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Anguillosyllis (Annelida: Syllidae) from multiple deep-water locations in the northern and southern hemispheres

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Abstract

Numerous specimens belonging to the syllid genus *Anguillosyllis* Day were collected during several deep-sea studies conducted between 1970 and 2011 in depths ranging from 180 to nearly 5000 m. These quantitative studies demonstrated that members of this genus are not as uncommon as once thought but can be among the 10 most common infaunal species at some deep-sea locations. Study areas included Georges Bank (New England), the North, Mid, and South Atlantic Continental Slope and Rise (east coast of North America), the Gulf of Mexico (off Louisiana), off San Francisco, California, the Clarion-Clipperton Fracture Zone (Pacific Ocean), the South China Sea (off Brunei), the abyssal plain in the South Atlantic Ocean, and Antarctica (Scotia Sea, Weddell Sea). Sixteen new species are described, bringing the total number of described *Anguillosyllis* species to 20; one additional species that cannot be fully characterized is also noted. The new species include eight with palps that are entirely or partially free (*Anguillosyllis aciculata* **n. sp.**, *A. acsara*, **n. sp.**, *A. carolina* **n. sp.**, *A. denaria* **n. sp**., *A. hadra*, **n. sp.**, *A. hampsoni* **n. sp.**, *A. taleola* **n. sp**., and *A. truebloodi* **n. sp.**) and eight species with completely fused palps (*A. andeepia* **n. sp.**, *A. blakei* **n. sp.**, *A. bruneiensis* **n. sp.**, *A. elegantissima* **n. sp.**, *A. enneapoda* **n. sp.**, *A. hessleri* **n. sp.**, *A. inornata* **n. sp.**, and *A. sepula* **n. sp.**). Type specimens of *A. palpata* (Hartman) from off Cape Horn and *A. pupa* (Hartman) from off New England were examined; *A. capensis* Day from South Africa and *A. lanai* Barroso, Paiva, Nogueira & Fukuda from Brazil are discussed. All adult *Anguillosyllis* have a fixed number of setigers, either 8, 9, 10, or 11, with 11 setigers being the most common. Species differ in the number of setigers, degree of fusion of the palps, degree of development of parapodial lobes, structure and number of internal and external glands, number of setae in anterior setigers, shape and size of proventricle, and annulation of the dorsum. All species for which the anal cirri had not been lost were found to have four, including two long, thin, ventromedial ones and two shorter, usually oval, lateral ones. Reproduction is poorly known in the genus; the present study shows eggs are found in the posterior (post-proventricle) setigers of most species and enter the parapodia from the coelom of several specimens; egg diameters generally ranged from 50–85 µm with *A. sepula* **n. sp.** having eggs up to 120 µm, the largest reported for the genus.

Key words: ANDEEP, Antarctica, Atlantic Continental Slope and Rise, benthos, Borneo, Brunei, Clarion-Clipperton Fracture Zone, deep-sea, Georges Bank, New England, SF-DODS, South China Sea

Introduction

The syllid genus *Anguillosyllis* was established by Day (1963) for a single species, *A. capensis*, found in 183 m water depth on the Agulhas Bank off South Africa. The species was not recorded again until Böggemann & Purschke (2005) and Böggemann (2009), after examining the type specimen, reported new collections taken on the DIVA-1, DIVA-2, and BIOZAIRE expeditions off the west coast of Africa in 3945–5449 m. Aguado & San Martín (2008) examined a six-setiger anterior fragment of the type specimen and prepared a new illustration as part of their report on uncommon syllid genera. They also examined specimens of *Braniella pupa* Hartman, 1965, which was described from the continental slope off New England and northeastern South America (Hartman 1965), and *B. palpata* Hartman, 1967, from the Drake Passage and the deep sea off Cape Horn in the Antarctic (Hartman 1967). Noting the similarities between the two genera, Aguado & San Martín (2008) declared *Braniella* to be a junior synonym of *Anguillosyllis*; that synonymy has been accepted and is also followed here. In addition to these three named species, Aguado *et al.* (2012) referenced an undescribed species from Costa Rica in their cladistic analysis of the Syllidae; Barroso *et al.* (2017) described a new species, *A. lanai*, from 1035–2997 m on the continental slope off southeastern Brazil, and Langeneck *et al.* (2018) proposed a potential new species from the Mediterranean but did not name or fully describe their specimen even though illustrations were provided. Thus, the four currently accepted species in the genus are *Anguillosyllis capensis* Day, 1963; *A. pupa* (Hartman, 1965); *A. palpata* (Hartman, 1967); and *A. lanai* Barroso, Paiva, Nogueira & Fukuda, 2017.

Both Day (1963) and Hartman (1965) placed the genus in the subfamily Exogoninae based on the fused palps of *A. capensis* and *B. pupa*, respectively; however, this placement was questioned by Aguado & San Martín (2008, 2009), who listed it in the subfamily Eusyllinae (Aguado & San Martín 2009, Table 2, supplementary material) but considered it an "enigmatic and poorly known" genus. They subsequently considered *Anguillosyllis* as *incertae sedis* after an extensive morphological and molecular analysis indicated that this genus is a sister group to all other syllid genera and represents an early diversionary line (Aguado *et al.* 2012). Aguado & San Martín (2008, 2009) also noted the lack of information on the mode of reproduction, but assumed reproduction by epigamy, the most primitive form of reproduction in syllids.

Approximately 1400 specimens belonging to *Anguillosyllis* were collected during several deep-sea studies conducted between 1970 and 2011; 1369 have been assigned to two previously named taxa (*A. palpata* and *A. pupa*) and 16 newly described species, bringing the total number of species in the genus to 20. In addition to descriptions of new species, the collections allowed some observations on egg sizes in this genus. The quantitative studies demonstrated that members of this syllid genus are sometimes among the 10 most common benthic species at some deep-sea locations.

Material and methods

Collections of *Anguillosyllis* from offshore the U.S. Atlantic and Gulf coasts were made in the 1980s and 1990s during (1) the Georges Bank Benthic Infauna Monitoring Program (GBMP, aka BIMP) conducted for the U.S. Department of the Interior, Bureau of Land Management (BLM), now the Bureau of Ocean Energy Management (BOEM); (2) the deep-water U.S. Atlantic Continental Slope & Rise Program (ACSAR, aka ASLAR) also conducted for BOEM (at the time called the Minerals Management Service or MMS); and (3) deep-water oil and gas explorations off Louisiana, performed for Total E&P USA. Specimens from off northern California were collected as part of site-selection and monitoring of deep-water dredged-material disposal at the San Francisco Deep Ocean Disposal Site (SF-DODS) between 1990 and 2006.

Specimens from the abyssal plain of the Clarion-Clipperton Fracture Zone (CCFZ) in the North Equatorial Pacific Ocean were collected in 1983 by the U.S. National Oceanic and Atmospheric Administration (NOAA) as part of their Deep Ocean Mining Environmental Study (DOMES) (Wilson 2017) and in 1993–1994 as part of the NOAA Benthic Impact Experiment (BIE) (Trueblood & Ozturgut 1997). Specimens from off Brunei in the South China Sea were collected as part of deep-water baseline studies conducted for Total E&P Deep Offshore Borneo B.V. (TOTAL) and Petronas Carigali Brunei Ltd (PETRONAS). Specimens from off Antarctica were collected and living specimens photographed by Dr. James A. Blake (JAB) as part of the ANDEEP I–II surveys in 2002 on the R/V *Polarstern*; the specimen from the Southern Atlantic Ocean off the Meteor Rise was collected during ANDEEP III in 2005.

In the field, samples were sieved on either a 500-µm-mesh or a 300-µm-mesh sieve, preserved in 10% formalin, and later transferred to 70% ethyl alcohol (EtOH). Specimens were examined with light microscopy using a high-quality Wild M-5 stereomicroscope and a Zeiss research compound microscope equipped with phase contrast and Nomarski optics. Of the entire collection of 1400 specimens, 1369 were assigned to a species; the remainder were either damaged or incomplete, or the material was otherwise insufficient to be fully characterized. Photomicrographs were taken with a Nikon D7100 camera mounted on the stereo- and compound microscopes. Some specimens were stained with Shirlastain A to highlight surficial morphology; other specimens were stained with a saturated solution of either Methyl Green (MG) or Methylene Blue (MB) in EtOH to elucidate staining patterns, which are usually associated with glandular structures that preferentially retain stain. Both of the latter stains dissipate completely in fresh EtOH and were used interchangeably. Measurements of body width (across the widest anterior setiger, usually setiger 5) and length were made using an ocular micrometer on the Zeiss microscope. Where possible, setal blades were also measured and drawn, but often the details of the blade, such as possible serrations and the full length, could not be resolved sufficiently by light microscopy. Line drawings were made in pencil using a drawing tube (*camera lucida*) on the Zeiss; the sketches were scanned and imported into Adobe Illustrator where vector line drawings were made. Plates were prepared using Adobe Power Point and Adobe Photoshop software. Specimens retained by the author are indicated as NJM.

Organization of this paper. *Anguillosyllis capensis*, the type species of the genus, is discussed first, followed by *A. palpata*, which is discussed at length because of its widespread nature and the extensive material available. *Anguillosyllis lanai* is discussed only in comments under *A. elegantissima* **n. sp.** The remaining species are discussed alphabetically within two palp morphology groupings that were created for convenience: (1) palps that are entirely or partially fused (Table 1) and (2) palps that are completely fused with no separation (Table 2).

Abbreviations of sampling programs and institutions referred to in this paper:

ACOE	Army Corps of Engineers
ACSAR	Atlantic Continental Slope & Rise (*aka* ASLAR)
AHF	Allan Hancock Foundation
ANDEEP	ANtarctic benthic DEEP-sea biodiversity
ASLAR	Atlantic Slope and Rise (*aka* ACSAR)
BIE	Benthic Impact Experiment
BOEM	Bureau of Ocean Energy Management
BLM	Bureau of Land Management
BIMP	Benthic Infauna Monitoring Program (*aka* GBMP)
BMNH	British Museum of Natural History
CASIZ	California Academy of Sciences Invertebrate Zoology
CCFZ	Clarion-Clipperton Fracture Zone
DOMES	Deep Ocean Mining Environmental Study
GBMP	Georges Bank Monitoring Program (*aka* BIMP)
EPA	Environmental Protection Agency
LACM	Los Angeles County Museum
MCZ	Museum of Comparative Zoology, Harvard University
MMS	Minerals Management Service
NOAA	National Oceanic and Atmospheric Administration
SMF	Senckenberg Museum Frankfurt
USNM	Smithsonian Institution, National Museum of Natural History
WHOI	Woods Hole Oceanographic Institution

Results

Family Syllidae

Genus *Anguillosyllis* Day, 1963

Type species *Anguillosyllis capensis* Day, 1963

Diagnosis (amended). Body very small, meiofaunal, adults with limited and fixed number of setigers. Palps elongated, free to the base or fused partly to completely; prostomium with three club-shaped antennae, without eyes; peristomium with one pair of tentacular cirri similar to or smaller than prostomial antennae. Dorsal cirri smooth, long, filiform, present or (usually) absent on setiger 2. Ventral cirri digitiform, inserted medially to distally on parapodia. Parapodia uniramous, rectangular, truncate, with anterior and posterior lobes developed to varying degrees; with superior (dorsal) lobe that may be contractile (*fide* Day 1963). Compound setae heterogomph, with falcigers and spiniger-like blades; setae emerging from distal tip and ventral face of parapodium between insertion of ventral cirrus and distal tip. Pharynx straight, eversible, with two (or three) crowns or sections, external one formed by pharyngeal sheath, distal one surrounded by several (10–12) soft papillae, tooth absent. Proventricle barrel- or heart-shaped, usually tapered posteriorly, muscle rows obscure; with associated glandular structure (caeca) wrapped around post-ventricle. Four pygidial cirri, two lateral, two ventromedial.

Remarks. This generic diagnosis elaborates on that provided by Aguado & San Martín (2008). The number of setigers in adults of each species of *Anguillosyllis* is remarkably consistent: adult specimens can be separated based on the number of setigers, which ranges from eight to eleven (or twelve, if Day's (1963) account of the 13-segment non-type specimen of *A. capensis* is included).

Aguado & San Martín (2008) described the antennae and tentacular cirri as papilliform, as did Day (1967), but these structures may be well-formed in some species and much larger than the minute nipple-like structure implied by the term "papilliform." The proventricle is usually barrel-shaped but may also be distinctly cordate; it usually narrows, sometimes abruptly, toward the posterior end. The muscle rows of the proventricle do not appear as the typical rows of dots or points seen in other syllids; they are fuzzy dark bands that are difficult to see clearly and to count, especially at the anterior and posterior ends of the structure (Böggemann & Purschke 2005; Aguado & San Martín 2008; this study).

The post-ventricle in syllids often has an associated pair of caeca (Haswell 1921) that are called "T-shaped glands" (Jeuniaux 1969) and have been figured as such (Weidhase *et al.* 2016). Jeuniaux (1969) stated that these glands are filled with water and probably act as a swim-bladder. Aguado *et al.* (2015) suggested a glandular function based on their results of staining with MB; they also proposed the possibility of an endocrine function related to reproduction, but later ruled this out and limited the potential role of the caeca to digestion (Weidhase *et al.* 2016). In the present study, the caeca were clearly visible in the majority of *Anguillosyllis* specimens; often appearing to encircle the post-ventricle and with a circlet of cells on the dorsal side that stained deeply with MB or MG.

The dorsal lobe or setal hood on *A. capensis* was described by Day (1963) as "curious" and "unique" but was not subsequently discussed beyond an uncertain reference by Böggemann & Purschke (2005) and Böggemann (2009) to a small structure seen on the parapodia. This dorsal lobe was seen on all species examined for this study and is included here as a genus-level character. While it cannot be confirmed to be retractile as Day (1963) suggested, larger lobes in, for example, *A. palpata* were sometimes folded back towards the medial line of the body while smaller ones in other species (e.g., *A. andeepia* **n. sp.** and *A. sepula* **n. sp.**) appeared as rounded knobby structures; in many species, these lobes appeared to contain glandular structures that exited through the distal part.

Recently, Barroso *et al.* (2017) amended the generic diagnosis to eliminate the presence of dorsal cirri on setiger 2. However, in the present study, although a cirrus on setiger 2 was almost never seen (i.e., lost or absent), it was observed on two specimens of *A. palpata* and one specimen of *A. hampsoni* **n. sp.** and basal cirrophores were observed on setiger 2 in *A. truebloodi* **n. sp.** Also, Day (1963) clearly described and illustrated *A. capensis* as having a dorsal cirrus on all setigers, including setiger 2, and stubs were illustrated by Böggemann (2009); Hartman's description of *A. palpata* implied and the illustration showed a cirrus on setiger 2. Therefore, at this time, this character is retained as a present-or-absent character of the genus.

Anal cirri are easily and often lost but numerous specimens with a partial or full complement of two long, thin, coiled ventromedial ones similar to the dorsal cirri and two wider lateral oval ones allowed clarification of this

TABLE 1. Characters of *Anguillosyllis* species with palps that are partly or entirely free.

Species/ Character	Type Locality	Depth (m)	# Set.	Max. length (mm)	Annulation	Palps
***aciculata* n. sp.**	South China Sea	2162	11	2.9	None, but slight wrinkling in middle setigers	Free dorsally, joined ventrally on proximal half
***acsara* n. sp.**	North Carolina, USA	1505–1996	11	2.5	Clearly biannulate setigers 2–5 (larger one)	Free dorsally, joined ventrally
***capensis* Day, 1963**	Cape Town, SA	183	11 (?)	3.5	Not mentioned	Fused halfway or more; tips free
***capensis sensu* Böggemann & Purschke (2005)**	West coast of Africa	5389–5449	up to 11	2.5	Not mentioned, but possibly biannulate anteriorly (Fig. 1A–B)	Fused with notch
***carolina* n. sp.**	North Carolina, USA	720–2999	10	1.2	Slightly biannulate anteriorly	Free dorsally, possibly slightly joined ventrally on proximal half
***denaria* n. sp.**	South China Sea	1171–1967	10	1.9	None	Fused 1/2–2/3, tips free
***hadra* n. sp.**	South China Sea	1015–1329	11	1.5	Slightly biannulate anteriorly	Free dorsally, joined ventrally on proximal half
***hampsoni* n. sp.**	New England shelf	142–151	11	2	Slightly biannulate anteriorly	Free dorsally, joined ventrally on proximal three-quarters
***palpata* Hartman, 1967**	Antarctica	210–4652	11	2.8	Slightly biannulate anteriorly	Free dorsally, joined ventrally on proximal half
***taleola* n. sp.**	South China Sea	1294–1958	10	1.8	None	Entirely separate both dorsally and ventrally
***truebloodi* n. sp.**	Pacific Ocean, CCFZ[1]	4516–4861	11	1.2	None	Fused 1/2, tips free

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TABLE 1. (Continued)

Species/ Character	Nuchal organs	Proventricle: # setigers, shape	# Muscle rows	Posterior parapodial lobe	Dorsal lobe	Internal parapodial glands
***aciculata* n. sp.**	Obvious	3, elongated cordate	Not clear	Absent	Small, rounded, glandular, on setigers 1–3	Elongate, smooth
***acsara* n. sp.**	Large patches, obvious	3, short barrel, then narrows	ca. 15	Absent	Rounded, curled	Few, elongate
***capensis* Day, 1963**	Not mentioned	Broad, barrel-shaped	Day: 30, Aguado & San Martín: 25–30	Day 1963: Fig. 5C–D suggests it is well developed	Obvious	No information
***capensis sensu* Böggemann & Purschke (2005)**	Not mentioned	2, barrel-shaped	ca. 13–18	Not mentioned	Tapered, seems to be retractile	No information
***carolina* n. sp.**	Obvious	3, oval or barrel-shaped	Not clear	Posterior setigers only, small	Small	Elongate, few
***denaria* n. sp.**	Present but not obvious	2–3 setigers, barrel-shaped	ca. 14–20	Becoming large, glandular	Small	Elongate, intertwined
***hadra* n. sp.**	Lateral, not obvious	4–5, barrel-shaped	ca. 25	Absent	Small	Few, elongate, smooth, with rosette of cells at one end
***hampsoni* n. sp.**	Lateral bands, not overly large	2–3, barrel-shaped	ca. 30–35	Small throughout	Large	None observed
***palpata* Hartman, 1967**	Especially large ovals	3, cordate, tapered	ca. 30–35	Becoming large	Very large	Elongate
***taleola* n. sp.**	Large patches, obvious	4, cylindrical to barrel-shaped	ca. 13–18	Absent	Small	Elongate, along posterior edge of parapodia
***truebloodi* n. sp.**	Not obvious	3, barrel-shaped	Not clear	Becoming large	Large	Round, walnut-shaped

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TABLE 1. (Continued)

Species/ Character	Max number setae (ant; post)	Falcigers	Aciculae	Eggs (greatest diameter, µm)	Other notable characters
***aciculata* n. sp.**	30 falcigers, 10 spiniger-like setae; ca. 20	Blunt dark tip	4, emergent; anteriormost with bent tip	None observed	
***acsara* n. sp.**	ca. 30–50 falcigers setigers 1–6; spiniger-like setae increasing from 2–4 set 1 to several through set 6; numbers decrease set 7–11 to 16–20	Blunt, rounded tip	2, may have bent tips	Not measured	Small round glands on peristomium and across dorsum in posterior portion of segment
***capensis* Day, 1963**	Not specified	Blunt, fine tip	0 (none mentioned by Day, none observed in 6 setigers by Aguado & San Martín)	No information	Dorsal lobes thought to be retractile, *fide* Day (1963, 1967)
***capensis sensu* Böggemann & Purschke (2005)**	Numerous	Blunt tip, serrated along length	2–7 anterior, 1–4 posterior, with pointed tips	No information	Posteriormost setigers with upper and lower simple setae. Based on Fig.1B, palps are fused, not free. Likely a new species.
***carolina* n. sp.**	25–35, falcigers and spiniger-like setae; fewer	Blunt, rounded tip	2	60–85	Prostomium appearing to have two parts; small external glands
***denaria* n. sp.**	20; 10–12	Blunt to fine tip	2	50–85	Prostomium appearing to have two parts
***hadra* n. sp.**	20–22; 10–12	Blunt tip	2–3, stout, pointed or posteriormost with distal tip bent	None observed	Small round glands across dorsum in posterior portion of segment
***hampsoni* n. sp.**	35–40 falcigers, 2–4 spiniger-like setae; 10	Hooked, likely not hooded	2–3	50–80	
***palpata* Hartman, 1967**	10 falcigers, up to 20 spiniger-like setae; fewer	Hooked and hooded	2, posterior one may have bent tip, others pointed	up to 75	
***taleola* n. sp.**	ca. 16–20 anterior; same posterior	Blunt, rounded tip	3–4	Seen but could not be measured	Prostomium appearing to have two parts. Shafts of setae can be up to 3x blade length
***truebloodi* n. sp.**	20–22 per parapodium	Slightly hooked	2	None observed	

[1]Clarion-Clipperton Fracture Zone

TABLE 2. Characters of *Anguillosyllis* species with palps that are entirely fused.

Species/ Character	Type Locality	Depth (m)	# Set.	Max. length (mm)	Annulation	Palps (anterior tip)	Nuchal organs
***andeepia* n. sp.**	Antarctica	4551	8	1+	None	Narrow, pointed	Not evident (no cilia seen)
***blakei* n. sp.**	Northern California	995–1820	10	1.4	Setiger 1 biannulate, sometimes setiger 2	Narrow, pointed	Small patch between pro-and peristomium
***bruneiensis* n. sp.**	South China Sea	1234	8	1	None	Wide, rounded	Small patch, visible with stain
***elegantissima* n. sp.**	South China Sea	1050–2162	10	3.4	Biannulate 1-4, then triannulate	Conical, arched dorsally	Not evident; largest specimen with possible sense organ.
***enneapoda* n. sp.**	South China Sea	1242–2117	9	1	None	Narrow, pointed	Small oval patches
***hessleri* n. sp.**	Pacific Ocean (CCFZ)[1]	4480–4518	11	3.8	None	Wide, blunt, small medial notch	Small patch, visible with stain but no cilia seen
***inornata* n. sp.**	Northern California	2005–3864	9	2	None	Narrow, pointed	Small oval patches
***lanai* Barroso *et al.*, 2017**	Brazil	1035–2997	10	2	Not mentioned	Narrow, acute	Not mentioned
***pupa* (Hartman, 1965)**	W Atlantic Ocean, continental slope off New England	168–805	9	2	None	Broad, rounded	Not evident
***sepula* n. sp.**	South China Sea	1234–1487	10	1.2	None	Narrow, slightly pointed	Not evident
sp.	Pacific Ocean (CCFZ)[1]	4851	9	1+	None	Narrow, pointed	Not evident

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TABLE 2. (Continued)

Species/ Character	Proventricle # setigers, shape	# Muscle rows	Posterior parapodial lobe	Dorsal lobe	Internal parapodial glands	External glands
***andeepia* n. sp.**	2	? (cannot discern)	Well developed	Rounded	None observed	None observed
***blakei* n. sp.**	2.5–4	ca. 20–25	Absent	Obvious	Single, large, tubular, clear, yellow	None observed
***bruneiensis* n. sp.**	2+	ca. 20	Well developed	Not observed	None observed (? large cell near ventral cirrus)	None observed
***elegantissima* n. sp.**	4, barrel, tapered posterior	30–35	Absent	Small, obvious on set. 1–5	In dorsal lobe	Yes, large, at anterior and posterior bases of parapodia
***enneapoda* n. sp.**	2–3	ca. 13–18	Absent	Small but obvious	Large, tubular, setigers 6–8	Yes
***hessleri* n. sp.**	2, blocky barrel filling body width	At least 10, but obscure	Absent	Low, not obvious	Large, elongated, sac-like, numbering 3–5 per parapodium	Yes, small, at anterior and posterior bases of parapodia
***inornata* n. sp.**	2.5–3	ca. 20 (18–22)	Absent	Small but obvious	None observed	None observed
***lanai* Barroso *et al.*, 2017**	2.5–3, barrel to heart shape	ca. 12	Short, inconspicuous; or gets larger posteriorly	Not mentioned	None mentioned	Yes, with granular inclusions seen in SEM
***pupa* (Hartman, 1965)**	3, spherical, tapered posteriorly	20–25 fide Aguado & San Martín 2008	Becoming very large posteriorly	Small, difficult to see	None observed	None observed
***sepula* n. sp.**	3–4	Indistinct, at least 10	Absent	Rounded, obvious set. 3–6	Single, obscured, tubular, yellow	None observed
sp.	2	? (cannot discern)	Well developed	Rounded	None observed	None observed

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TABLE 2. (Continued)

Species/ Character	Max number setae	Aciculae	Anal cirri (ventromedial; lateral)	Eggs (greatest diameter, µm)	Other notable characters
***andeepia* n. sp.**	22	2 large, bluntly pointed, yellow	lost	65–80	Peristomium 1.5x length prostomium
***blakei* n. sp.**	25 (setiger 6)	2	4	50–115 (median 70)	
***bruneiensis* n. sp.**	22	None observed	Most lost, one small oval cirrus present	50–75	
***elegantissima* n. sp.**	~50 ant, mid ~35–40; post. 20 or fewer	2 at least, up to 5 in posterior, most tapered, pointed, some bent	4, all thin, filiform	60–85	Heterogomph setal shafts with one side 3x length of other. 5–10 setae with very short blades in set 1, shafts curved anteriorly
***enneapoda* n. sp.**	16	4	4	50–60	
***hessleri* n. sp.**	26 anterior, then 12–16	4, anterior slimmer, posterior heavy, tips may protrude	2 filiform, 2 very large stalked oval	None observed	
***inornata* n. sp.**	24	2	4	70–85	Dark golden-brown pharynx
***lanai* Barroso *et al.*, 2017**	~15 setae anterior & mid; ~5-10 posterior	2, slightly enlarged subdistal to acute tip, often protrudes	Not mentioned	Not mentioned	
***pupa* (Hartman, 1965)**	18	2	4	70–95	Posterior lobes with glands
***sepula* n. sp.**	24 in setiger 1; 8–10 posteriorly	2	Presumed 4	85–120	
sp.	22	2 large, bluntly pointed, yellow	lost	75–95	

[1]CCFZ—Clarion-Clipperton Fracture Zone.

character. This arrangement was seen in all species of *Anguillosyllis* examined in this study, with the exception of two species (*A. aciculata* **n. sp**. and *A. carolina* **n. sp.**) that had lost all anal cirri. The fifth anal cirrus reported by Böggemann & Purschke (2005) and Böggemann (2009) for their *Anguillosyllis* from deep water off western Africa was not seen on any specimen of any species examined in this study.

The palps of *Anguillosyllis* appear to follow a continuum from being completely free to the base; to free dorsally but partly fused basally on the ventral side; to fused both dorsally and ventrally for half or more of their length, sometimes with only the tips free; to completely fused with a narrow more-or-less pointed or softly rounded anterior end. In this paper the species are divided into two groups strictly for convenience: (1) those with palps that appear free to the base or partially fused (including those with only the very distal portion free) and (2) those with palps completely fused with no separation (although two have a minor medial notch, the tips are not free). There are ten species with palps that are entirely free or partly fused, eight of which are named and described as new; and ten species with palps fused for their entire length, eight of which are named and described as new.

1. *Anguillosyllis* species with palps entirely or partially free:
    1. *Anguillosyllis aciculata* **n. sp.**
    2. *Anguillosyllis acsara* **n. sp.**
    3. *Anguillosyllis capensis* Day, 1963
    4. *Anguillosyllis carolina* **n. sp.**
    5. *Anguillosyllis denaria* **n. sp.**
    6. *Anguillosyllis hadra* **n. sp.**
    7. *Anguillosyllis hampsoni* **n. sp.**
    8. *Anguillosyllis palpata* (Hartman, 1967)
    9. *Anguillosyllis taleola* **n. sp**
    10. *Anguillosyllis truebloodi* **n. sp.**
2. *Anguillosyllis* species with palps completely fused:
    1. *Anguillosyllis andeepia* **n. sp.**
    2. *Anguillosyllis blakei* **n. sp.**
    3. *Anguillosyllis bruneiensis* **n. sp.**
    4. *Anguillosyllis elegantissima* **n. sp.**
    5. *Anguillosyllis enneapoda* **n. sp.**
    6. *Anguillosyllis hessleri* **n. sp.**
    7. *Anguillosyllis inornata* **n. sp.**
    8. *Anguillosyllis lanai* Barroso, Paiva, Nogueira & Fukuda, 2017
    9. *Anguillosyllis pupa* (Hartman, 1965)
    10. *Anguillosyllis sepula* **n. sp.**

Species in each group are compared in Tables 1 and 2 and are separated according to the following key. Except for *A. palpata* and possibly *A. pupa*, species appear to be restricted to geographical areas and depth ranges, so researchers should not assume that a species described from the South China Sea will occur, for example, off the coast of South America or Africa; in many cases, techniques in addition to morphological analyses may be required to separate species (e.g., Nygren 2014, Aguado *et al*. 2019).

