Zootaxa 4033 (1): 057–093
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.4033.1.3
http://zoobank.org/urn:lsid:zoobank.org:pub:9C0A63B6-5532-484D-BBD7-EDD5250D4ABA

New species of Scalibregmatidae (Annelida, Polychaeta) from the East Antarctic Peninsula including a description of the ecology and post-larval development of species of *Scalibregma* and *Oligobregma*

JAMES A. BLAKE[1,2]

[1]*Aquatic Research & Consulting, 24 Hitty Tom Road, Duxbury, MA 02332 USA.*
[2]*University of Massachusetts, Boston, 100 Morrissey Blvd., Boston, MA 02125 USA. E-mail: jablake9@gmail.com*

Abstract

A large collection of scalibregmatid polychaetes from the east Antarctic Peninsula in May 2000 has yielded specimens of three new species of *Scalibregma, Pseudoscalibregma*, and *Oligobregma*. The new species of *Scalibregma* is represented by more than 400 specimens that include post-larval and juvenile forms which, for the first time, provide data on the sequence of development of key characters of a scalibregmatid. These data demonstrate that taxonomic characters including the form of the prostomium and presence of branchiae develop late in ontogeny and that small specimens cannot be reliably referred to a species or genus without a growth sequence. Juvenile morphology is also presented for the new species of *Oligobregma*. The new species of *Scalibregma* is compared with five northern hemisphere species and differs in details of the peristomium, upper and lower lips of the mouth, dorsal and ventral cirri, and nature of the short spinous setae of setiger 1. The new species of *Pseudoscalibregma* is unique in the nature of asymmetrical ventral cirri of posterior setigers. The new species of *Oligobregma* has large acicular spines in both noto- and neuropodia and these are present in juveniles. However, the final adult configuration of the prostomium is not evident until late in development. The taxonomic significance of the timing of development of post-larval and juvenile morphology elucidated in this study is discussed in relation to the validity of certain taxa and the current system of genera used in the family.

Key words: Scalibregmatidae, *Pseudoscalibregma*, new species, Antarctica, Larsen Ice Shelf, Weddell Sea; reproduction, juvenile morphology

Introduction

Scalibregmatids are burrowing infaunal deposit feeding worms that are widely distributed but not commonly collected. They range from the intertidal to the deep-sea, with most species occurring deeper than 1000 m. Superficially, the bodies of most scalibregmatids have a rugged appearance because the cuticle is areolated with up to six annulated rows per segment. Their bodies are either elongate (arenicoliform) or maggot-shaped, and often inflated anteriorly. They typically have a bifid or T-shaped prostomium with frontal horns, which for *Polyphysia crassa* (Örsted, 1844) has been found to assist burrowing through the sediment (Elder 1973). Scalibregmatids have biramous parapodia that bear simple setae, including capillaries, lyrate setae, and acicular spines, some of which are large and conspicuous. Because scalibregmatids largely occur in deep water, little is known about their biology.

Scalibregmatids from Antarctic seas are generally well documented (Hartman 1967; Blake 1981; Schüller & Hilbig 2007; Schüller 2008). Collectively, these authors have reported 13 species from Antarctic and subantarctic locations distributed in the genera *Asclerocheilus* (1), *Oligobregma* (6), *Pseudoscalibregma* (3), *Scalibregma* (1), *Sclerocheilus* (1), and *Axiokebuita* (as *Kebuita*) (1). Of these 13 species, 12 are endemic to the Southern Ocean; the one species of *Scalibregma* has been referred by these and other authors to *S. inflatum* Rathke, 1843, the type-species.

A large, well-preserved collection of scalibregmatids was collected as part of a geological and biological survey along the eastern side of the Antarctic Peninsula in May 2000. Included among the more than 450 specimens is a full size range representing post-larval forms, juveniles, and fully developed and mature adults of a

Accepted by J. Williams: 28 Sept. 2015; published: 21 Oct. 2015

new species of *Scalibregma.* Study of the post-larval and juvenile specimens provided information of the developmental sequence of morphology in scalibregmatids for the first time. The new species of *Scalibregma* is compared with five previously described species, all from the northern hemisphere. In addition, three additional species of Scalibregmatidae are present in the collections, including one new species each of *Pseudoscalibregma* and *Oligobregma* and *P. bransfieldium* (Hartman, 1967) a previously known species.

Material and methods

The scalibregmatids used for this study were collected during a research cruise to the vicinity of the Larsen-A Ice Shelf (LIS-A) in May 2000 on the RVIB *Nathaniel B. Palmer* (Table 1). The objective of the survey was to describe the geology of the seafloor and to collect supporting benthic biology. A general account of the cruise including some geological results is found in Domack *et al.* (2001). Benthic biology samples were mostly obtained with a 0.1 m^2 Smith McIntyre grab. Each sample was physically divided in half by a Plexiglas divider. One half was used for geological assessment; the other half was for benthic infauna analysis resulting in a sample having a surface area of 0.05 m^2. Each sample was elutriated and sieved through a 300 µm mesh sieve and preserved in 10% formalin. After the cruise, the samples were shipped from the U.S. Antarctic Program base in Punta Arenas, Chile, to Port Hueneme, California, and from there to J.A. Blake in Woods Hole, MA, where the samples transferred to 70% ethanol. The samples were then sorted to major taxonomic category by a local laboratory, and subsequently distributed to the taxonomic team. A few additional samples were obtained with a megacore having core tubes with a diameter of 10 cm; some of these samples were processed on board the vessel in order to extract living polychaetes that were kept alive in culture dishes in the laboratory, observed, and photographed; other core tubes were preserved in 10% formalin for subsequent analysis. A few specimens of Scalibregmatidae were observed from these cores.

For the taxonomic analysis of scalibregmatids, all specimens were examined with light microscopy using a high-quality Wild M-5 stereomicroscope and a Zeiss RA research compound microscope equipped with phase contrast and Nomarski differential interference optics. Photomicrographs were taken with a Nikon D80 camera mounted on both the stereo- and compound microscopes. Some specimens were initially stained with a solution of Shirlastain A in water to highlight difficult-to-see surficial morphology. For this procedure, specimens were left in the stain until fine details of the morphology became evident by viewing with a stereomicroscope. Line drawings were developed with pencil using a drawing tube or Camera Lucida on the Zeiss RA and later transferred to drawing paper and inked. Additional specimens were prepared for scanning electron microscopy (SEM) at Hofstra University by dehydrating in an ascending ethanol series of 70–95% ETOH for 10 min each, followed by three changes of 100% ETOH for 15 min each. Specimens were critically point dried with a Samdri 795 Critical Point Dryer, mounted on aluminum stubs, coated with gold using an EMS-550 Sputter coater, and viewed with a Hitachi S-2460N SEM or FEI Quanta 250 SEM.

Specimens including type material are lodged at the Los Angeles County Museum of Natural History (LACM-AHF Poly); Museum of Comparative Zoology, Harvard (MCZ), and the U.S. National Museum of Natural History (USNM). A specimen from East Antarctica of the new *Scalibregma* species was from the Australian Antarctic program and is deposited in the Australian Museum (AM). Some non-type specimens are being retained by the author for further study and comparison with related species (JAB).

Terminology. Morphological terms used in this paper more or less follow those traditionally used in scalibregmatid descriptions. However, several morphological criteria differ from traditional usage and or have rarely been used in scalibregmatid descriptions. In addition, juveniles described herein differ from adults in several aspects. In order to avoid confusion raised by reviewers of this paper, the following glossary of terms is presented that emphasizes some of the main characters of taxonomic importance used in this article.

Acicular spines. In scalibregmatids these large spines are limited to a few anterior notopodia and sometimes neuropodia; spines are curved, usually sigmoid in shape, often covered with fibrils, and terminate in a blunt or pointed tip. These differ from the “spinous setae” described below.

Anal cirri. There are typically five or more elongate, fragile cirri located terminally on the pygidium; often lost during preservation.

TABLE 1. Benthic Sampling Stations—RVIB *Nathaniel B. Palmer* Cruise (NBP00-3), May 2000, Larsen Ice Shelf A and Prince Gustav Channel, East Antarctic Peninsula. Gear: SM, Smith-McIntyre Grab (0.1 m^2); MC, megacore.

Station	Location	Date	Latitude-S	Longitude-W	Depth (m)	Sampling Gear
NBP-01	Prince Gustav Channel	14-May	64°17.625′	058°34.678′	768	SM
NBP-02	Near Cape Longing	15-May	64°18.387′	058°37.911′	504	SM, MC
NBP-03	Off Lindenberg Island	15-May	64°53.533′	059°30.694′	385	SM
NBP-04	Larsen-A (Greenpeace Trough)	16-May	64°49.209′	060°32.033′	668	SM, Dredge
NBP-05	Larsen-A (Greenpeace Trough)	17-May	64°46.520′	060°10.720′	978	SM
NBP-06	Larsen-A (Greenpeace Trough)	17-May	64°45.518′	060°10.720′	733	SM, MC
NBP-07	Larsen-A (Greenpeace Trough)	18-May	64°43.523′	060°04.771′	839	SM, MC
NBP-09	Larsen-A (Greenpeace Trough)	18-May	64°57.314′	060°07.378′	305	SM
NBP-10	Larsen-A (Larsen B-transect)	18-May	64°57.368′	060°13.392′	332	SM
NBP-11	Larsen-A (Larsen B-transect)	18-May	64°56.669′	060°19.281′	350	SM
NBP-12	Larsen-A (Larsen B-transect)	19-May	64°55.101′	060°24.459′	317	SM
NBP-13	Larsen-A (Larsen B-transect)	19-May	64°53.517′	060°28.836′	323	SM
NBP-14	Larsen-A (Larsen B-transect)	19-May	64°51.818′	060°33.438′	419	SM
NBP-15	Larsen-A (Greenpeace Trough)	19-May	64°48.833′	060°36.786′	776	SM
NBP-16	Larsen-A (Greenpeace Trough)	19-May	64°43.897′	059°55.745′	713	SM
NBP-17	Larsen-A (Greenpeace Trough)	19-May	64°39.793′	060°07.662′	719	SM
NBP-18	Larsen-A (Greenpeace Trough)	20-May	64°39.381′	059°59.498′	665	SM
NBP-19	Larsen-A (Greenpeace Trough)	20-May	64°42.778′	060°20.846′	879	SM
NBP-20	Larsen-A (Greenpeace Trough)	20-May	64°44.984′	060°22.345′	899	SM
NBP-21	Larsen-A (Greenpeace Trough)	20-May	64°45.827′	060°19.450′	912	SM
NBP-22	Larsen-A (Greenpeace Trough)	20-May	64°46.632′	060°21.557′	868	SM
NBP-23	Larsen-A (Greenpeace Trough)	21-May	64°47.144′	060°21.566′	901	SM
NBP-25	Larsen-A (Greenpeace Trough)	22-May	64°43.314′	059°38.459′	628	SM
NBP-26	Larsen-A (Greenpeace Trough)	23-May	64°39.564′	059°13.226′	564	SM
NBP-27	Prince Gustav Channel	23-May	64°22.934′	058°36.976′	684	SM
NBP-28	Prince Gustav Channel	23-May	64°22.018′	058°30.942′	794	SM
NBP-29	Prince Gustav Channel	24-May	64°21.361′	058°26.637′	690	SM
NBP-30	Prince Gustav Channel	24-May	64°16.875′	058°26.985′	843	SM
NBP-32	Prince Gustav Channel	24-May	64°16.877′	058°40.025′	887	SM
NBP-33	Prince Gustav Channel	24-May	64°11.959′	058°41.857′	587	SM
NBP-34	Prince Gustav Channel	24-May	64°10.995′	058°34.140′	865	SM
NBP-35	Prince Gustav Channel	25-May	64°10.471′	058°28.505′	651	SM

Annulated rings. The segments of scalibregmatids bear 1–6 annular rings composed of separate raised or elevated pads or blocks. The number of rings and the size and organization of the pads are of taxonomic importance. Histologically, the raised pads comprising these annular rings are entirely different from the surficial papillae of the closely related *Travisia* species.

Arenicoliform. Body-shape where the anterior end is expanded, narrowing posteriorly.

Branchiae. In scalibregmatids, branchiae are limited to a few anterior parapodia and organized into clusters of dichotomously or pectinately branched filaments.

Dorsal and ventral cirri. Cirri of various shapes and forms occur on some genera and are limited to middle and posterior setigers.

Fusiform shape. Body shape where the middle of the body is expanded and the anterior and posterior ends are narrow.

Frontal and lateral horns. These are outgrowths of the anterior or subapical margins of the prostomium, often providing the prostomium with a T-shaped appearance. These horns are situated on a wedge-shaped anterior end that supports burrowing not feeding. These are superficially similar in appearance to prostomial or lateral horns of some genera of Spionidae. For scalibregmatid species where these horns are exceptionally long, ciliated and apparently grooved, they have been termed "palps" and have been determined to have a role in feeding rather than burrowing.

Lyrate setae. These are forked setae located anterior to capillaries having two thin branches with equal or unequal tynes tapering to filamentous tips and with numerous delicate plate-like bristles on the inner margins.

Maggot-shaped. Body shape where the entire body is thick from anterior to posterior with no part being noticeably wider or narrower; also termed sausage-shaped.

Pygidial lobes. A ring of lobes surrounding the pygidium; number variable from 3 to many; usually with some lobes bearing anal cirri.

Spinous setae. These are short, spines located anterior to capillaries or acicular spines on a few anterior segments of adults where lyrate setae do not occur; these are considered to be homologous to lyrate setae because they occupy the same position as lyrate setae on following segments and some are described with split or forked tips, other are blunt or aristate. In juveniles, these spinous setae occur on a greater number of segments and prior to the appearance of any lyrate setae. When lyrate setae do appear, they replace the spinous setae except for those anterior segments where lyrate setae do not develop.

Tubular glands. Unicellular tubular glands are present in dorsal and ventral cirri of some species; similar glands have been reported in clusters on some anterior noto- and neuropodia.

Upper and lower lips of the mouth. The upper and lower lips of the mouth are arranged in groups of elevated lobes or pads (forms are species-specific).. The upper lip is entirely derived from the peristomium; the lower lip is also derived from the peristomium, but may have contributions from the first setiger.

Ventral groove. A distinct mid-ventral groove containing 1–4 raised pads per segment forming a ridge line is present on species described in this paper.

Taxonomic account

Family Scalibregmatidae Malmgren 1867

Genus *Scalibregma* Rathke, 1843

Type Species: *Scalibregma inflatum* Rathke, 1843.
Synonym: *Oligobranchus* Sars, 1846. *Fide* Hartman 1959.

Diagnosis. Body elongate, arenicoliform. Prostomium T-shaped with lateral horns. Peristomium achaetous, surrounding prostomium dorsally and forming upper and lower lips of mouth ventrally. Parapodia of posterior segments with dorsal and ventral cirri; interramal papilla present; postsetal lamellae absent. Branchiae present in anterior segments. Setae include capillaries, lyrate setae, and sometimes inconspicuous blunt, pointed, or bifurcated spinous setae anterior to capillaries of setigers 1 or 1–2, representing homologues of lyrate setae; large conspicuous acicular spines absent. Pygidium with long anal cirri.

Remarks. Until recently, *Scalibregma inflatum* was considered to be cosmopolitan in its distribution. Mackie (1991), however, demonstrated sufficient variability in European populations to define an additional, closely related species, *S. celticum* Mackie, 1991. Among other observations, Mackie (1991) discovered that short slender spines were present anterior to the capillaries of a few anterior noto- and neuropodia anterior to the setigers where lyrate setae occurred. Prior to this study *Scalibregma* had been defined as lacking any type of spinous seta. The spinous setae discovered by Mackie were not the large, curved acicular spines that have been reported for species of *Asclerocheilus, Oligobregma, Parasclerocheilus Sclerobregma,* and *Sclerocheilus* but were instead inconspicuous companions of the capillaries. For *S. inflatum* Mackie (1991) found that some of these setae were forked or split on their tips. This observation plus their position in the setal fascicles suggested that they were homologous to the lyrate setae of following segments. Mackie further suggested that the larger recurved spines of other genera were homologous with capillaries.

Mackie (1991) redescribed *Scalibregma inflatum* based on specimens from the type locality in Norway as well as from Sweden, Scotland, Wales, and Ireland. The second species, *S. celticum*, was from Scotland, Wales, and France and differed in that the small spinous setae of setigers 1–2 were blunt-tipped instead of bifurcate. Additionally, eyes were present instead of absent and there were differences in the form of the peristomium, size and distribution of the epidermal pads above the notopodia, and in the number and arrangement of the pygidial cirri. *S. celticum* was subsequently reported from the Mediterranean by Çinar (2005) and Lomiri *et al.* (2012).

Mackie (1991) also re-examined *Sclerobregma stenocerum* Bertelsen & Weston, 1980, from shelf depths along the southeastern United States and found that the anterior acicular spines reported for the species by Bertelsen & Weston (1980) were of the small, inconspicuous kind found in *Scalibregma* species instead of the large, curved acicular spines found on other species of the *Sclerobregma*. *S. stenocerum* was therefore transferred by Mackie (1991) to *Scalibregma*. Mackie also examined the holotype of *S. branchiatum* Hartman, 1965, the type-species of *Sclerobregma* from deep water in the western North Atlantic and found short spinous setae anterior to the larger acicular spines of setigers 1 and 2. A similar situation exists in *Cryptosclerocheilus baffinensis* Blake, 1972, described from deep water in Baffin Bay. This species was reported to have slender, blunt-tipped spines in the noto- and neuropodia of setiger 2; these were replaced by furcate setae from setiger 3 (Blake 1972). A re-examination of prepared slides of these spines confirms that these are the same type of seta reported by Mackie (1991) for the three species of *Scalibregma* examined by him.

Following the lead of Mackie (1991), Blake (2000) examined specimens from California previously identified as *Scalibregma inflatum* and described a new species, *S. californicum* Blake, 2000. He also suggested that specimens from the U.S. Atlantic coast included at least one new species in addition to *S. stenocerum*. Most recently, Bakken *et al.* (2014) described *S. hanseni* Bakken, Oug & Kongsrud, 2014 from deep water off Norway. These authors also focused on the short, spinous setae anterior to normal capillaries in setigers 1–2 and found similar spines in *Pseudoscalibregma parvum* (Hansen, 1879). In my own work, numerous species of Scalibregmatidae have been examined and these short spinous setae, considered homologous to the lyrate setae, have been found in other genera including some with large curved acicular spines. I now believe that most species of Scalibregmatidae having lyrate setae will be found to have the same type of short spinous setae in segments anterior to where the lyrate setae begin.

To date, specimens of *Scalibregma* from Antarctic waters have been identified in several faunal and ecological accounts as *S. inflatum* (see reference list below). The only original illustrations of *Scalibregma* from Antarctica appear to be by Knox & Cameron (1998) of the anterior end and a branchiate parapodium from a specimen collected from the Ross Sea in 578 m.

Scalibregma australis **new species**

Figures 1–3

Scalibregma inflatum: Hartman 1967: 134, 1978: 181; Blake 1981: 1146; Siciński 1986: Table II, Fig. 5, 2000: 164, 2004: 82; Hartmann-Schröder 1986: 84; Hartmann-Schröder & Rosenfeldt 1989: 73, 1991: 75; Cantone & Sanfilippo 1992; Knox & Cameron 1998: 75, figs 141–142; Cantone 1994: 41; Cantone *et al*. 2000: 554; San Martín *et al.* 2000: 85, 91; Lovell & Trego 2003: 1813; Montiel *et al*. 2005: 199; Hilbig *et al.* 2006: 724; Schüller *et al.* 2009: 63; Barbosa *et al.* 2010:1155; Parapar *et al.* 2011a: 728; Pabis & Sobczyk 2015: 115–117. Not Rathke 1843.

