pinna with additional bifurcations	Chs 2 to 5, dense; arborescent
Branchia size	?	1<2<3	1~2<3	1~2<3	1<<2,3,4
Dorsal/ventral cirri	Middle and post cirri inflated becoming elongate in far post ch; int gls not reported	Short triangular from ch 13–14, then elongate, lanceolate post; with int yellow gls	Small, rounded from ch 14–15, then longer and digitiform post; with pigm int gls	Small, subtriangular to blunt from ch 16–17; both quickly gets full size (in about 3–5 chaetigers); in post about same size of parapodia; int gls absent	Small, rounded from ch 15–16, then triangular and lanceolate post; int gls present
Interramal papillae	Present	Present	Present	Present	Present

.....continued on the next page

TABLE 2. (Continued)

	<i>S. stenocerum</i>	<i>S. hansenii</i>	<i>S. lanai</i>	<i>S. drouali</i> sp. nov.	<i>S. celticum</i>
Acicular chaetae number in ch 1 and 2	Ch 1–2, short, slender, blunt tips; 2–6	Ch 1–2, curved, blunt tips; 4–6 in ch 1, 6–8 in ch 2	Ch 1–2, short, pointed tips; 8–9	Ch 1–2, short, slender, blunt tips; 5 in ch 1, 9–11 in ch 2	Ch 1–2, short, blunt tips; 7 in ch 1*, 13–14 in ch 2*
Lyrate number	Up to 14	7–8 in ch 3	4–6 post ch	Up to 13	12 in ch 25*
		8–12 further back			
Tines of lyrate chaetae	Unequal size	Unequal size	Equal size	Unequal size	Unequal size
Capillaries	Smooth	Hirsute	Smooth	Smooth with some hirsute	Hirsute and some smooth*
Body pigment	Not reported	Ch 3–5 with dors yellow tranverse pigment bands; dorsal and ventral cirri with yellow gls	Annular rings with or without small pigm gls; inconspicuous	No pigm or gls observed	Patches of pigment parapodia on ch 4–6; dorsally on ch 4–5.
Posteriormost region	?	?	Last 2–3 segs cirriferous and achaetous	With 2 segs cirrigerous and achaetous, tri annuli; one without chaetae or cirri	With 2–3 segs cirrigerous and achaetous; 1–3 pre-anal segs lacking all features
Pygidium	At least 3 anal cirri	Rounded, with ca. 10 short lobes; with 5 anal cirri	Anus with short lobes; with 3 long anal cirri (1 ventr and 2 mid-ventr)	With crenulated ring around anus; with 6 anal cirri (3 different lengths) inserted ventr	With crenulated ring around anus; with 5 long anal cirri, inserted ventr
Distribution	W Atlantic (SE USA, N Carolina to Florida); 17–218 m depth.	NE Atlantic (Norwegian sea, shelf and slope); 497–1,243 m depth	SW Atlantic (SE Brazil); 38–100 m depth	NE Atlantic (SW France to Moroccan coast); 55–102 m depth	NE Atlantic (UK, France, Mediterranean Sea); 6–89 m depth* (down to 300 m (OBIS 2025)
Reference	Bertelsen and Weston (1980), Kudenov (1984), Blake (2025)	Bakken <i>et al.</i> (2014), Blake (2025)	Mendes <i>et al.</i> (2023), Blake (2025)	Present study	Mackie (1991), Blake (2025), present study

Key to *Scalibregma* species with branchiae from chaetigers 3 to 5

1. Lyrate chaetae with equal size tynes *S. lanai*
- Lyrate chaetae with subequal size tynes 2
2. Simpler branchiae *S. hansenii*
- Brushy, dense branchiae 3
3. Ventral side with inconspicuous mid ventral line and showing smooth capillaries *S. stenocerum*
- Ventral side with conspicuous mid ventral line (double central pads) and showing hirsute capillaries *S. drouali* sp. nov.

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