Key to 20 known species of *Anguillosyllis*

1A. Palps free dorsally (may appear fused ventrally) or fused halfway with distal half or tips obviously free 2
1B. Palps fused completely, at most only a minor medial notch on anterior end of fused palps 11
2A. Aciculae distally emergent . . . . . *Anguillosyllis aciculata* **n. sp.** (South China Sea)
2B. Aciculae never emergent 3
3A. Adults with 10 setigers 4
3B. Adults with 11 setigers 6
4A. Palps fused halfway; with large posterior lobes on parapodia . . . . . *Anguillosyllis denaria* **n. sp.** (South China Sea)
4B. Palps entirely free or may be basally fused ventrally, with or without posterior parapodial lobes 5
5A. Without posterior lobes on parapodia; setae with very long shafts up to 3x blade length, anterior dorsum not biannulate . . . . . *Anguillosyllis taleola* **n. sp**. (South China Sea)

5B. With small posterior lobes on posterior setigers, setal shafts do not exceed 1.5–2x blade length; anterior dorsum slightly biannulate . . . . . *Anguillosyllis carolina* **n. sp.** (western North Atlantic)
6A. Palps fused for half to three-quarters length, tips clearly free 7
6B. Palps free to base dorsally, may be joined by thin membrane ventrally 8
7A. Palps fused only halfway, tips broad and rounded . . . . . *Anguillosyllis truebloodi* **n. sp.** (central Pacific, CCFZ)
7B. Palps fused more than halfway, tips slim and pointed . . . . . *Anguillosyllis capensis* Day, 1963 (South Africa)
8A. Falcigers with hooked tips (e.g., Figs.1H, 3F–G, 14B) 9
8B. Falcigers with blunt or pointed tips (e.g., Figs. 7D, 24B–C) 10
9A. Anterior setigers 1–3 with 50 or more setae, all but two or three blades are short falcigers . . . . . *Anguillosyllis hampsoni* **n. sp.** (western North Atlantic)
9B. Anterior setigers 1–3 with maximum of 20–25 setae, including short falcigers and several spiniger-like setae with long fine tips . . . . . *Anguillosyllis palpata* (Hartman, 1967) (Antarctica, widespread)
10A. Anterior setigers with 30–50 falcigers and 2–4 spiniger-like setae, number of setae per parapodium decreases to 16–20 in posterior setigers . . . . . *Anguillosyllis acsara* **n. sp.** (western North Atlantic)
10B. Anterior setigers with 20–22 setae, posterior setigers with 10–12 setae . . . . . *Anguillosyllis hadra* **n. sp.** (South China Sea)
11A. *(Note three choices.)* Palps completely fused; adults with 8 setigers. 12
11B. Palps completely fused; adults with 9 setigers 13
11C. Palps completely fused; adults with 10 or 11 setigers 15
12A. Peristomium 1.5x length of prostomium, fused palps with narrow anterior margin . *Anguillosyllis andeepia* **n. sp.** (Antarctica)
12B. Peristomium shorter than prostomium, fused palps with rounded, slightly notched anterior margin . . . . . *Anguillosyllis bruneiensis* **n. sp.** (South China Sea)
13A. Posterior parapodia with large posterior lobes . . . . . *Anguillosyllis pupa* (Hartman, 1965) (western Atlantic)
13B. Posterior parapodia without posterior lobes 14
14A. Parapodia with 4 aciculae, with large internal glands . . . . . *Anguillosyllis enneapoda* **n. sp.** (South China Sea)
14B. Parapodia with 2 aciculae, without internal glands . . . . . *Anguillosyllis inornata* **n. sp.** (eastern Pacific, California)
15A. Adults with 10 setigers, tips of posterior aciculae never emergent 16
15B. Adults with 11 setigers, tips of posterior aciculae emergent . . . . . *Anguillosyllis hessleri* **n. sp.** (central Pacific, CCFZ)
16A. Shafts of compound setae extremely heterogomph, some anterior setigers triannulate. . . . . *Anguillosyllis elegantissima* **n. sp.** (South China Sea)
16B. Shafts of compound setae not extremely heterogomph, anterior setigers never triannulate 17
17A. Parapodia with small posterior lobes . . . . . *Anguillosyllis lanai* Barroso *et al.*, 2017 (Brazil)
17B. Parapodia without posterior lobes 18
18A. Anterior dorsum (setigers 1–2) biannulate . . . . . *Anguillosyllis blakei* **n. sp.** (eastern Pacific, California)
18B. Anterior dorsum not biannulate . . . . . *Anguillosyllis sepula* **n. sp.** (South China Sea)

Anguillosyllis species with palps entirely or partially free

Remarks on *Anguillosyllis capensis* Day, 1963

Day's (1963) original description of the genus *Anguillosyllis* from 183 m on the Agulhas Bank off South Africa referenced large palps that were fused for "over half their length;" in his original illustration of the type species, *A. capensis*, he indicates an obvious furrow in the distal end of the otherwise closely applied palps. However, in his monograph (Day 1967), the illustration shows an obvious separation of the distal tips of the palps; this separation is also indicated in the drawing by Aguado & San Martín (2008). Other characters of the holotype included a maximal length of 3.5 mm; 12 segments (the other available specimen was described as having 13 segments, so the number of setigers of this species is uncertain); three short club-shaped antennae; two smaller tentacular cirri; a barrel-shaped proventriculus that occupied three setigers and had about 30 rows of points; long dorsal cirri on all setigers including setiger 2; slender ventral cirri inserted distally on the parapodia; and compound falcigerous setae with minutely serrated blades and blunt unidentate tips. The most intriguing part of the description and the character that Day singled out as unique was the "curious dorsal hood" on the parapodium (Day 1963: 401). Day further described this structure as tapering to a cirriform projection, which was all that was visible when the hood was retracted; the parapodia then appearing to have three points: anterior, posterior, and superior (i.e., dorsal). Day's (1967) subsequent description of this species in his monograph on South African polychaetes included at least two *lapsus calami* when he referred to its 5-mm length and 30 segments. Further, palps were described therein as fused for half their length (rather than *over* half their length), and the "short" prostomial antennae became "minute papilliform" structures, as did the tentacular cirri. The setae were now described as long and fine and ending in a blunt, apical tooth, but the illustration indicates a serrated falciger with a blunt tip. Thus, there is a bit of confusion over the characters of the species that Day (1963) used as the type of his new genus.

Anguillosyllis capensis was not reported again until new syllid material was collected during the DIVA-1, DIVA-2, and BIOZAIRE projects. Böggemann & Purschke (2005) and Böggemann (2009) reported *A. capensis* from the Angola, Cape, and Guinea Basins off the west coast of Africa at depths of 3945–5672 m. After comparison with the holotype and paratype, the new material was said to "predominantly agree" with Day's (1963) types but had up to 11 (10–11) setigers; compound setae with blades within each fascicle ranging in length from long spiniger-like setae to short falcigers; aciculae with pointed tips numbering anywhere from 2–7 in anterior setigers and 1–4 in posterior setigers; and superior and inferior simple setae in some specimens. The latter two characters (numerous aciculae and presence of simple setae) are especially striking differences from the original description. Böggemann & Purschke (2005) did not specifically comment on the presence or absence of dorsal cirri on setiger 2, but Böggemann (2009) illustrated basal cirrophores on all setigers, including setiger 2. Böggemann (2009) also illustrated five anal cirri, including a short digitiform medial cirrus on the ventral side in addition to two lateral pairs. Notably, Fig. 141A (Böggemann 2009) shows a specimen with 11 setigers whereas Fig. 141B shows a specimen with 10 setigers; in light of results of the present study, these two figures likely represent different species.

Aguado & San Martín (2008) redescribed *A. capensis* based on an examination of the holotype, which by that time had lost all antennae and dorsal cirri and was reduced to six setigers. The possibly retractile superior parapodial lobes were interpreted as posterior lobes (Aguado & San Martín 2008, Fig.1B–C). Although they described setal blades of varying lengths, thus agreeing with Böggemann & Purschke's (2005) observations of the material from the Angola Basin, they did not see aciculae or simple setae in the holotype. During a visit to the BMNH in 2007, Dr. J.A. Blake (pers. comm.) examined Day's (1963) type material and found that only fragments of setigers remained; thus, the type material must now be considered useless for confirming additional characters.

In discussing the molecular analysis of material identified as *A. capensis*, Böggemann (2009: 415) speculated on the need to clarify whether he was dealing with a widespread species or a complex of cryptic species. It is likely that Böggemann's (2009) deep SE Atlantic material represents at least two species, neither of which may be the original *A. capensis*. Further, Böggemann (2009: 405) suggested that *A. capensis* might be conspecific with *A. palpata* (Hartman, 1967); however, the two species have different palp and parapodial structures and Böggemann's suggestion is herein rejected (also see discussion on *A. palpata* below).

Anguillosyllis palpata (Hartman, 1967)

Figures 1–4

Braniella palpata Hartman, 1967: 55, pl.14; Blake *et al.* 2009: 1797.
Braniella nr. *palpata*: Blake & Grassle 1994: 850, 857; Hilbig 1994: 944; Hilbig & Blake 2006: 269.
Anguillosyllis palpata—Aguado & San Martín 2008: 38; Barroso *et al.* 2017: 422–424, Fig. 12.

Material examined. Antarctica. **Drake Passage.** Type material: 18 Sep 1963, USNS *Eltanin*, Station 740, 56°06–56°07'S to 66°19'–66°30'W, Blake trawl, 384–494 m, coll. H.L. Sanders, det. O. Hartman, **holotype**, USNM 55505; **off Cape Horn.** 4 Nov 1962, USNS *Eltanin*, Station 315, 57°11'–57°15′S to 66°19'–66°30′W, Menzies trawl, 3770–3806 m, coll. H.L. Sanders, det. O. Hartman, **paratype** USNM 55506.

Additional material: Antarctica. *(11 specimens from 11 stations)* ANDEEP I, coll. J.A. Blake. Drake Passage, Sta. PS61/042-6, 28 Jan 2002, 59°40.42′S, 7°35.75′W, 3692 m, large box corer, 1 specimen (SMF 24864); Sta. PS61/046-5, 30 Jan 2002, 60°38.13′S, 53°57.68′W, 2894 m, large box corer, 1 specimen (SMF 24865); —Scotia Sea, Sta. PS61/105-2, 14 Feb 2002, 61°24.14′S, 58°51,15′W, 2290 m, multicorer, 1 specimen (SMF 24866); Sta. PS61/114-9, 19 Feb 2002 61°43.58′S, 60°43.22′W, 2876 m, multicorer, 1 specimen (SMF 24867). ANDEEP II, Weddell Sea, Sta. PS61/131-8, 6 Mar 2002, 65°18.65′S, 51° 30.91′W, 3068 m, large box corer, 1 specimen (SMF 24868); Sta. PS61/132-4, 6 Mar 2002, 65°17.75′S, 53° 22.92′W, 2085 m, large box corer, 1 specimen (SMF 24869); Sta. PS61/132-5, 7 Mar 2002, 65°17.68′S, 53° 23.00′W, 2084 m, multicorer, 1 specimen (SMF 24870); Sta. PS61/139-7, 20 Mar 2002, 58°14.10′S, 24° 20.73′W, 3935 m, large box corer, 1 specimen (SMF 24871). ANDEEP III, coll. S. Doner. Weddell Sea, Sta. PS67/059-4, 14 Feb 2005, 67°30,99′S, 0°0,16′E, 4652 m, multicorer, 1 specimen (SMF 24872).—Weddell Sea, off Cape Norvegia, Sta. PS67/074-5, 20 Feb 2005, 71°18.11′S, 13°56.33′W, 1035 m, multicorer, 1 specimen (SMF 24873).—Southern Ocean, Powell Basin, Sta. PS67/121-10, 14 Mar 2005, 63°41.74′S, 50°42.99′W, 2621 m, large box corer, 1 specimen (SMF 24874).—**Gulf of Mexico, off Louisiana.** *(207 specimens from 20 stations).* Matterhorn Lateral Pipeline Survey, coll. J.A. Blake, Chief Scientist, R/V *Brooks Mc-*

Call, 10 July 2008, Sta. 5, 28°50.2021′N, 89°02.1818′W, 241 m, 99.5% silt-clay sediment, boxcorer, 15 specimens (MCZ 150563). Matterhorn Platform Survey, coll. J.A. Blake, Chief Scientist, 10 Nov 2008, boxcorer: Sta. 1N, 28°44.7163′N, 88°49.5337′W, 850 m, 97.5% silt-clay sediment, 17 specimens (MCZ 150564); Sta. 2N, 28°44.7798′N, 88°49.5334′W, 825 m, 98.5% silt-clay, 15 specimens (MCZ 150565); Sta. 3N, 28°44.8362′N, 88°49.5336′W, 840 m, 97.4% silt-clay, 15 specimens (MCZ 150566); Sta. 4N, 28°45.1034′N, 88°49.5331′W, 821 m, 99% silt-clay, 20 specimens (MCZ 150567). Sta. 1S, 28°44.3406′N, 088°49.5378′W, 875 m, 97.8% silt-clay, 11 specimens (MCZ 150568); Sta. 2S, 28°44.2796′N, 88°49.5347′W, 878 m, 98.3% silt-clay, 5 specimens (MCZ 150569); Sta. 3S, 28°44.2246′N, 88°49.5391′W, 884 m, 98.7% silt-clay, 19 specimens (MCZ 150570); Sta. 4S, 28°43.9584′N, 88°49.5465′W, 908 m, 98.7% silt-clay, 1 specimen (MCZ 150571); Sta. 5S, 28°43.4126′N, 88°49.5373′W, 955 m, 98.1% silt-clay, 1 specimen (MCZ 150572). Sta. 1E, 28°44.5352′N, 88°49.3039′W, 867 m, 98.6% silt-clay, 6 specimens (MCZ 150573); Sta. 3E, 28°44.5244′N, 88°49.2116′W, 868 m, 98.8% silt-clay, 5 specimens (MCZ 150574); Sta. 4E, 28°44.5232′N, 88°48.8942′W, 891 m, 98.6% silt-clay, 8 specimens (MCZ 150575). Sta. 1W, 28° 44.52630′N, 88°49.7627′W, 851 m, 97.4% silt-clay, 8 specimens (MCZ 150576); Sta. 2W, 28°44.5327′N, 88°49.8318′W, 853 m, 97.8% silt-clay, 10 specimens (MCZ 150577); Sta. 3W, 28°44.5279′N, 88°49.8851′W, 850 m, 98.5% silt-clay, 21 specimens (MCZ 150578); Sta. 4W, 28°44.5305′N, 88°50.2023′W, 839 m, 99.2% silt-clay, 8 specimens (MCZ 150579); Sta. 5W, 28°44.5332′N, 88° 50.8139′W, 818 m, 98.8% silt-clay, 15 specimens (MCZ 150580). Matterhorn Lateral Gas Export Pipeline Survey, coll. S. Aubrey, Chief Scientist, R/V *Ocean Intervention*, 4 June 2009, Sta. 8C, 28°51.797′N, 088°59.055′W, 241 m, 99.5% silt-clay, 6 specimens (MCZ 150587); Sta. 9C, 28°53.821′N, 088°56.766′W, 229 m, 99.5% silt-clay, 1 specimen (MCZ 150588).—**Western North Atlantic continental slope and rise.** *(196 specimens in 27 samples from 7 stations).* **off Delaware, USA.** US Mid Atlantic ACSAR Program, coll. R. Petrecca (WHOI), Chief Scientist, Sta. Mid 4, Cruise M4, R/V *Oceanus*, 16 May 1985, Rep. 1, 38°44.44′N, 72°41.24′W, 2100 m, 1 specimen (USNM 1480243).—**North Carolina, USA, off Cape Lookout,** U.S. South ACSAR Program, coll. J.A. Blake (Battelle), Chief Scientist. Sta. South 1, Cruise SA2, R/V *Cape Hatteras*, 27 Mar 1984, Rep. 2, 34°15.81′N, 75°46.01′W, 583 m, 1 specimen (USNM 1480217); Rep. 3, 34°15.81′N, 75°45.78′W, 593 m, 2 specimens (USNM 1480218); Cruise SA3, R/V *Gyre*, 15 July 1984, Rep. 1, 34°16.4′N, 75°45.8′W, 584 m, 2 specimens (USNM 1480219). Sta. South 2, Cruise SA1, R/V *Columbus Iselin*, 12–13 Nov 1983, Rep. 1, 34°14.87′N, 75°43.79′W, 1013 m, 22 specimens (USNM 1480220); Rep. 2, 34°14.23′N, 75°43.89′W, 1000 m, 4 specimens (USNM 1480221); Rep. 3, 34°14.07′N, 75°44.06′W, 995 m, 7 specimens (USNM 1480222). Cruise SA2, R/V *Cape Hatteras*, 27 March 1984, Rep. 1, 34°15.04′N, 75°43.66′W, 1019 m, 25 specimens (USNM 1480223); Rep. 2, 34°14.46′N, 75°43.85′W, 1003 m, 2 specimens (USNM 1480224); Rep. 3, 34°14.56′N, 75°43.35′W, 1000 m, 20 specimens (USNM 1480225). Cruise SA3, R/V *Gyre*, 15 July 1984, Rep. 1, 34°14.5′N, 75°43.9′W, 984 m, 26 specimens (USNM 1480226); Rep. 2, 34°15.0′N, 75°43.7′W, 1002 m, 25 specimens (USNM 1480227); Rep. 3, 34°15.2′N, 75°43.6′W, 1007 m, 8 specimens (USNM 1480228).—**North Carolina, USA, Off Cape Fear.** Sta. South 11, Cruise SA5, R/V *Gyre,* 23 Sep 1985, Rep. 1, 33°04.83′N, 76°25.19′W, 796 m, 2 specimens (USNM 1480229); Rep. 2, 33°04.83′N, 76°25.17′W, 896 m, 2 specimens (USNM 1480230); Rep. 3, 33°04.86′N, 76°25.12′W, 797 m, 1 specimen (USNM 1480231); Cruise SA6, R/V *Cape Hatteras*, 22 Nov 1985, Rep. 3, 33°04.84′N, 76°25.06′W, 807 m, 1 specimen (USNM 1480232). Sta. South 12, Cruise SA6, R/V *Cape Hatteras*, 21 Nov 1985, Rep. 1, 33°00.55′N, 76°07.45′W, 1992 m, very soft mud, 1 specimen (USNM 1480233).—**South Carolina, USA, northern Blake Plateau, off Charleston, SC.** Sta. South 14, Cruise SA4, R/V *Cape Hatteras*, 20 May 1985, Rep. 1, 32°23.64′N, 77°01.13′W, 805 m, 6 specimens (USNM 1480234); Rep. 2, 32°23.64'N, 77°01.19'W, 802 m, 8 specimens (USNM 1480235); Rep. 3, 32°23.67′N, 77°01.12′W, 803 m, 2 specimens (USNM 1480236). Cruise SA5, R/V *Gyre*, 19 Sep 1985, Rep. 1, 32°23.67′N, 77°01.18′W, 796 m, pteropod ooze/green mud, 2 specimens (USNM 1480237); 20 Sep 1985, Rep. 3, 32°23.63′N, 77°01.11′W, 799 m, 10 specimens (USNM 1480238). Cruise SA6, R/V *Cape Hatteras*, 18 Nov 1985, Rep. 1, 32°23.73′N, 77°01.10′W, 799 m, 7 specimens (USNM 1480239); Rep. 2, 32°23.67′N, 77°01.09′W, 799 m, 3 specimens (USNM 1480240); Rep. 3, 32°23.70′N, 77°01.06′W, 799 m, 5 specimens (USNM 1480241). Sta. South 16, Cruise SA6, R/V *Cape Hatteras*, 20 Nov 1985, Rep. 3, 31°35.16′N, 75°10.22′W, 3012 m, 1 specimen (USNM 1480242).—**Gulf of the Farallones, California continental slope.** *(137 specimens in 65 samples).* **US Navy, 103 Site Selection Survey, west of the Farallon Islands,** coll. J.A. Blake. Sta. B2, 19 Jul 1991, 37°40.36′N,123°27.96′W, 2701 m, 1 specimen (CASIZ 230506); Sta. B3, 20 Jul 1991, 37°40.06′N, 123°23.69′W, 2385 m, 2 specimens (CASIZ 230505); Sta. B8, 24 Jul 1991, 37°38.58′N, 123°29.86′W, 2985 m, 2 specimens(CASIZ 230504).—**EPA 102 Site Survey, off San Francisco,** north of Pioneer Canyon, R/V *Point Sur*, coll. J.A. Blake. Sta. 3-8, 13 Sep 1991, 37°27.13′N, 123°23.02′W, 2005 m, 1 specimen (NJM); Sta. 3-13, 15 Sep

1991, 37°24.30′N, 123°20.02′W, 1780 m, 2 specimens (LACM-Poly 10477); Sta. 3-18, 15 Sep 1991, 37°22.31′N, 123°19.24′W, 1990 m, 3 specimens (CASIZ 230518); Sta. 3-19, 16 Sep 1991, 37°26.05′N, 123°19.99′W, 1760 m, 1 specimen (CASIZ 230519); south of Pioneer Canyon Sta. 4-15, 19 Sep 1991, 37°12.42′N, 123°15.81′W, 1730 m, 1 specimen (LACM-Poly 10478).—**San Francisco Deep Ocean Disposal Site (SF-DODS),** west of the Farallon Islands, coll. JA Blake. Sta. 6, 16 Oct 2000, 37°39.97′N, 123°26.95′W, 2730 m, 1 specimen (CASIZ 230502); 22 Sep 2002, 37°40.02′N, 123°27.00′W, 2697, 1 specimen (CASIZ 230503); Sta. 10, 8 Oct 1999, 37°39.96′N, 123°31.06′W, 3015 m, 3 specimens (LACM-AHF Poly 10479); 23 Oct 2001, 37°40.02′N, 123°31.00′W, 2985 m, 1 specimen (LACM-AHF Poly 10480); 22 Sep 2002, 37°40.00′N, 123°31.00′W, 2739 m, 4 specimens (CASIZ 230490); 14 Sep 2005, 37°39.970′N, 123°31.997′W, 2750 m, 1 specimen (CASIZ 230491); 26 Sep 2006, 37°40.197′N, 123°30.834′W, 2760 m, 1 specimen (CASIZ 230489). Sta. 11, 11 Dec 1996, 37°39.09′N, 123° 30.99′W, 2990, 1 specimen (NJM); 3 Nov 1997, 37°39.10′ N, 123° 31.03′ W, 2995, 2 specimens (CASIZ 230511). Sta. 12, 5 Dec 1996, 37°38.92′ N, 123° 29.85′ N, 3097 m, 3 specimens (CASIZ 230510). Sta. 16, 11 Jul 2007, 37°37.981′ N, 123°26.957′ W, 2699 m, 2 specimens (LACM-AHF Poly 10481). Sta. 17, 7 Oct 1998, 37°38.00′N, 123°27.99′W, 2830 m, 1 specimen (CASIZ 230500); 13 Oct 1999, 37°38.02′N, 123°20.00′W, 2770 m, 1 specimen (CASIZ 230501); 21 Oct 2001, 37°38.00′N, 123°28.03′W, 2862 m, 2 specimens (CASIZ 230499); 21 Sep 2002, 37°38.01′N, 123° 27.94′W, 2775 m, 6 specimens (LACM-AHF Poly 10482); 15 Sep 2005, 37°37.998′N, 123° 27.995′W, 2750 m, 1 specimen (LACM-AHF Poly 10483). Sta. 18, 30 Oct 1997, 37°37.95′N, 123°28.89′W, 2905 m, 1 specimen (CASIZ 230520); 8 Oct 1999, 37°37.86′N, 123°28.86′W, 2900 m, 1 specimen (CASIZ 230521). Sta. 19, 7 Oct 1998, 37°38.04′N, 123°30.02′W, 3030 m, 4 specimens (LACM-AHF Poly 10484); 15 Oct 2000, 37°37.95′N, 123°29.95′W, 2940 m, 2 specimens (CASIZ 230483); 22 Oct 2001, 37°37.98′N, 123°30.03′W, 3123 m, 2 specimens (CASIZ 230484); 22 Sep 2002, 37°38.01′N, 123°30.00′W, 3000 m, 3 specimens (CASIZ 230482); 25 Sep 2006, 37°37.975′N, 123°30.013′W, 3083 m, 2 specimens (CASIZ 230481); 11 Jul 2007, 37°38.166′N, 123°30.213′W, 3100 m, 2 specimens (LACM-AHF Poly 10485). Sta. 20, 15 Oct 2000, 37°37.96′N, 123°31.06′W, 3060 m, 2 specimens (LACM-AHF Poly 10486); 23 Oct 2001, 37°38.04′N, 123°31.01′W, 3142 m, 1 specimen (LACM-AHF Poly 10487); 22 Sep 2002, 37°38.06′N, 123°31.01′W, 3050 m, 4 specimens (CASIZ 230496); 15 Sep 2005, 37°37.987′N, 123°30.989′W, 3037 m, 4 specimens (CASIZ 230497); 25 Sep 2006, 37°37.960′N, 123°30.996′W, 3052 m, 1 specimen (CASIZ 230495); 11 Jul 2007, 37°38.163′N, 123°31.265′W, 2980 m, 1 specimen (CASIZ 230498). Sta. 23, 10 Dec 1996, 37°37.13′N, 123°29.08′W, ~2950 m, 2 specimens (CASIZ 230514); 3 Nov 1997, 37°37.06′N, 123°29.15′W, ~2950 m, 3 specimens (CASIZ 230513); 6 Oct 1998, 37°37.23′N, 123°29.18′W, 2970 m, 1 specimen (CASIZ 230517); 9 Oct 1999, 37°36.96′N, 123°28.93′W, 2970 m, 6 specimens (CASIZ 230516); 26 Sep 2002, 37°36.95′N, 123°29.02′W, 2954 m, 1 specimen with possible dorsal egg mass (CASIZ 230515); 24 Sep 2003, 37°36.86′N, 123°28.85′W, 2821 m, 5 specimens (LACM-AHF Poly 10488); 25 Sep 2006, 37°36.984′N, 123°28.928′W, 2929 m, 1 specimen (LACM-AHF Poly 10489); 13 Jul 2007, 37°37.170′N, 123°29.222′W, 2995 m, 1 specimen (LACM-AHF Poly 10490). Sta. 24, 19 Oct 2000, 37°36.97′N, 123°27.92′W, 2650 m, 1 specimen (CASIZ 230479); 22 Oct 2001, 37°36.94′N, 123°27.93′W, 2680 m, 4 specimens (CASIZ 230480). Sta. 27, 16 Oct 2000, 37°40.97′N, 123°31.98′W, 2740 m, 3 specimens (LACM-AHF Poly 10491); 22 Oct 2001, 37°40.98′N, 123°31.95′W, 2770 m, 1 specimen (CASIZ 230508); 23 Sep 2002, 37°40.96′N, 123°31.94′W, 2825 m, 4 specimens (CASIZ 230507); 11 Jul 2007, 37°41.141′N, 123°32.078′W, 2832 m, 1 specimen (CASIZ 230509). Sta. 57, 22 Oct 2001, 37°42.96′N, 123°32.97′W, 2750 m, 1 specimen (CASIZ 230485). Sta. 64, 25 Sep 2002, 37°36.01′N, 123°33.01′W, 3136 m, 7 specimens (CASIZ 230494); 14 Sep 2005, 37°36.079′N, 123°32.954′W, 3120 m, 1 specimen (CASIZ 230492); 27 Sep 2006, 37°35.968′N, 123°32.989′W, 3145 m, 1 specimen(CASIZ 230493); 13 Jul 2007, 37°36.028′N, 123°33.078′W, 3115 m, 1 specimen (LACM-AHF Poly 10492). Sta. 92, 24 Sep 2006, 37°45.080′N, 123°35.134′W, 2815 m, 1 specimen (LACM-AHF Poly 10493). Sta. 116, 25 Sep 2002, 37°34.99′N, 123°28.98′W, 2975 m, 4 specimens (CASIZ 230488; 14 Sep 2005, 37°34.927′N, 123°28.935′W, 2733 m, 2 specimens (CASIZ 230486; 27 Sep 2006, 37°35.051′N, 123°29.034′W, 3052 m, 3 specimens (CASIZ 230487); 13 Jul 2007, 37°35.080′N, 123°29.039′W, 2908 m, 3 specimens (LACM-AHF Poly 10494). Sta. DR2A, 29 Sep 2006, 37°22.924′N, 124°01.001′W, 3775 m, 3 specimens (LACM-AHF Poly 10495). Sta. DR2B, 29 Sep 2006, 37°22.924′N, 124°01.001′W, 3775 m, 2 specimens (CASIZ 230512). Sta. DR3B, 13 Jul 2007, 37°17.537′N, 124°09.192′W, 3864 m, 1 specimen (LACM-AHF Poly 10496).—**Abyssal Pacific, Clarion-Clipperton Fracture Zone.** *(2 specimens from 2 samples).* NOAA DOMES Site C, coll. R.R. Hessler, ECHO I, sample H352, Sandia box corer, 14 June 1983, 14°38.21'N, 125°26.32'W, 4502 m, 1 specimen (LACM-AHF Poly 10172); sample H353, Sandia box corer, 18 June 1983, 14°42.09'N, 125°24.27'W, 4516 m, 1 juvenile (LACM-AHF Poly 10173).—**South China Sea, off Brunei.** *(38 specimens from 20 stations).* coll. J.A. Blake, Chief Scientist. Sta.

6, 7 Jun 2011, 5°51′40.17938″N, 114°10′54.32730″E, 1353 m, 1 juvenile (NJM); Sta. 9, 6 June 2011, 5°52′38.23770″N, 114°13′42.28254″E, 1459 m, 3 specimens (MCZ 148547); Sta. 11, 6 June 2011, 5°50′27.84205″N, 114°10′56.95330″E, 1405 m, 5 specimens (MCZ 148548); Sta. 23, 5 June 2011, 5°50′24.47069″N, 114°14′04.40344″E, 1411 m, 1 specimen (MCZ 148549); Sta. 27, 5 June 2011, 5°46′11.81146″N, 114°09′16.72096″E, 1510 m, 3 specimens (MCZ 148550); Sta. 28, 4 June 2011, 5°44′29.74715″N, 114°07′42.47198″E, 1557 m, 1 specimen (MCZ 148551); Sta. 29, 4 Jun 2011, 5°43′01.15997″N, 114°06′07.18190″E, 1537 m, 1 specimen (MCZ 148552); Sta. 34, 4 June 2011, 5°50′32.29819″N, 114°15′47.44656″E, 1369 m, 3 specimens, poor condition (NJM); Sta. 38, 3 June 2011, 5°42′59.40134″N, 114°09′16.14114″E, 1353 m, 1 specimen (MCZ 148553); Sta. WH-Jokit-NE, 6 Jun 2011, 5°53′28.38401″N, 114°11′57.24436″E, 1400 m, 4 specimens (MCZ 148554); Sta. WH-Jokit-SW, 5 Jun 2011, 5°46′27.76503″N, 114°07′33.98027″E, 1487 m, 2 specimens (MCZ 148555). Sta. WH-Jaring-SWB, 4 June 2011, 5°43′13.87265″N, 114°08′13.15762″E, 1463 m, 3 specimens (MCZ 148556).—coll. P. Neubert, Chief Scientist. Sta. AN5, 27 Jun 2011, 5°26′51.39448″N, 113°46′41.57612″E, 1632 m, 2 specimens (MCZ 148557); Sta. ME7, 4 July 2011, 5°22′08.21298″N, 113°37′25.97978″E, 1725 m, 1 specimen (MCZ 148558); Sta. SA6, 29 June 2011, 5°36′19.08413″N, 113°37′45.57822″E, 2178 m, 1 specimen (MCZ 148559); Sta. TU2, 24 June 2011, 5°18′25.22812″N, 113°48′13.59077″E, 1224 m, 1 specimen (MCZ 148560); Sta. TU4, 25 Jun 2011, 5°12′34.01837″N, 113°42′17.60077″E, 1439 m, 1 specimen (MCZ 148561); Sta. TU7, 4 Jul 2011, 5°19′24.21956″N, 113°47′15.61845″E, 1327 m, 2 specimens (MCZ 150560); Sta. TU8, 24 June 2011, 5°21′35.85828″N, 113°49′14.10977″E, 1325 m, 1 specimen (MCZ 150561); Sta. TU14, 23 June 2011, 5°22′23.91273″N, 113°48′25.59116″E, 1444 m, 1 specimen (MCZ 150562).

Description. Body with 11 setigers, linear in overall shape (Figs. 1A, 3A), maximal length 2.8 mm without anal cirri, most specimens 1.0 mm long; maximal width 1.0 mm without setae; juveniles with 9–10 setigers 0.5 mm long or less.

Palps elongated bean shape (Figs. 1A, 3A, 4A), free to base but often appearing closely applied on proximal half, dorsally with distinct furrow and separation, ventrally joined giving fused appearance at low magnifications; prostomium longer than wide, convex medially resulting in dome-shaped appearance, with three club-shaped antennae in nearly transverse row, two lateral antennae slightly anterior to medial one; eyes lacking; large oval nuchal pits between prostomium and peristomium filled with long cilia (Figs. 1A, 3B). Peristomium shorter than prostomium, with two tentacular cirri similar in shape to prostomial antennae, shorter than prostomial antennae but sometimes appearing inflated. Eversible pharynx with distal ring of 10 soft papillae; tooth absent. Proventricle in three setigers, distinctly heart-shaped with abruptly tapered posterior end (Figs. 1A, 3A–E); rows of muscle cells somewhat indistinct, perhaps 30–35; post-ventricle caeca wrapped around ventricle (Figs.1A, 3E), with dorsal circlet of cells retaining deep MB stain (Fig. 3A, I).

Dorsum with first 2–3 setigers sometimes appearing slightly biannulate. Parapodia uniramous, elongated, rectangular, shortest on first and last setiger; with anterior and posterior lobes small on anterior setigers, becoming larger through posterior setigers (Figs. 1B–G, 2A–I); posterior lobe larger than anterior lobe in middle and posterior setigers; large dorsal lobe or hood present on all setigers, rounded, largest on setigers 5–6, may be extended over setae or curled or folded back toward midline. Posterior margin of parapodial lobe with pad of cells that retain MB stain (Figs. 1C, 4B); elongate internal parapodial glands extending up into dorsal lobe (Fig. 1E–G). Dorsal cirri with basal cirrophores, cirri extremely long, thin, measuring up to 2.5 times body length when gently stretched out or in life (Fig. 4E), may be coiled into corkscrew or relaxed; cirri present on setiger 1, usually lacking on setiger 2 but sometimes present (Fig. 4A, C), present on setigers 3–11. Ventral cirri short, widest at base, tapering toward distal end, inserted midway between body and distal end of parapodia on all setigers.