Material examined. East Antarctic Peninsula, RVIB *Nathaniel B. Palmer* Cruise 2000-03, Collector, J.A. Blake.—**Prince Gustav Channel**, Sta. NBP-01, 768 m, 62 **paratypes** (LACM-AHF Poly 7001); Sta. NBP-27, 684 m, 12 **paratypes** (USNM 1281913); Sta. NBP-28, 794 m, 4 specimens (JAB); Sta. NBP-29, 690 m, 11 **paratypes** (LACM-AHF Poly 7007); Sta. NBP-30, 843 m, 13 specimens (JAB); Sta. NBP-33, 587 m, 19 specimens (JAB); Stas. NBP-35, NBP-35A, NBP-35B, 651 m, 3, 6, and 14 specimens, respectively, from three grabs (JAB).—**Off Cape Longing,** Sta. NBP-02, 504 m, 19 **paratypes** (LACM-AHF Poly 7002).—**Off Lindenberg Island**, Sta. NBP-03, 385 m, 12 **paratypes** (USNM 1281909).—**Larsen Ice Shelf Area, Greenpeace Trough**, Sta. NBP-04, 668 m, **holotype** and 17 **paratypes** (LACM-AHF Poly 7003, 7004); Sta. NBP-05, 798 m, 7 specimens (JAB); Sta. NBP-06, 733 m, 7 **paratypes** (LACM-AHF Poly 7005); Sta. NBP-07A, 839 m, 8 **paratypes** (USNM 1281910); Sta. NBP-07B, 839 m, 15 **paratypes** (MCZ 60891); Sta. NBP-16, 713 m, 14 **paratypes** (MCZ 60892); NBP-17, 719 mm, 7 **paratypes** (MCZ 60893); Sta. NBP-18, 665 m, 11 specimens (JAB); Sta. NBP-19, 879 m, 2 specimens (JAB); Sta. NBP-20, 899 m, 1 specimen (JAB); NBP-22, 3 specimens (JAB); Sta. NBP-23, 901 m, 7 specimens (JAB).—**Larsen Ice Shelf Area, transect along border with Larsen Ice Shelf B**, Sta. NBP-10, 332 m, 18 **paratypes** (USNM 1281911); Sta. NBP-11, 350 m, 3 specimens (JAB); Sta. NBP-12, 317 m, 27 **paratypes** (LACM-AHF Poly 7006); NBP-13, 323 m, 16 **paratypes** (USNM 1281912); Sta. NBP-14, 8 specimens (JAB).—**Weddell Sea off LIS-A Area**, Sta. NBP-25, 628 m, 9 specimens (JAB).—**East Antarctica, Wilkes Land, Vincennes Bay, Casey Station**, coll. Australian Antarctic Division, O'Brien Bay, SRE-1, Control R2, 12 Nov 1997, 66.295°S; 110.536°E, diver cores, 12–25 m, 1 specimen (AM).

Description. A large species, body elongate, arenicoliform, expanded in anterior half to variable degree, usually from about setiger 4–5 continuing to mid-body, then tapering to narrow abdominal region (Fig. 3C). Body surface covered with numerous annulated rings; most annulations formed of separate elevated pads or blocks (Figs. 1A–E, 2A). Holotype from Sta. NBP-04 ovigerous female, 32 mm long, 4.5 mm wide across expanded anterior region, with 40 setigerous segments; large paratype from Sta. NBP-01, 21 mm long, 4.5 mm wide anteriorly, for 41 setigers; six smaller paratypes from same sample, 7–10 mm long, 1.1–2.1 mm wide for 32–40 setigers. Numerous smaller specimens including post-larval forms as small as 1 mm long or less with as few as 10 setigers common in samples. Color in alcohol light tan with no yellow-orange caste as in other species; some specimens with distinct dark reddish-colored glands forming a row across dorsum of setigers 4–5 (Fig. 3A); similar isolated pigmented glands consisting of numerous twisted tubules on some anterior neuropodia (Fig. 2B); these glands likely retaining color derived from Rose Bengal stain used in sample processing; similar reddish-colored glands in dorsal and ventral cirri of posterior parapodia (Figs. 2C–D, 3D–G).

Prostomium T-shaped, with lateral processes or horns well developed, pointed laterally, sometimes oriented dorsally or anteriorly (Figs. 1A–C, 2A, 3A–C); posterior margin of prostomium visible dorsally (Fig. 1A–B); eyes absent. Nuchal organs not everted on any specimens; ciliated grooves apparent between prostomium and peristomium on some specimens. Peristomium achaetous, not concealing posterior margin of prostomium, consisting of single ring complete dorsally (Figs. 1A–C), split into three rings ventrally forming the upper lip of the mouth and together with annulated rows from setiger 1 forming the lower lip of the mouth (Figs. 2A, 3B). Mouth surrounded by broad lateral lips divided anteriorly into a row of small elongate lobes forming upper lip of mouth and posteriorly by 4–5 large paired lobes or blocks forming lower lip of mouth at level of setiger 1 (Fig. 2A). Juvenile morphology suggests that upper and lower lip morphology entirely derived from peristomium (see below). Proboscis smooth sac when everted.

Dorsally, setiger 1 biannulate and setigers 2–3 triannulate (Figs. 1A–B); ventrally, setigers 1–3 triannulate (Fig. 2A); subsequent anterior setigers of expanded region quadriannulate, narrow posterior segments initially quadriannulate, then becoming pentannulate and quadriannulate in far posterior setigers (Fig. 1D). Each annulation divided into separated elevated pads or square-shaped blocks, providing complex areolated appearance to body surface. Ventral midline from setiger 2 with group of four large epidermal pads per segment in anterior segments (Figs. 2A, 3B), merging into a single pad in middle and posterior segments, forming ridge line within mid-ventral groove; mid-ventral groove and ridge line continuing posteriorly (Fig. 3C).

Arborescent or dendritically branched branchiae present on setigers 2–5 posterior to notosetae (Figs. 1A, C, 2A–B, 3B). Parapodia reduced, inconspicuous anteriorly (Figs. 1C, 2B) becoming larger and more conspicuous in middle and posterior setigers (Figs. 1D, 2C–D); Dorsal and ventral cirri develop from about setigers 17–20 or mid-body; dorsal cirri initially short, triangular (Figs. 2C, 3D), becoming slightly longer and narrower by about setiger 30 (Figs. 1E, 2D, 3F), continuing to posterior end; ventral cirri narrower than dorsal cirri, oval, tapering to rounded tip. Each dorsal and ventral cirrus with darkly pigmented glands; each gland formed of tubules appearing to exit dorsally on dorsal cirri and ventrally on ventral cirri (Figs. 3D–G). Interramal papillae small, inconspicuous in anterior setigers, becoming larger in middle and posterior parapodia (Fig. 2C).

All setigers with noto- and neuropodial fascicles of slender capillaries, with those of anterior fascicles more numerous, arranged into 2–3 rows, with setae of posterior row longest; capillaries of middle and posterior setigers arranged in 1–2 rows; all capillaries with numerous short bristles along length, representing emerging fibril endings (Figs. 1F–G); setiger 1 with additional anterior row of inconspicuous short, slender, pointed aristate spinous setae (Figs. 1F–G; 2E) with occasional spine having two thin branches (Fig. 2E); spines numbering 8–12 on large specimens, fewer on specimens of 10 mm or less in length. Setigers 2 and following with lyrate setae in same anterior position as short spines of setiger 1; each lyrate seta with nearly equal tynes tapering to filamentous tips and with numerous flattened, plate-like bristles on inner margins (Fig. 1H–I, 2F), details best seen with SEM.

Pygidium of largest specimens with anal opening surrounded by about 12 elongate lobes (Fig. 1D), pygidium inflated in smaller specimens with fewer poorly defined lobes poorly defined (Fig. 2G); pygidium with five long, thin anal cirri, two dorsal, two ventral and one mid-ventral (Fig. 2G); these cirri fragile, missing on most specimens. **Ecology.** Sediment particle size distributions analyzed from the same grabs as the biology samples from vertical subcores taken to a depth of 12 cm were reported by Gilbert & Domack (2003). A core closest to the Antarctic Peninsula in the LIS-A area (Sta. NBP-05) was dominated by silt and clay, but exhibited higher concentrations of coarse sand and gravel of up to 30% near the surface; adjacent cores taken further offshore (Stas. NBP-06 and -07) had a more uniform particle size distribution of fine silt with depth. Out of 16 subcores analyzed from the LIS-A area, ten showed the maximum amount of gravel to occur in the upper 2.5 cm; of the remaining six subcores, four showed a decrease of coarse particles at the surface and two had subsurface maxima. Of nine subcores collected from the Prince Gustav Channel, seven had a sand-gravel maximum at the surface. Of the 26 subcores collected and analyzed for particle size, 65% had a sand-gravel maximum near the surface overlying fine silt and clay.

With respect to diversity, the dominance of silt + clay overlain with coarse sediments provides a variable sedimentary habitat to support an interesting mix of benthic invertebrates (Blake & Maciolek unpublished data). Out of 32 successful grab samples (21 from the LIS-A area; 11 from the Prince Gustav Channel), a total of 270 species of benthic invertebrates were identified, 128 of which were polychaetes. Of the total invertebrate fauna, *Scalibregma australis* **n. sp.** was the fifth most abundant species identified, with a total of 419 specimens. Two cirratulid polychaetes, *Tharyx homosetosus* (Hartmann-Schröder & Rosenfeldt, 1989) (891 specimens) and *Chaetozone* sp. 1 (828 specimens), a bivalve, *Yoldiella* cf. *vallettei* (Lamy, 1906) (704 specimens) and a scaphopod, *Siphonodentalium* sp. (688 specimens) were the four most abundant species.

Elsewhere in Antarctica, high benthic biomass (1.3 g/0.1 m^2) and high density (37.3 ± 20.6 ind/0.1 m^2) for *S. inflatum* was reported by Pabis & Sobczyk (2015) from a glacial fjord on King George Island, South Shetland Islands having strong currents, away from glacial influence, and with poorly sorted sandy sediments.

Typically, scalibregmatid polychaetes do not occur in high densities in benthic communities. Therefore, the dominance of *Scalibregma australis* **n. sp.** in sediments along the east Antarctic Peninsula is unusual and reminiscent of similar high densities of *S. inflatum* in continental slope sediments (600–1500 m) off Cape Hatteras, NC (Blake 1993; Blake & Hilbig 1994). Live phytoplankton cells were recovered at 14 cm depth in the sediments from the Cape Hatteras sediments, suggesting rapid subduction (Cahoon *et al.* 1994) and possibly caching by deposit feeders such as *S. inflatum*. Blair *et al.* (1996) documented rapid *in situ* uptake of 13C-labeled *Chlorella* sp. by *S. inflatum* and rapid subduction of labeled material from the same area. Similar efforts to understand organic content of sediments along the east Antarctic Peninsula have not been undertaken. R.E. Ruff (personal communication) also provided evidence of high densities of *S. californicum* in one sample from the NE Pacific in the San Juan Archipelago from 24 m in silt and clay (376 specimens, 14 June 2012) and another from Bellingham Bay, 26 m in silt and clay (683 specimens, 08 Apr 2014). Most scalibregmatids are believed to be burrowing subsurface deposit feeders (Jumars *et al.* 2015).

Available data on the reproduction and post-larval development of *S. australis* **n. sp.** is presented in a separate section (below).

Remarks. *Scalibregma australis* **n. sp.** from Antarctica is compared with five previously known species, all from the northern hemisphere (Table 2). All of the six known species have a T-shaped prostomium with laterally or anteriorly directed fronta l horns, short spinous setae anterior to capillaries in setigers 1 or 2, lyrate setae from

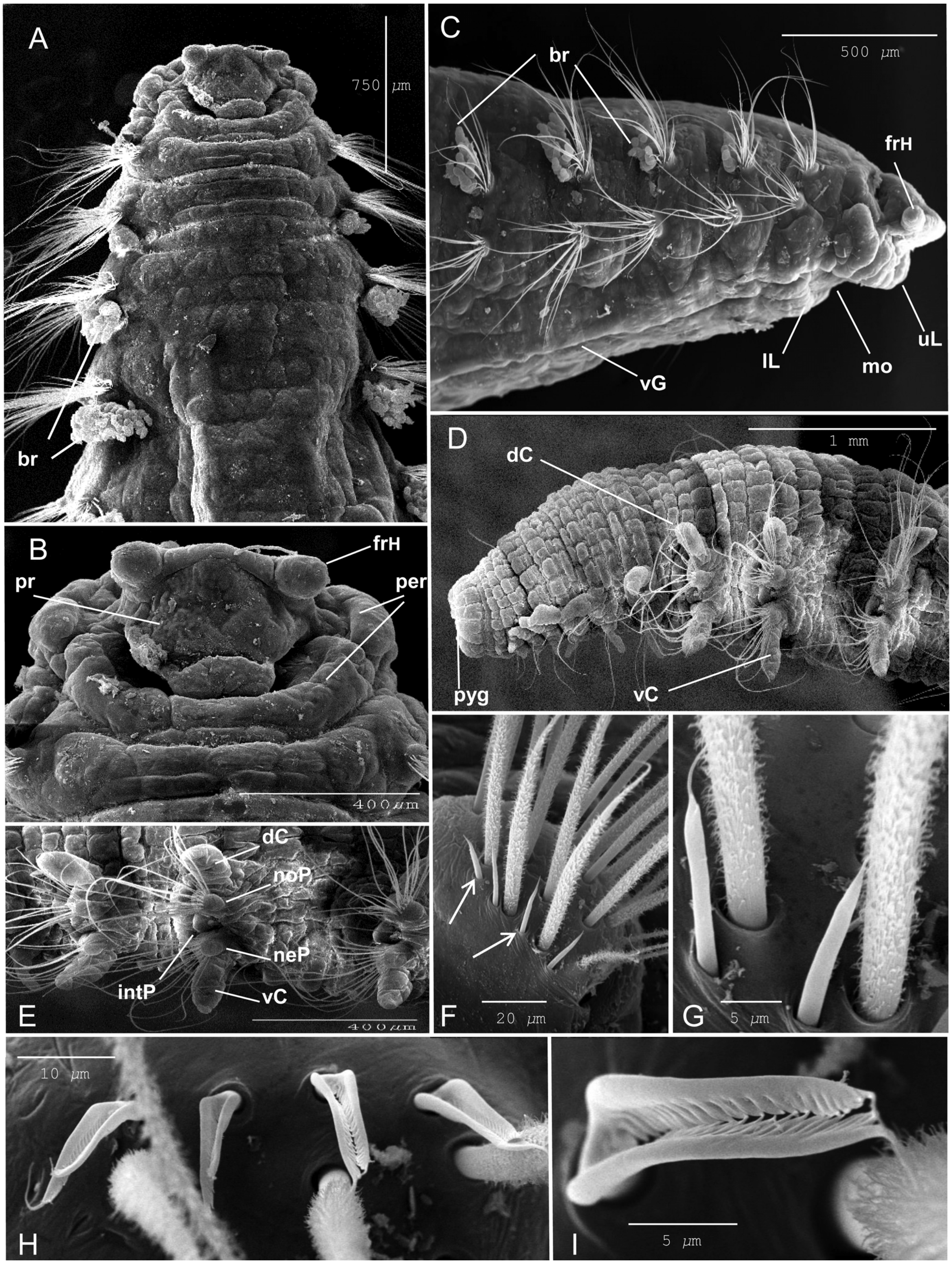

FIGURE 1. *Scalibregma australis* **n. sp.** SEMs from Sta. NBP 29: A, anterior end, dorsal view; B, same specimen showing details of prostomium, peristomium, and setiger 1; C, anterior end of another specimen, right lateral view; D, posterior end, right lateral view; E, parapodia from posterior setigers, right lateral view; F, notosetae from setiger 1, with anterior row of short spinous setae (arrows) and three rows of capillaries; G, detail of two short neuropodial spinous from setiger 1 and bases of two capillaries with numerous short bristles or fibril endings; H, four lyrate neurosetae from setiger 2; I, same, detail of a single lyrate seta with plate-like bristles along interior margin of tynes. Abbreviations: br, branchiae; dC, dorsal cirrus, frH, frontal horn, intP; interramal papilla; lL, lower lip of mouth; mo, mouth; neP, neuropodium; noP, notopodium; per, peristomium; pr, prostomium; pyg, pygidium; uL, upper lip of mouth, vC, ventral cirrus; vG, ventral groove.

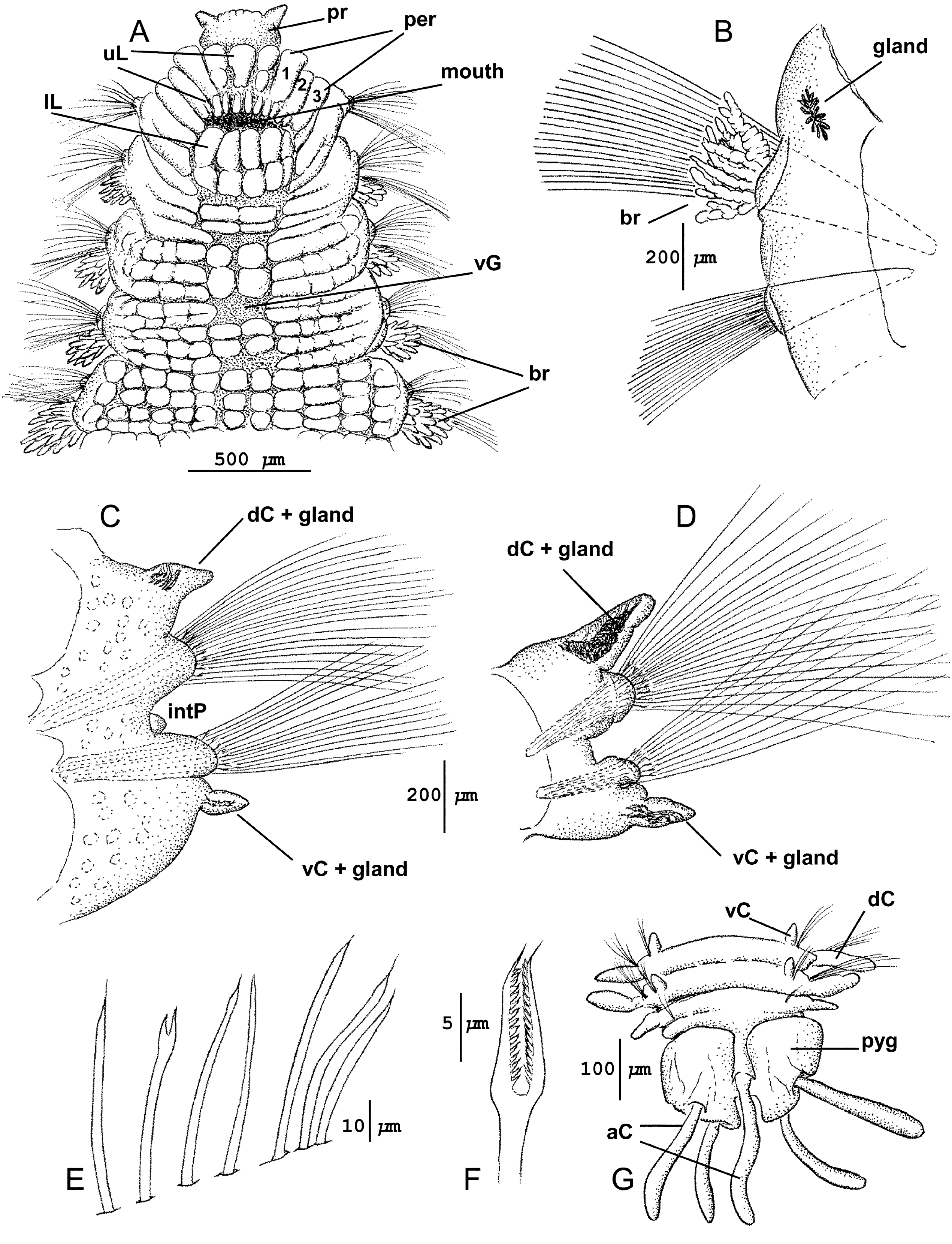

FIGURE 2. *Scalibregma australis* **n. sp.** Paratypes Sta. NBP-01 (LACM AHF Poly 7001): A, anterior end, ventral view; B, setiger 4, right side, anterior view; C, mid-body setiger, left side, anterior view; D, posterior setiger, left side, anterior view; E, short spinous setae from setiger 1; F, lyrate seta from middle body segment; G, pygidium, ventral view. Abbreviations: aC, anal cirri; br, branchiae; dC, dorsal cirrus, intP; interramal papilla; lL, lower lip of mouth; per, peristomium; pr, prostomium; pyg, pygidium; uL, upper lip of mouth, vC, ventral cirrus; vG, ventral groove. Numbers 1, 2, & 3 denote three rings of the peristomium.