All setae compound, with heterogomph shafts; up to 20 long-bladed setae emerging from distal end of parapodium, additional group of up to 10–12 short-bladed falcigerous setae emerging in two rows from ventral face of parapodium between insertion of ventral cirrus and distal end (Fig. 3H); fewer setae in posterior setigers. Setal shafts measuring 70–130 μm long, with shorter ones ventral, shafts often equal to blade length, never exceeding 3x length of blades. All setae serrated; falcigers 20–50 μm long, with small shoulder before hooked tip, tip dark, with small clear hood between tip and shoulder of blade (Fig. 1H, 3F–G). Longer, spiniger-like blades up to 200 μm long. Each parapodium with acicula in both anterior and posterior edges (Fig. 1B); tip of posterior acicula sometimes appearing bent at nearly right angle in posterior setigers.

Pygidium with four anal cirri: two lateral, oval and two ventromedial, thin, filiform, often coiled (Fig. 1A); cirri easily lost.

Reproductive characteristics. Several specimens from each location were found to have eggs in the coelom

starting after the end of the proventricle in setiger 6 or 7 and continuing to the end of the body. The eggs measured up to 75 μm in diameter and were usually on either side of the midline, pushed up against the parapodia; in the material from California and the western North Atlantic, eggs were seen squeezing into the parapodia and in at least one specimen the eggs appeared to have dark inclusions (Fig. 1D–G). One specimen (Sta. 23, 2002, CASIZ 230515) had an attached mass (Fig. 3D) that appeared to contain at least one round object; whether this might be an external brood pouch is uncertain. Dorsal brooding was recently documented in *A. lanai* by Fukuda & Barroso (2019).

Methyl Green staining pattern. All specimens retained light MG stain on the pharyngeal papillae, the cells along the posteroventral edge of the parapodia, and the broad, oval anal cirri. Deep stain was retained by the area immediately anterior to the proventricle and a dorsal circlet of cells on the post-ventricle (Fig. 3A).

Ecological Notes. *Anguillosyllis palpata* often co-occurred with other species of *Anguillosyllis*, usually a fused-palp species. For example, in the collections from California, *A. palpata* was found with *A. inornata* **n. sp.** In some areas, notably ASCAR South Sta. 2, *A. palpata* occurred in numbers up to 20–26 in each 0.1-m^2 box-core sample, resulting in this species being among the dominant 20 species in the benthic community (Blake & Grassle 1994, as *Braniella* nr. *palpata*).

Remarks. *Anguillosyllis palpata* is one of the larger species of the genus, reaching 2.8 mm in length in the Antarctic material (Hartman 1967, this study) and 4.3 mm in length for specimens from Brazil (Barroso *et al.* 2017). The California, North Atlantic slope, and Gulf of Mexico material also included some exceedingly small specimens that measured no more than 0.3–0.5 mm in length; these usually had fewer than 11 setigers (i.e., 8 or 9 setigers) and are considered to be juveniles.

The present description is based primarily on 10 specimens from Antarctica, including the type specimens and eight additional specimens collected by Dr. J.A. Blake during ANDEEP surveys in 2002–2005. Extensive collections (593 specimens in all) from the South China Sea, the abyssal Pacific, the North American Pacific and Atlantic coasts, and the Gulf of Mexico were carefully compared to the Antarctic material. All material assigned to *A. palpata* in this study had 11 setigers (with the exception of the few juveniles mentioned above), parapodia with anterior and posterior lobes as described for the Antarctic material, and the distinctive hooked and hooded tip on falcigers along the length of the body. Differences in morphology among populations in different locations (e.g., size of the nuchal area, which in some material appeared more as a band than a large oval patch; the degree of biannulation, which was not observed in some material; the number of setae in anterior parapodia, which varied slightly among locations; and the number and ease of observation of internal parapodial glands) were not considered indicative of representing a different species. Specimens referred to *A. palpata* by Barroso *et al.* (2017) differ from the Antarctic material examined here in being of a larger size and having more setae in the first setigers, many fewer muscle rows in the proventricle, and longer spiniger-like blades. It is not clear from their description if the Brazilian specimens have the hooked and hooded tips on the falcigers, while Fig. 12G in Barroso *et al.* (2017) suggests that a small hood might be present, this character should be verified. It is possible that molecular studies would find differences between the various populations, but that technique was not available for this study. Eight additional species similar to *A. palpata* were separated out after careful morphological examination; those specimens have distinctive characters that distinguish them from *A. palpata*, including number of setigers, shape of the falcigers, and the development or lack of parapodial lobes.

A further discussion of the variability in several characters of *A. palpata* is presented below and comparison with other species that have free or partially free palps is presented in Table 1.

Degree of fusion of the palps: The palps were described by Hartman (1967) as "separated to the base" but other authors have referred to the palps as fused halfway (Aguado & San Martín 2008) or sometimes more than halfway (Barroso *et al.* 2017). While many specimens in the present collections had palps clearly separate to the base, some adults had palps that appeared to be joined for half their length. The confusion may arise because when the dorsal surface is in focus, the palps appear separate to the prostomium, but when the focus is adjusted ventrally, the palps appear joined along the lower half. Photographs of living specimens taken by J.A. Blake from Antarctic samples show palps that are clearly separate for the distal half, perhaps with a membrane joining the palps basally; this condition appears similar to that pictured in Barroso *et al.* (2017, Fig. 12).

Nuchal patches: The nuchal patches were described by Hartman as "transverse ridges" but are strikingly large oval patches in the Antarctic material; they are visible without staining, but their size and density are especially obvious when stained with Shirlastain A. They are similarly large in some of the material from California, the Gulf of Mexico, and the South China Sea; other specimens from those collections appear to have smaller, less obvious areas of nuchal cilia and some, from other geographic areas, have nuchal areas that are not obvious, even with stain.

Specimens from the US Atlantic continental slope off North Carolina had narrow ridges of cilia rather than large oval patches. It is possible that these areas can contract to various degrees, allowing some of the cilia to be retracted and hidden. Conversely, the size of the patch might be indicative of cryptic species.

Peristomial and tentacular cirri: The tentacular cirri were described by Hartman (1967) as "short, cirriform tentacles which resemble the prostomial antennae." Both Aguado & San Martín (2008) and Barroso *et al.* (2017) referred to them as "papilliform," a term that suggests a much smaller structure than is actually present. They are typically only a bit smaller than the prostomial antennae but, in some specimens, including living specimens from the Antarctic, the peristomium appears swollen and the tentacular cirri are noticeably large.

Pharynx: The pharynx is straight and lacks a medial tooth (Hartman 1967); the everted pharynx has two crowns with 10 large papillae associated with the distal crown (Barroso *et al.* 2017, this study). In most specimens, the papillae are long and oval and retain MB stain, but in some samples from the Gulf of Mexico, many specimens appeared to have a plain rim on the everted pharynx, while others had small papillae and still others had large papillae. These differences might be attributable to difficulty in observing this character in small specimens, but possibly the degree of development of the papillae is related to growth, as the smallest specimens had the least obvious papillae.

Proventricle: The proventricle in *A. palpata* is distinctly heart-shaped or cordate, with an indented anterior edge and a tapered posterior end that becomes very narrow (Barroso *et al.* 2017, this study). Hartman (1967) described it only as "barred"; individual muscle rows are obscure and hard to count reliably even when the proventricle is free of overlying tissue. In this study, the proventricle of *A. palpata* was estimated to have 30–35 muscle rows (dark bands or stripes) (Antarctica), ca. 25 (California), ca. 20^{+} (Gulf of Mexico), and ca. 20–25 (southeastern US slope). Barroso *et al.* (2017) reported 12 muscle rows for their specimens from Brazil.

Dorsal cirri: Hartman implied but did not state specifically whether dorsal cirri are present on setiger 2, but her illustration (Hartman 1967: Plate 14B) shows long filiform cirri on all setigers. Aguado & San Martín (2008) used this character in their key (presumably those cirri were present on the non-type specimen that they examined, or they relied on Hartman's published illustration, which often included more details than those mentioned in her texts). In the present material, dorsal cirri were often mostly lost, but the basal stubs of missing cirri could usually be seen easily; no such bases were noted on setiger 2 of the large majority of specimens although often those same specimens had cirri present on setigers 1 and 3. However, two specimens from off California did have long filiform dorsal cirri on setiger 2 (CASIZ 230481, Fig. 4A,C and LACM-AHF Poly 10492); these exceptions demonstrate the unreliability of using this character, especially at the generic level. Barroso *et al.* (2017) amended the generic definition to reflect the lack of dorsal cirri on setiger 2 of all four of the then-known *Anguillosyllis* species. However, the presence of dorsal cirri on setiger 2 of some *Anguillosyllis* material, including *A. palpata* and other species described in this study precludes making this a genus-level character.

Parapodial lobes: The dorsal or superior lobe is obvious on all specimens of *A. palpata*; it was often visible as a large rounded flap, sometimes extended as a hood over the setae and sometimes curled back toward the midline. Barroso *et al.* (2017) described a "semicircular flap" on the dorsal surface of the parapodia. This lobe or flap does not appear retractile as described by Day (1963) for *A. capensis*. Many internal parapodial glands appear to enter this lobe in several if not all of the *Anguillosyllis* species.

Setae: Hartman's (1967) original description mentioned composite setae that included both falcigers and spinigers, but although the narrow hooked or twisted tips and the serration of the falcigers were illustrated, they were not specifically described in the text. The falcigers as illustrated also appear to have a small membrane that is reminiscent of the hoods seen in other polychaetes reaching from the tip to the shaft. The obvious serration of both the falcigers and longer spiniger-like blades was seen on the type specimens and new material from the Antarctic. The serrations on the blades were more difficult to see in some collections than in others, with the material from the Gulf of Mexico having the smallest and hardest-to-see serrations (although visible at 1000x); whereas, the blades on the specimens from the US Mid- and South Atlantic had coarse serrations that were more easily seen. The hooked and hooded tips on the falcigers are considered to be a defining character for this species and were seen on all specimens referred to *A. palpata* in this study. It is not clear if material from Brazil has similar tips on the falcigers, the figured seta may or may not have a small hood (Barroso *et al.* 2017, Fig. 12G).

Number of setae per parapodium: The specimens from Brazil were reported by Barroso *et al.* (2017) to have 30+ setae in the first few anterior setigers. Most of the material examined in this study had fewer setae in the anterior setigers, usually 20, in a few cases (GOM) as many as 25, but never more than 30.

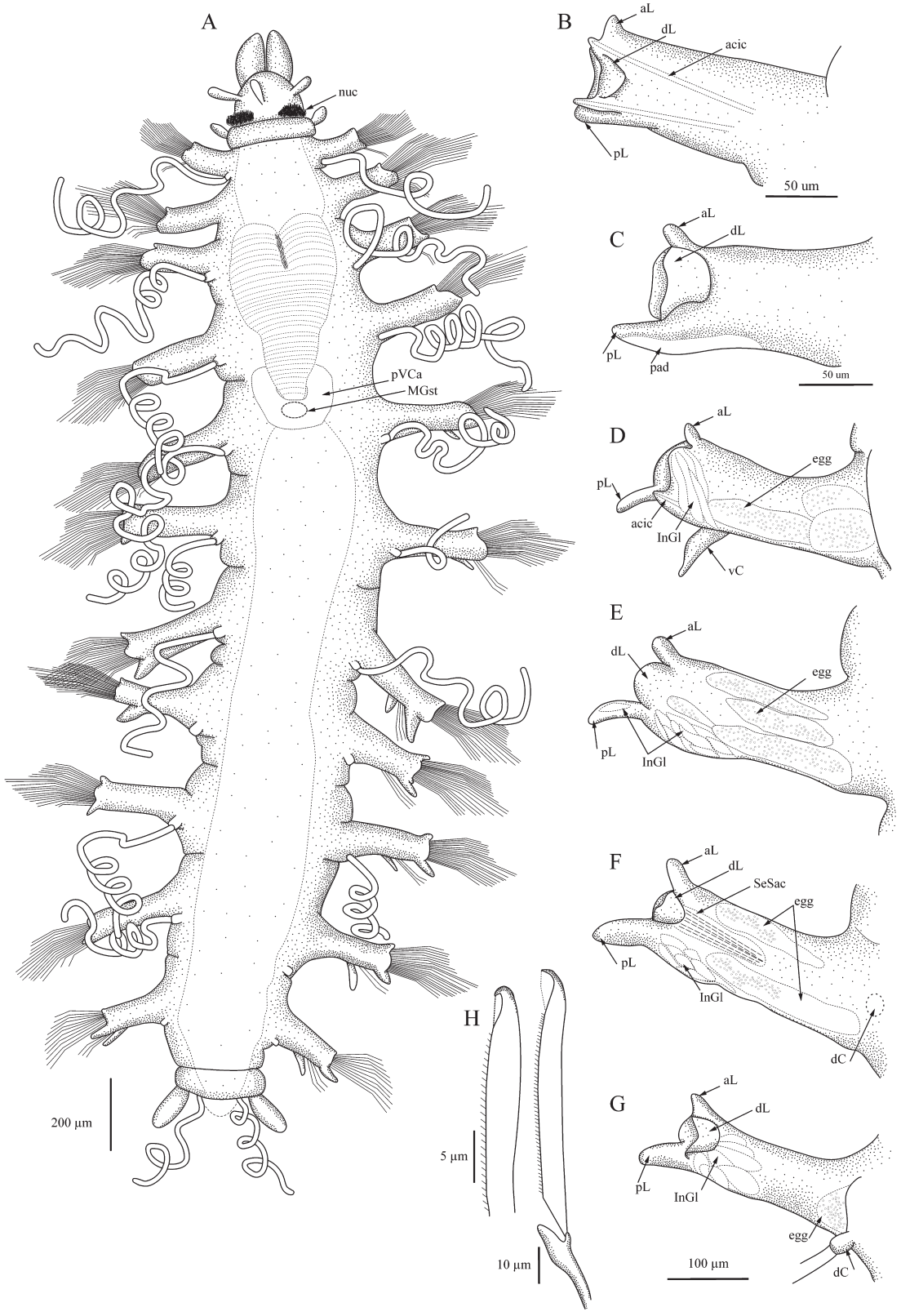

FIGURE 1. ***Anguillosyllis palpata*** **(Hartman, 1967).** ANDEEP sta.74-5 (SMF 24873): A, entire specimen dorsal view. ANDEEP sta. 105-2 (SMF 24866): B, setiger 1, dorsal view. ANDEEP sta. 121-10 (SMF 24874): C, setiger 3, dorsal view. Gulf of the Farallones, SFDODS sta. 19 (CASIZ 230481), dorsal view: D, setiger 8; E, setiger 9; F, setiger 10; G, setiger 11. ANDEEP sta.74-5, (SMF 24873): H, two setae from same setiger. Abbreviations: acic—acicula, aL—anterior lobe, dC—dorsal cirrus, dL—dorsal lobe, MGst—cells stained with Methyl Green pL—posterior lobe, pVCa—post-ventricle caeca, InGl—internal gland, SeSac—setal sack, vC—ventral cirrus.

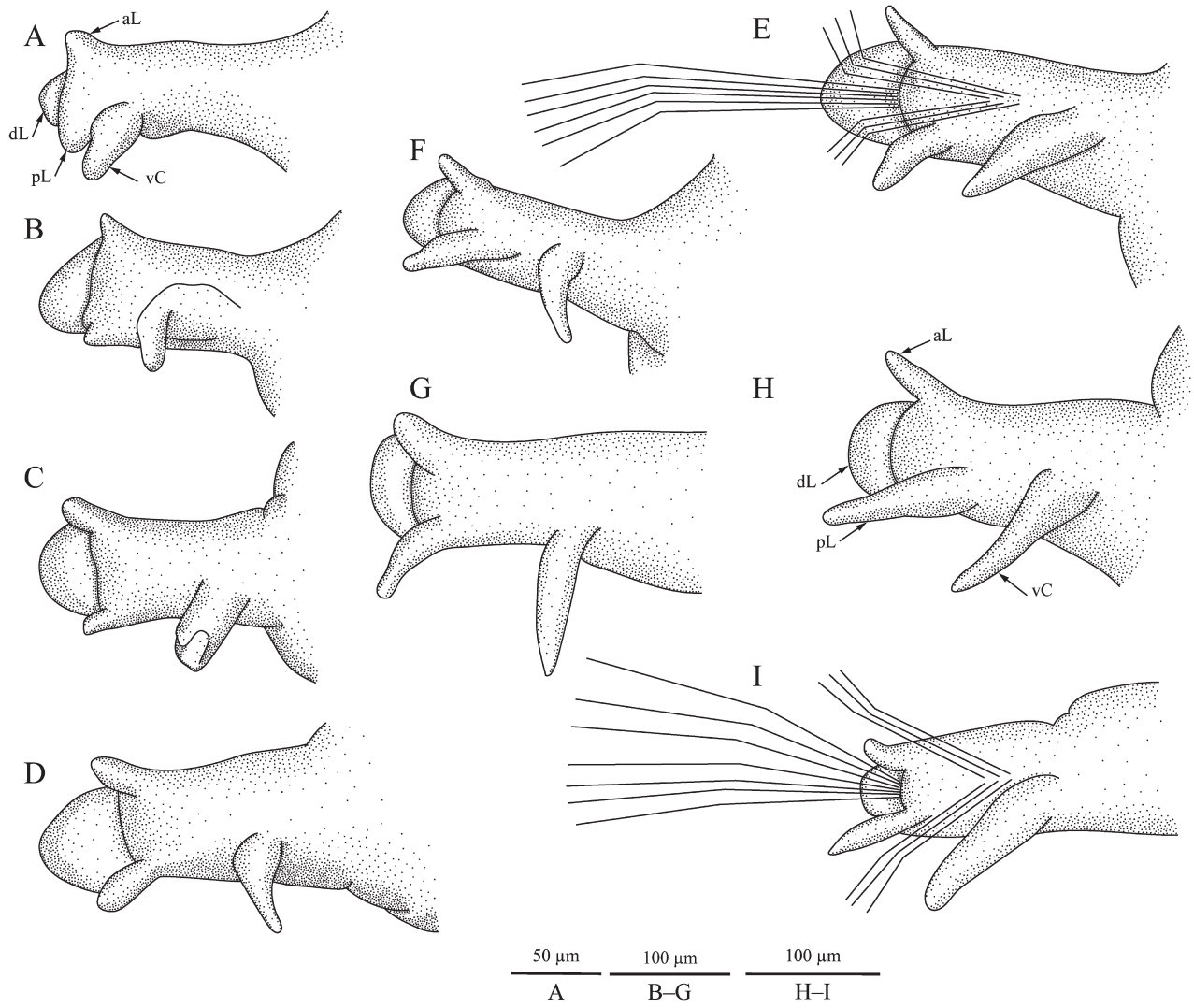

FIGURE 2. ***Anguillosyllis palpata*** **(Hartman, 1967).** Antarctica, ANDEEP sta. 74-5 (SMF 24873), parapodia, ventral view: A, setiger 1; B, setiger 2; C, setiger 3; D, setiger 4; E, setiger 5; F, setiger 6; G, setiger 7; H, setiger 9; I, setiger 11. Abbreviations: aL—anterior lobe, dL—dorsal lobe, pL—posterior lobe, vC—ventral cirrus.

Length of setal blades: In the Brazilian specimens (Barroso *et al.* 2017), the shortest setal blades were reported as measuring 20–30 µm, similar to the 20–50 µm measured for the Antarctic material; the longest blades measured 320–450 µm, which is twice the length measured here for the Antarctic material (200 µm).

Aciculae: The two aciculae per parapodium were not mentioned by Hartman (1967) but were seen by Barroso *et al.* (2017) and this study. The specimens from Brazil have aciculae that are subdistally slightly enlarged and distally acute, whereas those from the Antarctic sometimes have bent tips but no noticeable subdistal enlargement. All aciculae are encased in parapodial tissue and are not emergent.

Parapodial glands: Almost all material had elongated tubular glands in the middle to distal sections of the parapodia. The glands are usually oriented diagonally across the parapodium and feed into the dorsal lobe or distal portion of the parapodium.

Pygidial cirri: Hartman's (1967:53) description limited pygidial cirri to two lateral digitate cirri; however, the full complement actually includes four cirri: two long, thin, coiled ones similar to the dorsal cirri and two wider lateral elliptical ones as illustrated by Hartman (1967).

Discussion. The material examined for the present study is consistent across all geographic locations in major morphological characters, including the number of setigers, the shape and degree of (or lack of) fusion of the palps, the shape and size of the proventricle, the presence of obvious dorsal lobes, as well as anterior and posterior parapodial lobes, and the kind and distribution of acicula and setae. Minor variability appears to occur in the number

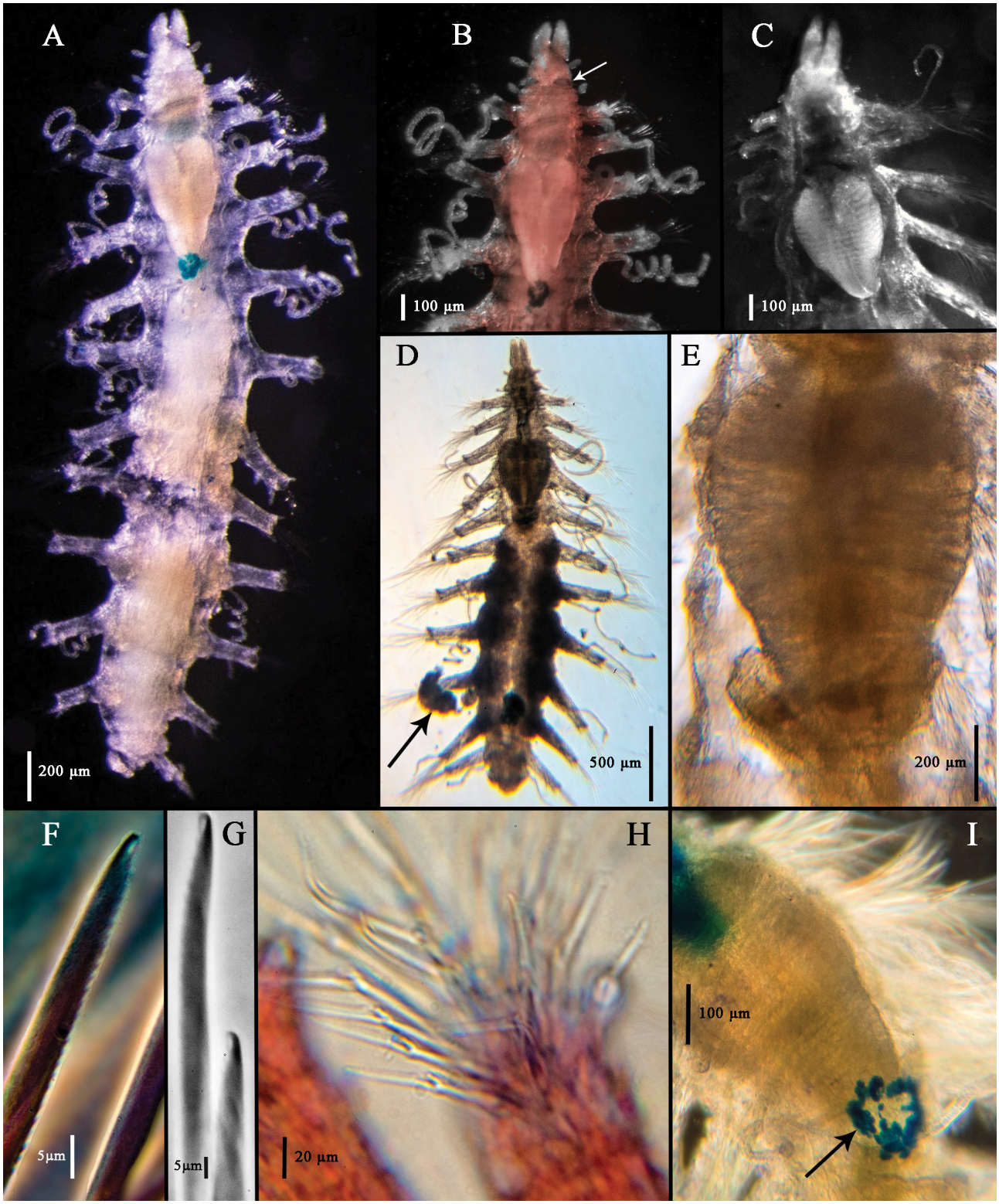

FIGURE 3. ***Anguillosyllis palpata*** **(Hartman, 1967).** ANDEEP sta. 74-5 (SMF 24873): A, entire specimen with MG stain, dorsal view; B, anterior end with Shirlastain A, dorsal view, arrow indicates nuchal patch. South China Sea (MCZ 150560): C, anterior end, dorsal view. SFDODS Sta. 23 (CASIZ 230515): D, entire specimen, dorsal view, arrow indicates attached mass. ACSAR South Sta. 14 (USNM 1480238): E, proventricle and post-ventricle, dorsal view. ACSAR South Sta.14 (USNM 1480234): F, setal blade with serrated edge and hooked tip with hood. ANDEEP Sta. 59-4 (SMF 24872): G, setal blade with hooked tip. H, ventral view of parapodium, showing rows of emerging setae. South China Sea, sta. 9 (MCZ 148547): I, dorsal view of proventricle, arrow indicates MG—stained circle of cells in post-ventricle.

of muscle rows in the proventricle (a very difficult character to observe), the degree of serration of the setal blades (which could be due to the angle of observation), the number of setae in anterior setigers, and the degree of development of the parapodial lobes (especially in the material from the South China Sea, which often had damaged tissue where the parapodial lobes would be).

At this time, it appears that *Anguillosyllis palpata* is very widespread, reported from the Antarctic to the South China Sea, and from depths ranging from 210 to 4652 m. Further investigations as to whether any of these populations represent separate species will necessitate the use of additional technologies, including SEM and molecular studies.

Records. Antarctica: Drake Passage, Bransfield Strait, Weddell Sea, 210–4652 m. **Brazil**: continental slope 393–3028 m. **Gulf of Mexico:** off Louisiana**,** 229–955 m. **Western Atlantic:** off Delaware, 2100 m; southeastern U.S. continental slope and rise, off North Carolina and South Carolina, 583–3012 m (*most common at 800–1000 m*). **Eastern Pacific:** off San Francisco, California, 1780–3864 m. **South China Sea:** off Brunei, 1224–2135 m

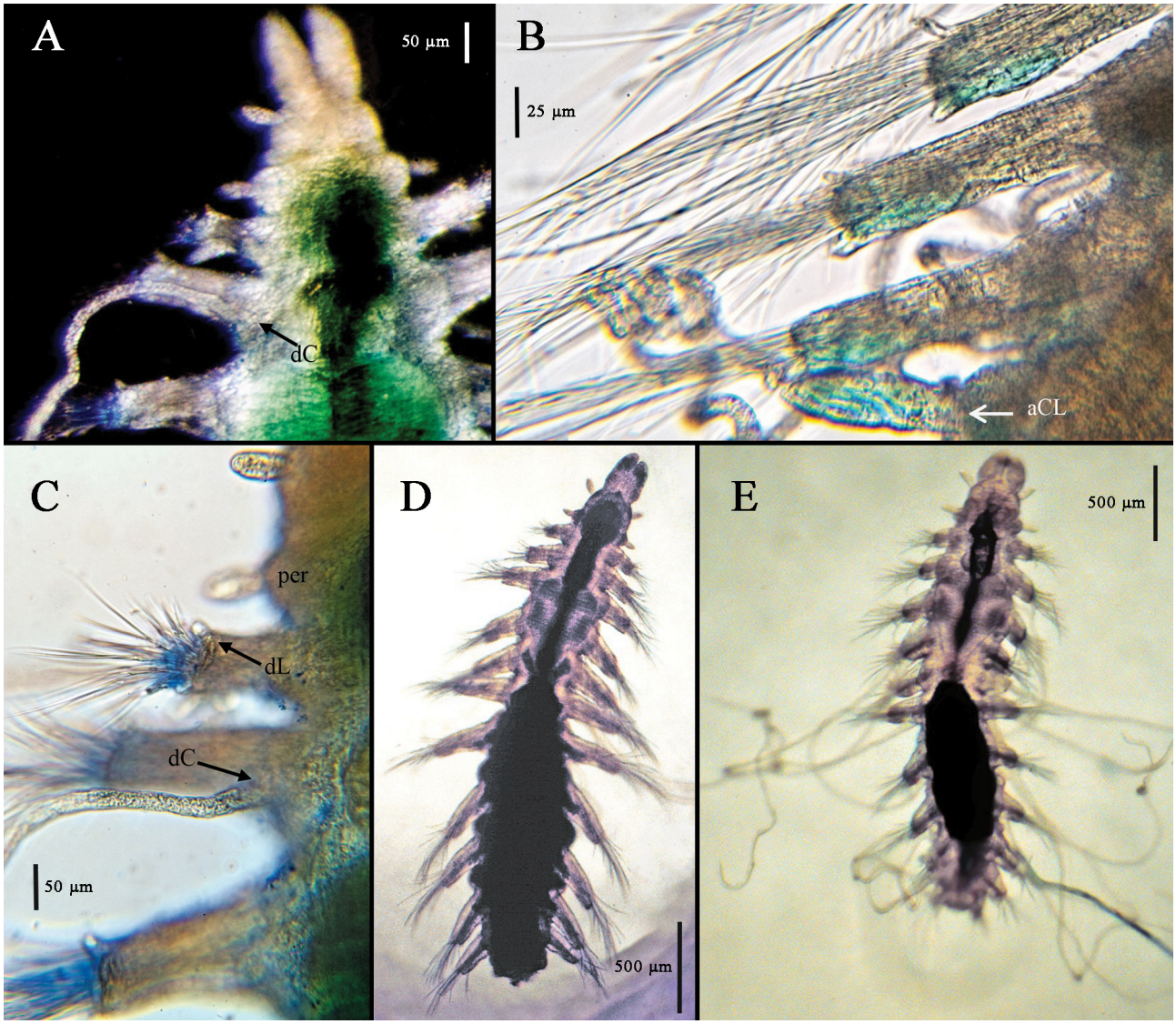

FIGURE 4. ***Anguillosyllis palpata*** **(Hartman, 1967)**. Gulf of Farallones, CA (CASIZ 230481): A, anterior end with dorsal cirrus on setiger 2. ACSAR South Sta. 11 (USNM 1480229): B, dorsal view of setigers 9–11, showing pad of MG—stained glands on posteroventral edge of parapodia and lateral anal cirrus. Gulf of Farallones (CASIZ 230481): C, another view of anterior end with dorsal cirrus on setiger 2. D–E: photographs taken by J.A. Blake of live specimens from ANDEEP Sta. PS61-46-6, Drake Passage, 2894 m (JAB). Abbreviations: aCL—anal cirrus lateral, dC—dorsal cirrus, dL—dorsal lobe, per—peristomium.

***Anguillosyllis aciculata* n. sp.**
Figures 5–6
urn:lsid:zoobank.org:act:2BA6947B-CA04-4C48-9040-94F9AF6ABA3E

Material examined. (*1 specimen)* **South China Sea**, off Brunei. Coll. P. Neubert, Chief Scientist. Sta. SA5, 29 Jun 2011, 5°36′56.59222″N, 113°41′07.37801″E, 2162 m, **holotype** (MCZ 147935).

Description. Body with 11 setigers (Fig. 5A), arched dorsally; 2.9 mm long, width 0.6 mm at setiger 5 without parapodia, 1.0 mm with parapodia but without setae, ca. 1.6 mm with setae, Palps slim, elongated, bean-shaped, appear free to base on dorsal surface but connected by membrane on ventral surface; tips of palps retain MB stain. Prostomium roughly circular (Figs. 5A, 6A); eyes lacking; no antennae or remnants of antennae seen, presumed lost. Prostomium and peristomium with glands on medial dorsal surface. Nuchal patches obvious, lateral, between prostomium and peristomium; division between pro- and peristomium otherwise not clear. Peristomium with two small, oval tentacular cirri.

Proventricle in three setigers, elongated heart shape, rounded anteriorly, tapered at posterior end (Figs. 5A, 6A–C); muscle rows not clearly defined, visible in mid-region in high-contrast light as thin dark bands; post-ventricle caeca with dorsal gland cells lacking or not retaining MB stain.

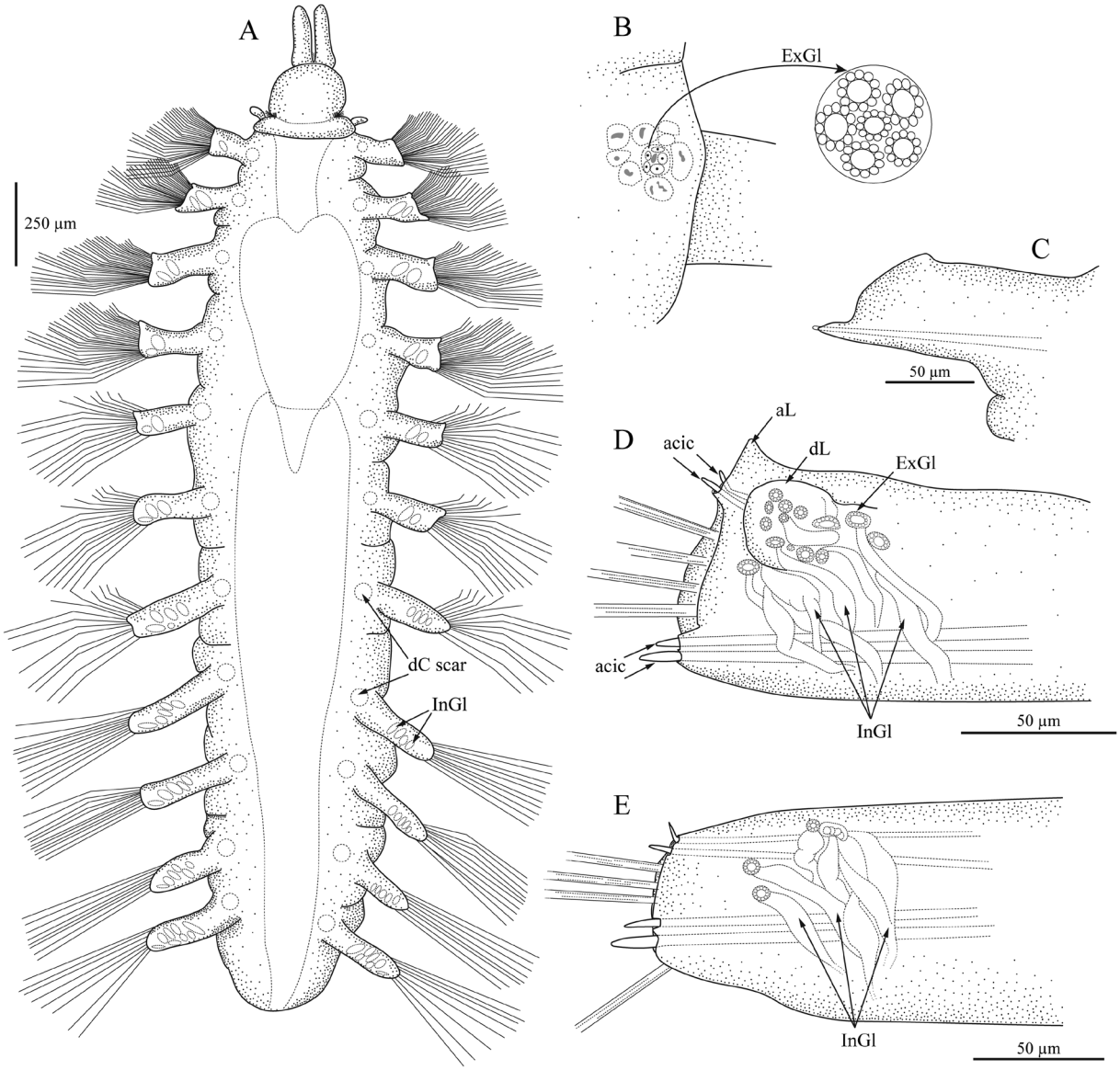

FIGURE 5. ***Anguillosyllis aciculata* n. sp.** Holotype (MCZ 147935): A, entire specimen, dorsal view; B, external glands, inset not to scale. C, setiger 1; D, setiger 3; E, setiger 10. Abbreviations: acic—acicula, aL—anterior lobe, dC—dorsal cirrus, dL—dorsal lobe, ExGl—external gland, InGL—internal gland.

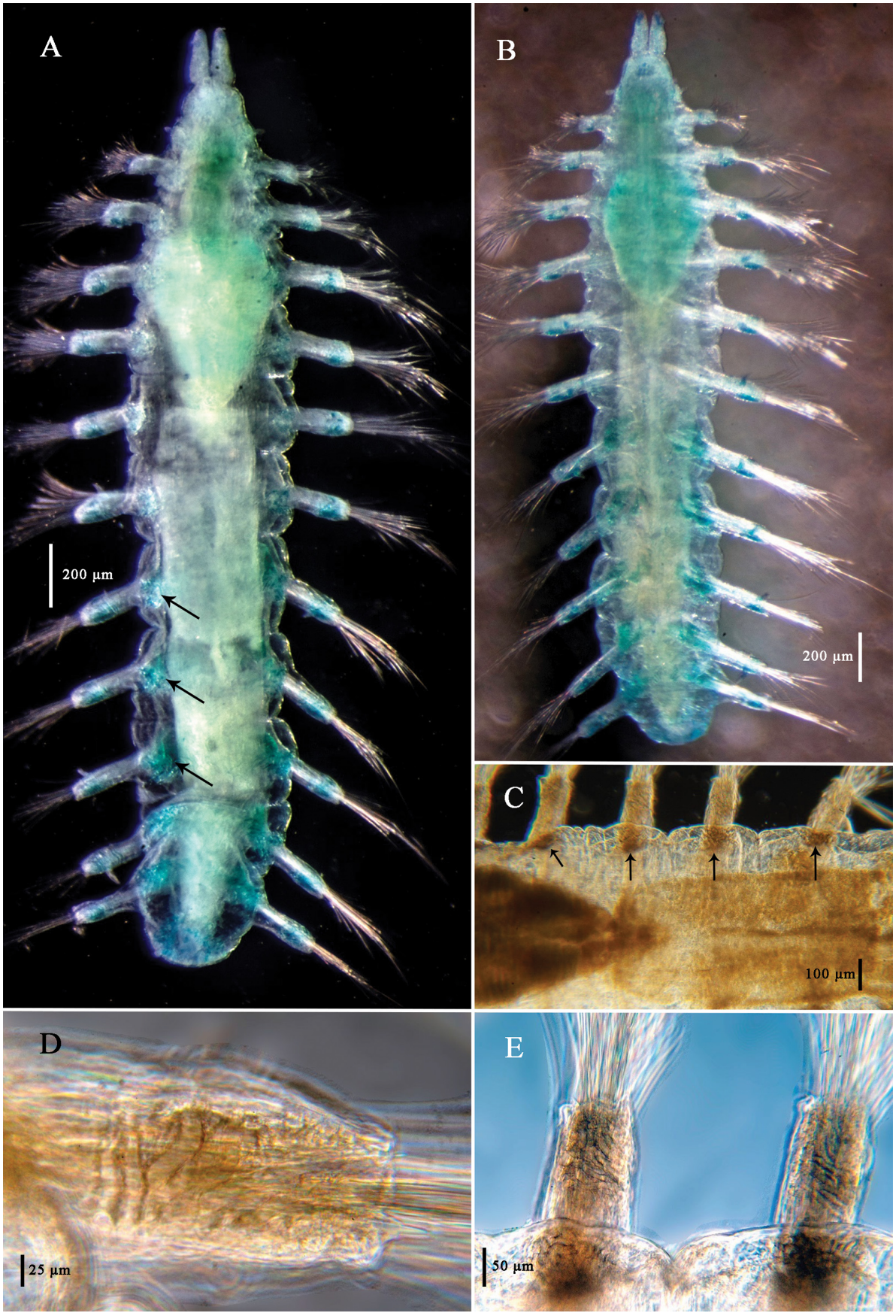

FIGURE 6. ***Anguillosyllis aciculata*** **n. sp.** Holotype (MCZ 147935): A, entire specimen, dorsal view; B, entire specimen, ventral view; C, setigers 3–7, left side; D, setiger 9, right side; E, setigers 5–6, right side. A, C: arrows indicate external glands.

Dorsum uniannulate, a few median setigers with slight wrinkling or indication of biannulation. Elongate tubes and clusters of cells numerous, extending across dorsum on all setigers, round glands similar to those noted on prostomium and peristomium (Figs. 5B, 6A, C). Parapodia uniramous, shortest and nearly square on setiger 1, becoming longer, slimmer, rectangular over subsequent setigers; with small but obvious translucent triangular anterior lobe on setigers 2–6, largest on setigers 3 (Fig. 5D) and 4; posterior lobe lacking; dorsal lobe small, rounded, glandular, obvious only on setigers 1–3. Parapodia with smooth elongate internal glands associated with external clusters of tightly packed cells (Figs. 5D–E, 6D–E), distal end of tube narrowing and exiting through dorsal lobe or surface of parapodium, glands becoming more numerous progressing posteriorly, last few setigers packed with glands. Venter of setigers 1–5/6 with scattered glands. Dorsal cirri lost, cirrophores seen on some setigers. Ventral cirri small, slim, with wider base tapering to narrower tip, inserted midway on parapodia; cirri with glands retaining MB stain (Fig. 6B).

All setae compound with heterogomph shafts, with short to long blades; falcigers 40–80 µm long, with serrated blades, dark blunt tip; spiniger-like blades up to 350 um long, serrated along length, with plain fine tips; setae numbering up to 10 long-bladed and 30 short-bladed setae in setiger 1, fewer short-bladed setae in setigers 2–3; setae reduced to ca. 20 in setigers 5–11; most setae emerging from distal end of parapodium, cluster emerging from ventral face Up to four aciculae per parapodium: two anterior aciculae thin, one with distal end bent at nearly right angle, other pointed; two posterior aciculae large, stout, pointed; tips of all aciculae emerging from tissue of parapodium (Fig. 5D–E).

All anal cirri lost.

No eggs seen.

Remarks. *Anguillosyllis aciculata* **n. sp.** is unique in having up to four emergent aciculae in each parapodium (setiger one appears to have only two aciculae whereas the remaining setigers have 4; Fig. 5C shows only one acicula). The distal tip of the anteriormost acicula is bent at an angle; the posteriormost acicula is especially large and stout. In *A. acsara* **n. sp.**, the tip of one anterior acicula was seen to be minimally emergent from the parapodium, and in *A. hessleri* **n. sp**., the tips of some aciculae emerge from the body wall, but in all other known species of *Anguillosyllis,* the aciculae are not emergent.

The single specimen available appears to have glands on the surface of the prostomium rather than being smooth; antennae and insertions for antennae were not seen. It would be expected that this species would have three antennae as do all other species in the genus, but because of the limited amount of material, the nature of the prostomium could not be further understood.

This species is similar to *A. palpata* and *A. hadra* **n. sp.** in having 11 setigers and clearly separated palps, but differs in the number and nature of the setae and in lacking posterior lobes on the parapodia; the dorsal lobes in *A. aciculata* **n. sp.** are much smaller than those observed in either *A. palpata* or *A. hadra* **n. sp.** Both *A. palpata* and *A. aciculata* **n. sp.** have a cordate proventricle that is narrowly tapered at the posterior end; in *A. hadra* **n. sp**. the proventricle is shaped differently and is only slightly tapered at the posterior end.

The areas of *A. aciculata* **n. sp.** that stain deeply with MB include the tips of the palps, the tentacular cirri, the ventral cirri, the glands in the distal portion of the parapodia, and the clusters of glands on the lateral edges of the dorsum. This pattern differs from that seen in other *Anguillosyllis* species, which do not retain stain on the tips of the palps but, unlike *A. aciculata* **n. sp.**, do retain stain in the dorsal cells of the post-ventricle gland that wraps around the posterior end of the proventricle (see, for example, *A. palpata* above).

Etymology. From Latin *acus* meaning needle or small pin, the root of the term *aciculum*, in reference to the large emergent aciculae of this species.

Records. South China Sea, off Brunei, 2162 m.

Anguillosyllis acsara **n. sp.**

Figures 7–8

urn:lsid:zoobank.org:act:AA60704C-9ED0-4EDD-9F70-29C17E76117C

Material examined. Western North Atlantic continental slope and rise. *(3 specimens in 3 samples from 2 stations).* **off North Carolina,** U.S. South ACSAR Program, coll. J.A. Blake (Battelle), Chief Scientist. Sta. 3, Cruise SA1, R/V *Columbus Iselin*, 15 Nov 1983, Rep. 1, 34°14.13′N, 75°40.41′W, 1505 m, 1 juvenile (NJM). Cruise SA2,

R/V *Cape Hatteras*, 27 March 1984, Rep. 1, 34°14.51′N, 75°40.33′W, 1523 m, **holotype** (USNM 1480212). Sta. 12, Cruise SA4, R/V *Cape Hatteras*, 22 May 1985, Rep. 1, 33°00.31′N, 76°07.39′W, 1996 m, **paratype** (USNM 1480213).

Description. Body with 11 setigers (Fig. 8A), holotype large, significantly arched dorsally, flat ventrally (Fig. 7A, E; 8A–B); 2.5 mm long, 0.8 mm wide without parapodia, 1.2 mm wide with parapodia but without setae, other specimens much smaller, up to 1.5 mm long. Palps blunt-tipped, robust ovals, appear free to base on dorsal surface, connected by membrane on ventral surface. Prostomium wider than long, pentagonal; eyes lacking; three club-shaped antennae in nearly transverse row, lateral antennae slightly anterior to medial antenna. Peristomium with two oval tentacular cirri smaller than prostomial antennae; peristomium weakly biannulate, with glandular band across posterior half. Nuchal cilia in large oval patches between prostomium and peristomium.

Proventricle in three setigers, barrel-shaped, slightly narrowed at posterior end; ca. 15 muscle rows (Figs. 7C); post-ventricle caeca with dorsal circle of gland cells retaining MB stain (Figs. 7C, 8A–B).

Setigers dorsally biannulate, weakly so on setigers 1 and 5, obscured on setigers 6–10, visible on setiger 11 and pygidium (Figs. 7A–B, 8A–C); anterior annulation much shorter than posterior, posterior portion of each segment with gland cells scattered across dorsum (Fig. 7A), similar gland cells visible on setiger 11; additional area of dark gland cells at base of parapodia (Fig. 7A); venter biannulate on setigers 2–5. Parapodia uniramous, mitten-shaped, shortest on setiger 1, becoming longer, rectangular in subsequent setigers; with small, translucent anterior lobe on setigers 2–3 (Fig. 7F), lobe decreasing in size through setiger 6, then either smaller or absent through end of body; posterior lobe lacking on all setigers; dorsal lobe small, knobby, curled dorsally, clearest on setigers 1–5/6. Dorsal cirri retained on setiger 1, otherwise absent or lost; cirri thin, smooth, filiform. Ventral cirri thin, digitate, inserted midway on parapodia. Parapodia with smooth elongate internal glands, distal end narrowing and exiting through dorsal lobe (Fig. 7F).

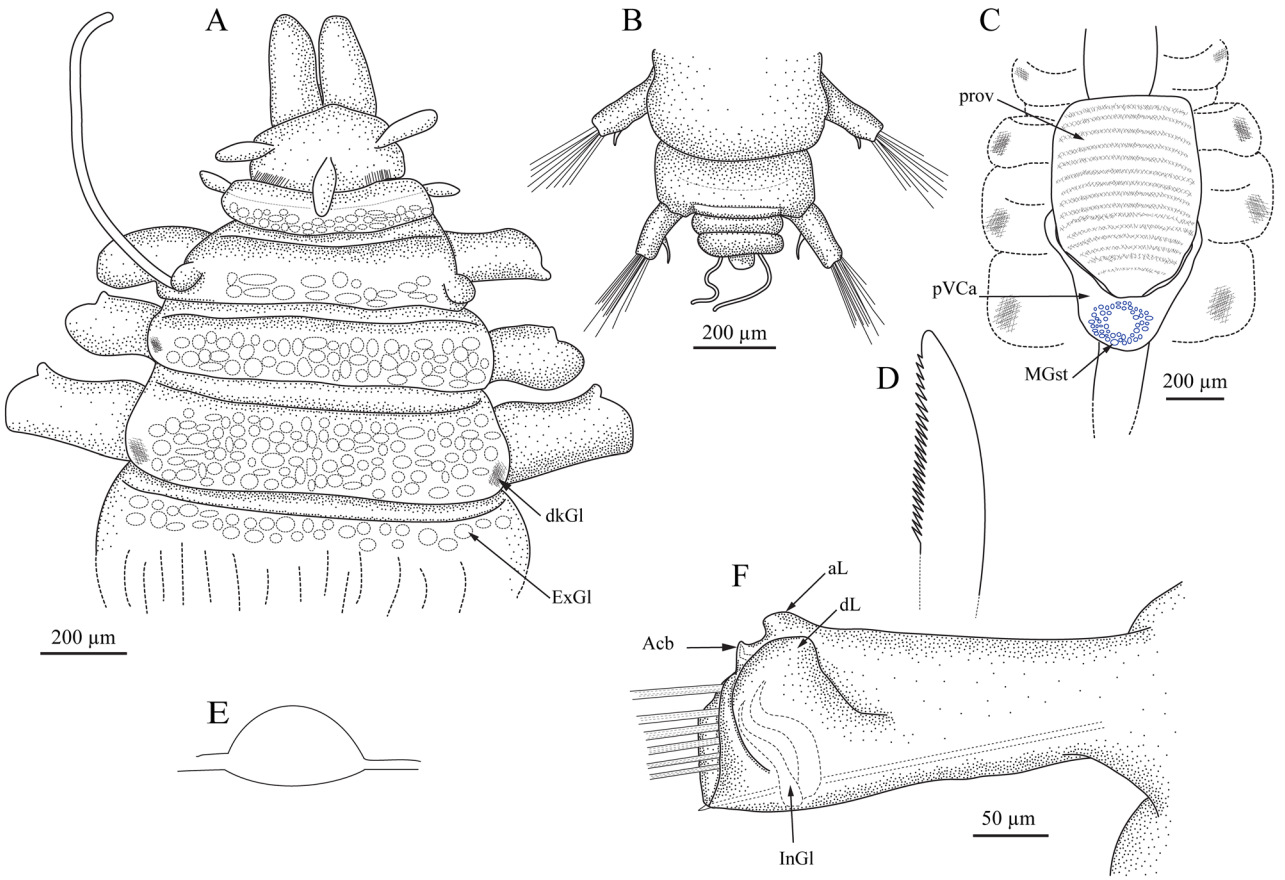

FIGURE 7. ***Anguillosyllis acsara*** **n. sp.** Holotype (USNM 1480212): A, anterior end, dorsal view; B, posterior end, dorsal view; C, proventricle; D, tip of falciger; E, cross-section of body, not to scale. Paratype (USNM 1480213): F, setiger 3, dorsal view. Abbreviations: Acb—acicular bump, aL—anterior lobe, dL—dorsal lobe, dkGl—dark gland, ExGl—external gland, MGst—cells stained with Methyl Green, prov—proventricle, pVCa—post-ventricle caeca.

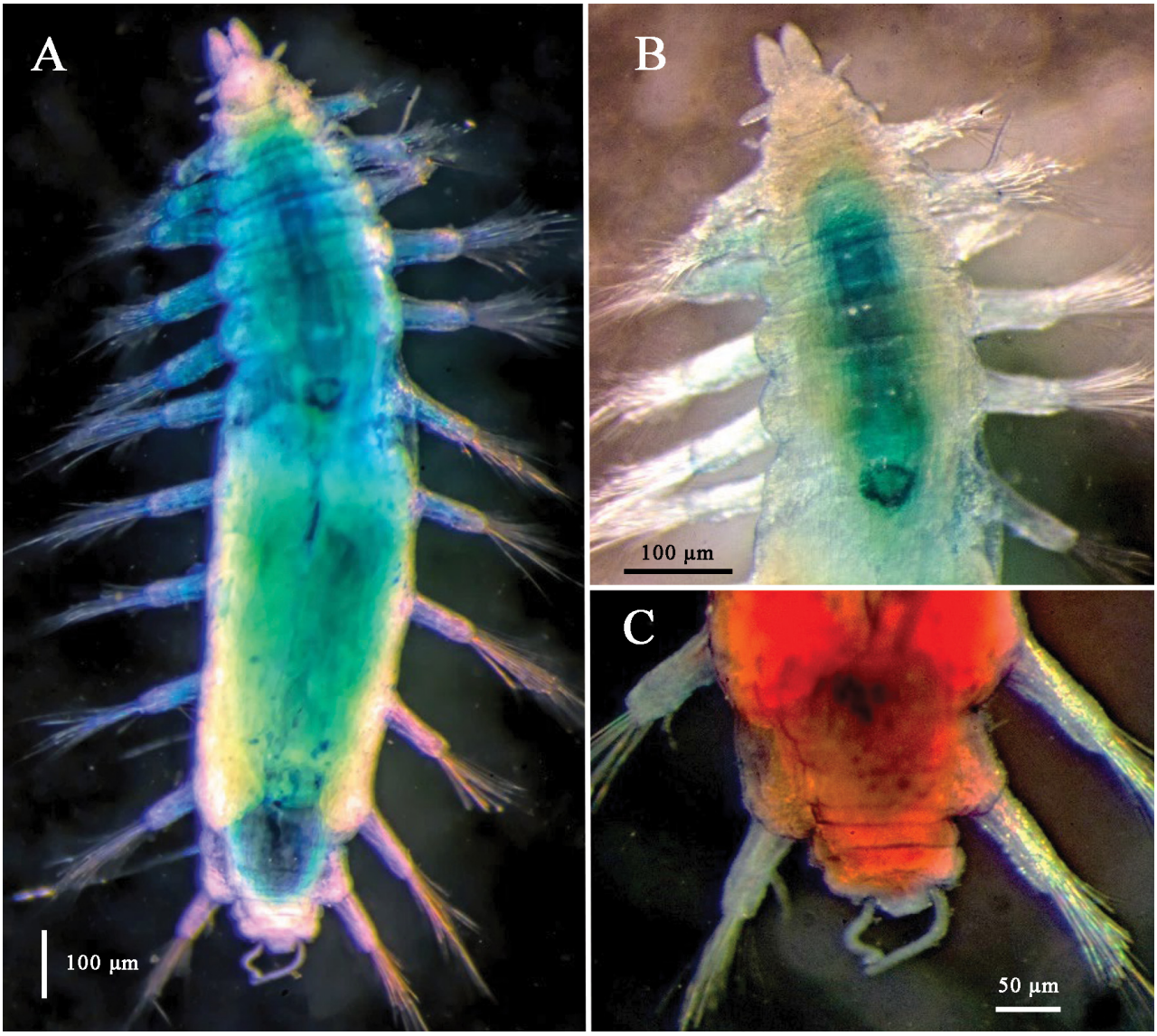

FIGURE 8. ***Anguillosyllis acsara*** **n. sp.** Holotype (USNM 1480212): A, entire specimen, dorsal view; B, anterior end, dorsal view; C, pygidium. A–B, with MG stain; C, with Shirlastain A.

All setae compound with heterogomph shafts, with short to long blades; setae emerging from distal end and ventral face of parapodium. Ventral falcigers with deeply serrated blade, bluntly rounded tip (Fig. 7D); spiniger-like blades clearly serrated at base, becoming plain near thin, fine tips; setiger 1 with ca. 30 falcigers ca. 70–90 µm long and 2–4 spiniger-like setae with long, fine tips up to 200 µm long; setigers 2–3 similar but with more spiniger-like setae; setigers 4–6 with ca. 50 setae, number of setae decreasing in setigers 7–11 to ca. 16–20; spiniger-like setae becoming more numerous and falcigers reduced in number posteriorly. Two aciculae per parapodium, both embedded or tip barely emergent, pointed (Fig. 7F); anterior acicula appearing bent in posterior setigers (Fig. 7F).

Pygidium biannulate, with two ventromedial filiform cirri, other cirri lost (Figs. 7B, 8C).

Reproductive features. Holotype with setigers 6–10 filled with possible gonadal products but individual eggs not detectable (Fig. 8A); juvenile specimen ca. 0.5 mm long, biannulation not evident.

Remarks. *Anguillosyllis acsara* **n. sp.** from North Carolina is similar to the widespread *A. palpata* and *A. hampsoni* **n. sp.** from shelf depths off New England in having 11 setigers and unfused palps, but differs in having a heavier habitus, smaller nuchal area, and falcigers with plain rather than hooked tips; more importantly, *A. acsara* **n. sp.** also lacks the posterior parapodial lobes of the other two species. Both *A. acsara* **n. sp.** and *A. hadra* **n. sp.** from the South China Sea have 11 setigers and bulky, dorsally arched bodies, and both lack posterior lobes on the parapodia; they differ in the larger size, clearer biannulation, smaller proventricle, more obvious nuchal patches, and

greater number of setae in anterior setigers of *A. acsara* **n. sp.** compared with *A. hadra* **n. sp.** *Anguillosyllis acsara* **n. sp.** differs from almost all other *Anguillosyllis* in having numerous small glands covering the posterior half of the peristomium and first few setigers; only *A. hadra* **n. sp.** has similar dorsal glands on anterior segments.

Etymology. The species name is based on ACSAR, the acronym for the Atlantic Continental Slope and Rise program, during which this species was collected

Records. Off North Carolina, USA, 1505–1996 m.

Anguillosyllis carolina **n. sp.**

Figures 9–10A

urn:lsid:zoobank.org:act:70825BC8-0893-49EC-8BD2-4A705D2E3D24

Material examined. *(4 specimens from 3 stations)*. **off North Carolina,** U.S. South ACSAR Program, coll. J.A. Blake (Battelle), Chief Scientist. Sta. 1, Cruise SA1, R/V *Columbus Iselin*, 11 Nov 1983, Rep. 1, 34°16.40′N, 75°45.01′W, 720 m, **paratype** (USNM 1480215). Sta. 12, Cruise SA6, R/V *Cape Hatteras*, 21 Nov 1985, Rep. 1, 33°00.55′N, 76°07.45′W, 1992 m, very soft mud, **paratype** (USNM 1480216). Sta. 13, Cruise SA6, R/V *Cape Hatteras*, 20 Nov 1985, Rep. 1, 32°55.16′N, 75°50.25′W, 2999 m, **holotype** (USNM 1480214).

Description. Body with 10 setigers (Figs. 9A, 10B), slender, linear; all specimens 1–1.3 mm long, 0.25 mm wide without parapodia, 0.6 mm wide with parapodia but without setae. Palps slim, bean-shaped ovals, free to base. Prostomium wider than long, appearing to be in two parts with inner part smaller, dome-shaped anteriorly, slightly raised and outer part inflated, surrounding inner part like a collar (Fig. 9A); eyes lacking; antennae long, club-shaped, presumed to be three in total but individual specimens with only one or two. Peristomium with two large tentacular cirri. Nuchal cilia in obvious patches between prostomium and peristomium. Proventricle in 3–4 setigers, oval, barrel-shaped, posterior end not tapered (Figs. 9A, 10A); muscle rows not clearly defined, at least 8–10; cells of post-ventricle caeca do not retain MB stain (holotype), or stain very faintly (USNM 1480215).

Dorsum of setiger 1 weakly biannulate, others uniannulate, posterior setigers distorted by eggs. Parapodia uniramous, shortest on setiger 1, becoming longer on setigers 2–3, elongated on setigers 4–10. Very small anterior lobe visible on anterior setigers (Fig. 9B–C); posterior lobe small on anterior setigers (Fig. 9B), more obvious on later setigers (Fig. 9C), especially setigers 8–9, absent on setiger 10 (Fig. 9D); dorsal lobe small rounded knob on all setigers. Elongate internal parapodial glands present in all setigers; these few, deep within tissue, some entering dorsal lobe; external glands present on dorsum at anterior and posterior bases of parapodia (visible on holotype in anterior setigers) (Fig. 9A). Dorsal cirri present on setigers 1 (holotype) and 4–8, others absent or lost; ventral cirri short, wider at base then tapered, inserted in middle of parapodium.

All setae compound with heterogomph shafts; most setae emerge from distal tip of parapodium, several others from ventral face of parapodium. Setiger 1–2 with ca. 25–35 setae, setiger 3 with ca. 25 setae; setae becoming less numerous in posterior setigers, ca. 16 in setiger 9. Blades ranging in length; shortest ventral falcigers 25 μm long, with narrow, fine (but blunt, not hooked) tips; longest dorsal spiniger-like setae up to 130 μm long, with long fine tips; all blades with deeply serrated proximal area. Parapodia each with two aciculae, not emerging but forming anterior and posterior bumps at distal end of parapodia (Fig. 9B–D); aciculae bluntly pointed.

All anal cirri lost.

Oocytes in coelom of setigers 6–9 of all specimens, measuring 60–85 μm greatest diameter; large oocytes entering parapodia.

Remarks. The palps of *Anguillosyllis carolina* **n. sp.** are clearly free on the dorsal surface and, while they also appear free to the base, they possibly are connected by a membrane on the ventral surface close to the base: some of the fine structural details of these small specimens were difficult to confirm with light microscopy and the pharynx was everted on one. The prostomium is unusual in appearing to be a structure with two parts, with the inner area slightly raised and the outer portion bearing the antennae; the prostomia of *A. denaria* **n. sp.** and *A. taleola* **n. sp.** from Brunei are similar.

Anguillosyllis carolina **n. sp.** differs from most of the other *Anguillosyllis* species with free or mostly free palps in having 10 rather than 11 setigers. Only *A. denaria* **n. sp.** and *A. taleola* **n. sp.**, both from the South China Sea, also have 10 setigers. *Anguillosyllis carolina* **n. sp.** and *A. taleola* **n. sp.** are similar in having palps that are entirely free (at least on the dorsal side), whereas *A. denaria* **n. sp.** has palps that are fused halfway both dorsally and ventrally.

Anguillosyllis carolina **n. sp.** and *A. taleola* **n. sp.** are also similar in having large nuchal patches in comparison to the small ones of *A. denaria* **n. sp.** *Anguillosyllis carolina* **n. sp.** and *A. taleola* **n. sp.** differ in that the former species has small posterior lobes on the posterior setigers except setiger 10, and *A. taleola* **n. sp.** lacks these posterior lobes; *A. carolina* **n. sp.** has more setae in anterior setigers, and finer-tipped falcigers than *A. taleola* **n. sp.**, and also has shorter setal shafts relative to blade length (see below).

Etymology. The species name *carolina* refers to the collection of this species at stations off the coast of North Carolina, USA, during the ACSAR program.

Records. Off North Carolina, USA, 720–2999 m.