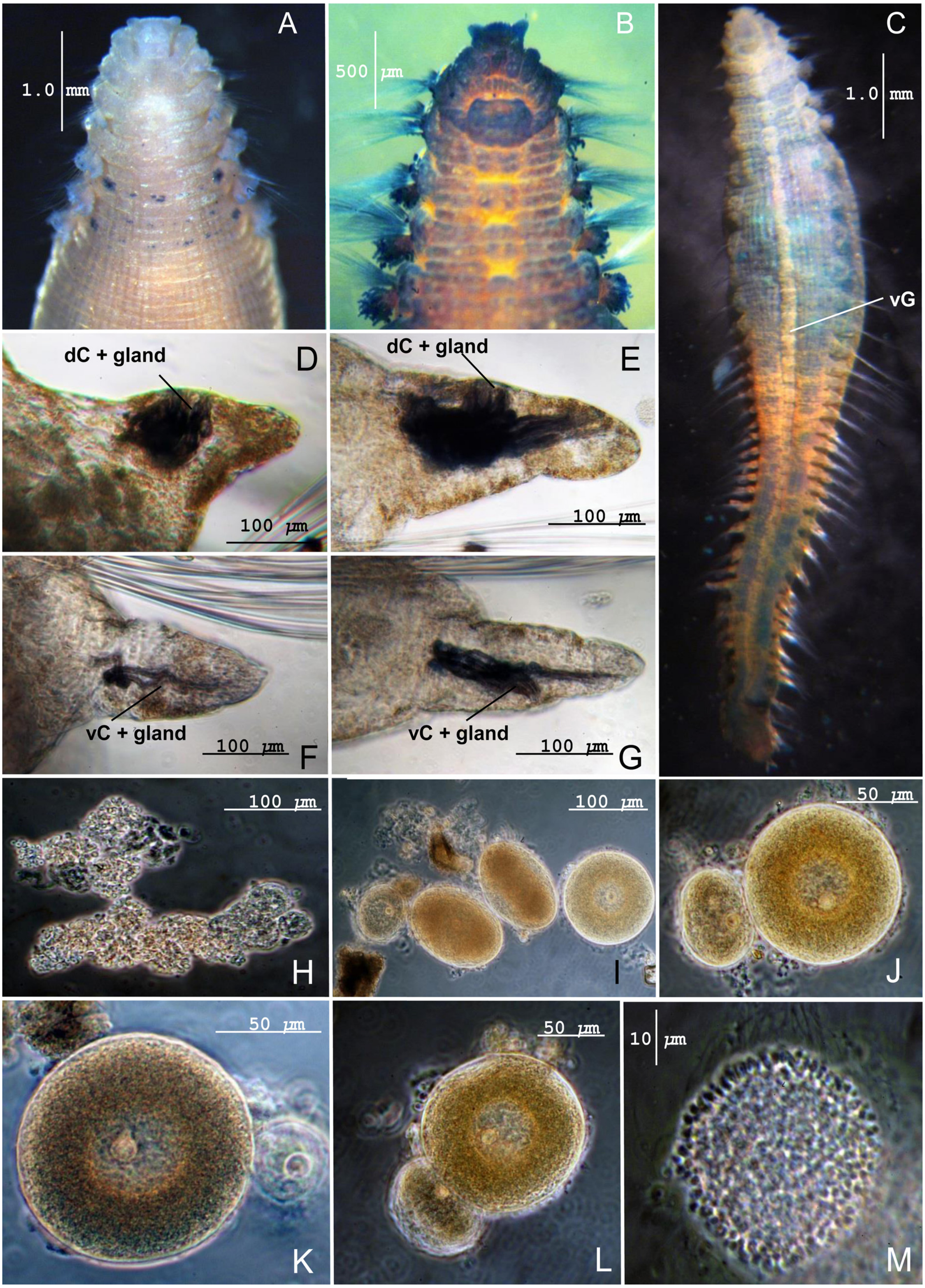

FIGURE 3. *Scalibregma australis* **n. sp.** Photomicrographs of Paratypes Sta. NBP-01 (LACM-AHF Poly 7001): A, anterior end, dorsal view; B, anterior end, ventral view; C, entire animal, ventral view; D–E, dorsal cirri from middle (D) and posterior (E) parapodia showing internal glands; F–G, ventral cirri from middle (F) and posterior (G) parapodia showing internal glands; H, oocytes, from parts of ovaries; I–L, oocytes in different stages of maturation; M, sperm packet with sperm nuclei and flagella visible. Abbreviations: dC, dorsal cirrus, vC, ventral cirrus; vG, ventral groove.

TABLE 2. Comparison of Morphology among Adults of Six Species of *Scalibregma.*

Species/Morphology	*Scalibregma inflatum* (Ashworth, 1902)	*Scalibregma celticum* Mackie, 1991	*Scalibregma californicum* Blake, 2000	*Scalibregma stenocerum* (Bertelsen & Weston, 1980)	*Scalibregma hanseni* Bakken, Oug & Kongsrud, 2014	*Scalibregma australis* n. sp.
Prostomium	T–shaped, lateral processes pointed laterally or anterolaterally	T–shaped, lateral processes pointed laterally or anterolaterally	T–shaped, lateral processes pointed anterolaterally	T–shaped, lateral processes pointed anterolaterally	T–shaped, lateral processes anterior/lateral	T–shaped, lateral processed pointed anterolaterally; narrow posterior to projections, then becoming wide and inflated
Eyes	Absent	Pair of dark brown to black subdermal eyes	Absent	Posterolaterally located, V-shaped with points directed anteriorly	Absent	Absent
Peristomium	A single ring dorsally; approximately 3 rings ventrally, merging with the upper lips of the mouth	Dorsally expanded, hood–like, covering eyes and posterior prostomium	Does not conceal posterior margin of prostomium, 2 rings merge dorsally and encompass mouth ventrally	Achaetous and apodous	Two dorsal rings, partial covering of posterior prostomium; ventrally narrow	One dorsal ring encompassing prostomium; three rings ventrally forming anterior and posterior lips of mouth
Nuchal Organs	Present, eversible, dorsolateral on either side of the prostomium	Present, eversible, on lateral side of prostomium immediately behind eyes	?	Branched, originating at posterolateral margins of prostomium	?	Ciliated; present laterally on both sides of prostomium
Mouth	Upper lip a large biannulate and tessellate pad, lower lip narrow, single row of pads	Upper lip with distinct longitudinal median fold, lower lip large with radiating wrinkles	Surrounded by broad lateral lips; small rounded upper lip; lower lip with 4–5 short lobes	?	Broad anterior and dorsal lips	Upper lip with a row of narrow pads; lower lip with two rows of 5–6 large pads; small lobes laterally
Proboscis	Smooth sac	Smooth sac	Smooth sac	Smooth sac	Folded, undulating rim	Smooth sac
Annulation	Setigers 1–3 triannulate, quadriannulate or pentannulate after	Setiger 1 triannulate, quadriannulate or pentannulate after	Setigers 1–4 triannulate, pentannulate after	Transverse annulation	Setigers 1–4 quadriannulate; subsequent with 5–6 annulations	Anterior most segments triannulate or quadriannulate, posterior segments pentannulate
Ventral Midline/ Groove	From setiger 2 (hexagonal or pentagonal on 2 (possibly 3–4) rectangular or biannulate after)	From setiger 2 (broad rectangular to trapezoidal and biannulate on 2, then rectangular and biannulate after)	From setiger 2, deep groove containing large epidermal pads	Narrow ventral groove depicted in drawing, but not described	Present, 1 pad per segment	From setiger 2, four raised pads in mid-ventral groove, continuing along body; groove deep in narrow posterior segments
Branchiae	Present, setigers 2–5	Present, setigers 2–5	Present, setigers 2–5	Present, setigers 3–5	Present, setigers 3–5	Present, setigers 2–5
Dorsal/Ventral Cirri	Initially small and rounded, then becoming triangular, then becoming lanceolate	Initially small and rounded, then becoming triangular, then becoming lanceolate	Bulbous, low and rounded at first, then becoming larger and triangular	Short, inflated, becoming more elongate in posterior segments	Short triangular at first, becoming lanceolate in posterior segments	Short, triangular at first, then elongate, fingerlike
Glands on dorsal and ventral cirri	Present	Present	Black spots on dorsal and ventral cirri	Dorsal and ventral cirri retain reddish brown pigment in alcohol	Present, yellowish color	Present, dark reddish

TABLE 2. Comparison of Morphology among Adults of Six Species of *Scalibregma*.

Interramal Sense Organ	Small, from setiger 1	Small, from setiger 1	Small, inconspicuous, from setiger 1	Small and rounded, middle and posterior parapodia	Present from about setiger 15	Small and rounded, from setiger 1
Setiger 1 and/or 2 with short spinous setae in 1st row anterior to capillaries	Present setiger 1, pointed and bifurcate ca. equal numbers	Present setigers 1–2, short, blunt, smooth	Present setiger 1, row of 10–12, short pointed spines	Present, setigers 1–2	Present setigers 1–2, short, curved blunt tipped	Present setiger 1, most aristate, rare bifurcate
Lyrate Setae	From setiger 2	From setiger 3	From setiger 2	From setiger 3	From setiger 3	From setiger 2
Lyrate Setae Tynes	Unequal (ratio of about 1.2)	Unequal (ratio of about 1.3)	Nearly equal	Unequal	Nearly equal	Nearly equal
Pygidium	Crenulate margin around anal aperture	Crenulate margin around anal aperture	Numerous lobes	?	About 10 lobes	Crenulate/multilobate margin around anal aperture
Anal Cirri	Five filiform anal cirri (1 median ventral and 2 pairs ventrolateral)	Five long, ventrally inserted filiform anal cirri	Five long, thin anal cirri arising from ventral most lobes	0–3 on specimens examined, located ventrally and ventrolateral	Up to 5 cirri	Five long, thin anal cirri; 2 dorsal, 2 ventral, 1 mid–ventral
Body pigment	Small glandular patches dorsal and ventral to parapodia on setigers 4–5	Solitary patches stained with Rose Bengal ventral to parapodia on setigers 4–6; and dorsally on setigers 4–5	Body yellow-orange, with black spots on some annulated rings and dorsal and ventral cirri	?	Setigers 3–5 with dorsal yellow transverse pigment bands; dorsal and ventral cirri with yellow glands	Band of spots dorsally between setigers 3–4 and 4–5 on some specimens, some isolated spots ventral on setigers 2–3. These apparent when stained with Rose Bengal

setigers 2 or 3, dendritically branched branchiae on four or five anterior setigers, well-developed dorsal and ventral cirri on middle and posterior setigers, and a ventral groove containing elevated pads running the length of the body.

Scalibregma australis **n. sp.** is most closely related to *S. inflatum* and *S. californicum* Blake, 2000. All three species have lyrate setae from setiger 2; the other three species have them from setiger 3; branchiae are on setigers 2–5, two other species have them on setigers 3–5; eyes are absent, two other species have eyes (Table 2).

The main characters that separate *S. australis* **n. sp**., *S. inflatum*, and *S. californicum* from one another are (1) details of the peristomium, (2) the development of the upper and lower lips that surround the mouth, (3) the shape of the dorsal and ventral cirri along the body, and (4) the structure of the short spinous setae in setiger 1.

Peristomium. The peristomium of *S. inflatum* consists of a single ring dorsally and approximately four rings ventrally, merging with the upper lips of the mouth (Mackie 1991); in *S. californicum* the peristomium has two rings dorsally that extend ventrally to merge with the lateral lips of the mouth (Blake 2000); in *S. australis* **n. sp**., the single dorsal peristomial ring divides into three ventral rings that merge with the upper lip of the mouth.

Upper and lower lips surrounding mouth. The morphology of the upper and lower lips of the mouth differs considerably among *S. inflatum, S. californicum,* and *S. australis* **n. sp.** In *S. inflatum*, the upper lip of the mouth consists of a biannulate row of large pads and the lower lip by a narrow single row of pads; in *S. californicum*, padded rows are not present, instead there is a small rounded upper lip, long lateral lips, and a ventral lip consisting of 4–5 short lobes; in *S. australis* **n. sp.**, the upper lip has a curved row of numerous narrow pads, small lobes laterally, and two rows of 5–6 large pads ventrally.

Dorsal and ventral cirri. In *S. inflatum*, the dorsal and ventral cirri transition from a rounded triangular shape anteriorly to a lanceolate shape posteriorly; in *S. californicum*, these same cirri transition from a bulbous to a triangular shape along the body; in *S. australis* **n. sp.**, the cirri are initially short and triangular, becoming elongate and finger-like posteriorly, with the dorsal cirri always larger than the ventral ones.

Short spinous setae on setiger 1. In *S. inflatum*, these spines are simple pointed or distally bifurcate in approximately equal numbers; in *S. californicum*, all spines are pointed, never bifurcate; in *S. australis* **n. sp.** the spines are mostly simple and aristate, rarely bifurcate.

Additionally, there may be differences in the arrangement of the five anal cirri, but given that these structures are fragile and often missing from preserved specimens, their position and location on mature specimens is not well documented. For *S. inflatum,* Mackie (1991) indicated that one mid-ventral cirrus and four ventrolateral cirri are present; for *S. californicum*, Blake (2000) reported that the five cirri arise from a ventral position; in the present study, *S. australis* **n. sp**. has a single ventral cirrus, two dorsolateral cirri, and two ventrolateral cirri.

Etymology. *Australis* is Latin for southern.

Distribution. Widespread on both sides of the Antarctic Peninsula: Weddell Sea, Larsen Ice Shelf area, Prince Gustav Channel; Elephant Island, South Shetland Islands, 45–1000 m. Bellingshausen Sea, ~500 m. Ross Sea: Terra Nova Bay, 320–670 m; off Daniell Peninsula, north of McMurdo; 567–578 m. East Antarctica, Wilkes Land, O'Brien Bay, 10–25 m.

Reproduction of Scalibregmatids and Observations on the Gametes and Post-larval Development of *Scalibregma australis* n. sp.

Figures 3H–M, 4–5

Reproduction. There is little information available regarding the reproductive biology of scalibregmatids. Adults of *Scalibregma inflatum* have been observed swimming in the plankton; this behavior is believed to be associated with spawning (Ditlevsen 1911; Clark 1954). Clark (1954) also reported *Lipobranchus jeffreysii* (McIntosh, 1869) swarming in the plankton in February 1953. Fage & Legendre (1927) reported swarming of *S. inflatum* at Concarneau in the Mediterranean, but they also reported the presence of a pair of eyes on their specimens, which are lacking in *S. inflatum*. Those specimens are likely *S. celticum* according to Mackie, (1991). In most cases, these swimming scalibregmatids exhibited long, natatory-like setae.

Size-frequency data on *S. inflatum* in continental slope sediments (600 m depth) off North Carolina did not exhibit any strong evidence of seasonality and only weak evidence of summer recruitment (Blake 1993); the data suggest year-around reproduction.

The observations that some species of Scalibregmatidae develop long natatory-like setae and swim in the plankton at certain times of the year suggest that spawning takes place in the water column. However, there are no published observations to confirm this or even to understand how eggs are fertilized or the fate of such fertilized eggs if they are released in the water. There are no accounts of the embryology or early development of larvae; there are no reports of larvae in the plankton. In the present study, well-preserved early post-larval stages of *S. australis* **n. sp.** were collected from the sediment samples.

According to Ashworth (1901), the anlage of reproductive organs in *S. inflatum* are groups of cells associated with the nephridia. These cells are eventually released into the coelom and the oocytes thus follow extra-ovarian development, deriving their nutrition from coelomic fluid (Eckelbarger 2005, 2006).

A full range of oocytes in various stages of development was observed for *S. australis* **n. sp.** from coelomic smears of several large specimens ranging from 15–20 mm or more in length. Groups of small cells believed to be parts of the ovaries themselves were removed from attachment points during dissection. One set most certainly comprised developing oocytes because the larger cells were clearly round or oval in shape (Fig 3H). The largest eggs observed from the coelomic smears were oblong 120 x 84 µm; when rounded up, they were about 110 µm in diameter. A distinct nucleolus in the germinal vesicle was apparent in these larger ova (Figs. 3 I–L). Smaller stages of oocyte development lacked visible evidence of a nucleus. Some of the smaller oocytes were observed in apparent union with large ova, suggesting a nurse cell pattern of oocyte maturation in the coelom after release from the ovaries (Figs. 3J–L). However, this cannot be confirmed without further study. Thin sections are required in order to determine if the smaller cells are connected to the larger ones by cytoplasmic intercellular bridges (Eckelbarger 2005).

Oval sperm platelets were observed in coelomic smears from a few large specimens (20 mm or more in length) of *Scalibregma australis* **n. sp**. (Fig. 3M). In light microscopy with Phase Contrast illumination at 1000 x magnification, the individual sperm of these platelets, when broken free, were observed to have a short oval nucleus, a middle piece consisting of 2–4 smaller spherical structures that are likely mitochondria, and a long tail or flagellum. This type of sperm agrees with the short-headed or “primitive” type of sperm defined by Franzén (1956) as being spawned into seawater. Primitive sperm were subsequently referred to as “ect-aquasperm” that were freely spawned into seawater and that fertilize eggs in the water column (Jamieson & Rouse 1989).

Post-larval development. Well-preserved post-larvae and juveniles of *S. australis* **n. sp**. having 10–30 setigerous segments were available for study. Measurements provided in Table 3 suggest that length and width within each developmental category (i.e., number of setigers attained) is variable; however, this is because absolute size as measured increases within growth periods as segments are added. Further, contraction during preservation has undoubtedly affected the size of individual organisms.

The overall body shape of the post-larvae and juveniles is initially fusiform (Fig. 4A, C–E, 5J) with the characteristic inflated thoracic region not becoming prominent until the elongate and narrow posterior segments with dorsal and ventral cirri have developed by the 22-setiger stage (Figs. 4F, H–I, 5K–L). The only pigment on the body is associated with glands that develop within the dorsal and ventral cirri of posterior segments and similar glands that develop dorsally and ventrally on setiger 4 by about the 20-setiger stage (Fig. 5N). The mid-ventral longitudinal groove with paired elevated pads begins to differentiate early. The 14-setiger post-larva exhibits some differentiation along the ventral mid-line (Fig. 4C); medial pads are evident in anterior setigers by about the 16-setiger stage and along the entire body after 20 setigers are developed. A 30-setiger juvenile has large mid-ventral pads from setiger 2 (Fig. 5N); with development, these single pads will eventually divide into two and then four per segment in adults and form a prominent ventral ridge line within the ventral groove (See Figs. 2A, 3B–C).

The prostomium is initially bulbous and rounded (Fig. 4A), then becomes wider and somewhat triangular, narrowing anteriorly to a conical tip (Figs. 5A–C, specimens with 16, 17, and 20 setigers, respectively). Subsequently, two lateral peaks develop and, as these peaks thicken, the anterior margin becomes broadly rounded (Fig. 5D, 22 setigers). The two lateral peaks transition to short lateral horns by 28 setigers (Fig. 5E, M); with the prostomial horns fully developed and assuming the adult form by the 30-setiger stage (Fig. 5F). Eyes are absent in all stages of development. Nuchal organs are apparent only as cilia within a groove between the peristomium and posterior-lateral margin of prostomium. Everted nuchal organs were not observed in any specimens available, either juvenile or adult. The proboscis was not everted on any of the juvenile specimens.

The peristomium consists of a single ring both dorsally and ventrally through the 16-setiger stage (Fig. 4D). Thereafter, while the dorsal side of the peristomium remains a single ring, the ventral side becomes enlarged by about the 18-setiger stage and begins to form the upper lip of the mouth; by the 28-setiger stage, the peristomium encompasses both the upper and lower lips of the mouth; by the 30-setiger stage, short narrow pads are present on the upper lip and large pads are present on the ventral lip as in adults (Fig. 5N).

Although elevated epidermal pads are evident along the body in early post-larvae, they are irregular in their position (Fig. 4D, E, H) and do not become fully organized into distinct annulations until about the 25- or 26-setiger stage.

Dorsal cirri are the first to develop and are typically present in mid-body setigers (8–9) by the 16-setiger stage. Additional dorsal cirri develop as segments are added. Ventral cirri do not develop until the 20-setiger stage, and are initially limited to the last one or two posterior setigers; thereafter they develop rapidly on the other segments that bear dorsal cirri. Dorsal cirri are always longer than ventral cirri; both, however, bear pigmented internal glands, with those of the dorsal cirri being more prominent (Fig. 5I, L).

Branchiae do not appear until late in development. The first evidence of branchiae is a single bulge from the wall of the parapodia of setigers 3–4 of a 22-setiger juvenile; these are believed to be anlage of branchiae. A 24-setiger juvenile exhibited single branchial filaments on setigers 3–5; a 28-setiger juvenile had branchiae on setigers 2–5, with 1, 2, 3, and 4 lobes respectively and with evidence of branching (Fig. 4J–K). Juveniles with 30 setigers exhibited branchiae on setigers 2–5, with branching evident on branchiae of setigers 3–5.

Capillary setae are present in both noto- and neuropodia on all setigers of all specimens having 10–30 setigers. In addition, short, spinous setae are present on setigers 1–4, anterior to the capillaries in noto- and neuropodia. Lyrate setae are entirely absent on post-larvae of 10–15 setigers. The first lyrate setae appear on setigers 3–4 of a 16-setiger post-larva and then on setigers 2–4 of juveniles in the 17–20 setiger range. Thereafter lyrate setae developed on middle and posterior setigers together with many more capillaries. It is noteworthy that through the 24-setiger stage, both spines and lyrate setae occurred together with capillaries on setigers 2–4; thereafter spines were observed only on setiger 1 as in the adults

The spinous setae taper to a fine point (Fig. 4B, L–M), sometimes drawn out into an aristate like tip; these are similar to those observed on adults. Each lyrate seta is similar to the adult form with two nearly equal tynes and fine, plate-like bristles on the interior margin (Fig. 4M). On the smallest 10-setiger post-larva, there are two spines and three capillaries (Fig. 4B); on a 28-setiger juvenile there are four spines and about 12 capillaries in two rows (Fig. 4L); spines are less than half the thickness of the capillaries and only about one-fourth as long; each spine is sharply pointed. Capillaries have numerous short bristles or emergent fibril endings as in adults (Fig. 4B, L–M).

The pygidium is initially a simple bulbous segment, weakly divided into two lateral halves (Fig. 4A, C). The first evidence of pygidial cirri is at about the 15-setiger stage where four or five short oval cirri are evident (Fig. 4D). All five cirri are definitely present with development of 18 setigers; initially these are somewhat pointed on the tips (Fig. 5 G–H). The five cirri are arranged with two dorsolateral, two ventrolateral, and one mid-ventral. With continued development, the pygidial cirri become elongate, cirriform and rounded on the tips (Figs. 4I, 5I).