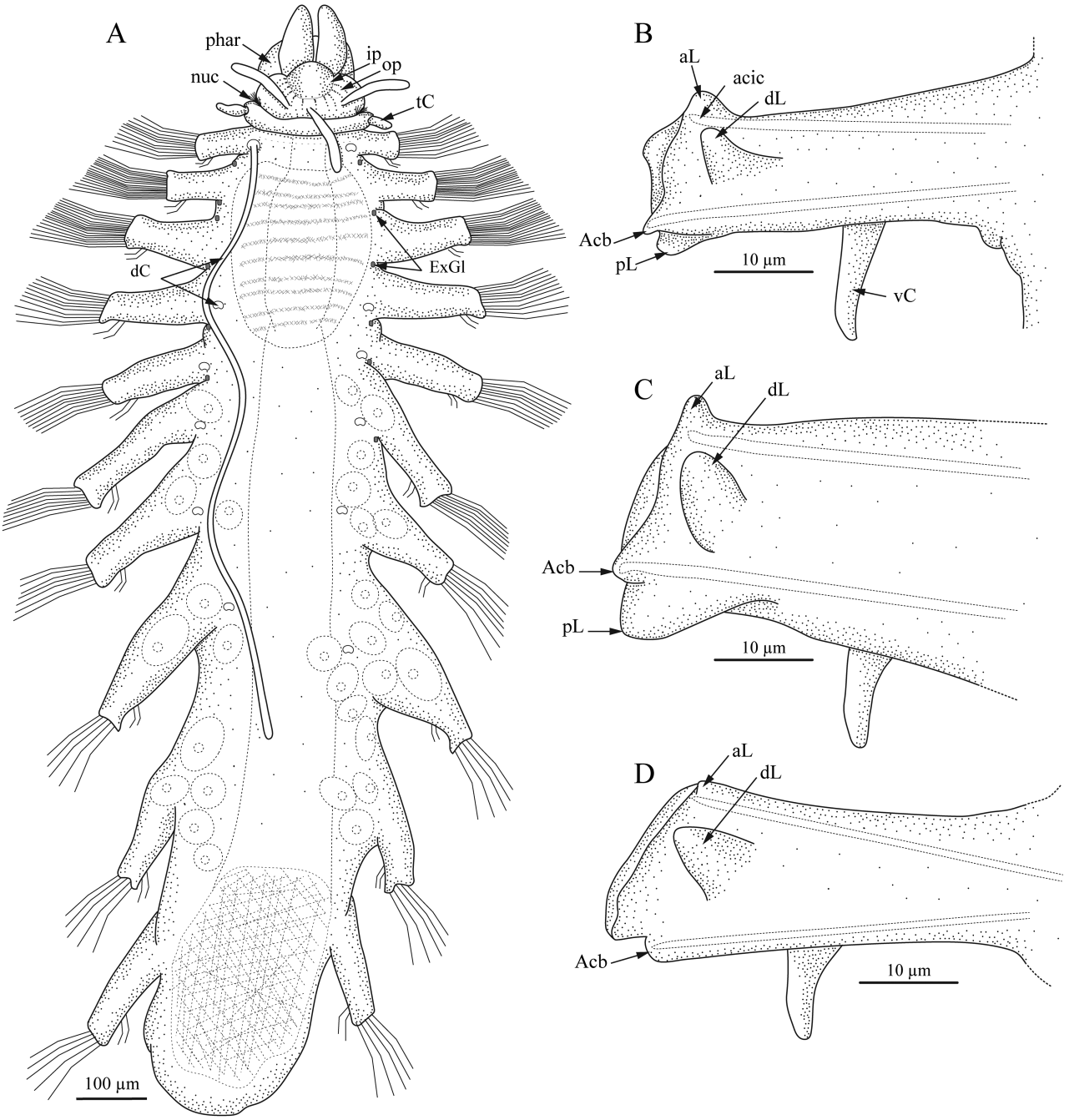

FIGURE 9. ***Anguillosyllis carolina*** **n. sp.** Holotype (USNM 1480214): A, entire specimen, dorsal view. B, setiger 2; C, setiger 5; D, setiger 10. Abbreviations: Acb—acicular bump, acic—acicula, aL—anterior lobe, dC—dorsal cirrus, nuc—nuchal cilia, ip—inner prostomium, op—outer prostomium, phar—pharynx, pL—posterior lobe, prst—prostomium, tC—tentacular cirrus, vC—ventral cirrus.

***Anguillosyllis denaria* n. sp.**
Figures 10B–E, 11
urn:lsid:zoobank.org:act:8D103C88-69D7-4944-9EFF-BC1FB6D5829A

Material examined. *(39 specimens from 23 stations)* **South China Sea, off Brunei.** Coll. J.A. Blake. Sta. 6, 7 Jun 2011, 5°51′40.17938″N, 114°10′54.32730″E, 1353 m, 2 specimens (MCZ 151148); Sta. 9, 6 Jun 2011, 5°52′38.23770″N, 114°13′42.28254″E, 1459 m, **paratype** (MCZ 151147); Sta. 21, 5 Jun 2011, 5°50′25.56269″N, 114°12′30.71125″E, 1424 m, 1 specimen (MCZ 151149); Sta. 29, 4 Jun 2011, 5°43′01.15997″N, 114°06′07.18190″E, 1537 m, 1 specimen (MCZ 151150); Sta. 33, 4 Jun 2011, 5°48′54.28228″N, 114°14′02.81573″E, 1370 m, 2 specimens (MCZ 151151); Sta. 34, 4 Jun 2011, 5°50′32.29819″N, 114°15′47.44656″E, 1369 m, **holotype** (MCZ 151152); Sta. 35, 3 Jun 2011, 5°47′37.12906″N, 114°14′10.75153″E, 1329 m, 2 specimens (MCZ 151153); Sta. 40, 3 Jun 2011, 5°41′48.58019″N, 114°08′57.21297″E, 1379 m, 2 **paratypes** (MCZ 151154); Sta. 42, 3 Jun 2011, 5°45′13.06236″N, 114°13′06.77111″E, 1252 m, 2 specimens (MCZ 151155); Sta. 44, 2 Jun 2011, 5°47′22.97393″N, 114°15′36.22932″E, 1294 m, 1 specimen (MCZ 151156); Sta. 45, 2 Jun 2011, 5°48′57.88185″N, 114°17′18.08262″E, 1260 m, 2 specimens (poor condition) (MCZ 151157); Sta. 48, 2 Jun 2011, 5°45′28.93802″N, 114°15′23.44165″E, 1219 m, 2 specimens (MCZ 151158); Sta. 49, 2 Jun 2011, 5°44′24.32540″N, 114°13′59.60803″E, 1199 m, **paratype** (MCZ 151159); Sta. 50, 2 Jun 2011, 5°42′55.91978″N, 114°12′23.51666″E, 1214 m, 2 specimens (MCZ 151160); Sta. 51, 1 Jun 2011, 5°41′53.71760″N, 114°10′26.14608″E, 1308 m, 1 specimen (MCZ 151161); Sta. 54, 9 Jun 2011, 5°42′10.95536″N, 114°13′11.98424″E, 1171 m, 2 specimens (MCZ 151162); Sta. 56, 1 Jun 2011, 5°45′04.58388″N, 114°16′27.71012″E, 1179 m, 1 specimen (MCZ 151163); Sta. 61, 31 May 11, 5°40′32.90422″N, 114°13′15.64893″E, 1050 m, 1 specimen (NJM), Sta. WH-Jokit-NE, 6 Jun 2011, 5°53′28.38401″N, 114°11′57.24436″E, 1400 m, 3 specimens (MCZ 151164). Coll. P. Neubert, Chief Scientist, Sta. JA4, 30 Jun 2011, 5°30′54.36931″N, 113°37′21.11932″E, 1967 m, 2 specimens (NJM); Sta. TU2, 24 Jun 2011, 5°18′25.22812″N, 113°48′13.59077″E, 1224 m, **paratype** (MCZ 151165); Sta. TU7, 4 Jul 2011, 5°19′24.21956″N, 113°47′15.61845″E, 1327 m, 3 specimens (MCZ 151166); Sta. TU9, 23 Jun 2011, 5°23′40.02974″N, 113°51′04.16812″E, 1306 m, 2 specimens (MCZ 151167); Sta. TU10, 23 Jun 2011, 5°24′42.72532″N, 113°51′35.81868″E, 1354 m, 2 specimens (NJM).

Description. Body with 10 setigers (Figs. 10B, 11A), colorless, delicate, linear in shape; maximum size 1.9 mm (holotype 1.5 mm) long without anal cirri, 0.3 mm wide without parapodia, 0.6 mm wide with parapodia but excluding setae. Palps fused both dorsally and ventrally on proximal half to two-thirds, tips free, rounded, faint medial furrow visible on some specimens (Fig. 11A); eyes lacking; prostomium more-or-less oval in shape, with three oval to club-shaped antennae, medial antenna slightly longer than lateral antennae; peristomium slightly inflated, with two short oval tentacular cirri. Nuchal cilia in lateral patches between prostomium and peristomium. Proventricle in two or three setigers, barrel-shaped with blunt anterior edge, slightly tapered posteriorly (Figs. 10B–C, 11A), rows of muscle cells indistinct at either end, numbering ca. 14–20; post-ventricle caeca surrounding posterior proventricle, with dorsal oval loop of cells retaining MG stain (Fig. 10C).

Parapodia uniramous, shortest on setiger 1, becoming longer, rectangular over next few setigers; small anterior lobe present on all setigers, largest on middle setigers then becoming very small (Fig. 11B–E); posterior lobe small on setiger 1, becoming increasingly larger through setiger 10, especially large, with large gland(s) on setigers 8–10 (Fig. 11B–E); dorsal lobe small, rounded knob on all setigers. Several internal parapodial glands present in setigers 5–10, elongated, intertwined, appearing to exit through dorsal lobe (Figs. 10E, 11D–E). Dorsal cirri present on setiger 1 on most specimens, cirri or basal cirrophores of cirri seen on setigers 3–10; ventral cirrus short, wider at base then tapered, inserted in middle of parapodium.

All setae compound with heterogomph shafts; most setae emerge from distal tip, several others from ventral face of parapodium. Ventral blades shorter with narrow, blunt tips, 22–45 µm in length; longer dorsal spiniger-like blades with fine, pointed tips, up to 120 µm long; all blades with serrated proximal area. Setigers 1–8 with ca. 18–20 setae, setigers 9–10 with 8–12 setae. Parapodia each with at least two, possibly three, aciculae, not emerging but forming anterior and posterior bumps at distal end of parapodia; one acicula with bent tip, others pointed.

Pygidium with four cirri: two large oval glandular lateral and two filiform ventromedial (Figs. 10B, E, 11A).

Oocytes in coelom of setigers 6–9 (Fig. 10B, D), measuring 50–85 µm greatest diameter (ave.= 59.8 ± 8.9 µm, n=20); large oocytes entering parapodia (Fig. 10A).

Remarks. *Anguillosyllis denaria* **n. sp.** has palps that are fused both dorsally and ventrally for half to 2/3 their length; a faint median furrow is visible on some specimens. The separate tips of the palps are softly rounded rather than narrow as in *A. palpata*, but may be elongated, thus appearing narrow, or contracted, thus appearing shorter

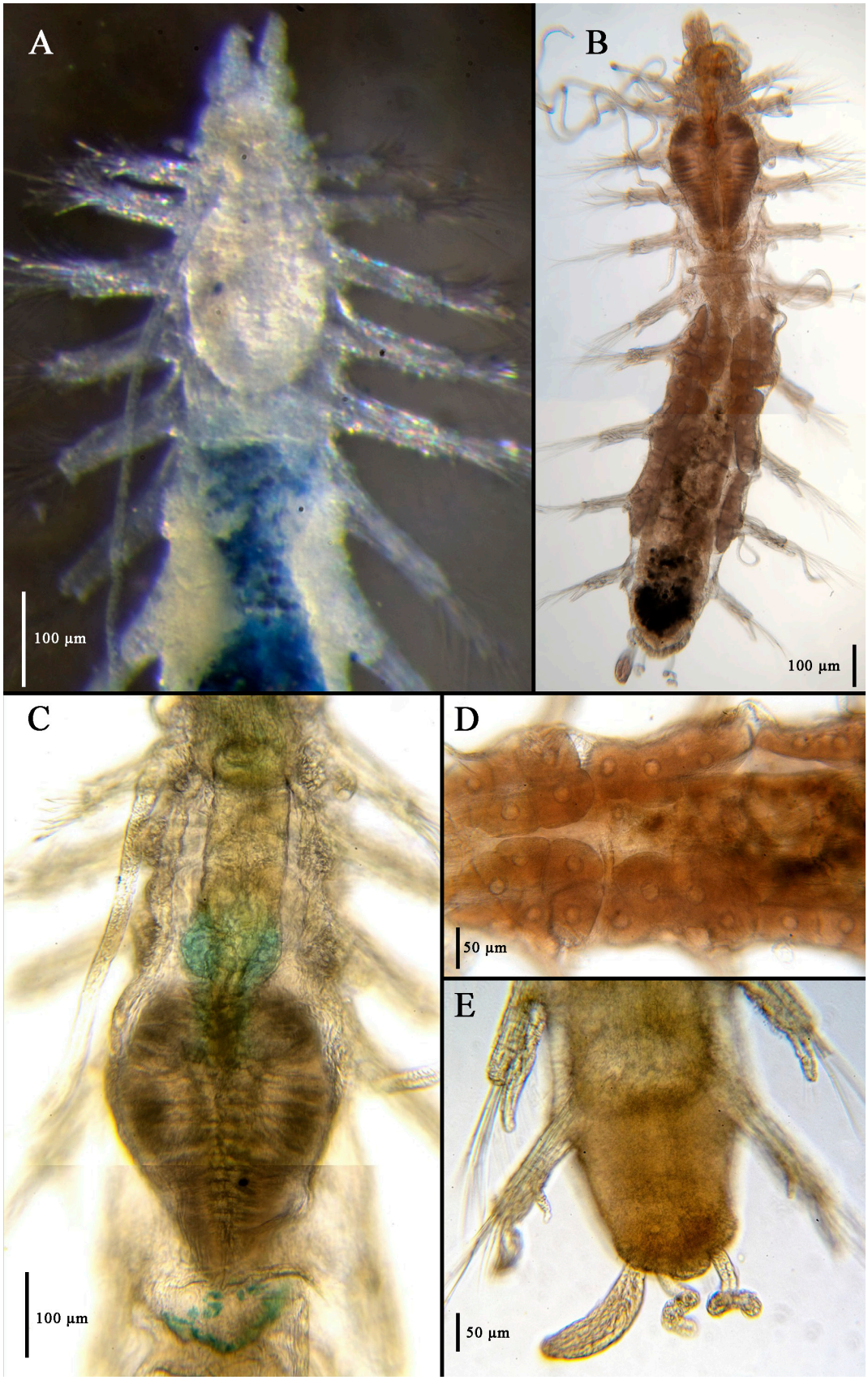

FIGURE 10. ***Anguillosyllis carolina*** **n. sp.** Holotype (USNM 1480214): A, anterior end, dorsal view.—***Anguillosyllis denaria*** **n. sp.** Holotype (MCZ 151152): B, entire specimen, dorsal view. Paratype (MCZ 151147): C, setigers 1–5, dorsal view, pharynx, proventricle and post-ventricle MG-stained cells. Holotype (MCZ 151152): D, eggs in coelom of setigers 7–9. Paratype (MCZ 151152): E, setigers 9–10 and pygidium.

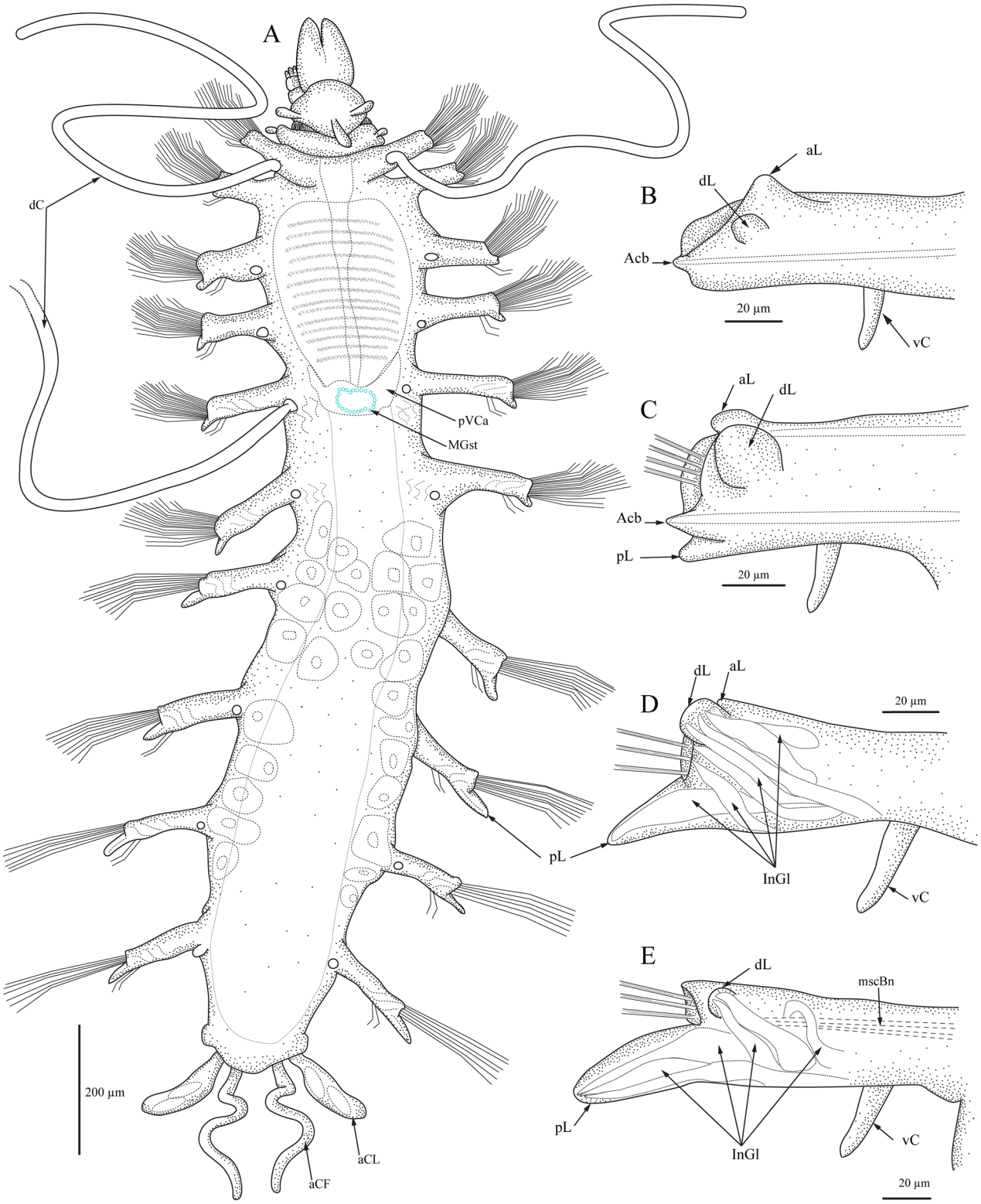

FIGURE 11. ***Anguillosyllis denaria*** **n. sp.** Holotype (MCZ 151152): A, entire specimen, dorsal view. Paratype (MCZ 151147): B, setiger 1; C, setiger 2. Holotype (MCZ 151152): D, setiger 7; E, setiger 10. Abbreviations: Acb—acicular bump, aCL—anal cirrus lateral, aCF—anal cirrus filiform, aL—anterior lobe, dC—dorsal cirrus, dL—dorsal lobe, InGl—internal gland, MGst—cells stained with Methyl Green, mscBn—muscle bundle, pL—posterior lobe, vC—ventral cirrus.

and wider. The only other *Anguillosyllis* species with similar palps is *A. truebloodi* **n. sp.**, described below; all other species have palps that are either completely free dorsally or are completely fused except for the very tip. *Anguillosyllis denaria* **n. sp.** is similar to *A. carolina* **n. sp.** and *A. taleola* **n. sp.** in having 10 setigers but differs from both in having large posterior lobes and small nuchal patches, rather than absent or small posterior lobes and large nuchal patches.

The setal blades of *A. denaria* **n. sp.** have blunt to fine tips, but are never hooked or hooded as they are in *A. palpata* and *A. hampsoni* **n. sp.** The cells that retain MB stain in the post-ventricle tend to form a loose loop rather than a tight circle as seen in *A. palpata* and other species.

Etymology. From the Latin adjective *denaria*, meaning "containing ten each;" in reference to the ten setigers of this species.

Records. South China Sea, off Brunei; 1171–1967 m.

Anguillosyllis hadra **n. sp.**

Figures 12–13

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Material examined. *(14 specimens from 9 samples)*. **South China Sea**, off Brunei. Coll. J. A. Blake, Chief Scientist. Sta. 35, 3 Jun 2011, 5°47′37.12906″N, 114°14′10.75153″E, 1329 m, **paratype** (MCZ 148520); Sta. 44, 2 Jun 2011, 5°47′22.97393″N, 114°15′36.22932″E, 1294 m, 1 specimen (MCZ 148521); Sta. 46, 2 Jun 2011, 5°48′02.68476″N, 114°18′10.00693″E, 1234 m, **holotype** (MCZ 148522); Sta. 47, 2 Jun 2011, 5°47′21.86444″N, 114°17′10.72194″E, 1242 m, 3 specimens (MCZ 148523); Sta. 48, 2 Jun 2011, 5°45′28.93802″N, 114°15′23.44165″E, 1219 m, 1 specimen (MCZ 148524); Sta. 49, 2 Jun 2011, 5°44′24.32540″N, 114°13′59.60803″E, 1199 m, 2 specimens (MCZ 148543); Sta. 58, 1 Jun 2011, 5°44′45.95938″N, 114°17′28.05056″E, 1127 m, 1 specimen (MCZ 148544); Sta. 61, 31 May 11, 5°40′32.90422″N, 114°13′15.64893″E, 1050 m, 1 specimen (MCZ 148545); Sta. WH Jagus E Subthrust, 1 Jun 2011, 5°46′34.64026″N, 114°17′24.73418″E, 1214 m, 3 specimens (MCZ 148546).

Description. Body with 11 setigers (Fig. 12A), bulky, opaque, arched dorsally; up to 1.5 mm long, 0.4 mm wide without parapodia, 0.6 mm wide with parapodia but without setae. Palps slim, bean-shaped ovals, appear free to base on dorsal surface, connected by membrane on ventral surface. Prostomium wider than long; eyes lacking; three club-shaped antennae in nearly transverse row. Peristomium with two tentacular cirri smaller than prostomial antennae; peristomium not clearly demarcated from prostomium, together appearing nearly square. Nuchal cilia present between prostomium and peristomium, but not obvious. Proventricle in 4–4.5 setigers, barrel-shaped, only slightly narrowed at posterior end (Fig. 12A); ca. 24 muscle rows not clearly defined; post-ventricle caeca with dorsal gland cells lacking or not retaining MB stain.

Dorsum biannulate through first four setigers, posterior annulation with small dorsal glands that retain MB stain (Fig. 12A). Parapodia uniramous, short, rectangular, length equal to about half or less body width (may appear short in dorsal view because of bulkiness of arched dorsum); with small, translucent anterior lobe increasing slightly in size through setiger 5 then decreasing through end of body (Figs. 12B–D, 13B); posterior lobe lacking; dorsal lobe small, sometimes curled dorsally, clearest on setigers 1–5/6. Dorsal cirri retained on setiger 1, otherwise absent or lost; cirri thin, smooth, filiform. Ventral cirri with wider base tapering to narrower tip, inserted midway on parapodia. Parapodia with smooth elongate internal glands, one end associated with cluster of tightly packed pentagonal cells, distal end of tube narrowing and exiting through dorsal lobe or surface of parapodium, rarely retaining faint MB stain (Figs. 12C–E, 13A–D).

All setae compound with heterogomph shafts, with shorter falcigers and longer spiniger-like blades; falcigers with deeply serrated, blunt-tipped blade; spiniger-like blades clearly serrated at base, becoming plain near thin, fine tips; setae numbering 20–22 in setigers 1–4; 12–14 in setigers 5–8, 10–12 in setigers 9–11; setae emerging from distal end and ventral face of parapodium. Two or three stout pointed embedded aciculae per parapodium, posterior acicula with distal end bent (MCZ 148520), others straight and pointed.

Pygidium with four cirri: two, large, inflated lateral cirri and two filiform ventromedial cirri (Fig. 12A).

Reproductive features. None of the specimens had eggs, but one sample included a very tiny specimen (<0.5 mm) with 10 setigers that could be a juvenile of this species.

Glands. The specimen from Sta. 35 (MCZ 148520) differed from the other specimens in having clear, elongated, internal glands on the dorsum as well as at the distal end of the parapodia (Figs. 12E, 13A, E). The glands

on the dorsum started on setiger 4 at the base of the parapodia and on subsequent setigers became more numerous and higher on the dorsal surface, extending to near the midline. These clear structures were connected at one end to rosettes or clusters packed with small cells that appeared pentagonal or octagonal; these rosettes most likely surround the external opening of the tubular gland, but thin sections and histological staining are necessary to clarify the structure of these glands. Neither the long tubes nor the clusters of small cells retained any MB stain.

Remarks. *Anguillosyllis hadra* **n. sp.** is most similar to *A. aciculata* **n. sp.**, also from the South China Sea, and to *A. acsara* **n. sp.** from off North Carolina: all three species have 11 setigers, palps that are free or mostly free to the base, and significant numbers of glands both in the parapodia and on the dorsum; all three species lack posterior lobes on the parapodia. *Anguillosyllis hadra* **n. sp.** differs most noticeably from *A. aciculata* **n. sp.** by lacking the emergent acicula that characterize the latter species and from *A. acsara* **n. sp.** by a different arrangement of dorsal glands, smaller proventricle, less obvious nuchal patches and dorsal biannulation, and fewer setae in anterior setigers.

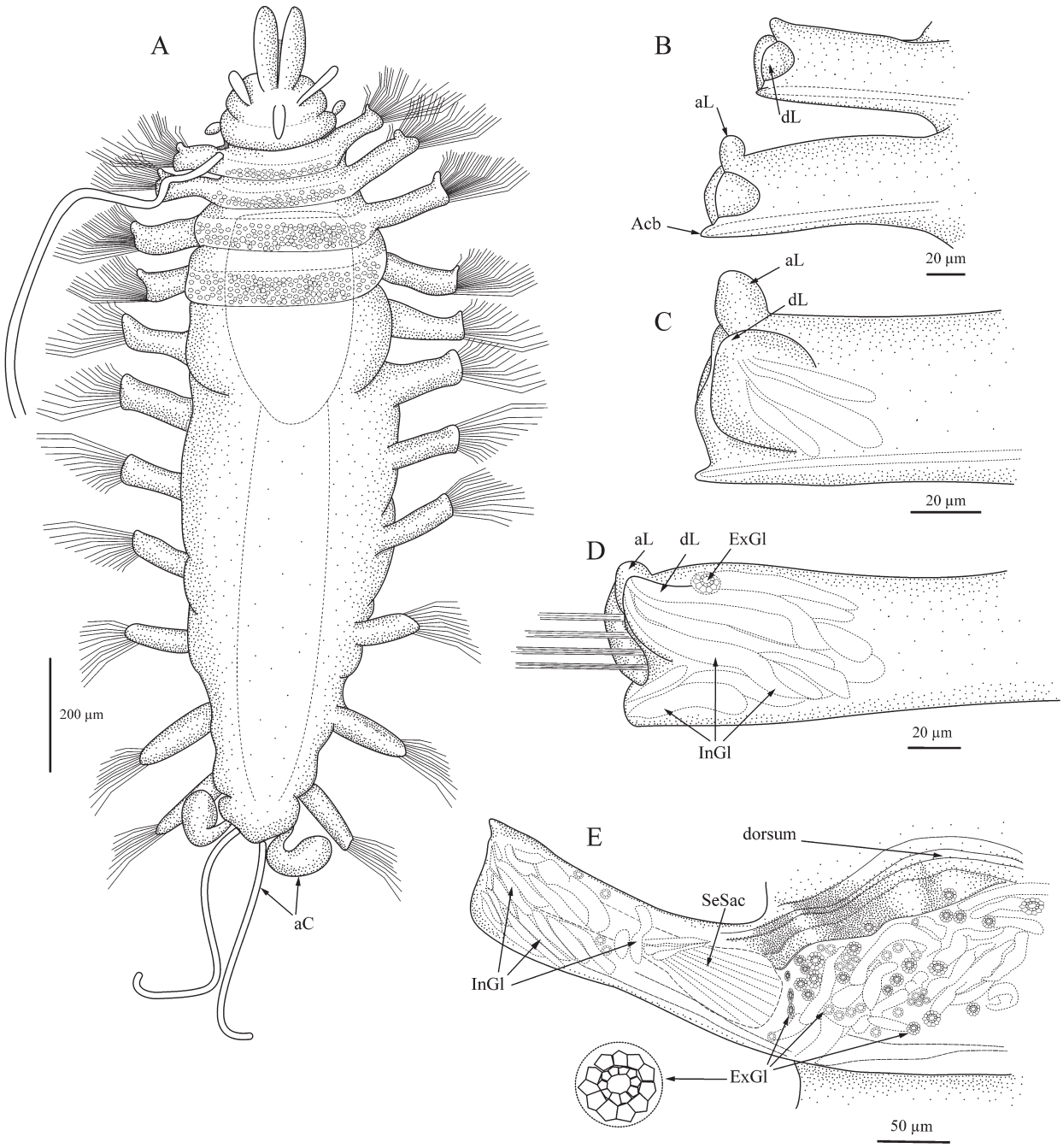

FIGURE 12. ***Anguillosyllis hadra*** **n. sp.** Holotype (MCZ 148522): A, entire specimen, dorsal view; B, setigers 1–2; C, setiger 3; D, setiger 6. Paratype (MCZ 148520): E, setiger 5, inset not to scale. Abbreviations: ac—anal cirri, Acb—acicular bump, aL—anterior lobe, dL—dorsal lobe, ExGl—external gland, InGl—internal gland, SeSac—setal sac.

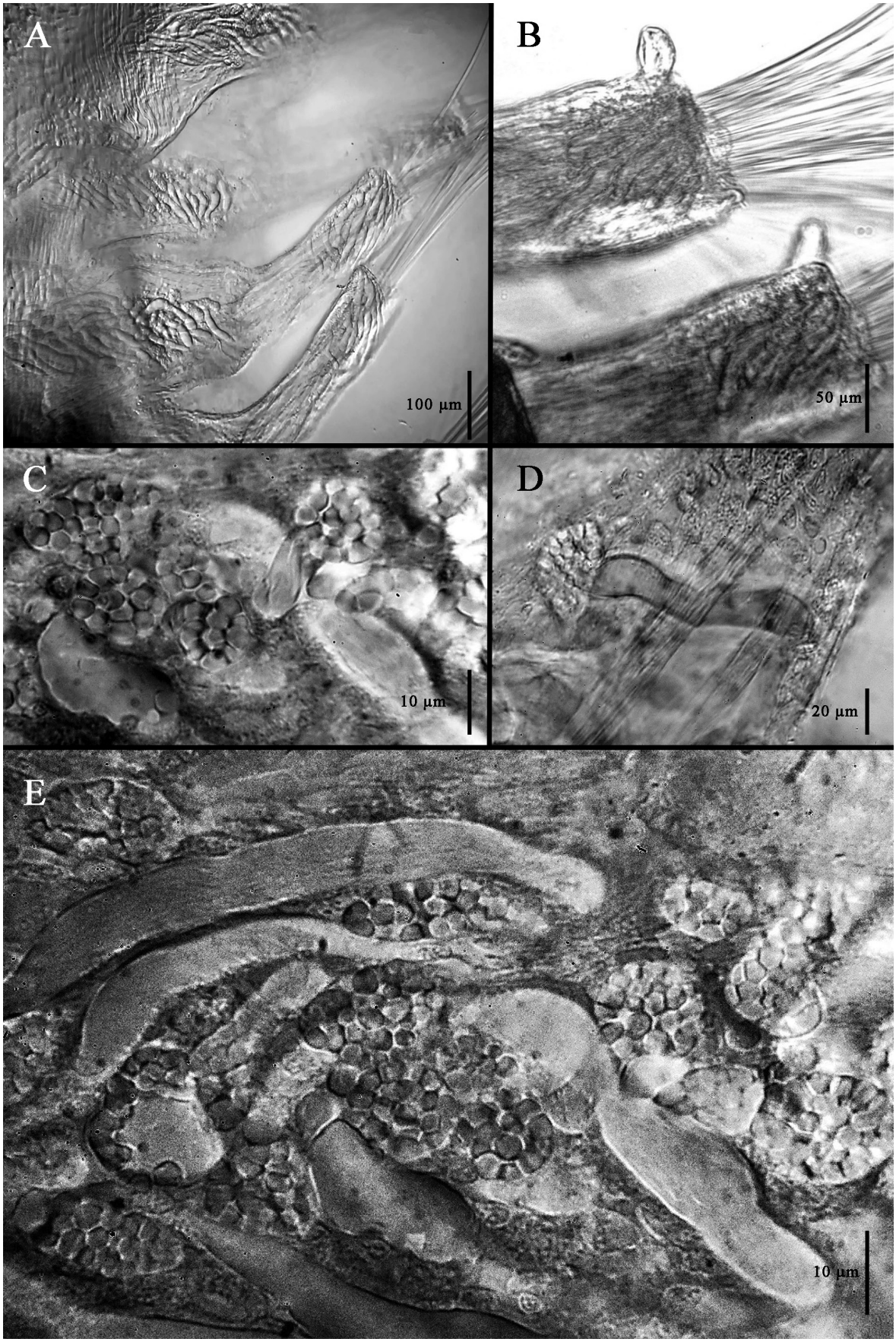

FIGURE 13. ***Anguillosyllis hadra*** **n. sp.** Paratype (MCZ 148520): A, setigers 4–7; B, setigers 4–5; C, parapodial glands, setiger 5; D, parapodial gland, setiger 5; E, dorsal glands, setiger 5.