Remarks. Although the mode of early development is not known, these observations on post-larvae and juveniles of a species of *Scalibregma* provide data on the timing of development of adult characters (Table 3). The progression of the prostomium from a rounded, somewhat bulbous shape to the characteristic T-shaped form of the adults with prominent frontal horns passes through growth phases where the prostomium actually has the appearance reported for adults of other scalibregmatids (Blake 1981; Kudenov 1985; Schüller & Hilbig 2007). This transition from a rounded anterior margin on the prostomium to a squared off or flattened anterior margin where lateral horns develop is similar to what has been reported during larval development for the spionid genera *Marenzelleria, Malacoceros, Rhynchospio*, and *Spiophanes* (Day 1934; George 1966; Guérin 1975; Bochert & Bick 1995; Blake 2006).

The dorsal peristomial ring is single and entire during development and is similar to the adult morphology. The ventral part of the peristomium, however, undergoes considerable modification by forming the upper lip of the mouth with short, narrow pads and the lower lip with large, inflated pads; the final form is that which is described for the adult in this paper. It is apparent that little attention has been paid to the morphology of peristomial involvement in the mouth, yet this appears to be distinctive and species-specific. The ventral groove with elevated pads that extends posterior to the mouth to near the end of the body is another structure rarely mentioned in scalibregmatid descriptions. The paired pads that occur in the groove develop by about the 17-setiger stage or relatively early in development, but the entire morphology associated with this groove and the final arrangement of the paired pads is not complete until about 30 setigers have developed.

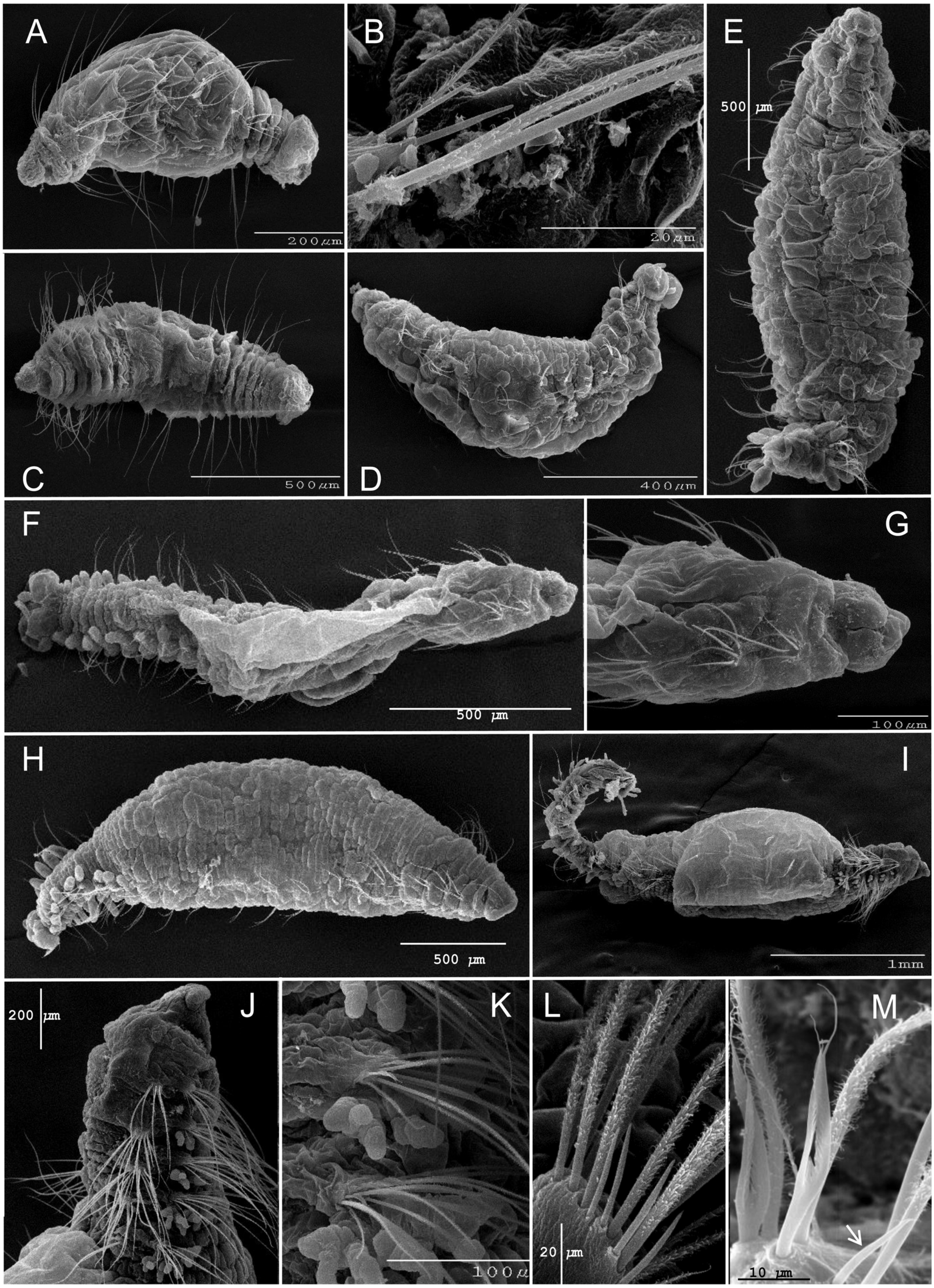

FIGURE 4. *Scalibregma australis* **n. sp.** SEMS of post-larvae and juveniles from Sta. NBP-35: A, 10-setiger post-larva, left lateral view; B, short spinous setae and capillaries from setiger 1; C, 16-setiger post-larva, ventral view; D, 15-setiger post-larva, lateral view; E, 18-setiger juvenile, dorsal view; F, 20-setiger juvenile, right lateral view; G, same, detail of prostomium, peristomium, and setigers 1–3; H, 22-setiger juvenile, right lateral view; I, 26-setiger juvenile, right lateral view; J, same, detail of prostomium, peristomium, and setigers 1–5 showing development of branchiae on setigers 2–5; K, same, detail of setigers 2–4, showing early development of branchiae; L, same specimen showing short spinous setae and capillaries from setiger 1; M, two lyrate setae and a single short spinous seta (arrow) from setiger 4 from 24-setiger juvenile.

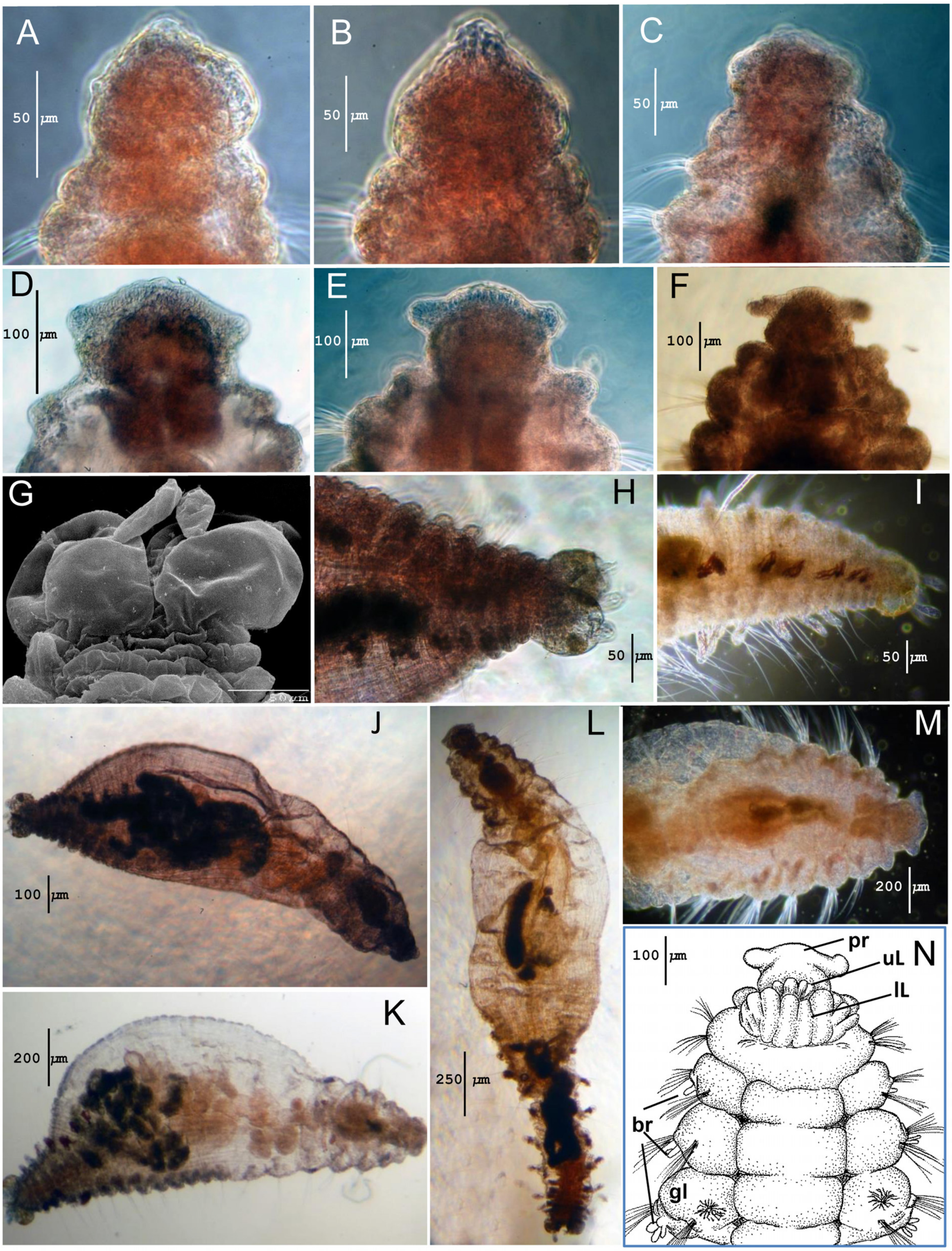

FIGURE 5. *Scalibregma australis* **n. sp.** Photomicrographs of post-larvae and juveniles: A–F, developmental series of the prostomium (A, 16 setigers; B, 17 setigers; C, 20 setigers; D, 22 setigers, E, 28 setigers; F, 30 setigers); G–I, developmental series of the pygidial cirri (G, 20 setigers; H, 18 setigers; I, 28 setigers with pigmented glands in dorsal cirri); J–L, changes in body shape, narrowing of posterior end (J, 18 setigers; K, 20 setigers; L, 22 setigers with pigmented glands in dorsal cirri); M, anterior, 28-setiger specimen; N, 30-setiger juvenile, ventral view showing development of the upper and lower lips of the mouth, branchiae, gland on setiger 4, and ventral ridge line. Abbreviations: br, branchiae; gL, gland, lL, lower lip of mouth; pr, prostomium; uL, upper lip of mouth.

The development of dorsal and ventral cirri differ in timing, with the larger dorsal cirri first appearing by the 16-setiger stage and the ventral cirri not present until 20 setigers have developed. Both sets of cirri have internal pigmented tubular glands that appear to be characteristic of species of *Scalibregma* (Ashworth 1901; Mackie 1991; Bakken *et al.* 2014) and other genera (see below for new species *of Pseudoscalibregma* and *Oligobregma*).

The short spinous setae found in setiger 1 of adults have been postulated to be homologous to the lyrate setae of setiger 2 and subsequent segments (Mackie 1991; Blake 2000). However, in the post-larvae and juveniles observed for *Scalibregma australis* **n. sp.**, the spines were present in the earliest post-larval (10–setiger) stage that was available for study and were present on setigers 1–4 in both noto- and neuropodia. These setae are thus established early in development, whereas the lyrate setae do not appear until about the 16-setiger stage and occur together with the spinous setae on setigers 2–4 until after 24 setigers have developed with a body length of about 3 mm. Lyrate setae are entirely absent from middle and posterior setigers until 22–24 setigers have developed. In adults, short spines do not co-occur on segments having lyrate setae. These results suggest that the short spinous setae appear first in a few anterior setigers, and then are replaced by lyrate setae on the segments where they develop.

There are several taxonomic implications of the results of this study. The morphological changes from the earliest rounded prostomial shape until the development of the broad anterior margin and lateral horns demonstrates that *S. australis* **n. sp.** passes through developmental phases that are morphologically similar to the prostomium described for adults of other species. This plus the late appearance of branchiae suggests that species described from small specimens of various genera should be revaluated. Based on these morphological results, and the observation that gametes were only present in larger adults (15 mm or more in length), any species described measuring less than 4.0 mm and lacking branchiae needs to be considered a possible juvenile of another species, possibly in another genus. A similar conclusion was reached as part of an unpublished study of deep-water specimens of a presumed new species of *Oligobregma* and adults of *Sclerobregma branchiatum* Hartman, 1965 collected from the U.S. Atlantic continental slope (Blake & Luzak unpublished). The specimens of *Oligobregma* were all small and lacked branchiae; study of a growth sequence of the smaller presumed *Oligobregma* specimens with the larger *S. branchiatum* identified a complete overlap in the development of the prostomium and branchiae.

Genus *Pseudoscalibregma* Ashworth, 1901

Type-species: *Scalibregma parvum* Hansen, 1879.

Diagnosis. Body elongate, arenicoliform. Prostomium T-shaped with lateral horns. Peristomium achaetous, surrounding prostomium dorsally and forming upper and lower lips of mouth ventrally. Parapodia of posterior segments with dorsal and ventral cirri; interramal papillae present; postsetal lamellae absent. Branchiae absent. Setae include capillaries, lyrate setae, and sometimes few inconspicuous spinous setae among capillaries of setigers 1–2, blunt, pointed, or bifurcated, representing homologues of lyrate setae; large conspicuous spines absent. Pygidium with long anal cirri.

Remarks. Apart from a more variable morphology of dorsal and ventral cirri, the only character that separates *Pseudoscalibregma* from *Scalibregma* is the absence of branchiae. The presence of short spinous setae in the first 1–2 setigers as occurs in species of *Scalibregma* was confirmed by Imajima (2009) as part of his description of *P. orientalis* Imajima, 2009 from Japan and Bakken *et al.* (2014) as part of their redescription of the type species, *P. parvum*. I can also confirm after a re-examination of the holotype that *P. usarpium* Blake, 1981 from Antarctica also has these setae.

Four species of *Pseudoscalibregma* have been reported from Antarctic seas: (1) *P. bransfieldium* (Hartman, 1967), (2) *P. usarpium,* (3) *P. papilla* Schüller, 2008, and (4) *P. hartmanae* (Blake, 1981), **new combination.** A fifth species was found in the LIS-A collections and is described here. Additional descriptive notes are provided for *P. bransfieldium*.

TABLE 3. Development of Morphological Characteristics in Post-larval and Juvenile *Scalibregma australis* **n. sp.**

Character/No. Setigers	10	14–15	16	17–18	20	22–24	28	30
Length	630 µm	850–900 µm	945–990 µm	960–1,221 µm	1300–1875 µm	2.6–2.8 mm	3.5 mm	5.67 mm
Width	70 µm	220–232 µm	305–325 µm	353–407 µm	450–580 µm	0.62 mm	0.75 mm	0.95 mm
Prostomium	Bulbous, rounded	Bulbous, extended apically	Rounded, pointed apically	Inflated, lateral bulges, tapering apically to rounded tip	Becoming wide, thickened subterminally, then tapering to rounded anterior peak	Broad, thickened across anterior margin, lateral horns developing	Lateral horns well developed	Lateral horns fully developed
Peristomium	Single ring dorsally and ventrally	Single ring dorsally and ventrally	Single ring dorsally and ventrally	Single narrow ring dorsally becoming expanded ventrally, with pads developing	single ring dorsally; ventrally enlarging anterior to mouth	Single ring dorsally, ventral ring expanding to encompass upper lip of mouth	Single ring dorsally; ventral ring forming upper and lower lips of mouth	Single ring dorsally; three rings ventrally encompassing the mouth
Branchiae	Absent	Absent	Absent	Absent	Absent	22 Setigers: One branchial anlage, setigers 3–4; 24 Setigers: One branchial lobe on setigers 3–5	Branchiae present setigers 2–5; with 1, 2, 3, and 4 lobe(s) respectively	Branchiae present setigers 2–5 with individual lobes branching
Dorsal cirri	Absent	Absent	Present, from about setiger 8–9	Present	Present	Present	Present	Present
Ventral cirri	Absent	Absent	Absent	Absent	1–2 present, posterior most setigers	Present	Present	Present
Dorsal pigmented glands setiger 4	Absent	Absent	Absent	Absent	Present	Present	Present	Present
Pygidium	Bulbous, rounded, 2 weakly developed halves	Bulbous, divided into 2 halves	Bulbous, divided into 2 halves	Bulbous, divided into 2 halves, with additional divisions or lobes developing	With additional divisions or lobes developing	With additional divisions or lobes developing	With additional divisions now distinct	With 5–6 additional divisions distinct
Pygidial cirri	Absent	3: 1 mid-ventral, 2 dorsolateral	3 cirri present	3–5 cirri present	5 cirri present	5 cirri present	5 cirri present	5 cirri present
Spinous setae, lyrate setae, & capillaries	1–2 spines, setigers 1–4; lyrate setae absent; 2–3 capillaries all setigers	1–2 spines setigers 1-4; lyrate setae absent; 3–4 capillaries all setigers	1–2 spines setigers 1–4; 1–2 lyrate setae setigers 3–4 only; 3–4 capillaries all setigers	2–3 spines setigers 1–4; 1–2 lyrate setae setigers 2-4; 3–5 capillaries all setigers	3–4 spines setigers 1–4; 1–2 lyrate setae setigers 2-4; 5–6 capillaries all setigers	3–4 spines setigers 1-4; 2–3 lyrate setae setigers 2-4, and present most middle and posterior setigers; 6–8 capillaries all setigers	3–4 spines setiger 1; 2–4 lyrate setae all setigers from setiger 2; 8–10 capillaries all setigers	4–5 spines setiger 1; 3–4 lyrate setae all setigers from setiger 2; 12 or more capillaries all setigers
Ventral groove	Absent	Initial development, with paired pads	Medial paired pads present	Distinct, surrounded by paired pads	Longitudinal row of paired pads	Longitudinal row of paired pads	Longitudinal row of paired pads	Large pads in groove from setiger 2 to posterior end
Nuchal organs	Not apparent	Not apparent	Not apparent	Not apparent	Large, lateral ciliated grooves anterior to dorsal peristomial ring	Large, lateral ciliated grooves anterior to dorsal peristomial ring	Lateral ciliated grooves anterior to dorsal peristomial ring	Lateral, ciliated grooves anterior to dorsal peristomial ring

Pseudoscalibregma palmeri new species

Figures 6A–E; 7

Material examined. East Antarctic Peninsula, RVIB *Nathaniel B. Palmer* Cruise 2000-03, Collector, J.A. Blake.—**Prince Gustav Channel**, Sta. NBP-01, 768 m, 1 **paratype** (LACM Poly 7008).—**Weddell Sea,** Off Lindenberg Island, Sta. NBP-03, 385 m, **holotype** (LACM-AHF Poly 7009).

Description. Holotype incomplete, 6.2 mm long, 1.5 mm wide for 21 setigerous segments; paratype incomplete, 3.2 mm long, 1.2 mm wide with 16 setigerous segments. Body with weakly expanded thoracic region, narrowing posteriorly. Color in alcohol light tan, with reddish pigmented glands dorsally on setigers 3–4 and ventrally on setigers 3–6 (Figs. 6A–B); anterior and middle segments with small reddish pigment spots along individual annulae (Figs. 7A–B). Body segments with transverse rows of pads; setigers 1–2 biannulate with large, prominent pads dorsally, not evident ventrally; subsequent setigers quadriannulate with numerous small pads closely spaced, becoming triannulate from about setiger 16. Venter with prominent ventral groove bearing large elevated pads from setiger 2, continuing posteriorly forming ventral ridge line with rounded, elevated pad at mid-point of each segment within groove (Figs. 6B, 7B). Branchiae absent; pygidium not present on either specimen.

Prostomium with two long, diverging lateral horns directed anterolaterally (Figs. 6A–B); eyes absent, nuchal organs not observed; proboscis not everted. Peristomium a single lobed ring around prostomium dorsally (Fig. 6A), ventrally forming upper and lower lips of mouth; upper lip with 9–10 narrow lobes; lower lip with about seven large, elongate inflated lobes (Fig. 6B).

Parapodia with elongate conical podial lobes throughout Fig. 7B–C). Dorsal and ventral cirri from setiger 14, these short, inconspicuous at first, becoming longer and more prominent posteriorly (Fig. 7C); dorsal cirri triangular, broad basally, tapering to pointed tip (Figs. 7C–D); ventral cirri asymmetrical with broad basal attachment and elongated, rounded tip (Figs. 7C, E); both dorsal and ventral cirri with prominent darkly pigmented internal glands; glands on dorsal cirri exiting toward apex and glands on ventral cirri exiting along ventral surface (Fig. 7D–E). Interramal papillae present between noto- and neuropodia, more developed in posterior parapodia (Figs. 6C, 7C); these papillae with glandular contents, not ciliated (Fig 6C).

Noto- and neuropodial capillary setae in 2–4 rows throughout, successive rows with longer setae. Setigers 1–2 with anterior group of 3–4 short, blunt-tipped spinous setae (Fig. 6D); these homologous to lyrate setae that begin from setiger 3 and continue on subsequent segments. Lyrate setae, short, anterior to capillaries with unequal tynes bearing short bristles (Fig. 6E); lyrate setae numbering 3–4 per noto- and neuropodium in anterior segments and 9–10 in posterior most segments.

Remarks. *Pseudoscalibregma palmeri* **n. sp.** resembles *P. usarpium* Blake, 1981 in the shape of the prostomium, single lobate peristomial ring, and by having prominent rows of annulated pads on anterior setigers. Major differences are that in *P. usarpium* the first two segments are quadriannulate, with subsequent segments having five annulae and with all annulae being large and prominent (Blake 1981). In contrast, in *P. palmeri* **n. sp.** the annulae of setigers 1–2 are biannulate, with large, prominent pads, followed by quadriannulate segments where the rows are narrow and have numerous small inconspicuous pads bearing pigment spots.

The asymmetrical form of the ventral cirri in *Pseudoscalibregma palmeri* **n. sp.** is unique for the genus. The pigmented glands of the dorsal and ventral cirri are similar to those described for *Scalibregma australis* **n. sp**. earlier in this paper. Similar glands in the dorsal and ventral cirri of the closely related *P. usarpium* were reported by Blake (1981) but not described in detail. It is likely that these glands are widespread in scalibregmatids but have been largely overlooked. Similarly, the dorsal and ventral glands that occur in some anterior setigers from setiger 4 are similar to those of *Scalibregma* species but are newly reported for *Pseudoscalibregma*. The extensive array of pigment spots across the annulae in *P. palmeri* **n. sp.,** however, is unique and has not been reported for other scalibregmatids.

The short anterior spinous setae of setigers 1–2 present in *P. palmeri* **n. sp.** were not reported for *P. usarpium*. However, an examination of the holotype (USNM 60583) showed that such setae are present, but not as short as in *P. palmeri* **n. sp.**

Etymology. This species is named for the RVIB *Nathaniel B. Palmer*, research vessel of the United States Antarctic Program, on which most of the specimens reported in this paper were collected. Additionally, this research vessel was in turn named for Nathaniel B. Palmer, an American whaler, who is reputed to be among the first to sight the Antarctic continent.

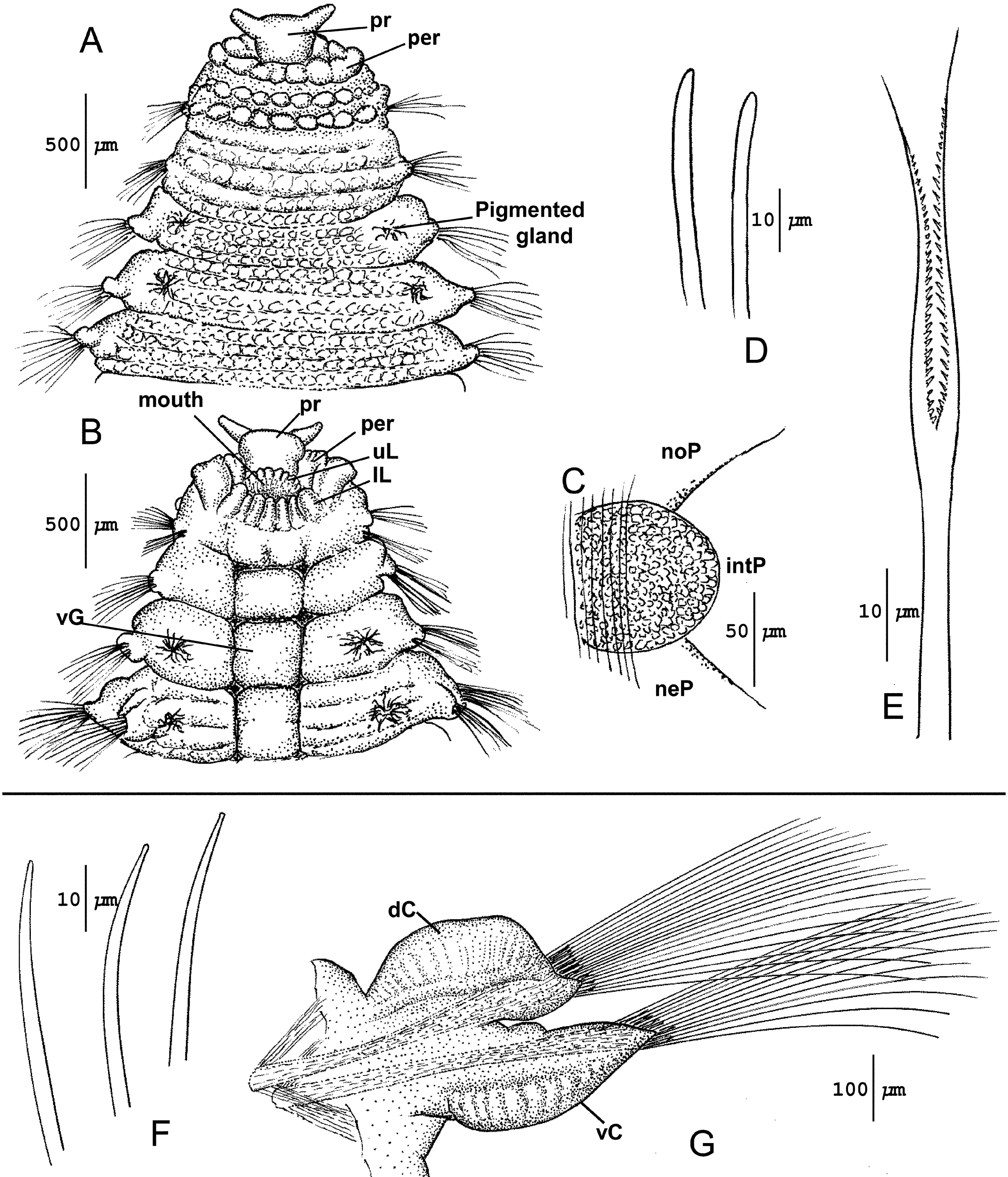

FIGURE 6. *Pseudoscalibregma palmeri* **n. sp.** Holotype, Sta. NBP-03 (LACM-AHF-Poly 7009): A, anterior end, dorsal view; B, anterior end, ventral view; C, detail of interparapodial papilla; D, short spinous setae from setiger 1; E, lyrate seta from middle body setiger.—*Pseudoscalibregma bransfieldium*: F, short spinous setae from setiger 1; G, posterior parapodium, anterior view. Abbreviations: dC, dorsal cirrus, intP; interramal papilla; lL, lower lip of mouth; neP, neuropodium; noP, notopodium, per, peristomium; pr, prostomium; uL, upper lip of mouth, vC, ventral cirrus; vG, ventral groove.

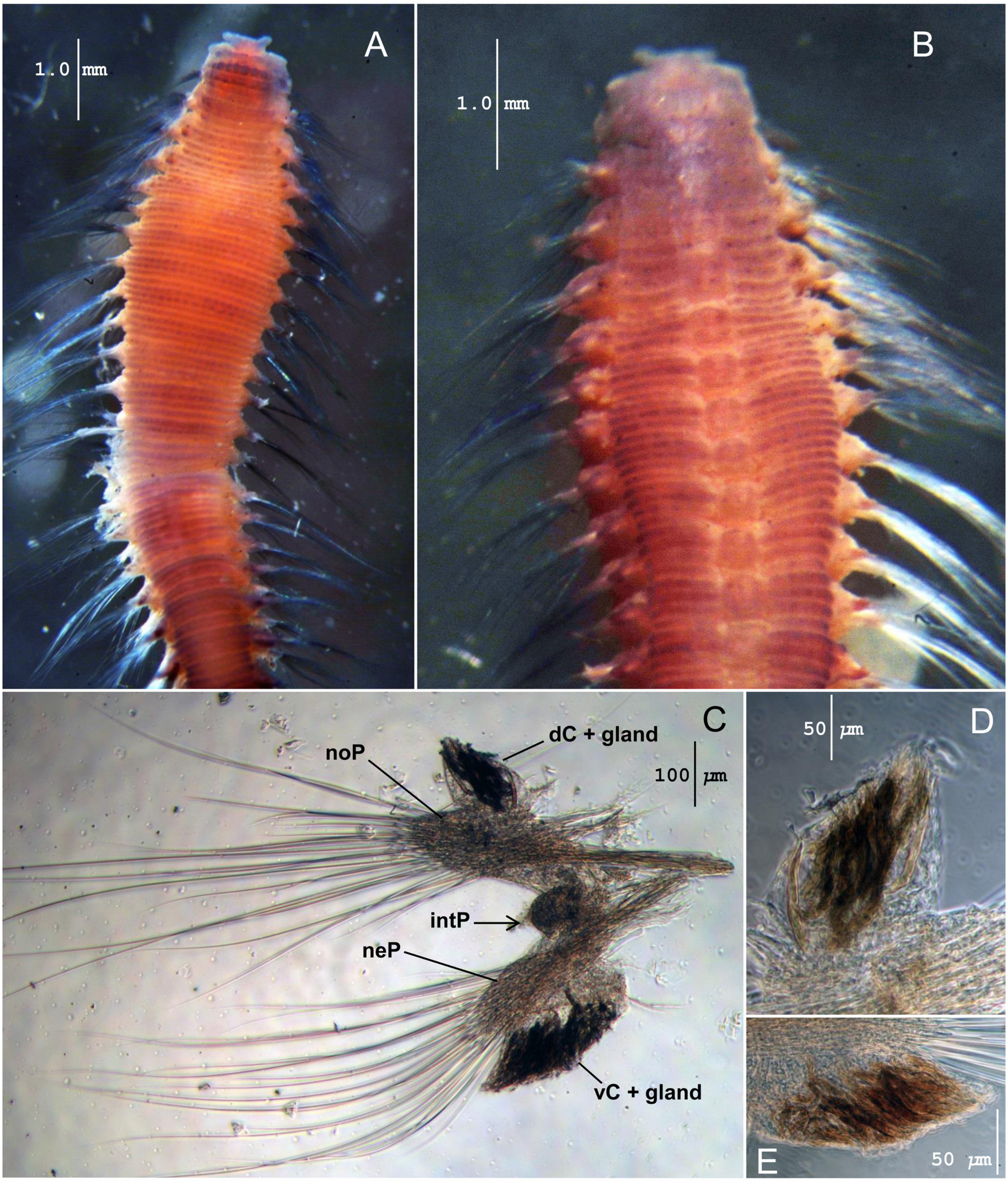

FIGURE 7. *Pseudoscalibregma palmeri* **n. sp.** Photomicrographs of holotype, Sta. NBP-03 (LACM-AHF-Poly 7009): A, anterior and middle body segments, dorsal view; B, anterior end, ventral view; C, posterior parapodium, posterior view; D, same, detail of dorsal cirrus; E, same, detail of ventral cirrus. Abbreviations: dC, dorsal cirrus, intP; interramal papilla; neP, neuropodium; noP, notopodium; vC, ventral cirrus.

Distribution. Known only from the vicinity of the Larsen Ice Shelf A area of the Weddell Sea side of the Antarctic Peninsula, 385–768 m.

Pseudoscalibregma bransfieldium (Hartman, 1967)

Figure 6 F–G

Eusclerocheilus bransfieldia Hartman, 1967: 130–131, pl. 39
Hyboscolex bransfieldia: Kudenov & Blake, 1978: 440.
Pseudoscalibregma bransfieldia: Hartman, 1978: 180–181, fig. 28
Pseudoscalibregma bransfieldium: Blake, 1981: 1143–1145, fig. 6; Hartmann-Schröder & Rosenfeldt, 1991: 75.

Material examined. East Antarctic Peninsula, RVIB *Nathaniel B. Palmer* Cruise 2000-03, Collector, J.A. Blake.—**Larsen-A Ice Shelf Area,** transect along border with Larsen B, Sta. NBP-10, 332 m, 1 specimen (LACM-AHF Poly 7010).

Additions to description. Single specimen complete, 10 mm long, 3 mm wide with 22 setigers; the body more maggot-shaped than arenicoliform. In alcohol, color light tan with no body pigment.

Prostomium bears two long frontal horns projecting anterolateral; dorsal surface of prostomium somewhat domed or elevated, clearly visible; eyes absent; nuchal organs not apparent. Peristomium a single dorsal ring surrounding the prostomium dorsally; ventrally forming upper and lower lips of mouth with upper lip relatively smooth and lower lip with three weakly developed lobes. A weakly developed ventral groove apparent along body from setiger 4; initially, groove formed by a single large segmental annulus that at the mid-point produces a notch between segments; in last 5–6 segments, a distinct furrow develops at segmental mid-point. The pygidium damaged, but bears five anal cirri.

Anterior parapodia weakly developed with low noto- and neuropodia; posteriorly podial lobes elongate, apically pointed, bearing distinctive dorsal and ventral cirri (Fig. 6G), both of which are bulbous extensions of the podial lobes; internal glands absent from cirri and elsewhere on body. Interramal papillae weakly developed.

Setae consist of numerous capillaries arranged in 2–3 rows throughout; lyrate setae from setiger 2; setiger 1 bears an anterior row of short, thin, spinous setae (Fig. 6F) anterior to capillaries, the homologues of lyrate setae now known to occur on numerous species of Scalibregmatidae.

Remarks. *Pseudoscalibregma bransfieldium* differs from other scalibregmatids by the distinctive dorsal and ventral inflated extensions of the podial lobes. The short anterior spinous setae of setiger 1 are newly reported.

Distribution. Widespread in Antarctic seas 332–916 m.

Genus *Oligobregma* Kudenov & Blake, 1978

Type-species: *Pseudoscalibregma aciculatum* Hartman, 1965, designated by Kudenov & Blake 1978.

Diagnosis. Body elongate and arenicoliform. Prostomium T-shaped with two prominent frontal horns; eyes present or absent; nuchal organs present. Peristomium achaetous, surrounding prostomium dorsally and forming upper and lower lips of mouth ventrally. Branchiae absent. Parapodia with well-developed dorsal and ventral cirri on posterior segments; interramal papilla present or absent. Large acicular spines present on anterior setigers. Capillaries present in all parapodia; lyrate setae present anterior to capillaries of setigers 2, 3, or 4; some species with short, slender, blunt or pointed spinous setae anterior to capillaries of setigers 1, 2 or 3, representing homologues of lyrate setae. Pygidium with anal cirri.

Remarks. *Oligobregma* is one of four genera with dorsal and ventral cirri: *Scalibregma* (with branchiae and without large anterior acicular spines); *Sclerobregma* (with branchiae and with large anterior acicular spines); *Pseudoscalibregma* (without branchiae or large anterior acicular spines); and *Oligobregma* (without branchiae and with large anterior acicular spines). The boundaries between these genera are not great and since the presence and absence of branchiae and large anterior acicular spines are characters occurring in other genera, it is obvious that the generic arrangement of scalibregmatids should be revised. In addition, the observations in this paper of branchiae developing late in juvenile *Scalibregma australis* **n. sp.** ontogeny means that they pass through a *Pseudoscalibregma*-like phase where the genus (and species) cannot be confirmed. A similar situation has been identified with *Sclerobregma branchiatum* in the western North Atlantic, where juveniles lacking branchiae were initially thought to represent a new species of *Oligobregma* (Blake & Luzak unpublished).

However, for the time being the definition of these genera and others provide a practical way to use a suite of characters to classify and identify them with the caveat that small specimens thought to be one genus might be a juvenile of another. At present, ten species have been described as *Oligobregma*, all except one from the southern ocean and hemisphere:

Oligobregma aciculata (Hartman, 1965). Western North Atlantic
Oligobregma blakei Schüller & Hilbig, 2007. Antarctica, Scotia Sea, 2889–2892 m. Juvenile, possibly belongs to a different genus.
Oligobregma collare (Levenstein, 1975). Subantarctic and Antarctic seas, 1622–6070 m.
Oligobregma hartmanae Blake, 1981. Antarctica, Weddell Sea, 505 m. Here referred to the genus *Pseudoscalibregma.*
Oligobregma lonchochaeta Detinova, 1985, North Atlantic, Reykjanes Ridge.
Oligobregma notiale Blake, 1981. Antarctica, widespread, shallow water to over 900 m.
Oligobregma oculata Kudenov & Blake, 1978. Off New Caledonia, 57 m.
Oligobregma pseudocollare Schüller & Hilbig, 2007. Antarctica, Scotia and Weddell Seas, 753–3050 m.
Oligobregma quadrispinosa Schüller & Hilbig, 2007. Antarctica, Scotia and Weddell Seas, 2258–4069 m.
Oligobregma simplex Kudenov & Blake, 1978. SE Australia, Westernport Bay, 11 m.

Of these species, all except *O. hartmanae* and *O. blakei* are validly placed in *Oligobregma. O. hartmanae* has only small spines in setigers 1–2 anterior to and smaller than the accompanying capillaries. These represent the small spinous setae that are considered to be homologues of lyrate setae that occur from setiger 3 and are not the large heavy acicular spines of other species. The short spinous setae have now been observed in many species in which they were not originally described. *O. hartmanae* is therefore referred to the genus *Pseudoscalibregma*. *Oligobregma blakei* is described from a very small specimen only 3 mm in length and less than the size where branchiae developed in *Scalibregma australis* **n. sp.** (see above) and may not be validly placed in *Oligobregma*. A new species of *Oligobregma* has been discovered in the LIS-A area and is described herein.

***Oligobregma mucronata* new species**

Figures 8–9

Material examined. **East Antarctic Peninsula,** RVIB *Nathaniel B. Palmer* Cruise 2000-03, Collector, J.A. Blake.—**Larsen-A Ice Shelf Area, Greenpeace Trough**: Sta. NBP-06, 733 m, 2 specimens poorly preserved (JAB); Sta. NBP-07A, 839 m, 3 **paratypes** (2 complete, LACM-AHF Poly 7011); Sta. NBP-07B, 839 m, 1 specimen (JAB); Sta. NBP-16, 713 m, 5 specimens (1 adult, 4 juveniles) (JAB); Sta. NBP-17, 719 m, 1 juvenile (JAB); Sta. NBP-18, 665 m, 3 **paratypes,** 1 adult, 2 juveniles (AHF-Poly 7012); Sta. NBP-19, 879 m, 1 specimen (JAB); Sta. NBP-20, 899 m, 7 **paratypes** (USNM 1281914); Sta. NBP-21, 912 m, **holotype** and 4 **paratypes** (LACM-AHF Poly 7013, 7014); Sta. NBP-22, 868 m, 4 specimens (JAB).—**LIS-A Area, transect along border with Larsen Ice Shelf B:** Sta. NBP-13, 323 m, 1 specimen (JAB).

Description. Holotype incomplete, 16 mm long, 3.5 mm wide for 30 setigerous segments; two complete paratypes from Sta. NBP-21, one 11 mm long, 1.4 mm wide with 27 setigerous segments; second 9.5 mm long, 1.5 mm wide with 28 setigerous segments. Body expanded through first eight setigers, thereafter narrowing to posterior end. Color in alcohol light pink, without body pigment. Body segments with transverse rows of weakly raised pads; setigers 1–3 uniannulate to biannulate (Fig. 8A–B); setigers 4 and subsequent segments becoming quadriannulate with low inconspicuous pads throughout (Fig. 9A). Venter with prominent ventral midline from setiger 2 composed of a row of large pads within a groove (Fig. 8B); each segment with at least two pads, each subdivided at middle by transverse groove, forming four structures per segment, corresponding to quadriannulate rows of segmental pads (Fig. 9A). Branchiae absent. Pygidium of holotype with indistinct lobes, with two cirri present; paratypes with up to four anal cirri (Fig. 8F).

Prostomium broadly curved across anterior margin, weakly expanded laterally, narrowing posteriorly; with two short, rounded lobes emerging subapically from anterior margin and extending forward forming short frontal horns (Figs. 8A–B, 9A); eyes absent; nuchal organs not observed; proboscis not everted. Peristomium a double-lobed ring around prostomium dorsally (Fig. 8A), ventrally forming upper and lower lips of mouth; upper lip with 4–5 narrow lobes; lower lip with about seven large, elongate inflated lobes, together forming a ring of elongate lobes around oral opening (Figs. 8B, 9A).