Considering other species from the east coast of North America, *Anguillosyllis hadra* **n. sp.** differs from *A. palpata* in lacking a posterior lobe on the parapodia, in having greatly enlarged lateral anal cirri, and having structurally complex parapodial glands, rather than having a large posterior lobe, small flattened lateral cirri, and a few simple internal glands; it also has a barrel-shaped proventricle compared to the cordate proventricle of *A. palpata*. *Anguillosyllis hadra* **n. sp.** differs from *A. hampsoni* **n. sp.** in having fewer very short falcigerous setae in the first few setigers as well as in the characters described for *A. palpata*.

Etymology. The specific epithet is an adjective taken from the Greek *hadros*, meaning well-developed or bulky; it refers to the broad bulky body of this species.

Records. South China Sea, off Brunei; 1015–1329 m.

Anguillosyllis hampsoni **n. sp.**

Figures 14–15

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Braniella cf. *palpata*: Maciolek-Blake *et al.* 1985.

Material examined. *(14 specimens from 3 stations, 10 samples)*. Western North Atlantic, off Massachusetts, Georges Bank, **BIMP Sta. 16,** 40°34.2′N, 67°12.3′W, coll. M. Rawson, Lamont-Doherty, Chief Scientist, Cruise M-2, R/V *Oceanus*, 18 Nov 1981, 142 m, 2 **paratypes** (USNM 1480259); coll. G. Hampson, WHOI, Chief Scientist, Cruise M-4, R/V *Cape Henlopen,* 12–13 May 1982, 140 m, **paratype** (USNM 1480260); Cruise M-8, R/V *Gyre*, 16 May 1983, 139 m, 2 **paratypes** (USNM 1480261); coll. R. Petrecca, Chief Scientist, Cruise M-10, R/V *Oceanus*, 15 Nov 1983, 142 m, 2 **paratypes** (USNM 1480262); coll. G. Hampson, Chief Scientist, Cruise M-11, R/V *Oceanus*, 3 Feb 1984, 142 m, **paratype** (USNM 1480263). **BIMP Sta. 17,** 40°35.0′N, 67°11.7′W, coll. M. Rawson, Lamont-Doherty, Chief Scientist, Cruise M-2, R/V *Oceanus*, 18 Nov 1981, 134 m, **paratype** (USNM 1480264); coll. G. Hampson, Chief Scientist, Cruise M-5, R/V *Oceanus*, 23 Jul 1982, 135 m, 2 **paratypes** (USNM 1480265). **BIMP Sta. 18**, 40°33.5′N, 67°13.7′W, coll. G. Hampson, Chief Scientist, Cruise M-3, R/V *Endeavor*, 17–18 Feb 1982, 145–147 m, **paratype** (USNM 1480266); Cruise M-5, R/V *Oceanus*, 23 Jul 1982, 140 m, **holotype** (USNM 1480267); Cruise M-6, R/V *Oceanus*, 21 Nov 1982, 144 m, **paratype** (USNM 1480268).

Description. Body with 11 setigers (Figs. 14A, 15A); most specimens ca. 1.0 mm long, maximal length 2.0 mm without anal cirri, maximal width 0.5 mm without parapodia, 1.1 mm with parapodia but without setae. Overall body shape linear (Fig. 15A) unless swollen with eggs (Fig. 14A), first three setigers with stiff, bristly appearance due to large number of setae. Palps bean-shaped, appear fused (at least ventrally) along proximal two-thirds to three-quarters, tips free, often turned ventrally; prostomium dome-shaped, with three short club-shaped antennae in nearly transverse row, two lateral antennae slightly anterior to medial one; eyes lacking; nuchal area between prostomium and peristomium short, oblong, extending toward midline, cilia obvious. Peristomium with two tentacular cirri, similar to but smaller than antennae; sometimes appearing large or swollen. Eversible pharynx with distal ring of 10 soft papillae. Proventricle in 2–3 setigers, anterior margin straight, widest in middle with slightly narrowing posterior end (Figs. 14A, 15A–B); rows of muscle cells indistinct, perhaps 30–35; post-ventricle caeca with numerous dorsal cells retaining MB stain (Fig. 15A).

Anterior setigers 1–3 faintly biannulate dorsally, clearly biannulate when stained. Parapodia uniramous, long, rectangular, with small anterior and slightly larger posterior lobes on all setigers (Fig. 14C–E); with large dorsal lobe on all setigers, often turned back, appearing as triangular flap (Fig. 14C–E). Dorsal cirri long, thin, coiled into tight corkscrews or relaxed, present on all setigers (including setiger 2 on one specimen); with basal cirrophores near posterior margin of parapodium. Ventral cirri inserted midway between body and distal end of parapodia on all setigers, wider at base, tapering toward distal end. No parapodial glands observed but dorsum with areas of dark glandular areas and clear sinuous channels on setigers 5–11.

All setae compound, with heterogomph shafts; several emerging from ventral face of parapodium, others emerging from distal end of parapodium. Setigers 1–3 with ca. 35–40 short-bladed falcigers, blades serrated, with hooked tips, 20–30 µm long (Fig. 14B); setigers 1–3 additionally with 2–4 falcigers with longer blades measuring 45–50 µm, these also serrate (Fig. 14B); longer-bladed setae becoming more numerous, with blades up to 110 µm long, in middle and posterior setigers. Setal shafts measuring 70–130 µm long. Number of setae decreasing to about 15 in

mid-region, 10 in posterior setigers. Each parapodium with stout, pointed acicula in anterior edge and 1–2 aciculae in posterior edge.

Pygidium with four cirri: two flat, oval lateral cirri and two thin, filiform, often coiled ventromedial cirri; all cirri easily lost (Figs. 14A, 15C).

Reproductive characteristics. Eggs measuring 50–80 µm were present in several specimens in the coelom after setiger 6 or 7. Specimens with eggs were collected in both November and July.

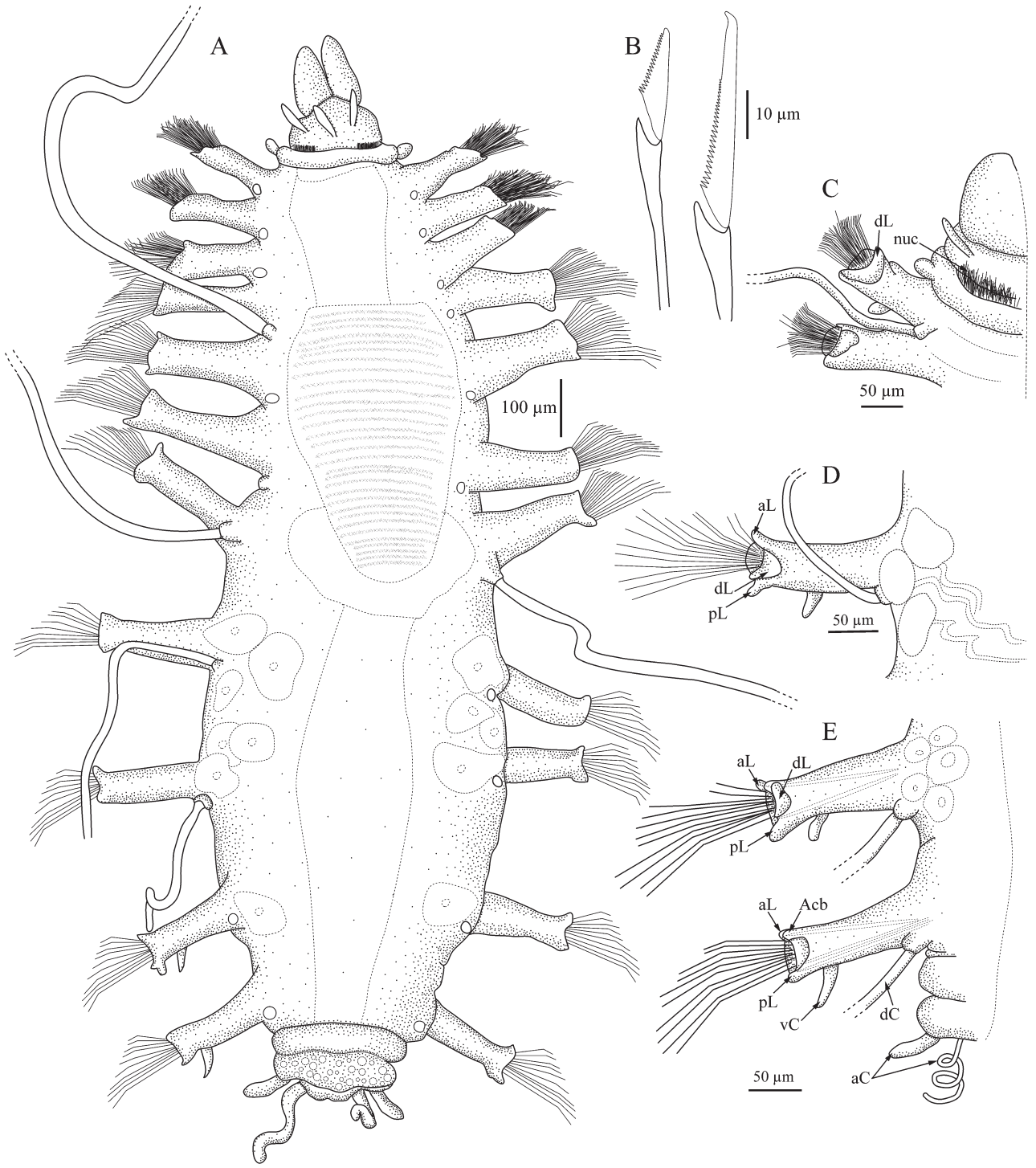

FIGURE 14. ***Anguillosyllis hampsoni*** **n. sp.** Paratype (USNM 1480263): A, entire specimen, dorsal view; B, falcigers from setiger 3; C, anterior end including setigers 1 and 2, dorsal view; D, setiger 8, dorsal view; E, setigers 10 and 11, dorsal view. Abbreviations: Acb—acicular bump, aL—anterior lobe, dC—dorsal cirrus, dL—dorsal lobe, nuc—nuchal cilia, pL—posterior lobe, vC—ventral cirrus.

Remarks. *Anguillosyllis hampsoni* **n. sp.** differs from *A. palpata* principally in the number and type of setae in anterior fascicles as well as in other subtler morphological details. There are three to four times as many short-bladed falcigers in setigers 1–3 in *A. hampsoni* **n. sp.** as in *A. palpata* and many fewer longer-bladed setae, none of which are spiniger-like. The palps of *A. hampsoni* **n. sp.** are usually more clearly fused along the ventral surface compared with the palps of *A. palpata*, although they may appear separate from the dorsal side. Additionally, the proventricle in *A. hampsoni* **n. sp**., which is basically the same size as that of *A. palpata*, is not cordate, but has a straighter anterior margin, and does not taper as abruptly as that of *A. palpata*. There are no obvious glands in the parapodia in *A. hampsoni* **n. sp.** as there are in *A. palpata*, and the huge lateral nuchal patches seen in *A. palpata* are much smaller and visible only as dorsal bands between the prostomium and peristomium in *A. hampsoni* **n. sp.** Finally, *A. hampsoni* **n. sp.** is generally a smaller species than *A. palpata*.

Etymology. This species is named for Woods Hole Oceanographic Institute scientist Mr. George Hampson (1938–2015), the skilled Chief Scientist on many of the Georges Bank and ACSAR cruises conducted in the 1980s. A friend and colleague, George exemplified the best in enthusiasm, competence, and careful attention to detail that made these sampling cruises a success.

Records. Northwest Atlantic, Georges Bank, 142–151 m.

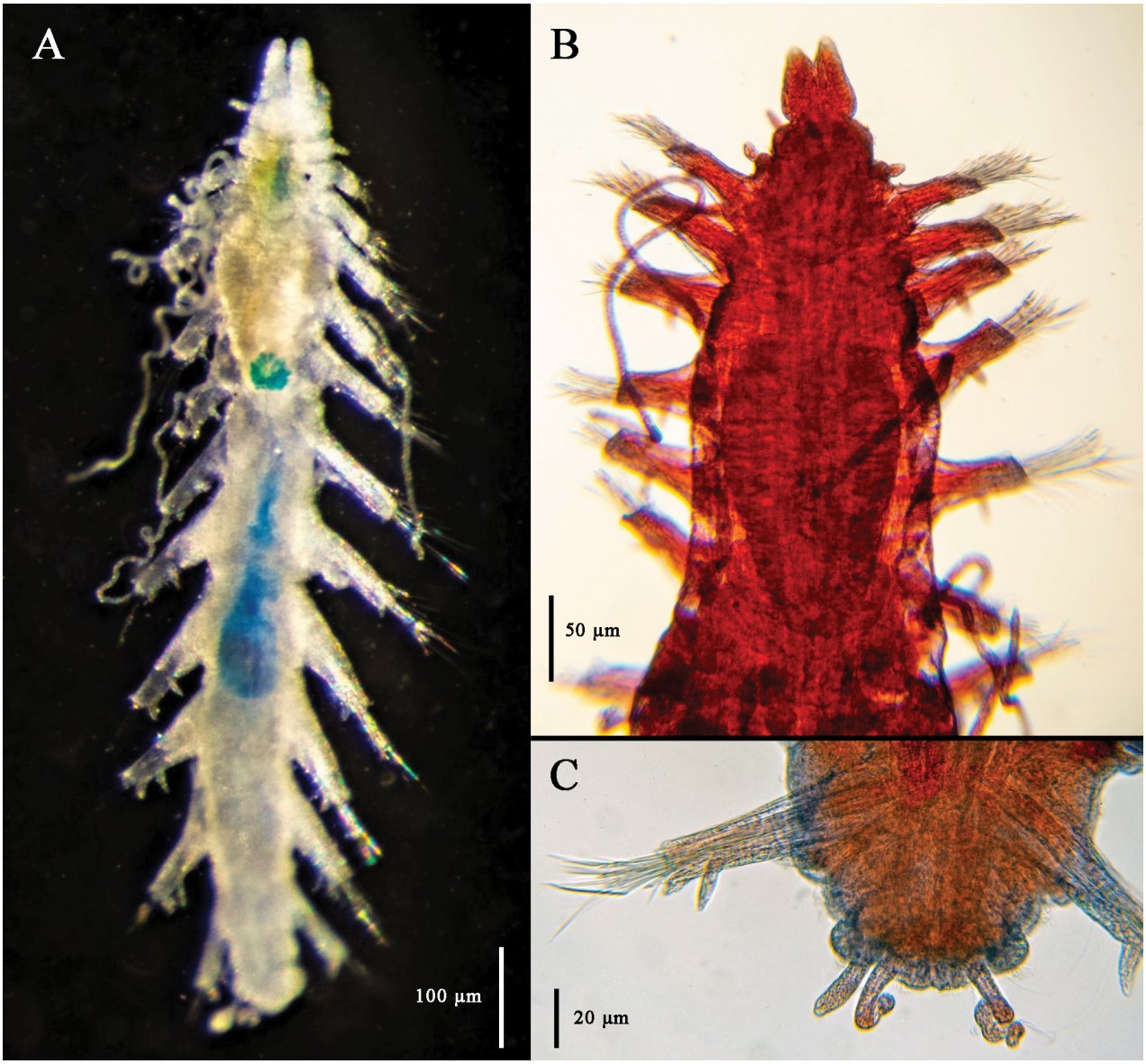

FIGURE 15. ***Anguillosyllis hampsoni*** **n. sp.** Paratype (USNM 1480263): A, entire specimen, dorsal view. Holotype (USNM 1480267): B, anterior end, dorsal view. Paratype (USNM 1480263): C, setiger 11 and pygidium, ventral view. B–C with Shirlastain A.

***Anguillosyllis taleola* n. sp.**
Figures 16–17
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Material examined. *(14 specimens from 10 stations)* **South China Sea, off Brunei.** Coll. J.A. Blake. Sta. 19, 5 Jun 2011, 5°47′28.77291″N, 114°09′18.99869″E, 1487 m, 2 specimens (MCZ 150599); Sta. 44, 2 Jun 2011, 5°47′22.97393″N, 114°15′36.22932″E, 1294 m, **paratype** (MCZ 150600). Coll. P.A. Neubert, Sta. AN8, 27 Jun 2011, 5°27′56.15653″N, 113°45′42.93641″E, 1783 m, 3 **paratypes** (MCZ 150601); Sta. DA2, 1 Jul 11, 5°24′13.64904″N, 113°28′04.25708″E, 1760 m, **paratype** (MCZ 150598); Sta. DA5, 1 Jul 11, 5°26′21.37195″N, 113°28′35.58907″E, 1958 m, 2 specimens (MCZ 150602); Sta. JA1, 30 Jun 2011, 5°28′22.57522″N, 113°36′38.54386″E, 1888 m, 1 specimen (MCZ 150603); Sta. JA2, 30 Jun 11, 5°27′55.53448″N, 113°32′57.69642″E, 1954 m, 1 specimen (NJM); Sta. JA3, 3 Jul 2011, 5°29′25.34994″N, 113°34′52.03519″E, 1922 m, 1 specimen (MCZ 150604); Sta. ME13, 26 Jun 2011, 5°23′16.81208″N, 113°37′16.44011″E, 1777 m, **holotype** (MCZ 150597); Sta. ME16, 26 Jun 2011, 5°24;24.44585″N, 113°35;28.03023″E, 1805 m, 1 specimen (MCZ 150605).

Description. Body with 10 setigers (Figs. 16A, 17A–B), colorless, delicate; holotype 2 mm long without anal cirri; other specimens including paratypes 1 mm long; maximum width 0.2 mm without parapodia, 0.5–0.6 mm with parapodia but excluding setae. First 5–6 setigers may be short, setigers 6–10 longer, more widely separated, or body may appear linear with setigers of relatively equal length (Fig. 17A–B). Palps elongate, bean-shaped, completely separate; prostomium wider than long, appearing to be faintly divided into two parts with smaller inner part dome-shaped, slightly raised and outer part inflated, surrounding inner part like a collar (Figs. 16A–B, 17D); three large club-shaped antennae on outer part, eyes lacking; peristomium slightly inflated, with two large tentacular cirri. Nuchal cilia in obvious patches between prostomium and peristomium. Proventricle filling body cavity in 3–4 setigers, cylindrical to barrel-shaped, with slightly rounded or straight anterior edge, very slightly narrowed at posterior end (Figs. 16A, 17A–C); rows of muscle cells particularly indistinct even under high power, ca. 18 irregular darker areas; post-ventricle caeca not retaining MG stain.

Parapodia uniramous, shortest on setiger 1, becoming longer, rectangular over subsequent setigers, after setiger 5 becoming elongated, slim, with rounded distal end; small anterior lobes present on setigers 1–4 (Figs. 16C, 17E), lobes becoming smaller and absent on subsequent setigers; posterior lobes lacking but posteroventral portion of parapodia may bulge with possibly glandular structures; dorsal lobe small, rounded (Fig. 16C). Dorsal cirri (or basal cirrophore) present on setiger 1 (Fig. 17A–C), other cirri absent or lost; ventral cirri short, wider at base then tapered, inserted in middle of parapodium. No elongated parapodial glands observed, but most specimens with fleshy looking posteroventral area of parapodia that might contain glands (Fig. 17E).

Setae emerging in fan-shaped fascicle from distal tip and ventral face of parapodium, all setae compound, with long heterogomph shafts measuring from ca. 70 µm up to 240 µm, shafts equal in length to blade or may be up to 4 times as long as blade, this especially noticeable in posterior setigers. Blades ranging in length from short falcigers 36–60 µm with blunt, rounded tip in ventral position to long spiniger-like blades up to 120 µm with fine, pointed tips, in dorsal position (Fig. 17E); all blades serrated. Setiger 1–5 of holotype with ca. 30 or more setae, becoming less numerous moving posteriorly; setiger 10 with ca. 15–20 setae; other, smaller, specimens with many fewer setae per setiger. Parapodia each with 3–4 aciculae, not emerging but forming anterior and posterior bumps at distal end of parapodia; one acicula with bent tip, others pointed.

Pygidium with four cirri: two large oval glandular lateral cirri and two ventromedial, filiform cirri (Figs. 16A, D; 17B, F).

Reproductive features. Several specimens had eggs moving into the parapodia after setiger 5; these eggs were not measured as they were distorted in the parapodia and eggs in the coelom were indistinct.

Remarks. *Anguillosyllis taleola* **n. sp.** is similar to *A. palpata* in having dorsally separate palps and an obvious nuchal patch; but differs in having 10 rather than 11 setigers, lacking posterior parapodial lobes, and having plain rather than hooked tips on the falcigers. *Anguillosyllis taleola* **n. sp.** is similar to *A. denaria* **n. sp.** in having 10 setigers, but *A. denaria* **n. sp.** has palps that are fused halfway rather than completely separate and has large glandular posterior parapodial lobes that are absent in *A. taleola* **n. sp.** The nuchal patches of *A. taleola* **n. sp.** are large and obvious rather than inconspicuous as in *A. denaria* **n. sp.** Similarly, *A. taleola* **n. sp** is similar to *A. sepula* **n. sp.** in having 10 setigers and lacking posterior parapodial lobes, but *A. sepula* **n. sp.** (see next section) has completely fused palps and setae with shafts that are shorter relative to blade length. *Anguillosyllis taleola* **n. sp.** is also similar to *A. denaria* **n. sp.** and *A. carolina* **n. sp.**, both of which have 10 setigers, in having a two-part appearance to the prostomium, with a smaller medial portion surrounded by an inflated area that bears the antennae.

Anguillosyllis taleola **n. sp.** differs from most other *Anguillosyllis* species in having setae with very long shafts relative to the blade length (Table 3). The shafts may be equal in length to the longest blades or up to four times the length of the shortest blades. In other species of *Anguillosyllis*, the shafts are not as long relative to blade length; in *A. palpata* the shafts may be up to three times as long as the blades but in other species they may be up to only as twice as long.

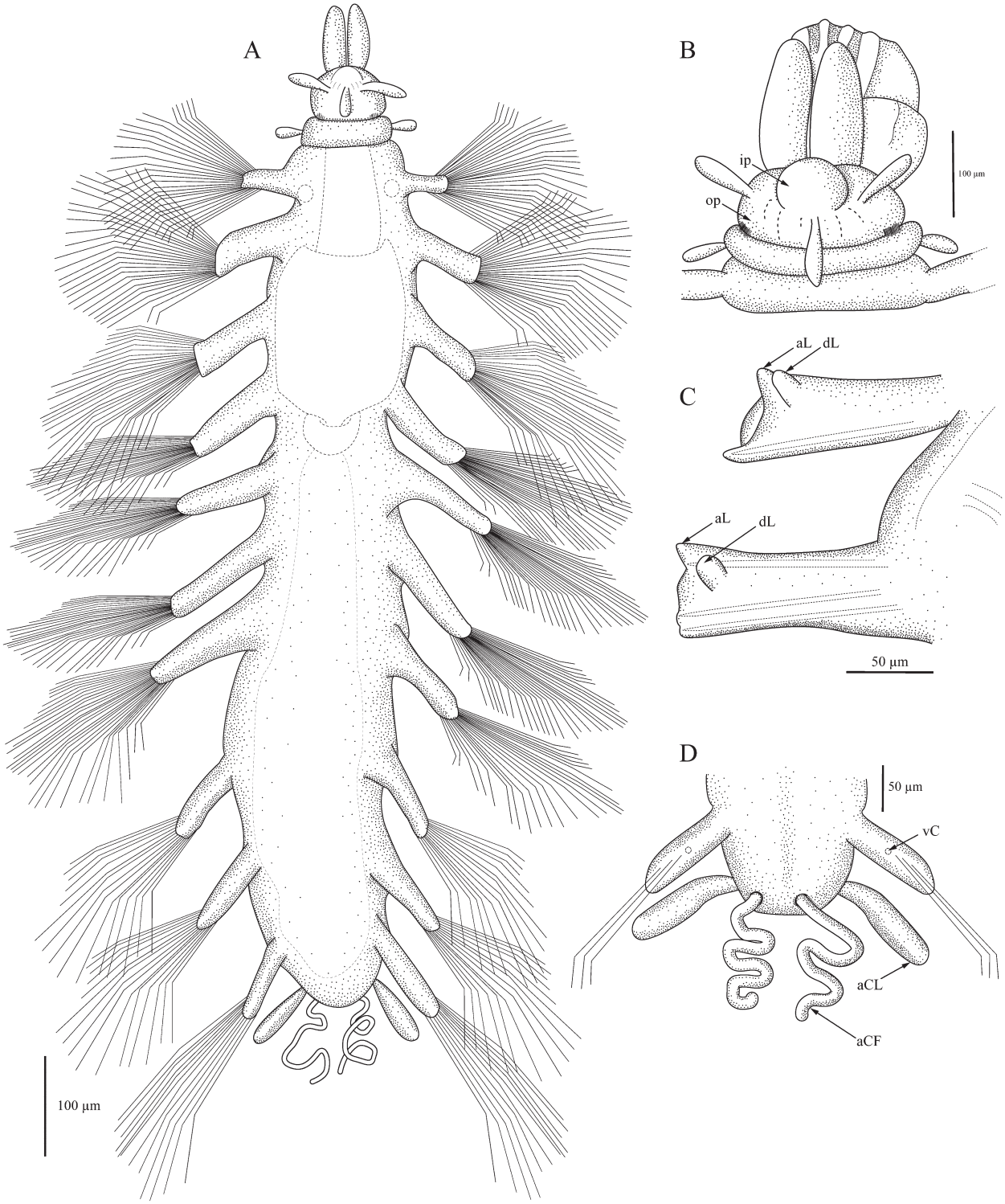

FIGURE 16. ***Anguillosyllis taleola*** **n. sp.** Paratype (MCZ 150598): A, entire specimen, dorsal view. Holotype (MCZ 150597): B, prostomium and peristomium, dorsal view; C, setigers 2–3, dorsal view; Paratype (MCZ 150598): D, setiger 10 and pygidium, ventral view. Abbreviations: aCL—anal cirrus lateral, aCF—anal cirrus filiform, aL—anterior lobe, dL—dorsal lobe, ip—inner prostomium, op—outer prostomium, vC, insertion point of ventral cirrus.

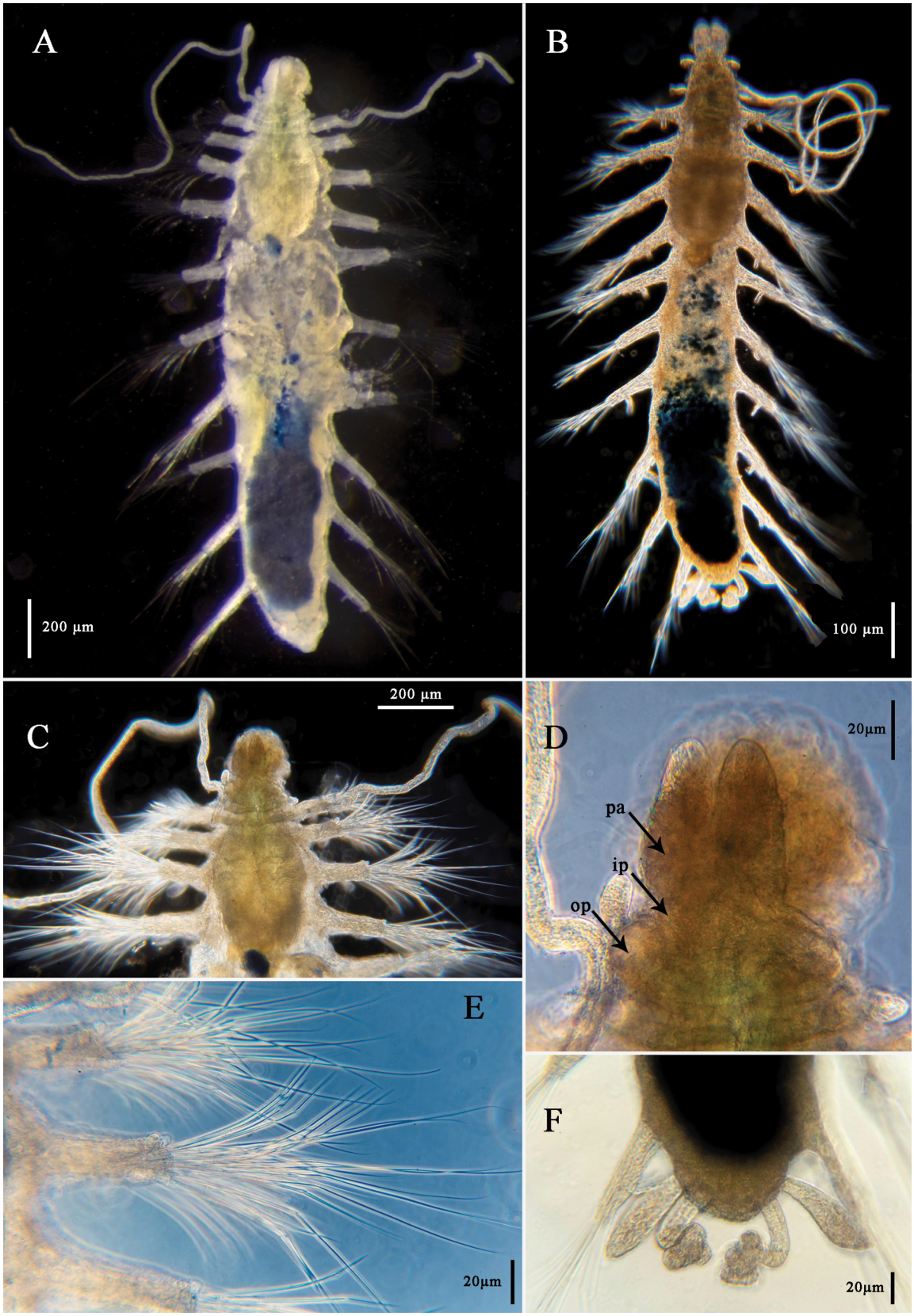

FIGURE 17. ***Anguillosyllis taleola*** **n. sp.** Holotype (MCZ 150597): A, entire specimen, dorsal view. Paratype (MCZ 150598): B, entire specimen, ventral view. Holotype (MCZ 150597): C, anterior end, dorsal view; D, palps, inner and outer prostomium, and peristomium, dorsal view; E, setigers 2–4, dorsal view; F, posterior end, ventral view. Dark spot near base of proventricle in A and C is stained ingested material rather than cells of post-ventricle caeca. Abbreviations: pa—palp, ip—inner prostomium, op—outer prostomium.

Etymology. The specific name, *taleola*, is the diminutive of the Latin *talea*, for slender staff or rod; it refers to the relatively long shafts of the setae in this species.