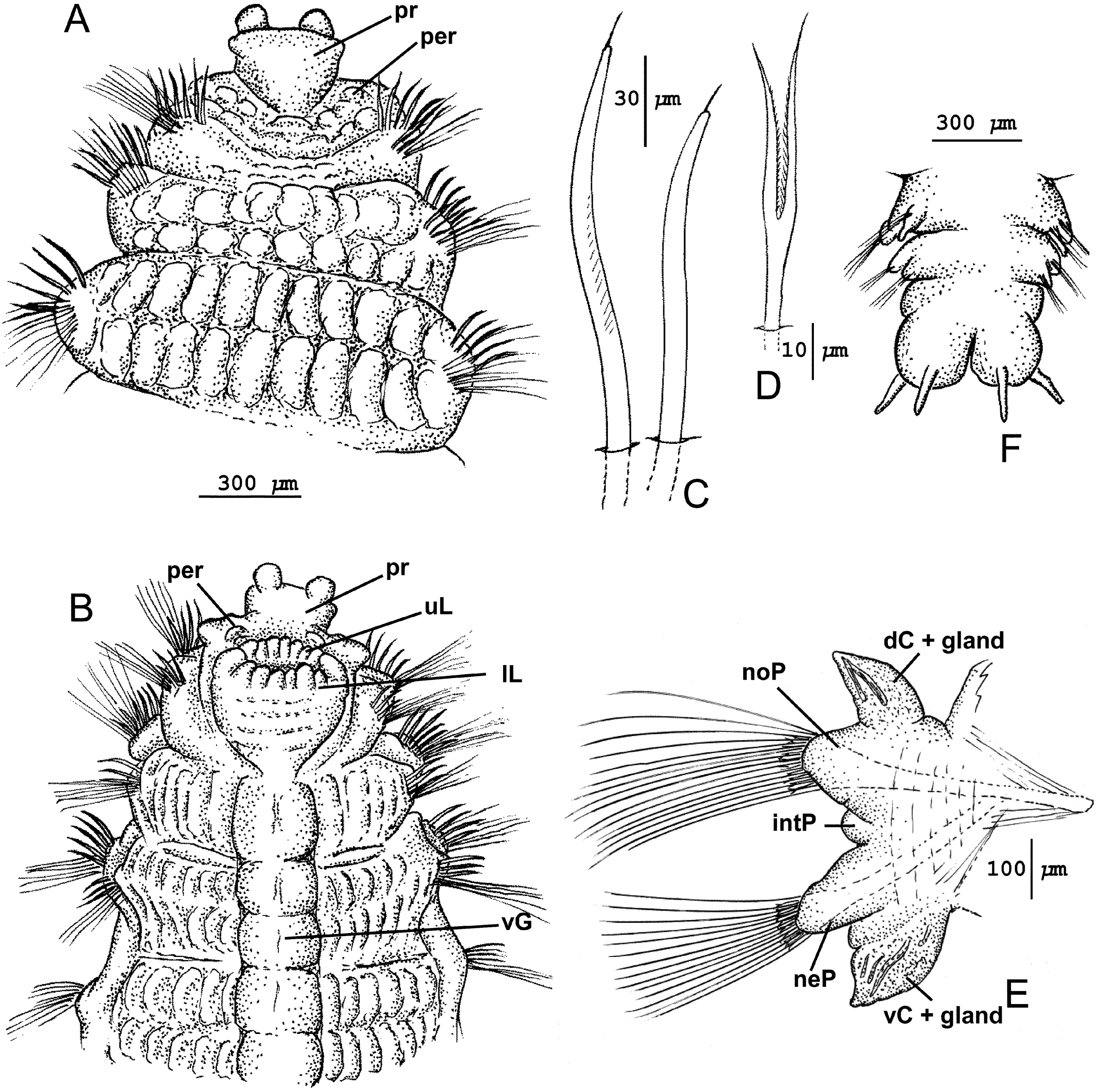

FIGURE 8. *Oligobregma mucronata* **n. sp.** Paratypes, Sta. NBP-21 (LACM-AHF-Poly 7014): A, anterior end, dorsal view; B, anterior end, ventral view; C, large notopodial spines from setiger 2; D, lyrate seta from posterior setiger; E, posterior parapodium, anterior view; F, pygidium, dorsal view. Abbreviations: dC, dorsal cirrus, intP; interramal papilla; lL, lower lip of mouth; neP, neuropodium; noP, notopodium; per, peristomium; pr, prostomium; uL, upper lip of mouth, vC, ventral cirrus; vG, ventral groove.

Parapodia with short, conical-shaped podial lobes in anterior third of body, becoming longer posteriorly; dorsal and ventral cirri from setiger 14 on holotype, these podial lobes inconspicuous anteriorly, becoming longer and more prominent posteriorly, both cirri asymmetrical; dorsal cirri triangular, broad, basally tapering to narrow nipple-like tip (Figs. 8E, 9B–C); ventral cirri strongly asymmetrical with broad basal attachment narrowing to elongated, nipple-like tip (Figs. 8E, 9B–D); both dorsal and ventral cirri with darkly pigmented internal tubular-shaped glands extending toward nipple-like tips (Fig. 9C–D). Interramal papilla present, best developed in posterior parapodia (Fig. 8E).

Heavy curved acicular spines present in both noto- and neuropodia of setigers 1–3 (Fig. 8A–B); notopodia with up to 12 spines arranged in two rows in setigers 1–2 and single row with up to seven spines in setiger 3, spines accompanied posteriorly by single row of capillaries; neuropodia with 3–5 spines in single row in setigers 1–3, accompanied by posterior row of capillaries; spines curved, narrowing to blunt tip bearing thin terminal arista (Fig. 8C); internal fibrils in spines apparent; notopodial spines more robust than those of neuropodia. Short spinous setae anterior to heavy spines absent. Setiger 4 with lyrate setae anterior to a row of short curved pointed setae and a third row of long, thin capillaries; setiger 4 therefore transitional between first three setigers bearing heavy curved spines and subsequent body segments having long thin capillaries. Lyrate setae continue on subsequent segments anterior to capillaries that generally occur in two rows from setiger 5. Lyrate setae from setiger 4, short, with unequal tynes bearing short bristles (Figs. 8D, 9K), numbering 3–4 per noto- and neuropodium in anterior segments and 8–10 in posterior most segments (Fig. 9K).

Reproduction. Sperm platelets were observed in one large paratype measuring 10 mm long and with 27 setigers of *Oligobregma mucronata* **n. sp.** from Sta. NBP-20 (Fig. 9J). These are similar in size and appearance to those described earlier for *Scalibregma australis* **n. sp.** Individual sperm were observed to have a short rounded nucleus, middle piece consisting of two spherical mitochondria and a long tail or flagellum. As with *S. australis* **n. sp**., the sperm structure for *O. mucronata* **n. sp**. suggests that they are ect-aquasperm, which are discharged into the sea.

Morphology of juveniles. The smallest juveniles available for study had 20–21 setigers and measured 2.3–2.8 mm long. The noto- and neuropodial acicular spines of setigers 1–3 develop early; these smallest juveniles had the full complement of notopodial spines on setigers 1–3, but spines were present only on neuropodia of setigers 1–2. A 24-setiger specimen that was 3.0 mm long had spines on setigers 1–3 in both noto- and neuropodia. Lyrate setae were present from setiger 4 in the smallest 20-setiger specimen examined.

While the setae or hard structures develop early, the soft morphology develops later. Changes to the prostomial morphology is shown in Figure 9: E, 20 setigers (2.3 mm long); F, 21 setigers (2.8 mm long); G, 24 setigers (3.0 mm long), H, 28 setigers (4.0 mm long); and I, 30 setigers (9.5 mm long). The initial prostomial shape in the available specimens is blunt across the anterior margin with a nearly square overall shape. With growth, the anterior margin becomes rounded or curved, eventually developing lateral bulges and a medial notch. The characteristic subapical lobes that become elongate and directed frontally do not develop until later, but were observed in 28-setiger juveniles that were 5–6 mm in length.

The development of segments in *O. mucronata* **n. sp.** appears to be limited to a maximal number of 28–30 setigers; within this range, the body length ranges from 4–16 mm indicating that continued growth of the worm is within a defined number of final segments. Parapodia develop dorsal and ventral cirri relatively early, at about 24 setigers and a length of 4.0 mm. These cirri also develop the tubular internal glands.

Remarks. These specimens of *Oligobregma mucronata* **n. sp**. were originally identified as *O. collare* due to the prostomium having two short anteriorly subapical frontal horns. Further study, however, showed that the large anterior acicular spines occurred on both the noto- and neuropodia of setigers 1–3 instead of only the notopodia and that most of these spines terminated in a thin arista. Further, the dorsal and ventral cirri were larger and of a different shape than in *O. collare*, with both cirri bearing internal glands similar to those described for *Scalibregma australis* **n. sp**. and *Pseudoscalibregma palmeri* **n. sp.** To date, *O. mucronata* **n. sp.** is the only species of the genus from Antarctic waters known to have large curved acicular spines in both noto- and neuropodia of anterior setigers. Examination of specimens of the type-species, *O. aciculata* (from deep-water off the Western North Atlantic collected as part of the Atlantic Continental Slope and Rise Program (ACSAR)) permitted elaboration of the original description which was based on a single incomplete specimen. *O. aciculata*, like *O. mucronata* **n. sp.** has acicular spines in noto- and neuropodia of setigers 1–3 and similar appearing frontal horns. However, a few short spinous setae occur anterior to the large acicular spines in *O. aciculata*, but are absent in *O. mucronata* **n. sp.** In addition, the form of the dorsal and ventral cirri differs significantly between the two taxa. In *O. aciculata* the dorsal cirrus is small oval and rounded on the tip and the ventral cirrus is larger, round and globular (not pointed as in Hartman (1965)); whereas in *O. mucronata* **n. sp.**, the dorsal cirrus is triangular and pointed at the tip and the ventral cirrus has a broad asymmetrical base and tapers to a pointed tip. Further, the acicular spines of *O. aciculata* taper to a long capillary-like tip and are not mucronate; blunt-tipped acicular spines reported by Hartman (1965) were not observed in the new material.

Oligobregma mucronata **n. sp.** bears some resemblance to *O. quadrispinosa* from deep water in the Weddell Sea. However, the prostomium and nature of the dorsal and ventral cirri is different in *O. quadrispinosa* and this species is reported to have heavy spines in the notopodia of setigers 1–4 but no neuropodial spines (Schüller & Hilbig 2007).

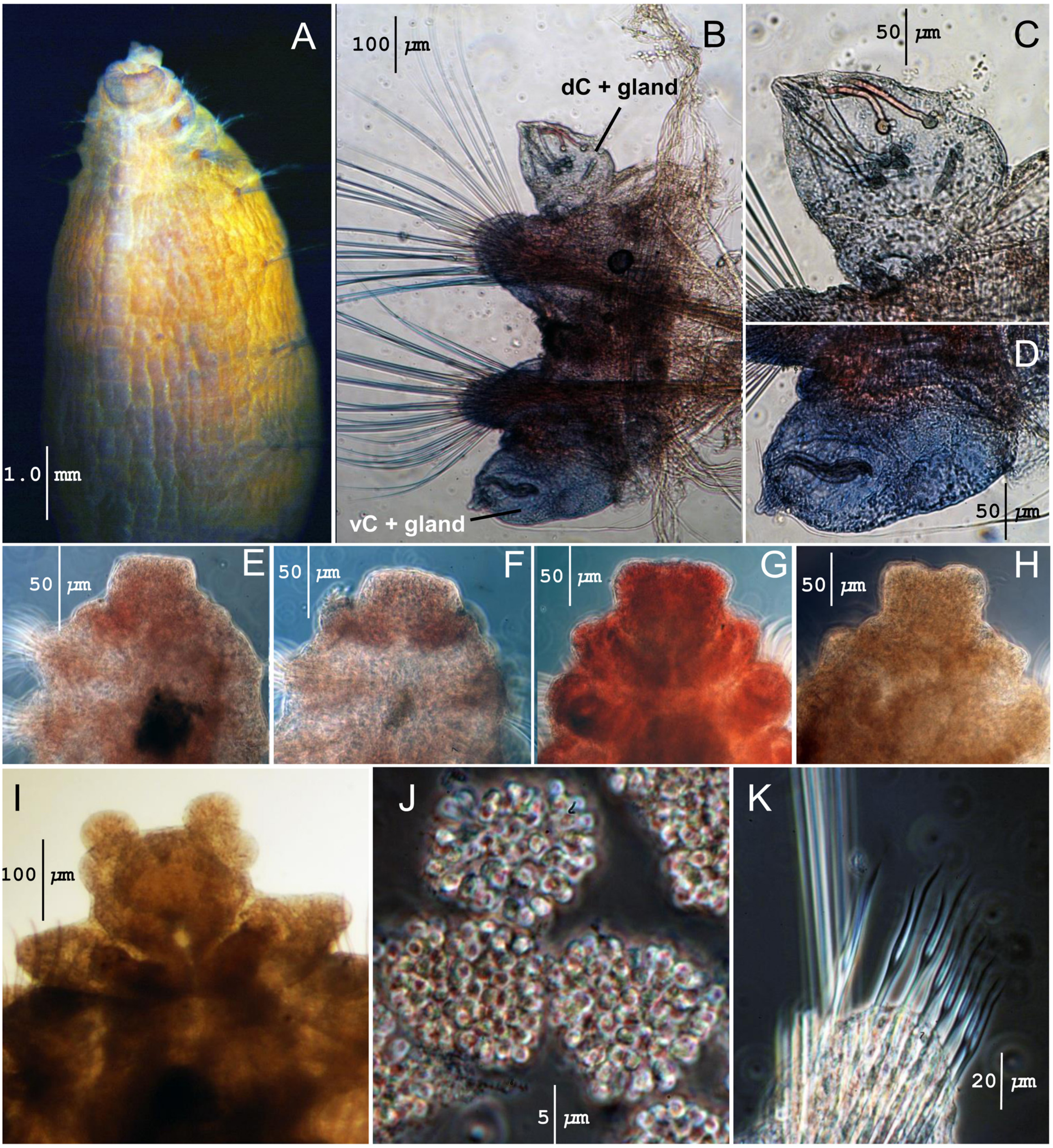

FIGURE 9. *Oligobregma mucronata* **n. sp.** Photomicrographs: A, holotype, Sta. NBP-21 (LACM-AHF Poly 7013), anterior half of body in ventral view; B, posterior parapodium, anterior view; C, same parapodium, detail of dorsal cirrus and internal glands; D, same parapodium, detail of ventral cirrus and internal glands; E–I, developmental series of the prostomium (E, Sta. NBP-18, 20 setigers, 2.4 mm long; F, Sta.NBP-21, 22 setigers, 2.8 mm long; G, Sta. NBP-04, 24 setigers, 3.0 mm long; H, Sta. NBP-13, 28 setigers, 4.0 mm long; I, Sta. NBP-21, 30 setigers, 9.5 mm long); J, sperm packets from specimen from Sta. NBP-20; K, capillaries and lyrate setae from a posterior notopodium from Sta. NBP-21. Abbreviations: dC, dorsal cirrus, vC, ventral cirrus.

The development of juvenile morphology indicates that the noto- and neuropodial acicular spines are present at least by the 20-setiger stage and with a length of 2.3 mm. In contrast, the characteristic form of the prostomium is not developed until at least 28 setigers with a length of 5–6 mm have developed. These results, like those for *Scalibregma australis* **n. sp.** suggest that small specimens of scalibregmatids cannot be specifically identified without sufficient numbers of specimens available to identify a growth sequence and transition of characters.

Before reaching the final configuration, the prostomium passes through growth phases that have been described for other species.

Etymology. The epithet is derived from the Latin *mucro*, referring to a sharply pointed thin aristate-like tip on some of the large acicular spines of setigers 1–3.

Ecology. Specimens of *Oligobregma mucronata* **n. sp.** collected as part of the LIS-A survey were mostly limited to the nearshore Greenpeace Trough, newly open to the sea and discovered by multibeam bathymetry during the survey in May 2000. These nearshore sediments were described from 20–25 cm cores as coarse-grained in the upper 5 cm near the surface, overlying fine-grained silt and clay size sediments with depth (Gilbert & Domack 2003). While the nature of coarse-grained surficial sediments and deeper fine-grained sediments provide a variable sedimentary habitat, the seafloor at this site also appeared to be in a constant state of disturbance due to the presence of numerous deposit-feeding elasapoid holothurians, *Elpidia glacialis* Théel, 1876, which were observed by video to be constantly moving over the surface. Several of the holothurians were observed on the surface of 10 x 10 x 50 cm megacore tubes collected in the Greenpeace Trough (Blake & Maciolek unpublished). As burrowing deposit feeders, scalibregmatids would be better adapted to such an environment than tube-building species. *Scalibregma australis* **n. sp.** was also abundant in these sediments.

Distribution. East Antarctic Peninsula, former Larsen Ice Shelf A area, 323–912 m.

Discussion

A single survey in an area formerly covered by an ice sheet has revealed a rich benthic fauna including three new species of scalibregmatid polychaetes. The description of *Scalibregma australis* **n. sp**. is distinct from the presumed cosmopolitan *S. inflatum* with which it had been previously identified in Antarctic seas and demonstrates that the latter is not a bipolar species, although it is closely related to *S. australis* **n. sp.**

Antarctic and subantarctic Scalibregmatidae. As noted earlier this paper, the scalibregmatids from Antarctic seas are well known from the works by Hartman (1967), Blake (1981), Schüller & Hilbig (2007), and Schüller (2008).The three new species of scalibregmatids described here bring to 15 the number of species known from Antarctic seas, all endemic. However, Parapar *et al.* (2011b) recently synonymized *Axiokebuita millsi* Pocklington & Fournier 1987, a deep-water species from the northern hemisphere, with *A. minuta* (Hartman, 1967), a deep-water species from Antarctica, thus producing a potential bipolar deep-water species. Known species of Scalibregmatidae from Antarctic seas are listed in Table 4.

Adult morphology and taxonomic characters. This study has revealed several characters that should be considered in any description of new scalibregmatid species. Further, previously described species should be re-examined for these characters.

Prostomium. The prostomium of the majority of scalibregmatids including the four species treated in this paper includes a pair of short frontal or subapical horns. Elder (1973) observed that *Polyphysia crassa* moves its head from side to side and uses prostomial horns to displace mud during burrowing. This behavior was confirmed by Dorgan *et al.* (2006) who observed *Scalibregma californicum* (as *S. inflatum*) to use a side-by-side motion of the horns to propagate a leading crack in mud as part of its burrowing. For scalibregmatids inhabiting soft sediments, therefore, the prostomium is used to support burrowing not feeding and these structures on mud-dwelling scalibregmatids do not conform to a feeding definition usually applied to palps.

However, a small group of scalibregmatids of the genera *Axiokebuita* and *Speleobregma* have very elongate horns that are ciliated and with shallow grooves that suggest they function to support feeding rather than burrowing (Parapar *et al.* 2011; Martínez *et al.* (2013, 2014) and have been termed 'palps." Use of these "palps" in feeding was confirmed for two marine cave-dwelling species of these genera that inhabit coarse sediments rather than the soft muddy sediment habitat typical of most scalibregmatids (Martínez *et al.* 2013).

Orrhage (1966, 1993) and Orrhage & Müller (2005) identified palp nerves in the scalibregmatid *Polyphysia crassa* that correspond to palp innervations in other polychaetes but no palps *per se* were identified suggesting that functional palps have been lost. Out of 12 palp nerve roots, *P. crassa* had one nerve (No. 6) attached to the ventral root and another (No. 9) attached to the dorsal root. The only other polychaete family having this arrangement were the Paraonidae. Before confirming these structures as palps in *Axiokebuita* and *Speleobregma,* evidence of their innervation is needed to determine similarities or differences with palp nerve roots previously identified for *P. crassa*.

TABLE 4. List of Antarctic Genera and Species of Scalibregmatidae (updated from Schüller 2008).

Species	Distribution	Depth Range (m)	References
Asclerocheilus ashworthi Blake, 1981	Antarctica: South Shetland Islands.—Subantarctic, W of Antipodes Island	223–2892	Blake (1981)
Axiokebuita minuta (Hartman, 1967)	Antarctica: Weddell Sea; South Sandwich Islands; Bellingshausen Sea; Antarctic Peninsula.—North Atlantic, SW Iceland; NW Spain.—SE Pacific, Easter Island	620–3049	Hartman (1967); Blake (1981); Parapar *et al.* (2011)
**Oligobregma blakei* Schüller & Hilbig, 2007	Antarctica: off Elephant Island	2889–2892	Schüller & Hilbig (2007)
Oligobregma collare (Levinstein, 1975)	Antarctica: Drake Passage; Weddell Sea; Ross Sea; Bellingshausen Sea	1622–3806	Levenstein (1975); Hartman (1967 in part, 1978); Blake (1981).—Synonymy Blake (1981)
Oligobregma mucronata **n. sp.**	Antarctica: East Antarctic Peninsula; Weddell Sea, Larsen Ice Shelf A area	323–912	This Study
Oligobregma notiale Blake, 1981	Antarctica: Weddell Sea; Antarctic Peninsula; Ross Sea; East Antarctica	18–923	Blake (1981)
Oligobregma pseudocollare Schüller & Hilbig, 2007	Antarctica: South Sandwich Islands; Weddell Sea; Off Elephant Island	752–3050	Schüller & Hilbig (2007)
Oligobregma quadrispinosa Schüller & Hilbig, 2007	Antarctica: Drake Passage; Weddell Sea; South Sandwich Islands	2258–4069	Schüller & Hilbig (2007)
Pseudoscalibregma bransfieldium (Hartman, 1967)	Antarctica: Weddell Sea; South Sandwich Islands; Antarctic Peninsula; Ross Sea	355–3690	Hartman (1967, 1978); Blake (1981); this study
Pseudoscalibregma hartmanae (Blake, 1981), **new combination**	Weddell Sea	585	Blake (1981); this study
Pseudoscalibregma palmeri **n. sp.**	Antarctica: East Antarctic Peninsula; Weddell Sea, Larsen Ice Shelf A area	385–768	This study
Pseudoscalibregma papilia Schüller, 2008	Antarctica: Off Elephant Island; Weddell Sea; South Sandwich Islands	2258–3690	Schuller (2008)
Pseudoscalibregma usarpium Blake, 1981	Drake Passage; Weddell Sea; off Elephant Island; Ross Sea	2143–3690	Blake (1981)
Scalibregma australis **n. sp.**	Antarctic Peninsula: Weddell Sea, LIS-A area; Prince Gustav Channel; Elephant Island; South Shetland Islands; Ross Sea; East Antarctica, Wilkes Land, O'Brien Bay	45–1000	This study
Sclerocheilus antarcticus Ashworth, 1915	Antarctic Peninsula; Bransfield Strait	45–426	Ashworth (1915); Blake (1981)

*Based on juvenile, may not be valid or juvenile of another species

Peristomium. The peristomium of scalibregmatids typically includes a single ring dorsally and ventrally, with the ventral ring dividing into three or more rings that encompass the upper and lower lips of the mouth. In the juveniles of *Scalibregma australis* **n. sp.** and *Oligobregma mucronata* **n. sp.** reported in this paper, the upper and lower lips of the mouth are entirely surrounded by peristomial tissue. However in adults of *S. australis*, pads of the lower lip become incorporated into setiger 1 as that segment develops.

Unique tubular-shaped glands in the dorsal and ventral cirri and on some anterior parapodia. Internal tubular-shaped glands are present within the dorsal and ventral cirri of all three new species described in this paper. Apart from Ashworth (1901) for *Scalibregma inflatum,* Bakken *et al.* (2014) for *S. hanseni*, and Blake (1981) for *Pseudoscalibregma usarpium*, these glands have rarely been mentioned in the literature or, if mentioned, have not been reported in detail. Ashworth (1901) provided details of these glands in *S. inflatum* using histology and determined that they were unicellular and stained deeply with haematoxylin. In *S. australis* **n. sp.** these glands are numerous and have exit points along the upper surface in the dorsal cirri and on the ventral surface and near the tip in the ventral cirri (Fig. 3D–F); this is similar to what Ashworth (1901: Pl. 13, Fig.10) reported and illustrated for *S. inflatum*. In *Pseudoscalibregma palmeri* **n. sp.** these glands are even more numerous and exit along the upper surface and around the entire tip of the dorsal cirri and along the entire ventral surface of the ventral cirri (Fig. 7C–E). In *Oligobregma mucronata* **n. sp.** the glands in the dorsal and ventral cirri are few in number and exit through the nipple-like tip of each cirrus (Fig. 9B–D). The tubular and unicellular nature of these glands was described by Ashworth (1901), but their function remains unknown.

In addition, similar tubular-shaped glands have been observed on anterior parapodia of some species (Ashworth 1901; this study). In *S. australis* **n. sp.** a row of these glands was observed originating above the notosetae and branchiae and extending across the dorsum of setigers 4–5 (Figs. 2B, 3A); a few isolated glands of this nature have also been observed on the neuropodia of some larger specimens. Individual pigmented glands have been observed on the notopodia and neuropodia of *Pseudoscalibregma palmeri* **n. sp.** (Figs. 6A–B, 7A). The presence/absence of glands in the dorsal and ventral cirri and anterior segments may prove to be important taxonomic characters.

Short, spinous setae anterior to capillaries in parapodia preceding lyrate setae. Mackie (1991) postulated that these spines were homologous to the lyrate setae and that conclusion is supported here. The short spinous setae that occur in setigers preceding the segment where lyrate setae begin in three species treated in this study likely occur but have not been reported from numerous additional species due to their inconspicuous nature. An inspection of the original description and illustrations of *Sclerocheilus antarcticus* Ashworth, 1915 from the South Orkneys indicates that short, straight, pointed setae occurred on setiger 1 anterior to the longer curved spines (Ashworth 1915: 407, fig. 1A).

As part of another study, type material of several species of Scalibregmatidae in the National Museum of Natural History, Washington DC (USNM) were examined and checked for the presence/absence of these short spinous setae of anterior setigers (Blake & Luzak unpublished). The following species were found to have these spines: *Asclerocheilus tropicus* Blake, 1981 (holotype, USNM 60570); *Hyboscolex equatorialis* Blake, 1981 (holotype, USNM 60571); *Neolipobranchus blakei* Kudenov, 1985 (holotype, USNM 97283); *Oligobregma notiale* Blake, 1981 (holotype, USNM 60576; 3 paratypes, USNM 58965–7); *Pseudoscalibregma usarpium* Blake, 1981 (holotype, USNM 60583); *Scalibregmides peruanus,* Blake, 1981 (holotype, USNM 60582); *Scalibregma celticum* Mackie, 1991 (confirmed observation of Mackie (1991), 5 paratypes (USNM 123353); *Scalibregma stenocerum* (Bertelsen & Weston, 1980) (confirmed observation of Mackie 1991, who transferred the species from *Sclerobregma* to the genus *Scalibregma* (holotype USNM 58955, 1 paratype 58956).

Numerous specimens of *Sclerobregma branchiatum* Hartman, 1965 and *Oligobregma aciculata* (Hartman, 1965) are available to me from the ACSAR collections from deep-water along the entire U.S. from Canada to South Carolina. Both species have notopodial acicular spines and a few very short and blunt-tipped spinous setae are present anterior to the large acicular spines in these species as well. Thus based on published works by Ashworth (1915), Mackie (1991), Imajima (2009), Blake (2000, this study), and Bakken *et al.* (2014) there are now 18 species of named Scalibregmatidae confirmed to have short spinous setae anterior to either capillaries or larger acicular spines on setigers preceding those with lyrate setae.

The following species did not have these short spinous setae: *Asclerocheilus mexicanus* Kudenov, 1985 (1 paratype USNM 97265); *Hyboscolex quadricincta* Kudenov, 1985: lyrate setae on all setigers (holotype USNM 97270; 5 paratypes (USNM 97271–3, 1 paratype 97275); *Axiokebuita millsi* Pocklington & Fournier, 1987 (entirely lacks lyrate setae, 2 paratypes USNM 46972, 46991); *Speleobregma lanzaroteum* Bertelsen, 1986 (entirely lacks lyrate setae, holotype USNM 60582).

As noted, among the species examined that were found to have the short spinous setae was *Asclerocheilus tropicus*, which was described from a single small specimen from Ecuador in shallow water (Blake 1981). Subsequently, Nogueira (2002) re-examined the holotype and compared it with similar appearing specimens from Brazil and southern California. He concluded that these additional specimens were the same species as described by Blake (1981) and provided a description of the new materials including new details and variability. He did not, however, report the presence of the short spinous setae anterior to the acicular spines of setiger 1. These very short setae are clearly evident at the base of the anterior row of large spines in SEMs published by Nogueira (2002: Figs. 3A–B). In Fig 3A, the anterior acicular spines are to the left; two very short curved light-colored setae at the base of the two uppermost spines are the short spinous setae; in Fig. 3B the anterior acicular spines are to the right; some tissue has lifted off at the base of the spines during preservation but several very thin setal shafts can be detected alongside the larger shafts of the acicular spines: these are the short spinous setae. In *A. tropicus* it appears that these short spinous setae are pointed. Unless one is looking for them, their very small size and inconspicuous nature makes them easy to overlook.

Large, acicular spines of anterior parapodia. In contrast to the short, inconspicuous spinous setae, the large acicular spines such as occur on *O. mucronata* **n. sp.** are considered to have a separate origin (Mackie 1991). This is supported by the observation that some species with large spines may also have the short spinous setae anterior to the large acicular spines.

Out of 12 species of *Asclerocheilus* reviewed by Blake (2000), only three species had large acicular spines in both the noto- and neuropodia. Of eight species of *Oligobregma*, excluding *O. hartmanae* (removed to *Pseudoscalibregma*) and *O. blakei* (a juvenile, not likely validly placed in *Oligobregma*), *O. mucronata* **n. sp.** and *O. aciculata*, the type-species are the only species recorded to date with acicular spines in both noto- and neuropodia.

In light microscopy, some of the acicular spines of *O. mucronata* **n. sp.** have a thin arista at the tip; such a character has not been previously reported for scalibregmatids with large acicular spines; further, the neuropodial spines appear to be thinner than the notopodial spines. With SEM, acicular spines of other species such as *Asclerocheilus tropicus* have been observed with a cloak of fibrils covering the tip of a pointed shaft (Nogueira 2002), but this does not appear to produce an arista when observed in light microscopy.

Among the variability noted by Nogueira (2002) for *O. tropicus* was that the acicular spines of setiger 1 of most specimens examined were sickle-shaped (Nogueira 2002: Figs. 1B, 3A) as was also reported and illustrated by Blake (1981: Fig. 1B) for the holotype. Three of Nogueira's specimens, however, were observed to have nearly straight shafts with curved tips (Nogueira 2002: Fig. 3B). In my experience this type of intraspecific variability in the structure of the acicular spines does not occur and I suggest that an additional species is present.

Ventral groove. A prominent ventral groove bearing elevated pads occurs in numerous species of Scalibregmatidae including the four reported in this paper; however, this groove with ridges has rarely been emphasized in previous descriptions. This character is an additional aspect of the overall morphology of scalibregmatids that deserves further study. The recent papers by Parapar *et al.* (2011b) and Martínez *et al.* (2013, 2014) on two closely related scalibregmatid genera, *Axiokebuita* and *Speleobregma*, suggest that a ventral groove or ridge line is completely absent in all described species of these two genera. If so, then, in conjunction with the complete absence of lyrate setae, acicular spines, branchiae, and parapodial cirri, together with the presence of an unusual prostomium with long ciliated lateral horns (termed palps by these authors) and an unusual peristomial sensory structure, this clade as reported by these authors differs considerably from other scalibregmatids.

The ventral groove of scalibregmatids is not of the same morphology as found in Opheliidae where the groove is a channel formed between two ridges of longitudinal ventral muscles. In scalibregmatids, the groove separates annulated rows of each segment along the mid-ventral line and continues from segment to segment along the entire venter of the body. Within this groove, elevated pads that approximate the number of annulated rows per segment fill the groove producing elevated lobes or a ridge line along the venter.

Reproduction. The presence of ect-aquasperm and eggs in the 110 µm size range in *Scalibregma australis* **n. sp.** together with similar sperm observed for *Oligobregma mucronata* **n. sp.** and published observations that adults of some species of scalibregmatids develop long natatory-like setae and swim in the plankton (Ditlevsen 1911; Clark 1954) suggests that spawning takes place in the water column for at least some species. There are, however, no previous accounts of fertilization, embryology, or early larval development for any scalibregmatid.

Post-larval and juvenile morphology. The study of post-larvae and juveniles of *Scalibregma australis* **n. sp.** and juveniles of *Oligobregma mucronata* **n. sp**. demonstrates that key morphology including shape and form of the prostomium, occurrence of branchiae, and patterns of setal development preclude accurate identification of small specimens unless a growth sequence is available. A similar pattern has been found with *Sclerobregma branchiatum*, a deep-water species off the U.S. Atlantic coast (Blake & Luzak unpublished). These findings have important consequences for species identifications and the definition of scalibregmatid genera. Some of the main findings are discussed below.

Setae. In *Scalibregma australis* **n. sp.** the short, spinous setae of the anterior row of setiger 1 found on adults develop on setigers 1–4 in post-larvae and juveniles. The lyrate setae that begin on setiger 2 in adults are entirely absent in the earliest post-larvae studied up to the 15-setiger stage. By 16–17 setigers lyrate setae appear on setigers 2–4, but unlike in adults, they co-occur with the short spinous setae until about the 24-setiger stage at which time the spinous setae of setigers 2–4 are entirely replaced by the lyrate setae and only retained on setiger 1 where lyrate setae never develop. Middle body and posterior segments do not fully exhibit lyrate setae until about 24 setigers have developed. In *O. mucronata* **n. sp.** the full complement of noto- and neuropodial acicular spines in setigers 1–3, lyrate setae from setiger 4, and capillaries throughout is first present in juveniles having 20–21 setigers and a length of 2.3 mm. The neuropodial spines of setiger 3, however, develop later than those of the notopodia.

Prostomial morphology. In both *Scalibregma australis* **n. sp**. and *Oligobregma mucronata* **n. sp.** the prostomium is initially a simple protuberance that is blunt or rounded on the anterior margin. With growth, the prostomium becomes broad and thickened across the frontal margin and develops lateral bulges that eventually form frontal horns in *S. australis* **n. sp**. In *O. mucronata* **n. sp**. there is a similar pattern, however, frontal horns do not develop, and instead separate subapical lobes develop late in ontogeny and protrude anteriorly.

Peristomial morphology. The most important finding of peristomial development is the elaboration of the ventral part of the peristomium into complex upper and lower lips surrounding the mouth. Differences in the nature of the lobes comprising these lips appear to be species-specific and is evident when the final adult morphology is attained. In contrast, the morphology of the dorsal peristomial ring remains largely constant during development.

Ventral groove. The ventral groove with elevated pads is established early in post-larval development. It typically originates from an anterior setiger and extends posteriorly in some form to near the posterior end. Individual pads within this groove begin as a single protuberance that later divides into 2–4 separate structures that generally approximate the number of annulated rows typically found on that segment.

Dorsal and ventral cirri and internal glands. The dorsal and ventral cirri that develop in juveniles are similar to those found in adults. However, in *Scalibregma australis* **n. sp.** the dorsal cirri develop before the ventral cirri. Based on the specimens available, both cirri appear to develop simultaneously in *Oligobregma mucronata* **n. sp.**

Both species develop internal tubular-shaped glands within the dorsal and ventral cirri; these glands occur with the earliest appearance of the cirri. These same glands were also observed in adults of *Pseudoscalibregma palmeri* **n. sp.** and are likely widespread among scalibregmatids, but have rarely been mentioned in the literature.

Development of branchiae. Branchiae have been found to develop late in the post-larvae and juveniles of *Scalibregma australis* **n. sp.** studied here. Since branchiae serve to support the definition of several genera such as *Scalibregma, Sclerobregma, Cryptosclerocheilus, Parasclerocheilus*, and *Polyphysia*, their late development in juveniles means that not only can one not identify small specimens of a species with confidence, but the genus cannot be identified as well. Therefore, based on the results of this study, specimens with a size limit of 3–4 mm and development of about 28 setigers cannot be morphologically classified to genus and species without a growth sequence of larger specimens that exhibit a full complement of adult characters. These size ranges may be greater however, because Cantone (1994) reported two specimens identified by him as *Scalibregma inflatum* from the Ross Sea where branchiae were present on setigers 3–4 on a 38 setiger specimen and setigers 2–5 on a 41 setiger specimen. These results support an observation by Day (1967: 584) that “It is important to note, however, that the number of gills increases with size of the worm and that small individuals may even lack gills entirely.” Støp-Bowitz (1945) synonymised *Lipobranchus jefferysi* McIntosh, 1869 with *Polyphysia crassa* because he was convinced that the former was a juvenile on which branchiae had not yet developed. Wesenberg-Lund (1950) subsequently disagreed with this after finding large abranchiate specimens of *L. jefferysi*.

Pygidial lobes and cirri. The development of the pygidium appears to be a gradual process from an expanded posterior end with perhaps two large lobes that becomes partitioned into five or more smaller lobes. Pygidial cirri are initially small and blunt then become elongate and cirriform. There is always a mid-ventral cirrus with other cirri positioned laterally. In the species studied here the maximal number of pygidial cirri was five. However, the cirri are fragile and can easily detach, therefore a large collection is usually needed in order to understand their number and arrangement. It is likely that scars of anal cirri can be detected with SEM. However, none were observed in the present observations of *Scalibregma australis* **n. sp.**

General taxonomic problems. The issues with late development of certain morphological characters in post-larval and juvenile morphology identified in this study calls into question the validity of some species described from very small specimens. The most serious problem appears to be the late development of branchiae that are known for five genera. In the unpublished data already mentioned, a presumed undescribed species of *Oligobregma* from deep-water off the U.S. Atlantic coast was found to be a juvenile of *Sclerobregma branchiatum* once a complete growth sequence was examined (Blake & Luzak unpublished). In the present study, juveniles of *Scalibregma australis* **n. sp.** less than 3.5 mm long would have been identified as a species of *Pseudoscalibregma* had a growth sequence not been available. The presence/absence of gametes usually used to define a mature adult were not present in small specimens of the species observed in this study and from the U.S. Atlantic slope.

Another character that can be confusing in smaller specimens is the morphology of the prostomium. In four species studied to date (two here and two from the western North Atlantic) frontal horns or lobes develop late in ontogeny (juveniles 3.5–4.0 mm long, with about 28 setigers) possibly leading to confusion in the identification of genera and species because the prostomial shape is one of the first characters one notices in scalibregmatids.

While the general features of dorsal and ventral cirri, when present, are good taxonomic characters, the presence of the internal tubular glands on anterior body segments and dorsal and ventral cirri have rarely been reported in scalibregmatid descriptions and if present have not been reported in sufficient detail to evaluate the nature of the tubular glands, their density, and where they exit the cirrus. The presence of these glands in all three of the new species described in this paper demonstrates that their presence/absence is an important taxonomic character and very likely widespread among species with these cirri but not reported as such. Further, while the glands are dense and numerous in *Scalibregma australis* **n. sp.** and *Pseudoscalibregma palmeri* **n. sp.**, they are sparse in *Oligobregma mucronata* **n. sp.** However, Ashworth (1901) observed that the density of these glands in dorsal and ventral cirri of *S. inflatum* increased in larger specimens.

It is apparent that some previously described species of Scalibregmatidae might be juveniles and not valid. The following are examples and not a comprehensive list:

(1) *Oligobregma blakei* Schüller & Hilbig 2009 based on a single specimen, only 3 mm long with 19 segments of which the posterior end was said to be regenerating. Gametes were not observed.

(2) *Asclerocheilus tropicus* Blake, 1981 was originally described from a single specimen only 1.8 mm long and with 29 segments from Ecuador. However, Nogueira (2002) re-examined the holotype and compared it with newly collected and much larger specimens (up to 9.5 mm long and with up to 37 segments) from Brazil and southern California and confirmed its validity. Gametes were not reported in either the original description by Blake (1981) or the updated description by Nogueira (2002).

(3) *Asclerocheilus ashworthi* Blake, 1981 is based on a specimen only 3.0 mm long and with 18 segments from off Elephant Island, Antarctica. However, newly collected material of this species is now available from deep-water from the Weddell Sea that includes larger specimens (Blake unpublished). Mature gametes were not observed in the original materials but are present in the new collections.

(4) *Neolipobranchus glabrus* Hartman & Fauchald, 1971 was described from off New England in abyssal depths of 4,436 m. The specimens were small, only 2.5–3.0 mm in length and largely based on negative characters, including any typical scalibregmatid morphology such as a bifurcated prostomium, segmental annulae, lyrate setae, branchiae, and pygidial cirri. Its inclusion in the Scalibregmatidae was not justified by the original authors. Gametes were not observed for this species. In order to evaluate the status of *N. glabrus*, the holotype (LACM-AHF Poly 896) was examined.

The holotype of *N. glabrus* is fragile with the body damaged ventrally in the middle where a segment has separated from the next. The specimen is fusiform in shape, with an expanded middle region, narrowing anteriorly and posteriorly; 2.9 mm long and 0.8 mm wide. There are no more than 22 segments of which setae were difficult to see and only confirmed on 18 segments. There is a faint ventral mid-line evident on the last six segments. The prostomium is a narrow lobe extending anteriorly and is rounded on the anterior margin. The peristomium is a singled lobed ring dorsally and appears to extend ventrally and border the upper or anterior lips of the mid-ventral mouth. In addition, there are three achaetous segments that together form an elongate region anterior to where segments begin to expand; these segments are considered peristomial and encompass the mouth; each of these segments is defined by a row of oblong lobes or elevated plates. These achaetous segments are followed by 13 segments that progressively increase in size forming the expanded middle region and then decrease in size to the narrow posterior end. The first nine of these segments are smooth, with surface morphology obscured or stretched with expansion; the following four segments become narrower and include the posterior part of the expanded region, each of these forms one or two distinct rings encircling the body, expanded on their posterior margins, but these rings are not annulated with elevated pads as is typical of scalibregmatids. The remaining nine segments become progressively narrow and elongate each with an expanded non-annulated ring on the posterior margin. The last segment is narrow and appears terminally damaged suggesting that the pygidial segment is missing. Parapodial tori and associated cirri or postsetal lamellae are not present; setae appear to emerge directly from the body wall. Setae are simple narrow capillaries with no more than 2–3 in either noto- or neuropodia. The specimen appears to be a post-larval juvenile possibly of a scalibregmatid, but the non-annulated rings and lack of parapodial tori are also typical of species of *Travisia.* The specimen had been feeding because the gut in the anterior half of the body is filled with silt. There are no distinctive morphological characters present to define this species. Characters that could characterize this specimen as a scalibregmatid such as annulated rings, lyrate setae, anterior spines, T-shaped prostomium, dorsal and/or ventral cirri, and anterior arborescent branchiae are entirely absent. The anterior achaetous region does have single rings of elongated plates and this is believed to be peristomial because it surrounds the lateral and ventral margins of the mouth and this suggest that missing characters would likely appear with growth and differentiation. However, without a growth sequence there is no way to determine what genus or species this specimen represents and the genus must therefore be *incertae sedis*.