Records. South China Sea, off Brunei; 1294–1958 m.

TABLE 3. Examples of ratio of setal shafts to blade length in *Anguillosyllis taleola* **n. sp.**

Specimen	Setiger	Shaft (µm)	Blade (µm)	Shaft:Blade Ratio
MCZ 150600	1	70	70	1:1
	2	85	110	0.8:1
	3	110	60	1.8:1
	6	144	120	1.2:1
	6	144	36	4:1
	9	120	60–120	2:1 to 1:1
MCZ 150601	8	180	110	1.6:1
	9	195	65	3:1
	9	240	110	2.2:1

Anguillosyllis truebloodi n. sp.

Figures 18–19

urn:lsid:zoobank.org:act:5D921292-4799-4AAD-B5FE-FDF6AFE64FB9

Material examined. Abyssal Pacific Ocean, Clarion-Clipperton Fracture Zone. *(8 specimens from 4 samples, 3 stations)* Coll. Dwight D. Trueblood for NOAA. Sta. 4-93, 11 August 1993, 12°55.595′N, 128°35.943′W, 4861 m, 2 **paratypes** (USNM 1480275). Sta. 12-93, 4 Sep 1993, 12°56.329′N, 128°35.698′W, 4851 m, 1 specimen (NJM). Sta. 1-94, 25 July 1994, 12°55.788′N, 128°35.843′W, 4851 m, **holotype** (USNM 1480273) and 2 **paratypes** (USNM 1480274). NOAA DOMES Site C, coll. R.R. Hessler, ECHO I, sample H351, nodule wash, Sandia box corer, 14 June 1983, 14°37.63′N, 125°26.38′W, 4516 m, 1 specimen (LACM-AHF Poly 10168).

Description. Body with 11 setigers (Fig. 18A); holotype measuring 1.2 mm long, 0.25 mm wide without parapodia, 0.6 mm wide with parapodia but without setae; other specimens less than 1.0 mm. Palps short, fused halfway to base, median furrow to base visible under high magnification, tips rounded, free and slightly divergent. Prostomium wider than long, oval, almost rectangular; eyes lacking; three club-shaped antennae in transverse row, lateral antennae slightly anterior to medial antenna. Peristomium with two tentacular cirri, smaller than prostomial antennae; peristomium not clearly visible on some specimens; nuchal cilia may be present between prostomium and peristomium but not obvious. Eversible pharynx with distal ring of 10 soft papillae. Proventricle in 2–3 setigers, barrel-shaped, anterior margin straight, posterior end slightly tapered (Fig. 18A); muscle rows not clearly apparent; post-ventricle caeca with dorsal gland cells lacking or not retaining MB stain.

Parapodia uniramous, elongated, rectangular, length equal to or greater than body width (Fig. 18A); small anterior lobe increasing in size through setiger 5 then decreasing through end of body; small posterior lobe from setiger 2, becoming increasingly larger through setiger 7, remaining large through last several setigers; dorsal lobe increasing in size through setiger 5 or 6, thereafter decreasing in size, usually curled dorsally (Fig. 18B, D–E). Parapodia from setiger 4 to end of body with increasing number of oval to round glands concentrated near distal tips and in dorsal parapodial lobes (Figs. 18D–E, 19A–C), glands retaining MB stain. Dorsal cirri mostly lost, those present thin, smooth, filiform; basal cirrophores visible on all setigers, including setiger 2. Ventral cirri inserted on distal half to quarter of parapodia, with wider base tapering to narrower tip.

All setae compound with long heterogomph shafts, with short to very long blades; falcigers with serrated blades 20–50 µm long, tip slightly hooked (Fig. 18C), spiniger-like blades up to 200 µm, clearly serrated at base, becoming very fine near plain tips. Largest specimen with 20–22 setae per parapodium, most emerging from distal end and a few emerging from ventral face of parapodium. Two stout, pointed aciculae per parapodium, seen most clearly starting from setiger 6.

Pygidium damaged on all specimens, but with at least one short filiform ventromedial cirrus, additional cirri likely lost.

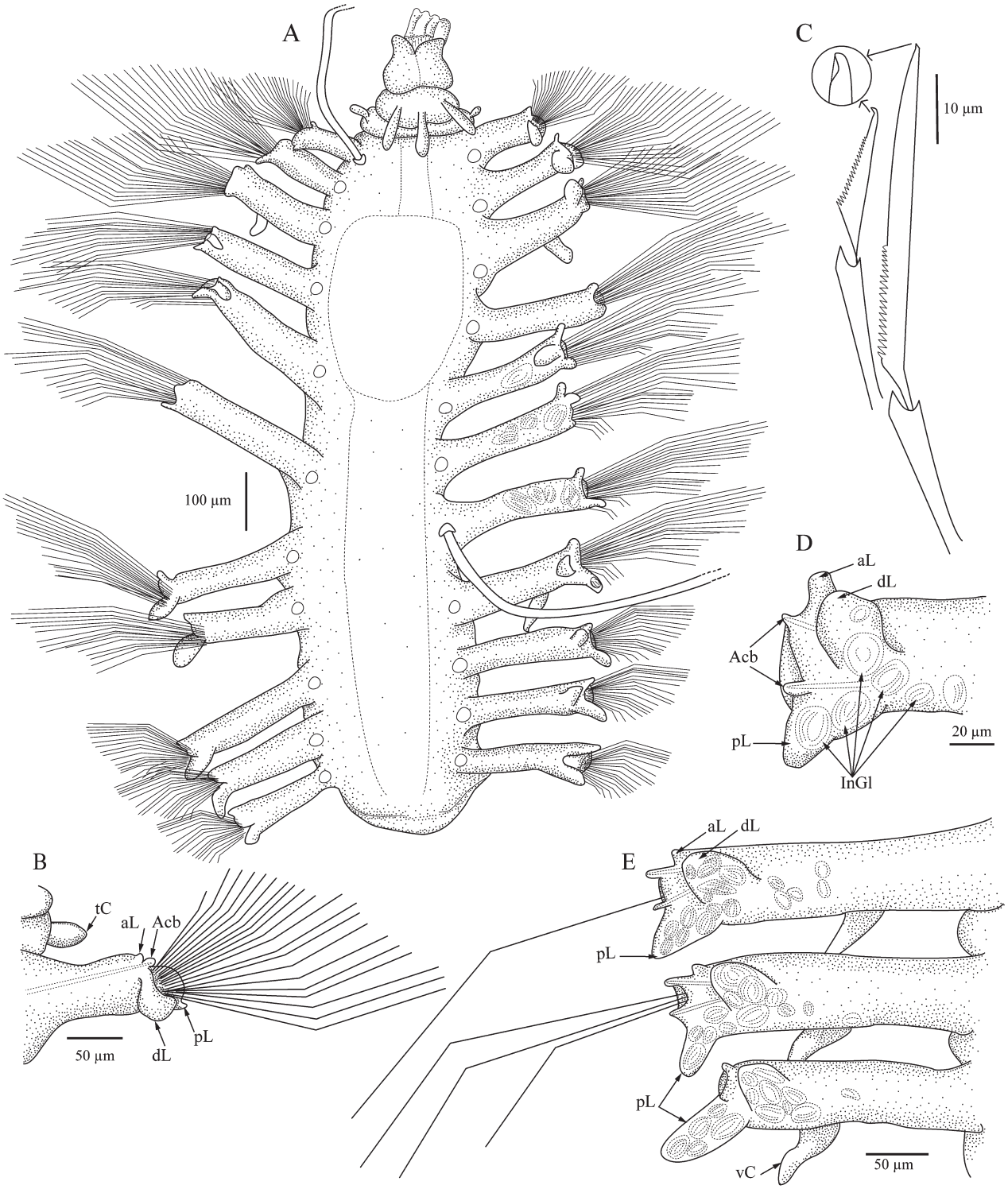

FIGURE 18. ***Anguillosyllis truebloodi*** **n. sp.** Holotype (USNM 1480273): A, entire specimen, dorsal view; B, setiger 1, dorsal view; C, falcigers, inset not to scale; D, setiger 8, dorsal view; E, setigers 9–11, dorsal view. Abbreviations: Acb—acicular bump, aL—anterior lobe, dL—dorsal lobe, InGl—internal gland, pL—posterior lobe, vC—ventral cirrus.

Remarks. *Anguillosyllis truebloodi* **n. sp.** is similar to *A. capensis* in having dorsal cirri (or indications of those cirri) on setiger 2 and posterior parapodial lobes; the two species differ in their overall size, with *A. capensis* reported to be up to 3.5 mm long and *A. truebloodi* **n. sp.** only one-third that size, and in the length and degree of fusion of the palps, which are longer and fused for more of their length in *A. capensis* compared with shorter and fused only halfway in *A. truebloodi* **n. sp**. *Anguillosyllis truebloodi* **n. sp.** is also similar to *A. denaria* **n. sp.** in the shape

and degree of fusion of the palps: in both species, the palps are fused both dorsally and ventrally for at least half their length. However, *A. truebloodi* **n. sp.** has 11 setigers whereas *A. denaria* **n. sp.** has 10 setigers. *A. truebloodi* **n. sp.** also differs from the remaining 11-setiger species in the degree of fusion of the palps, with those of *A. aciculata* **n. sp.**, *A. acsara* **n. sp.**, *A. hadra* **n. sp.**, *A. hampsoni* **n. sp.**, and *A. palpata* appearing free dorsally although possibly fused ventrally, and in having a large number of round walnut-shaped glands rather than elongated glands concentrated in the dorsal and posterior lobes of the parapodia. Recovered from the CCFZ, *Anguillosyllis truebloodi* **n. sp.** is the deepest-occurring species examined in the study, overlapping with *A. palpata*, *A. hessleri* **n. sp.**, and additional species that cannot be fully described due to the poor nature of the material.

With the exception of the holotype, the material is in very poor condition; while the anterior (head) region on all specimens allowed confirmation of the structures seen on the holotype, the remaining segments were somewhat decomposed.

Etymology. This species is named for Dr. Dwight D. Trueblood, who collected the majority of the specimens and made them available for study.

Records. Abyssal Pacific, 4516–4861 m.

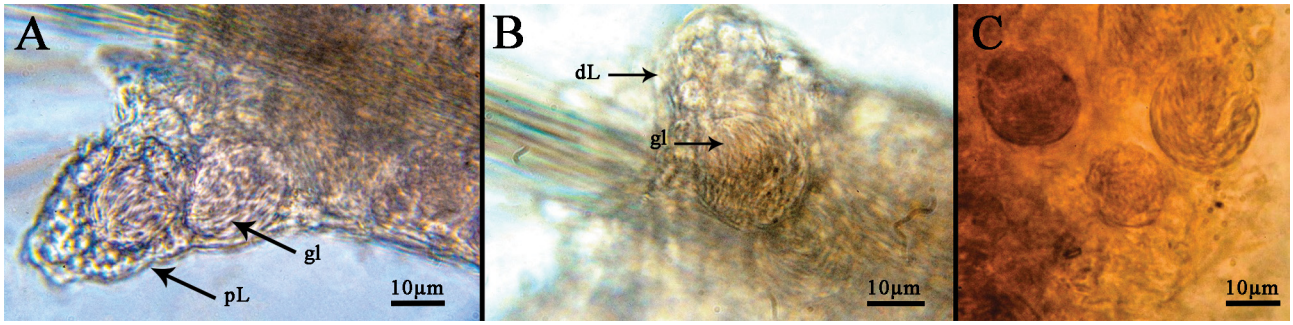

FIGURE 19. ***Anguillosyllis truebloodi*** **n. sp.** Holotype (USNM 1480273): A, setiger 8, glands in posterior lobe; B, setiger 8, gland in dorsal lobe; C, close up of glands. Stained with Shirlastain A. Abbreviations: dL—dorsal lobe, gl—gland, pL—posterior lobe.

Anguillosyllis species with palps completely fused

Anguillosyllis andeepia n. sp.

Figures 20–21

urn:lsid:zoobank.org:act:BA33786A-A665-40C1-AE6E-1CBA34BEB6FA

Material examined. South Atlantic Ocean, abyssal plain, South of Meteor Rise *(1 specimen from 1 station)* Coll. S. Doner ANDEEP III, Sta. PS67/21-3, 29 Jan 2005, 47°40.05′S, 4°14.84′E, large box corer, 4551 m, **holotype** (SMF 24863).

Description. Body with 8 setigers (Figs. 20A, 21A), colorless; holotype slightly longer than 1 mm without anal cirri, 0.2 mm wide without parapodia, 0.5 mm wide with parapodia but excluding setae; posterior appearing somewhat wide and flat due to distortion by eggs. Palps elongated, completely fused, narrowing to softly pointed anterior margin, with faint internal indication of median furrow; prostomium dome-shaped, not well demarcated from palps, with three antennae in transverse row; eyes lacking; peristomium 0.6 mm long, 1.5 times longer than prostomium (Figs. 20A, C; 21A), with two short oval tentacular cirri. No nuchal cilia visible even when specimen stained with Shirlastain A. Proventricle in two setigers, bluntly barrel-shaped anteriorly, slightly tapered posteriorly, rows of muscle cells indistinct (Figs. 20A, 21A).

Parapodia uniramous, shortest on setiger 1, becoming longer, rectangular over next few setigers; very small anterior lobe present on all setigers; posterior lobe smallest on setiger 1, becoming much larger through setiger 7, then slightly smaller on setiger 8 (Figs. 20B, 21B); dorsal lobe rounded; parapodia without internal glands. Dorsal cirri lost, basal cirrophores present on setigers 1, 3–8; ventral cirri short, digitiform, inserted in middle of parapodium.

All setae compound with heterogomph shafts; setiger 1 with 18–20 setae, setiger 2 with 20–22 setae, remaining setigers with similar numbers, fewer setae in setiger 8. Several setae emerging from distal tip of parapodium, others from ventral face of parapodium; ventral-most blades shortest, 25–50 µm, terminating in pointed tips; longer blades

85–110 µm, with long, fine, drawn-out tips; blades possibly with very fine serrations in proximal portion (difficult to see in light microscope even at 1500x). Parapodia each with two thick, bluntly pointed golden aciculae, not protruding but forming anterior and posterior bumps at distal end of parapodia.

Pygidial cirri lost.

Oocytes in coelom of setigers 5/ 6–8 (Fig. 21A), measuring 65–80 µm greatest diameter; some oocytes entering or within parapodia.

Remarks. *Anguillosyllis andeepia* **n. sp.** is unique in the proportions of the peristomium, which is 1.5 times the length of the prostomium and much longer than typical *Anguillosyllis* peristomia; it is also one of only two species encountered in this study that are reproductively mature with eight setigers. The completely fused palps align it with the group of species with similar palps. Of those, four species in addition to *A. andeepia* **n. sp.** have large posterior lobes on the parapodia: *A. denaria* **n. sp.** from the South China Sea, which has 10 setigers and elongated, slightly rounded palps; *A. pupa* from the North Atlantic, which has nine setigers and low, rounded palps; an unnamed 9-setiger species from the CCFZ, and *A. bruneiensis* **n. sp.** from the South China Sea, which also has eight setigers but has anteriorly rounded palps. In addition to differences in palp structure, all four species have a peristomium that is shorter than the prostomium, in contrast to the deep peristomium of *A. andeepia* **n. sp.**

Etymology. This species name is based on ANDEEP, the acronym for the expedition to study deep-sea biodiversity in Antarctica.

Records. Antarctica, 4551 m.

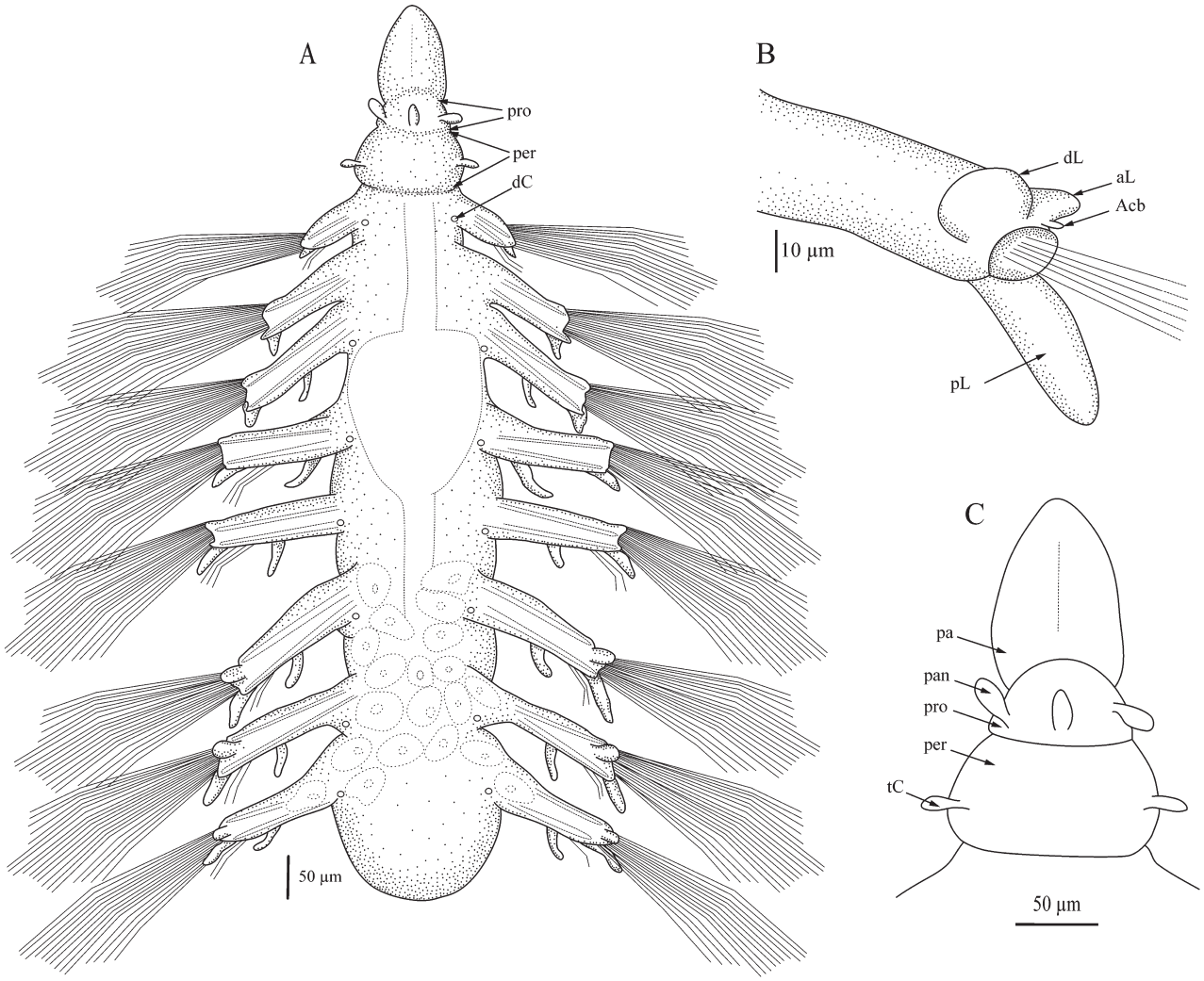

FIGURE 20. ***Anguillosyllis andeepia*** **n. sp.** Holotype (SMF 24863): A, entire specimen, dorsal view; B, setiger 1; C, prostomium and peristomium, dorsal view, segments delineated. Abbreviations: Acb—acicular bump, aL—anterior lobe, dC—dorsal cirrus, dL—dorsal lobe, pa—palp, pan—prostomial antenna, per—peristomium, pL—posterior lobe, pro—prostomium, tC—tentacular cirrus.

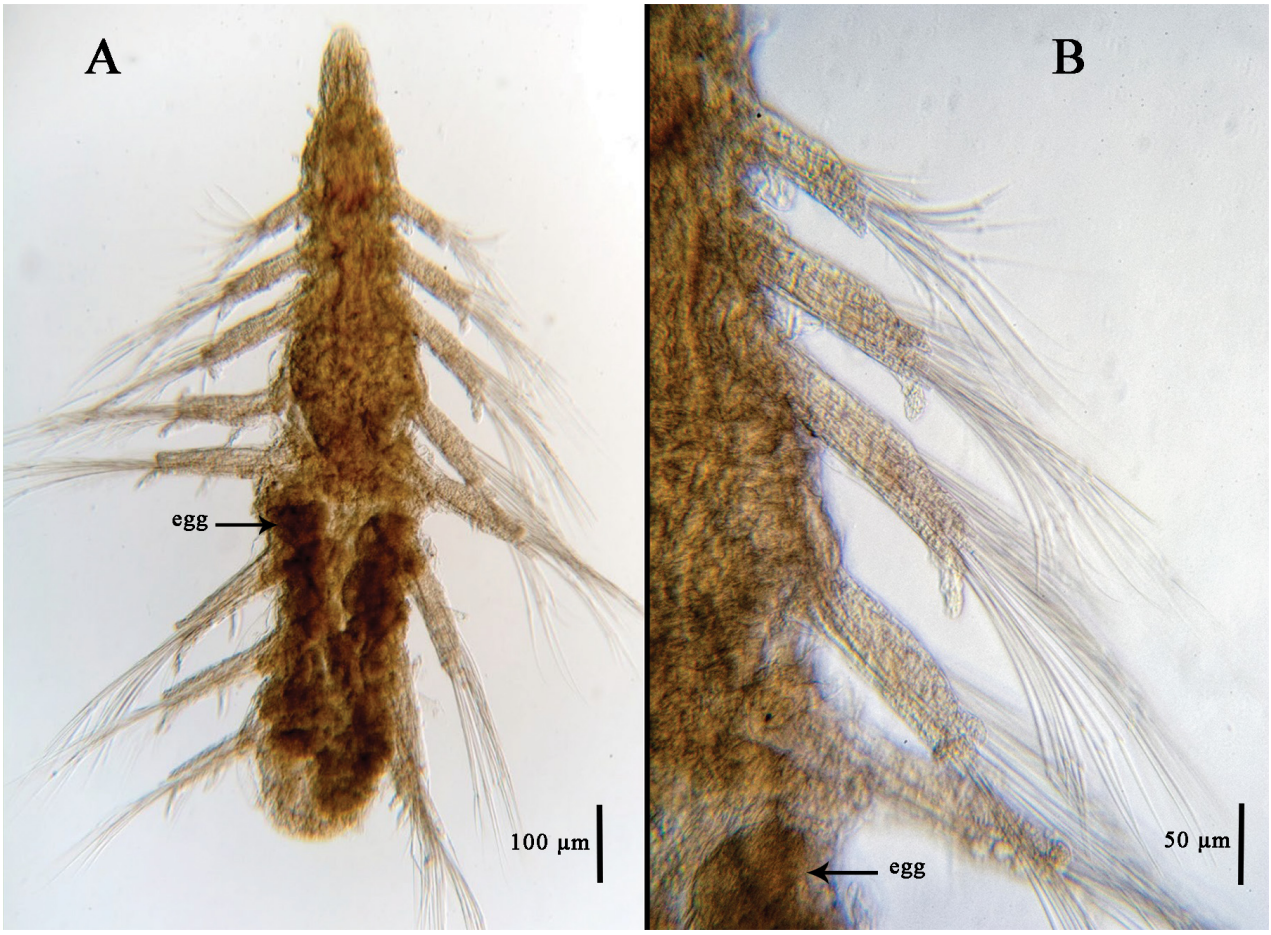

FIGURE 21. ***Anguillosyllis andeepia*** **n. sp.** Holotype (SMF 2463): A, entire specimen, dorsal view; B, setigers 1–5, right side, dorsal view.

Anguillosyllis blakei **n. sp.**
Figures 22–23
urn:lsid:zoobank.org:act:DB1D9215-3368-405B-88A6-37AAE08EEF8C

Braniella sp. 1: Hilbig & Blake 2006: 269.

Material examined. *(51 specimens from 8 samples, 8 stations)* **Gulf of the Farallones, California continental slope. EPA 102 Site Survey**, **south of Pioneer Canyon,** R/V *Point Sur*, coll. J.A. Blake. Sta. 3-7, 14 Sep 1991, 37°27.44′N, 123°19.50’W, 1675 m, 1 specimen (LACM-AHF Poly 10446); Sta. 3-12, 15 Sep 1991, 37°25.03′N, 123°18.00′W, 1745 m, 1 specimen (LACM-AHF Poly 10447); Sta. 4-2, 18 Sep 1991, 37°15.29′N, 123°07.13′W, 995 m, 1 specimen (LACM-AHF Poly 10448); Sta. 4-5, 17 Sep 1991, 37°13.54′N, 123°16.26′W, 1820 m, 6 specimens (LACM-AHF Poly 10449); Sta. 4-10, 17 Sep 1991, 37°11.26′N, 123°15.26′W, 1760 m, **holotype** (LACM-AHF Poly 10443), 6 **paratypes** (LACM-AHF Poly 10444), 11 **paratypes** (LACM-AHF Poly 10445); Sta. 4-12, 17 Sep 1991, 37 10.78′N, 123 09.87′W, 1480 m, **paratype** (LACM-AHF Poly 10450); Sta. 4-13, 17 Sep 1991, 37°10.34′N, 123°10.78′W, 1730 m, 9 specimens (LACM-AHF Poly 10451); Sta. 4-15, 19 Sep 1991, 37°12.42′N, 123°15.81′W, 1730 m, 14 **paratypes** (LACM-AHF Poly 10452).

Description. Body with 10 setigers (Figs. 22A, 23A), colorless; holotype complete, 1.4 mm long without anal cirri, 0.2 mm wide without parapodia, 0.6 mm wide with parapodia but excluding setae; other specimens maximum length 2 mm, maximum width with parapodia 0.75 mm. Palps elongated, completely fused, slightly wider at base, narrowing to weakly pointed anterior margin(Fig. 22A), indication of median furrow reaching to base on some specimens (Fig. 23B); prostomium oval, with three antennae in transverse row, eyes lacking; peristomium shorter

than either prostomium or setiger 1, with two short oval tentacular cirri. Nuchal cilia present as small patch between prostomium and peristomium. Eversible pharynx distally surrounded by 10–12 soft papillae, tooth absent. Proventricle in 2.5–4 setigers, bluntly barrel-shaped anteriorly, tapered posteriorly (Figs. 22A, 23C); ca. 20–25 rows of muscle cells; post-ventricle caeca with dorsal circlet of cells retaining faint MG stain.

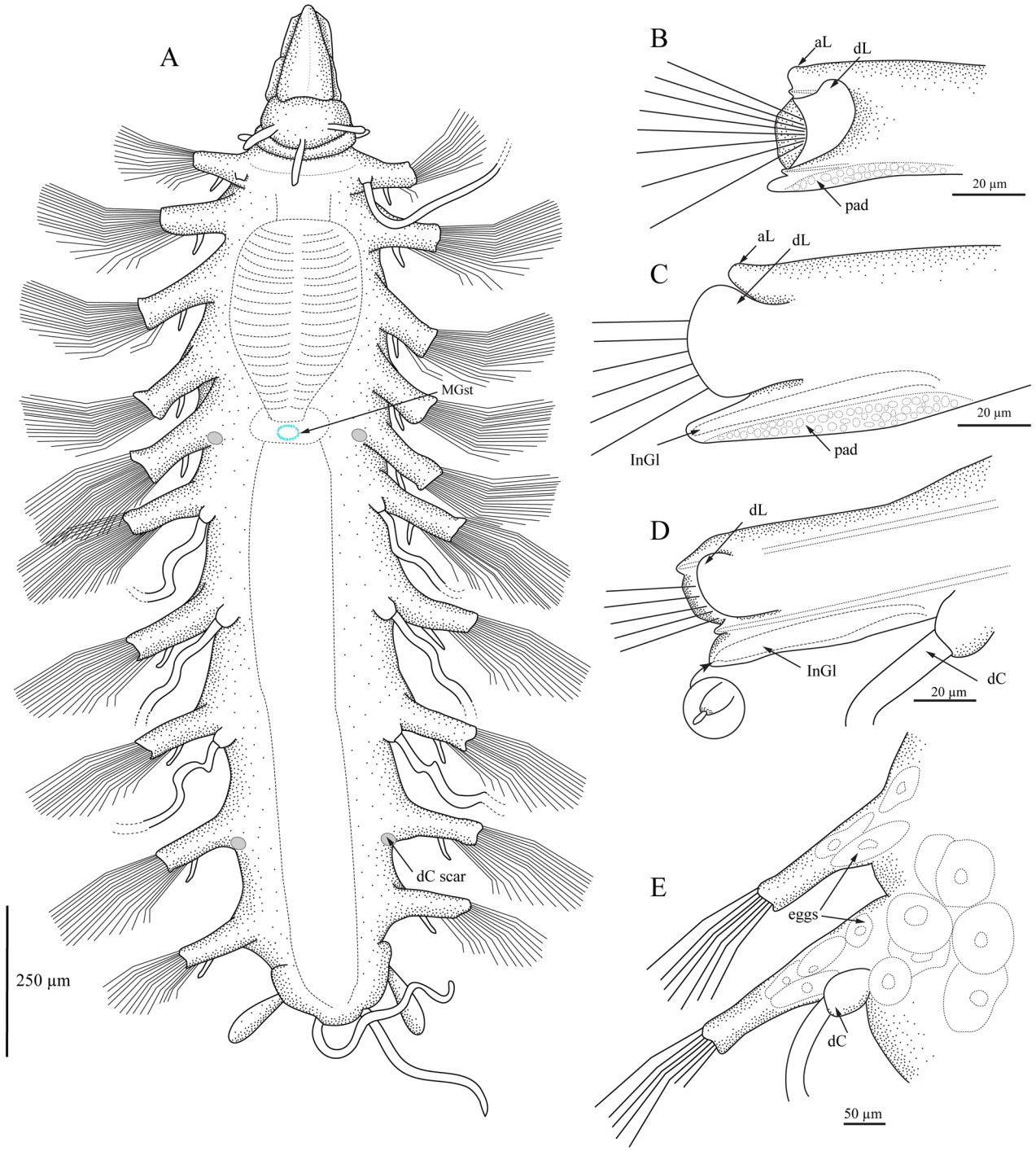

FIGURE 22. ***Anguillosyllis blakei*** **n. sp.** Holotype (LACM-AHF 10443): A, entire specimen, dorsal view. Paratype (LACM-AHF 10444): B, setiger 1, dorsal view, dorsal lobe folded back; C, setiger 2, dorsal view, dorsal lobe extended laterally. Holotype (LACM-AHF 10443): D, setiger 6, dorsal view, inset not to scale. Paratype (LACM-AHF 10444): E, setigers 7 and 8, dorsal view. Abbreviations: aL—anterior lobe, dC—dorsal cirrus, dCscar— dorsal cirrus scar, dL—dorsal lobe, InGl—internal gland, MGst—cells stained with Methyl Green.