(5) *Neolipobranchus blakei* Kudenov, 1985 the second species described for this genus was based on a single specimen from intertidal sediments on the western side of Florida; the specimen has a rounded prostomium, annular rings along the body, lyrate setae, and pygidial cirri, but was also small, only 3 mm long (Kudenov 1985) and a juvenile according to the results of the present study. Gametes were not observed. A growth sequence is needed in order to establish the identity of this species.

Acknowledgements

The field work with ship time for the survey at the site of the former Larsen Ice Shelf A was funded by the NSF Office of Polar Programs Grant OPP-9814383 to Drs. Eugene Domack and Patrick Reynolds, Hamilton College, Clinton, NY. Dr. Reynolds also arranged for my participation on the cruise and subsequent sorting of the benthic samples by Mr. Russ Winchell, Oceans Taxonomic Services. Completion of the polychaete taxonomy was funded by NSF Grant No. DEB-0118693 (PEET) to James A. Blake, University of Massachusetts, Boston. Dr. Jason Williams, Hofstra University, was a co-investigator on this grant and directed the preparation SEMs of these and other polychaetes. A subsequent reimaging of some earlier SEMs was supported by NSF Grant (DBI-1337525) to Jason D. Williams (Hofstra University). The manuscript was carefully reviewed by Dr. Nancy J. Maciolek. Comments by two anonymous greatly improved the manuscript.

References

Ashworth, J.H. (1901) The anatomy of *Scalibregma inflatum* Rathke. *Quarterly Journal of Microscopical Science*, 45, 237–309. [London]

Ashworth, J.H. (1915) On a new species of *Sclerocheilus*, with a revision of the genus. *Transactions of the Royal Society of Edinburgh*, 50 (2), 405–422.
http://dx.doi.org/10.1017/S0080456800036000

Bakken, T., Oug, E. & Kongsrud, J.A. (2014) Occurrence and distribution of *Pseudoscalibregma* and *Scalibregma* (Annelida, Scalibregmatidae) in the deep Nordic Seas, with the description of *Scalibregma hanseni* n. sp. *Zootaxa*, 3753 (2), 101–117.
http://dx.doi.org/10.11646/zootaxa.3753.2.1

Barbosa, L.S., Soares-Gomes, A. & Paiva, P.S. (2010) Distribution of polychaetes in the shallow, sublittoral zone of Admiralty Bay, King George Island, Antarctica in the early and late austral summer. *Natural Science*, 2 (10), 1155–1163.
http://dx.doi.org/10.4236/ns.2010.210143

Bertelsen, R.D. (1986) *Speleobregma lanzaroteum*, a new genus and species of Scalibregmatidae (Polychaeta) from a marine cave in the Canary Islands. *Proceedings of the Biological Society of Washington,* 99, 375–379.

Bertelsen, R.D. & Weston, D.P. (1980) A new species of *Sclerobregma* (Polychaeta: Scalibregmatidae) from off the southeastern United States. *Proceedings of the Biological Society of Washington*, 93, 708–713. Available from: http://www.biodiversitylibrary.org/item/107589 (Accessed 19 Oct. 2015)

Blake, J.A. (1972) Two new species of polychaetous annelid worms from Baffin Bay and the Davis Strait. *Bulletin of the Southern California Academy of Sciences*, 71, 127–132. Available from: http://www.biodiversitylibrary.org/item/106891 (Accessed 19 Oct. 2015)

Blake, J.A. (1981) The Scalibregmatidae (Annelida: Polychaeta) from South American and Antarctic Seas, collected chiefly during the cruises of the R/V *Anton Bruun*, R/V *Hero* and USNS *Eltanin*. *Proceedings of the Biological Society of Washington*, 94, 1131–1162. Available from: http://www.biodiversitylibrary.org/item/107603 (Accessed 19 Oct. 2015)

Blake, J.A. (1993) Life history analysis of five dominant infaunal polychaete species from the continental slope off North Carolina. *Journal of the Marine Biological Association of the United Kingdom*, 73, 123–141.
http://dx.doi.org/10.1017/S0025315400032689

Blake, J.A. (2000) Family Scalibregmatidae Malmgren, 1867. *In*: Blake, J.A., Hilbig, B. & Scott, P.H. (Eds.), *Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and the Western Santa Barbara Channel*. Santa Barbara Museum of Natural History, Santa Barbara, California, pp. 129–144.

Blake, J.A. (2006) Spionida. *In*: Rouse, G. & Pleijel, F. (Eds.), *Reproductive Biology and Phylogeny of Annelida.* Volume 4 of Series: Reproductive Biology and Phylogeny, Series Editor, B.G.M. Jamieson. Science Publishers, Enfield, New Hampshire, pp. 566–638,

Blake, J.A. & Hilbig, B. (1994) Dense infaunal assemblages on the continental slope off Cape Hatteras, North Carolina. *Deep-Sea Research II*, 41, 875–899.

Blair, N.E., Levin, L.A., DeMaster, D.J. & Plaia, G. (1996) The short-term fate of fresh algal carbon in continental slope sediments. *Limnology & Oceanography*, 41, 1208–1219.
http://dx.doi.org/10.4319/lo.1996.41.6.1208

Bochert, R. & Bick, A. (1995) Reproduction and larval development of *Marenzelleria viridis* (Polychaeta: Spionidae). *Marine Biology*, 123, 763–773.
http://dx.doi.org/10.1007/BF00349119

Cahoon, L.B., Laws, R.A. & Thomas, C.J. (1994) Viable diatoms and chlorophyll *a* in continental slope sediments off Cape Hatteras, North Carolina. *Deep-Sea Research II*, 41, 767–782.

Cantone, G. (1994) Polychaeta Sedentaria of Terra Nova Bay (Ross Sea, Antarctica): Orbiniidae to Oweniidae (Annelida). *Animalia*, 21, 35–47.

Cantone, G. & Sanfilippo, R. (1992) Polychaeta from Terra Nova Bay (Ross Sea, Antarctica). *In*: Gallardo, V.A., Ferretti, O., & Moyanao, I. (Eds.), *Oceanographia en Antartida*. ENEA-PNRA-EULA, Conception, Chile, pp. 372–377.

Cantone, G., Castelli, A. & Gambi, M.C. (2000) Benthic polychaetes off Terra Nova Bay and Ross Sea: Species composition, biogeography, and ecological role. *In*: Faranda, F.M., Guglielmo, L. & Ianora, A. (Eds.), *Ross Sea Ecology.* Springer Verlag, Berlin, Heidelberg, pp. 551–561.

Çinar, M.H. (2005) Polychaetes from the coast of northern Cyprus (eastern Mediterranean Sea), with two new records for the Mediterranean Sea. *Cahiers de Biologie Marine*, 46, 143–159.

Clark, R.B. (1954) Pelagic swarming of Scalibregmidae (Polychaeta). *Annual Report of the Scottish Marine Biological Association for 1952–1953*,1954, 20–22.

Day, J.A. (1934) Development of *Scolelepis fuliginosa* (Claparède). *Journal of the Marine Biological Association of the United Kingdom,* 19, 633–654.
http://dx.doi.org/10.1017/S0025315400046671

Day, J.H. (1967) A monograph on the Polychaeta of southern Africa. *British Museum of Natural History, Publication,* No. 66, 1–878.

Ditlevsen, H. (1911) Annelids from the Danmark-Expedition. Danmark-Ekspeditionen til Grønlands Nordøstkyst 1906–1908. *Meddelelser om Grønland, Kobenhaven***,** 45, 411–432, pls. 27–31.

Domack, E.A., Leventer, A., Gilbert, R., Brachfeld, S.K, Isman, S., Cmaerlenghi, A., Gavahan, K. Carlson, D. & Barkoukis, A. (2001) Cruise reveals history of Holocene Larsen Ice Shelf. *EOS, Transactions of the American Geophysical Union*, 82 (2), 13–17.
http://dx.doi.org/10.1029/01eo00009

Eckelbarger, K.J. (2005) Oogenesis and oocytes. *In*: Bartolomaeus, T. & Purschke, G. (Eds.), Morphology, Molecules, Evolution and Phylogeny in Polychaeta and Related Taxa. *Hydrobiologia*, 535/536, 179–198.
http://dx.doi.org/10.1007/1-4020-3240-4_11

Eckelbarger, K.J. (2006) Oogenesis. *In*: Rouse, G. & Pleijel, F. (Eds.), *Reproductive Biology and Phylogeny of Annelida. Volume 4 of Series: Reproductive Biology and Phylogeny, Series Editor, Jamieson*, *B.G.M.* Science Publishers, Enfield, New Hampshire, pp. 23–44.

Elder, H.Y. (1973) Direct peristaltic progression and the functional significance of the dermal connective tissues during burrowing in the polychaete *Polyphysia crassa* (Oersted). *Journal of Experimental Biology*, 58, 637–655.

Fage, L. & Legendre, R. (1927) Pèches planctoniques a la lumière effectuées a Banyuls-sur-Mer et à Concarneau. I. Annélides polychètes. *Archives de Zoologie Expérimentale et Générale, Paris*, 67, 23–222.

Franzén, Å. (1956) On spermiogenesis, morphology of the spermatozoon, and biology of fertilization among invertebrates. *Zoologiska Bidrag från Uppsala,* 31, 355–480, pls. 1–6.

Gilbert, R. & Domack, E.W. (2003) Sedimentary record of disintegrating ice shelves in a warming climate, Antarctic Peninsula. *Geochemistry, Geophysics, Geosystems,* 4 (4), 1–12.

George, J.D. (1966) Reproduction and early development of the spionid polychaete *Scolecolelides viridis* (Verrill). *Biological Bulletin,* 130, 76–93.
http://dx.doi.org/10.2307/1539954

Guérin, J.-P. (1975) Redescription des adultes et comparaision des divers states ontogénétiques des populalions méditerranéennes et atlantiques de *Scolelepis fuliginosa* Claparède (Annélide Polychète). *Cahiers de Biologie* Marine, 16, 21–37.

Hansen, G.A. (1879) Annelider fra den norske Nordhavsexpedition i 1876. *Nyt Magazin for Naturvidenskaern*, 24, 1–17.

Hartman, O. (1959) Catalogue of the polychaetous annelids of the world. *Allan Hancock Foundation, Occasional Paper*, 23, 1–628.

Hartman, O. (1965) Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. *Allan Hancock Foundation Publications Occasional Paper*, 28, 1–378.

Hartman, O. (1967) Polychaetous annelids collected by the USNS *Eltanin* and *Staten Island* cruises, chiefly from Antarctic seas. *Allan Hancock Monographs in Marine Biology*, 2, 1–387.

Hartman, O. (1978) Polychaeta from the Weddell Sea quadrant, Antarctica. *Antarctic Research Series*, 26, 125–223. Available from: American Geophysical Union]

Hartman, O. & Fauchald, K. (1971) Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas Part II. *Allan Hancock Monographs in Marine Biology*, 6, 1–327.

Hartmann-Schröder, G. (1986) Die Polychaeten der 56. Reise der "Meteor" zu den South Shetland-Inseln (Antarktis). *Mitteilungen des hamburgischen Zoologischen Museums und Instituts*, 83, 71–100.

Hartmann-Schröder, G. & Rosenfeldt, P. (1989) Die Polychaeten der "Polarstern" Reise ANT III/2 in the Antarktis 1984 Teil 2: Cirratulidae bis Serpulidae. *Mitteilungen des hamburgischen Zoologischen Museums und Instituts*, 86, 65–106.

Hartmann-Schröder, G. & Rosenfeldt, P. (1991) Die Polychaeten der "Walther Herwig" Reise 68/1 nach Elephant Island (Antarktis) 1985. Teil 2: Acrocirridae bis Sabellidae. *Mitteilungen des hamburgischen Zoologischen Museums und Instituts*, 88, 73–96.

Hilbig, B., Gerdes, D. & Montiel, A. (2006) Distribution patterns and biodiversity in polychaete communities of the Weddell Sea and Antarctic Peninsula area (Southern Ocean). *Journal of the Marine Biological Association of the United Kingdom*, 86, 711–725.
http://dx.doi.org/10.1017/S0025315406013610

Imajima, M. (2009) Deep-sea polychaetes off Pacific coast of the northern Honshu, Japan. *In*: Fugita, T. (Ed.), Deep-sea Fauna and Pollutants off Pacific Coast of Northern Japan. *National Museum of Nature and Science Monographs*, 39, 39–192.

Jamieson, B.G.M. & Rouse, G.W. (1989) The spermatozoa of the Polychaeta (Annelida) an ultrastructural review. *Biological Review*, 64, 93–157.
http://dx.doi.org/10.1111/j.1469-185X.1989.tb00673.x

Jumars, P.A., Dorgan, K.M. & Lindsey, S.M. (2015) Diet of worms emended: an update of polychaete feeding guilds. *Annual Review of Marine Science*, 7, 497–520 + Supplemental Appendix.
http://dx.doi.org/10.1146/annurev-marine-010814-020007

Knox, G.A. & Cameron, D.B. (1998) The Marine Fauna of the Ross Sea: Polychaeta. National Institute of Water and Atmospheric Research (NIWA). *NIWA Biodiversity Memoir*, 108, 1–127.

Kudenov, J.D. (1985) Four new species of Scalibregmatidae (Polychaeta) from the Gulf of Mexico, with comments on the familial placement of *Mucibregma* Fauchald & Hancock. *Proceedings of the Biological Society of Washington*, 98, 332–340. Available from: http://www.biodiversitylibrary.org/item/107750 (Accessed 19 Oct. 2015)

Kudenov, J.D. & Blake, J.A. (1978) A review of the genera and species of the Scalibregmidae (Polychaeta) with description of one new genus and three new species from Australia. *Journal of Natural History*, 12, 427–444.
http://dx.doi.org/10.1080/00222937800770291

Levenstein, R.Y. (1962) The polychaetes from three abyssal trenches in the Pacific Ocean. *Zoologisches Zhurnal,* Moscow, 41, 1141–1148. [in Russian with English summary]

Levenstein, R.Y. (1975) [The polychaetous annelids of the deep trenches of the Atlantic sector of the Antarctic Ocean]. *Trudy Institute Oceanologica*, 103, 119–142. [in Russian]

Lomiri, S., Vani, D., Tomassetti, P., Trabucco, B., Maggi, C., & Nonnis, O. (2012) First record of *Scalibregma celticum* (Annelida: Polychaeta: Scalibregmatidae) in Italian marine waters. *Marine Biodiversity Records,* 5, 1–4.
http://dx.doi.org/10.1017/S175526721100100X

Lovell, L.L. & Trego, K.D. (2003) The epibenthic megafaunal and benthic infaunal invertebrates of Port Foster, Deception Island (South Shetland Islands, Antarctica). *Deep-Sea Research II*, 50, 1799–1819.

Mackie, A.S.Y. (1991) *Scalibregma celticum* new species (Polychaeta, Scalibregmatidae) from Europe, with a redescription of *Scalibregma inflatum* Rathke, 1843 and comments on the genus *Sclerobregma* Hartman, 1965. *Bulletin of Marine Science*, 48, 268–276.

Martínez, A., Di Domenico, M., & Worsaae, K. (2013) Evolution of cave *Axiokebuita* and *Speleobregma* (Scalibregmatidae,

Annelida). *Zoologica Scripta*, 42 (6), 623–636.
http://dx.doi.org/10.1111/zsc.12024

Martínez, A., Di Domenico, M., & Worsaae, K. (2014) Gain of palps within a lineage of ancestrally burrowing annelids (Scalibregmatidae). *Acta Zoologica,* 95 (4), 421–429.
http://dx.doi.org/10.1111/azo.12039

Montiel, A., Gerdes,D., Hilbig, B. & Arntz, W.E. (2005) Polychaete assemblages on the Magellan and Weddell Sea shelves: comparative ecological evaluation. *Marine Ecology Progress Series*, 297, 189–202.
http://dx.doi.org/10.3354/meps297189

Nogueira, J.M.M (2002) *Asclerocheilus tropicus* Blake, 1981 (Polychaeta: Scalibregmatidae): redescription based on Brazilian specimens. *Proceedings of the Biological Society of Washington*, 115(2), 323–332. Available from: http://www.biodiversitylibrary.org/item/107750 (Accessed 19 Oct. 2015)

Orrhage, L. (1966) Über die Anatomie des zentralen Nervensystems der sedentären Polychaeten. *Archiv fur Zoologi,* 19, 99–133.

Orrhage, L. (1993) On the microanatomy of the cephalic nervous system of Nereidae (Polychaeta), with a preliminary discussion of some earlier theories on the segmentation of the polychaete brain. *Acta Zoologica* (Stockholm), 74, 145–172.
http://dx.doi.org/10.1111/j.1463-6395.1993.tb01231.x

Orrhage, L. & Müller, M. (2005) Morphology of the nervous system of Polychaeta (Annelida). *In*: Bartolomaeus, T. & Purschke, G. (Eds.), Morphology, Molecules, Evolution and Phylogeny in Polychaeta and Related Taxa. *Hydrobiologia*, 535/536, pp. 79–111.

Pabis, K. & Sobczyk, R. (2015) Small-scale variation of soft-bottom polychaete biomass in an Antarctic glacial fjord (Ezcurra Inlet, South Shetlands): comparison of sites at different levels of disturbance. *Helogland Marine Research*, 69, 113–121.
http://dx.doi.org/10.1007/s10152-014-0420-5

Parapar, J., Lopez, E., Gambi, M.C., Nunez, J. & Ramos, A. (2011a) Quantitative analysis of soft-bottom polychaetes of the Bellingshausen Sea and Gerlach Strait (Antarctica). *Polar Biology*, 34, 715–730.
http://dx.doi.org/10.1007/s00300-010-0927-4

Parapar, J., Gambi, M.C. & Rouse, G.W. (2011b) A revision of the genus *Axiokebuita* Pocklington and Fournier, 1987 (Annelida: Scalibregmatidae). *Italian Journal of Zoology*, 78 (S1), 148–162.
http://dx.doi.org/10.1080/11250003.2011.598350

Pocklington, P. & Fournier, J.A. (1987) *Axiokebuita millsi*, new genus, new species, (Polychaeta: Scalibregmatidae) from eastern Canada. *Bulletin of the Biological Society of Washington,* 7, 108–113.

Rathke, H. (1843) Beiträge zur Fauna Norwegens. *Verhandlungen Kaiserlichen Leopoldinisch-Carolinischen Akademie Naturforscher*, 20, 1–264. [Breslau]
http://dx.doi.org/10.5962/bhl.title.11613

San Martin, G, Parapar, J., Garcia, F.J. & Redondo, M.S. (2000) Quantitative analysis of soft bottoms infaunal macrobenthic polychaetes from South Shetland Islands (Antarctica). *Bulletin of Marine Science,* 67, 83–102.

Schüller, M. (2008) New polychaete species collected during the expeditions ANDEEP I, II, and III to the deep Atlantic sector of the Southern Ocean in the austral summers 2002 and 2005—Ampharetidae, Opheliidae, and Scalibregmatidae. *Zootaxa*, 1705, 51–68.

Schüller, M. & Hilbig, B. (2007) Three new species of the genus *Oligobregma* (Polychaeta, Scalibregmatidae) from the Scotia and Weddell Seas (Antarctica). *Zootaxa*, 1391, 35–45.

Schüller, M., Hilbig, B. & Wagele, J.-W. (2009) Community structure and diversity of polychaetes (Annelida) in the deep Weddell Sea (Southern Ocean) and adjacent basins. *Marine Biodiversity*, 39, 95–108.
http://dx.doi.org/10.1007/s12526-009-0009-4

Siciński J. (1986) Benthic assemblages of Polychaeta in chosen regions of the Admiralty Bay (King George Island, South Shetland Islands). *Polish Polar Research*, 7, 63–78.

Siciński, J. (2000) Polychaeta (Annelida) of Admiralty Bay: species richness, diversity, and abundance. *Polish Polar Research*, 21, 153–169.

Siciński, J. (2004) Polychaetes of Antarctic sublittoral in the proglacial zone (King George Island, South Shetland Islands, *Polish Polar Research*, 25 (1), 67–96.

Støp-Bowitz, C. (1945) Les scalibregmiens de Norvege. *Meddelelser fra det Zoologiske Museum,* 55, 63–87. [Oslo]

Wesenberg-Lund, E. (1950) Polychaeta. *The Danish Ingolf-Expedition*, 4 (14), 1–92, pls. 1–10.