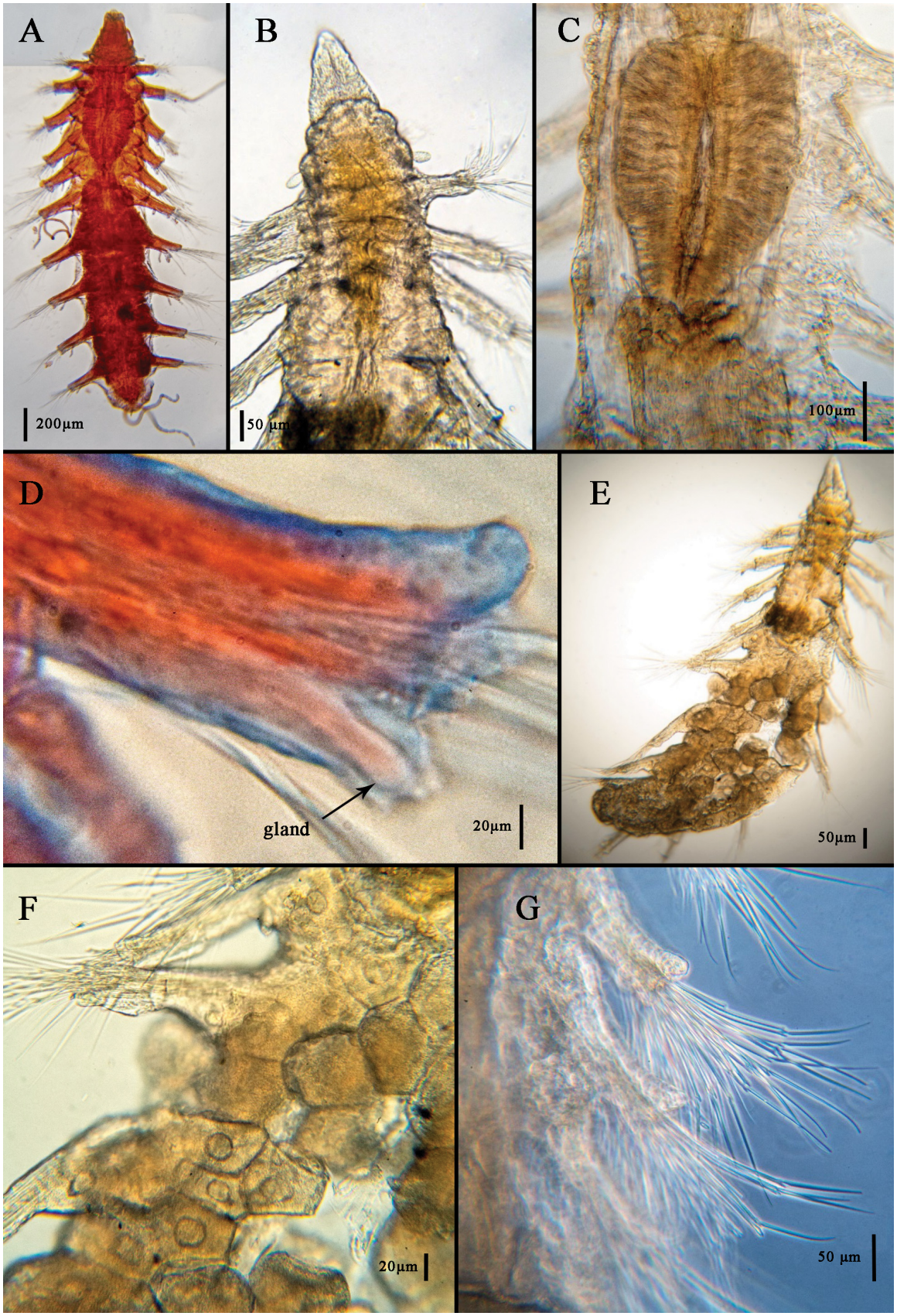

FIGURE 23. ***Anguillosyllis blakei*** **n. sp.** Holotype (LACM-AHF 10443): A, entire specimen, ventral view. Paratype (LACM-AHF 10452): B, anterior end, dorsal view. Paratype (LACM-AHF 10450): C, proventricle, dorsal view. Holotype (LACM-AHF 10443): D, large gland in setiger 8. Paratype (LACM-AHF 10452): E, entire specimen with eggs, dorsal view, damaged; F, eggs in setigers 6–8; Paratype (LACM-AHF 10450): G, setigers 3–5.

Dorsum biannulate on setiger 1 and sometimes setiger 2, anterior ring shorter. Parapodia uniramous, shortest on setiger 1, becoming elongated, rectangular over next few setigers, then slightly shorter again on setigers 9–10; very small anterior lobe present (Fig. 22B–C); dorsal lobe obvious, largest on several anterior and middle setigers (Fig. 22B–C), smaller posteriorly; posterior lobes absent; pad of cells that retain MG stain on posterior portion of parapodia (Fig. 22B–C). Single large golden tubular gland in all setigers, largest and most obvious in middle and posterior parapodia (setigers 5–9) (Figs. 22D, 23D), gland with elongated nipple-like structure at distal end (Fig. 22D inset). Dorsal cirri long, filiform, observed on setigers 1, 6, 7, 8, and sometimes 9; with basal cirrophores (Fig. 22D–E). Ventral parapodial cirri triangular to digitiform, inserted in middle of parapodium.

All setae compound with heterogomph shafts; number of setae per parapodium increasing through setiger 6 then decreasing in posterior setigers: setiger 1 with 14–20 setae, setiger 2 with 20–22, setiger 6 with 24–25, setigers 9–10 with up to 15 setae. Several setae emerging from distal tip of parapodium, remaining setae emerging from ventral face of parapodium between insertion of ventral cirrus and distal tip (Fig. 23G). Ventral falcigers with blunt-tipped blades measuring 12–25 µm, blades of distal spiniger-like setae long, thin, with finely tapered tips, measuring ca. 70 µm long in setiger 1, becoming longer in subsequent setigers, up to ca. 130 µm. All blades with fine proximal serrations. Parapodia each with two aciculae, not protruding but forming anterior and posterior bumps at distal end of parapodia; anterior acicula heavy, golden; posterior acicula less obvious.

Pygidium with two ventromedial, long, thin, filiform cirri and two lateral oval cirri; these often lost, but seen in various combinations, holotype with two filiform ventromedial cirri remaining (one lost during reexamination).

Reproductive specimens with oocytes in coelom of setigers 6–9 (Fig. 23E–F), oocytes measuring 50–115 µm greatest diameter (largest one is outlier, ave.=75.7 ± 14.6 µm, median diameter = 70 µm, n=18);some oocytes entering or within parapodia (Figs. 22E, 23E–F).

Remarks. Of the 51 specimens of *A. blakei* **n. sp.** examined in this study, all retained dorsal cirri on the first setiger and the majority had cirri on setigers 6–8 and sometimes setigers 5 and/or 9. Basal cirrophores were noted on the dorsal cirri and were seen on those setigers where the cirri had broken off; however, cirrophores were not seen on setigers 2–4 or 10, suggesting that cirri may be entirely absent from those setigers. A few specimens had fewer than 10 setigers and these are thought to be juveniles of the species. The smallest of these (Sta. 4-10, 7 setigers, 0.6 mm long) had palps that were somewhat softly rounded rather than the narrow and pointed palps of the larger specimens; also, the proventricle occupied only two setigers.

The single tubular gland in the posterior portion of middle and posterior parapodia is distinctively large and clear, often appearing golden in color; it appears to open externally through a nipple-like structure. A similar gland is seen in *A. sepula* **n. sp.**, described below, but in that species the gland is deep in the parapodium and obscured by a sheath of cells that stain with MG; whereas, in *A. blakei* **n. sp.**, the pad of cells is posterior to the gland and does not obscure it.

Other *Anguillosyllis* species with ten setigers include four from the South China Sea: *A. taleola* **n. sp.** and *A. denaria* **n. sp.**, which have large posterior lobes rather than lacking then as in *A. blakei* **n. sp.**; *A. elegantissima* **n. sp.**, which has unique heterogomph setal shafts that differ from those in *A. blakei* **n. sp.**; and *A. sepula* **n. sp.**, which lacks biannulation on setigers 1 and 2, has much larger eggs, and is generally a more robust species with palps that are wider anteriorly and have a defined medial notch. *Anguillosyllis lanai* from Brazil also has 10 setigers, but lacks the biannulation of setigers 1 and 2, has fewer setae that reach a greater length, lacks anterior lobes on the parapodia, has a smaller proventricle with half the number of muscle rows (1.5–2 setigers with ca. 12 rows in *A. lanai* vs. 2.5–4 setigers with ca. 20–22 rows in *A. blakei* **n. sp.**), and lacks the large internal tubular glands of *A. blakei* **n. sp.**

Etymology. This species is named in honor of Dr. James A. Blake, who collected the specimens and recognized them as an undescribed species.

Records. California continental slope, 995–1820 m.

Anguillosyllis bruneiensis n. sp.

Figure 24

urn:lsid:zoobank.org:act:7D6CD1C1-18EA-4F91-8C06-380881C6E3CF

Material examined. South China Sea, off Brunei. Coll. J.A. Blake. Sta. 46, 2 Jun 2011, 5°48′02.68476″N, 114°18′10.00693″E, 1234 m, 1 specimen**, holotype** (MCZ 147936).

Description. Body with 8 setigers (Fig. 24A), colorless; 1 mm long without anal cirri, 0.2 mm wide without parapodia, 0.4 mm wide with parapodia but excluding setae, posterior half distorted with eggs. Palps completely fused, anterior margin wide, softly rounded with slight medial indentation; eyes lacking; prostomium oval, with three club-shaped antennae; peristomium shorter but wider than prostomium, with two short, oval tentacular cirri. Nuchal area between prostomium and peristomium visible when stained with Shirlastain A. Proventricle in 2+ setigers, bluntly barrel-shaped anteriorly, tapered posteriorly, rows of muscle cells indistinct, ca. 20; post-ventricle caeca retaining MG stain on dorsal circlet of cells.

Parapodia uniramous, shortest on setiger 1, becoming longer, rectangular, over next few setigers; small anterior lobe present on all setigers; posterior lobe small on setigers 1–2, becoming larger through setiger 8 (Fig. 24A); dorsal lobe not observed; large clear cell or gland present in parapodium near base of ventral cirrus. Dorsal cirri present on setigers 4–7, others lost but basal cirrophores present on setigers 1, 3, and 8; ventral cirri short, digitiform, inserted in middle of parapodium.

All setae compound with heterogomph shafts; setiger 1 with 18–20 setae, setigers 2–7 with 20–22, setiger 8 with ca. 10 setae. Several setae emerge from distal tip, others from ventral face of parapodium. All blades with roughened proximal edge seen only with Phase Contrast at 1500x, terminating in pointed tips, length of blades 30–120 µm (Fig. 24B–C). Aciculae not seen.

Pygidial cirri lost, except one small oval cirrus possibly regenerating.

Oocytes in coelom of setigers 5–7, measuring 50–75 µm in greatest diameter; some oocytes entering or within parapodia (Fig. 24A).

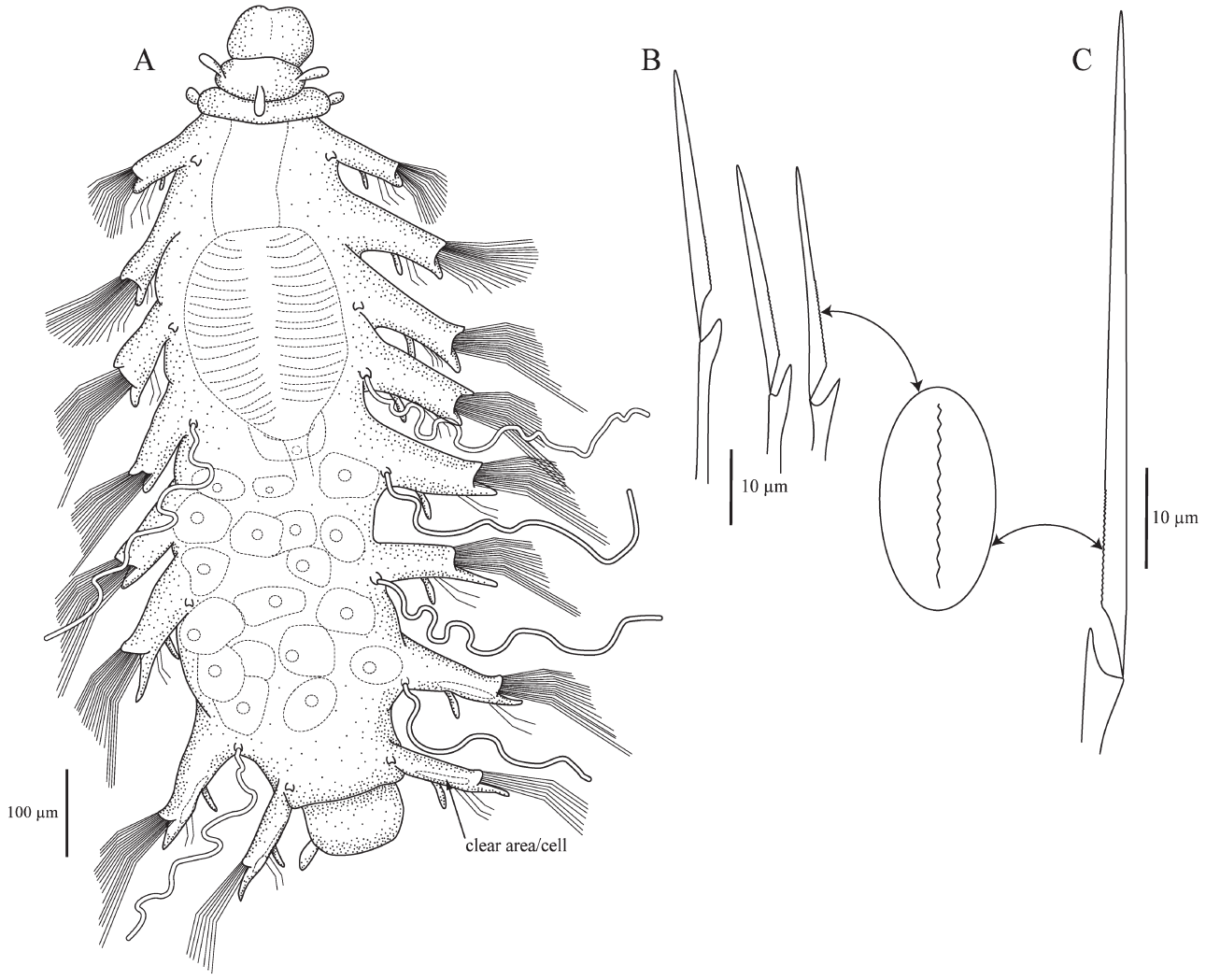

FIGURE 24. ***Anguillosyllis bruneiensis*** **n. sp.** Holotype (MCZ 147936): A, entire specimen, dorsal view; B–C, setae, inset not to scale.

Remarks. *Anguillosyllis bruneiensis* **n. sp.** from the South China Sea is, along with *A. andeepia* **n. sp.** from the Antarctic, reproductively mature with only eight setigers, thus precluding the possibility that these are juveniles of other species. The two species differ from each other principally in that *A. bruneiensis* **n. sp.** has a peristomium that is shorter rather than longer than the prostomium and fused palps that are short, wide, and anteriorly rounded rather than elongated and pointed anteriorly. Also, *A. bruneiensis* **n. sp.** lacks the obvious golden aciculae of *A. andeepia* **n. sp.**

Etymology. The species epithet reflects the collection location off Brunei in the South China Sea.

Records. South China Sea, 1234 m.

Anguillosyllis elegantissima **n. sp.**

Figures 25–26

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Material examined. (*44 specimens from 26 stations)* **South China Sea, off Brunei.** Coll. J.A. Blake, Chief Scientist: Sta. 29, 4 Jun 2011, 5°43′01.15997″N, 114°06′07.18190″E, 1537 m, **holotype** (MCZ 147937). Coll. P. Neubert: Sta. DA1, 1 Jul 2011, 5°24′13.24084″N, 113°30′31.39787″E, 1709 m, 3 **paratypes** (MCZ 147938); Sta. SA4, 29 Jun 2011, 5°36′08.70546″N, 113°40′11.51490″E, 2135 m, 2 **paratypes** (MCZ 147939); Sta. SE1, 28 Jun 2011, 5°33′07.24983″N, 113°46′11.03389″E, 1894 m, **paratype** (MCZ 147940). Coll. J.A. Blake, Chief Scientist: Sta. 25, 5 Jun 2011, 5°47′23.69441″N, 114°10′48.45326″E, 1402 m, 2 **paratypes** (MCZ 147941); Sta. 61, 31 May 2011, 5°40′32.90422″N, 114°13′15.64893″E, 1050 m, 2 specimens (MCZ 147942); Sta. WH-Jaring-SW, 4 Jun 2011, 5°43′13.87265″N, 114°08′13.15762″E, 1463 m, 1 specimen (MCZ 147943); Sta. WH-Jokit-NE, 6 Jun 2011, 5°53′28.38401″N, 114°11′57.24436″E, 1400 m, 2 specimens (MCZ 147944); Sta. WH-Jokit-SW, 5 Jun 2011, 5°46′27.76503″N, 114°07′33.98027″E, 1487 m, 4 **paratypes** (MCZ 147945). Coll. P. Neubert, Chief Scientist: Sta. AN7, 28 Jun 2011, 5°32′32.92542″N, 113°51′01.24946″E, 1585 m, 1 specimen (MCZ 147946); Sta. DA2, 1 Jul 2011, 5°24′13.64904″N, 113°28′04.25708″E, 1760 m, 2 specimens (MCZ 147947); Sta. DA4, 1 Jul 2011, 5°26′16.75004″N, 113°31′00.09025″E, 1851 m, 1 specimen (MCZ 147948); Sta. JA2, 30 Jun 2011, 5°27′55.53448″N, 113°32′57.69642″E, 1954 m, 2 specimens (MCZ 147949); Sta. JA6, 30 Jun 2011, 5°31′02.11247″N, 113°36′27.60639″E, 1999 m, 3 specimens (MCZ 147950); Sta. ME11, 25 Jun 2011, 5°20′47.88353″N, 113°33′12.39024″E, 1719 m, 2 specimens (MCZ 147951); Sta. ME14, 26 Jun 2011, 5°25′20.73778″N, 113°39′02.48164″E, 1792 m, 2 specimens (MCZ 147952); Sta. ME16, 26 Jun 2011, 5°24′24.44585″N, 113°35′28.03023″E, 1805 m, 1 specimen (MCZ 147953); Sta. SA1, 29 Jun 2011, 5°34′05.57104″N, 113°39′44.09821″E, 2075 m, 1 specimen (MCZ 147954); Sta. SA3, 3 Jul 2011, 5°35′09.05425″N, 113°38′49.25754″E, 2117 m, **paratype** (MCZ 147955); Sta. SA5, 29 Jun 2011, 5°36′56.59222″N, 113°41′07.37801″E, 2162 m, 1 specimen (MCZ 147956); Sta. SE2, 29 Jun 2011, 5°31′21.71605″N, 113°42′18.56434″E, 1955 m, 5 **paratypes** (MCZ 147957); Sta. SE5, 28 Jun 2011, 5°35′44.35485″N, 113°47′09.29726″E, 1947 m, 1 specimen (MCZ 147958); Sta. TA1, 1 Jul 2011, 5°23′48.33272″N, 113°24′08.80925″E, 1866 m, 1 specimen (MCZ 147959); Sta. TA2, 2 Jul 2011, 5°27′21.29666″N, 113°27′06.30764″E, 1981 m, 1 specimen (MCZ 147960); Sta. TA3, 1 Jul 2011, 5°24′43.00263″N, 113°23′10.96051″E, 1896 m, 2 specimens (MCZ 147961); Sta. TA5, 2 Jul 2011, 5°27′50.62360″N, 113°26′34.31837″E, 2008 m, 1 specimen (MCZ 147962).

Description. Body with 10 setigers (Figs. 25A, 26A–B) except for two juveniles with nine setigers each; up to 3.4 mm long, most specimens 1–1.5 mm long without anal cirri, holotype 2.3 mm; maximal width 1.0 mm without parapodia, 1.5 mm including parapodia but without setae; overall appearance widens from setigers 1 through 5 due to lengthening parapodia and increasingly long setae, then narrows through setiger 10. Palps long, oval, completely fused, often arched dorsally, narrowing to smoothly rounded anterior tip; palps with elongated internal structure with bulbous proximal end visible in several specimens (Fig. 25G, I); prostomium roughly oval in shape, with three club-shaped antennae in nearly transverse row, two lateral antennae only slightly anterior to medial one; eyes lacking. Peristomium shorter than following segments, with two very small rounded tentacular cirri. Nuchal cilia not evident, even when stained with Shirlastain A; small possible sense organ near lateral junction with prostomium seen on larger specimens (Fig. 26E). Eversible pharynx with three crowns, distal crown with 10 soft papillae (Fig. 25H–I); tooth absent. Proventricle in four setigers, barrel-shaped, posterior end gently (Fig. 26A) or sharply (Fig. 26B) tapered; ca. 30–35 rows of muscle cells; post-ventricle with dorsal circlet of cells retaining MG stain.

Dorsum biannulate through first three setigers, setiger 4 triannulate or quadriannulate, setigers 5–6 triannulate, annulations present but indistinct thereafter (Figs. 25A, 26D). Parapodia uniramous, short, broad, truncate on

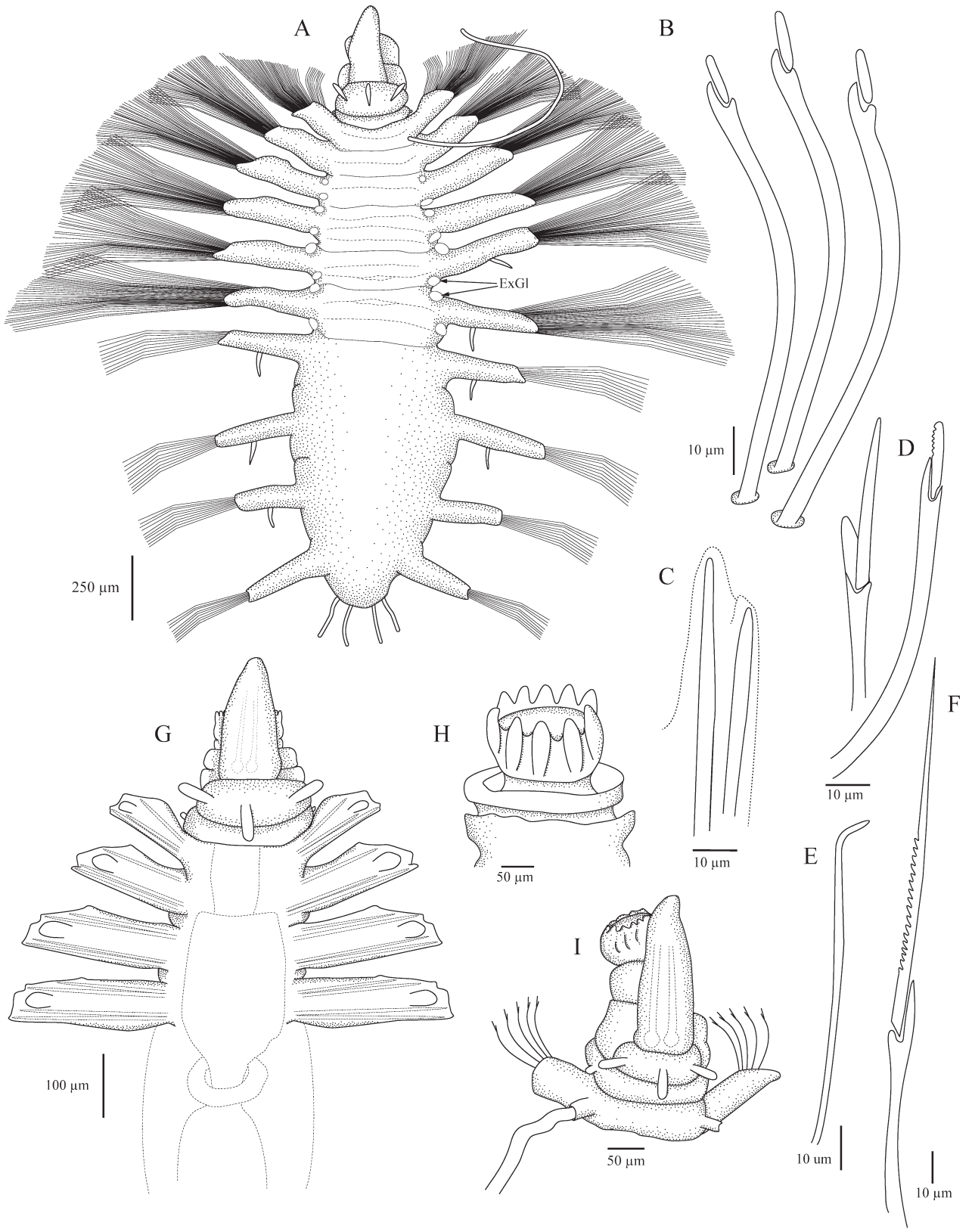

FIGURE 25. ***Anguillosyllis elegantissima*** **n. sp.** Holotype (MCZ 147937): A, entire specimen, dorsal view. Paratype (MCZ 147957): B, setae from setiger 1. Paratype (MCZ 147940): C, aciculae from setiger 3; D, setae from setiger 1; E, acicula from setiger 10; F, seta from setiger 6; G, anterior end. Paratype (MCZ 147955): H, everted pharynx. Paratype (MCZ 147957): I, anterior end, dorsal view, pharynx everted.

setiger 1, directed somewhat anteriorly (Figs. 25A, G; 26A–B, D); parapodia remaining broad but becoming longer through setiger 5, together with setae giving wide, triangular aspect to anterior body; parapodia narrower, elongated, rectangular in subsequent setigers. Parapodia with very small anterior lobe, posterior lobe absent; dorsal lobe glandular, short, rounded, most obvious on setigers 1–5 (Fig. 25G). Rounded external structures (glands?) on anterior and posterior margins of anterior parapodia (Fig. 25A, 26C). Dorsal cirri long, thin, seen only on setiger 1, possibly lost from additional setigers; ventral cirri very thin, filiform, inserted midway between body and distal end of parapodia on all setigers (Fig. 25A).

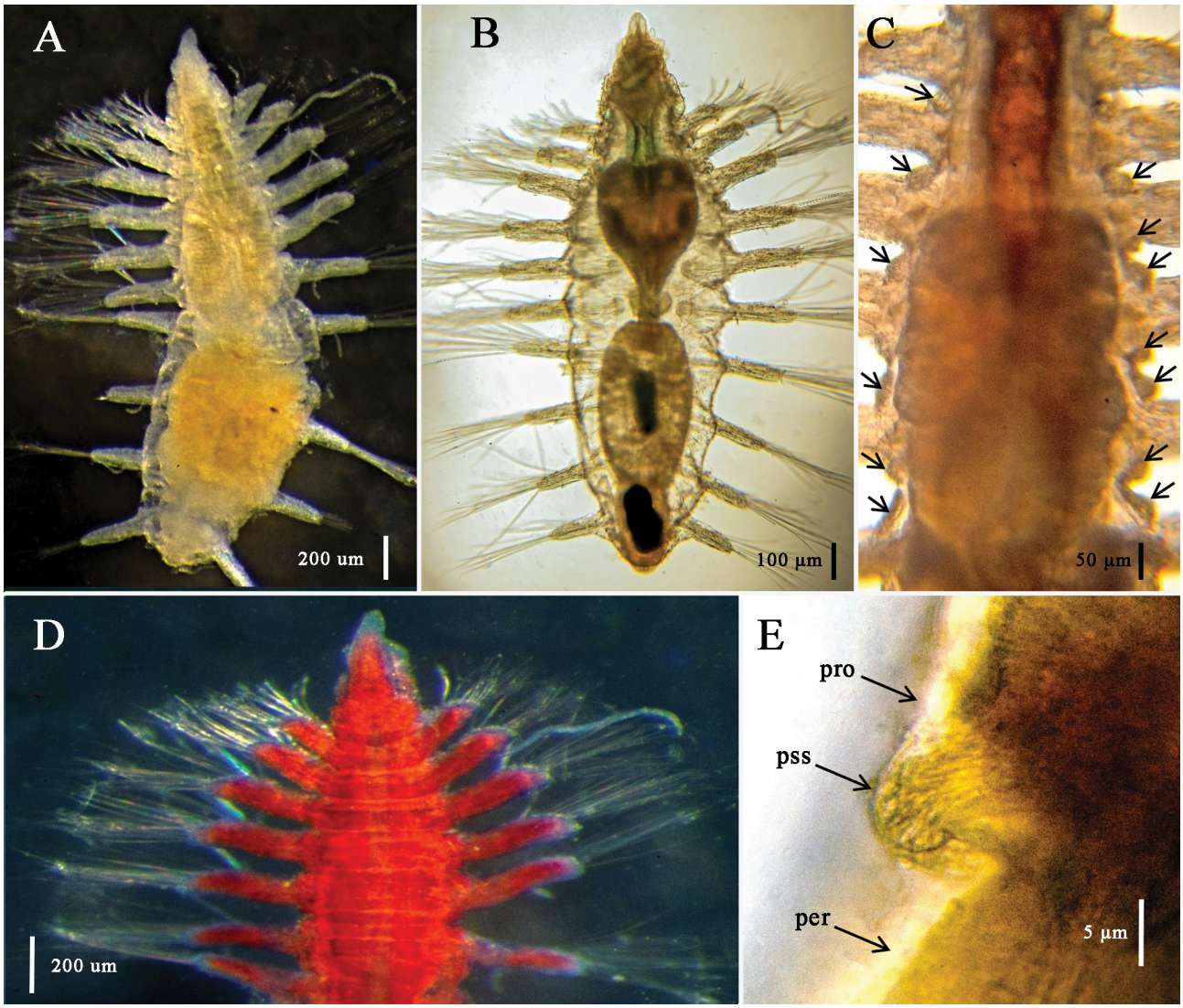

FIGURE 26. ***Anguillosyllis elegantissima*** **n. sp.** Holotype (MCZ 147937): A, entire specimen, dorsal view. Paratype (MCZ 147945): B, dorsal view; Paratype from Sta. DA-1 (MCZ 147938): C, setigers 1–6, dorsal view, arrows indicate glandular structures at anterior and posterior bases of parapodia. Holotype (MCZ 147937): D, anterior end with Shirlastain A, dorsal view, showing biannulate and triannulate segments. Paratype (MCZ 147941): E, dorsal view of possible sensory structure on prostomium. Abbreviations: per—peristomium, pro—prostomium, pss—possible sensory structure.

Setae emerging from distal end and ventral face of parapodia; ventral setae most numerous in anterior setigers, present but in reduced numbers in posterior setigers. All setae compound, with heterogomph shafts, one side measuring 3 times length of other (Fig. 25B, D). Setiger 1 with at least 50 setae: 5–10 dorsal setae with curved shafts arched anteriorly, with very short (8–10 µm) serrated falcigerous blades with rounded blunt tips (Fig. 25A, B); additional setae with shafts directed laterally, with longer (20–50 µm) blunt, serrated blades and even longer (100–120 µm) thin, sinuous blades with serrations visible at proximal end; curved shafts and shortest blades not present after setiger 1. Blades becoming even longer (150–300 µm) in subsequent setigers (Fig. 25F), including several with very long, fine, whip-like spiniger-like tips, these giving a full, flowing appearance to anterior setigers. Mid-body

setigers with about 35–40 setae, reduced to 20 or fewer in setigers 7–10. Each parapodium with stout aciculae in both anterior and posterior edges (Fig. 25C); aciculae numbering 3–5 per parapodium; some aciculae thinner, with bent tip (Fig. 25E), most with tapered pointed tip.

Pygidium with four thin, filiform cirri, easily lost (Fig. 25A).

Several specimens with eggs in coelom of setigers 6–10; specimens appearing bulky, bloated posteriorly; eggs measuring 60–85 μm in diameter.

Remarks. *Anguillosyllis elegantissima* **n. sp.** is most similar to *A. lanai* from Brazil; both species have elongated, tightly fused palps and 10 setigers, with the largest specimens of *A. lanai* measuring up to 2.0 mm in length and *A. elegantissima* **n. sp.** measuring up to 3.4 mm long. The free-palp species *A. palpata* and *A. aciculata* **n. sp.** are also large species, both reaching nearly 3 mm length; whereas, the majority of specimens of *Anguillosyllis* examined in this study were about 1 mm in length. At each of two stations (MCZ 147941 and MCZ 147947), one of two specimens of *A. elegantissima* **n. sp.** was considerably smaller than the other and had nine rather than ten setigers; these are considered to be juveniles. For example, at Sta. 25 (MCZ 147941), one specimen measured 2.8 mm long and the other measured a bit less than 1 mm long. The smaller specimen had nine fully developed setigers and a pointed bud with an acicula representing setiger 10.

Both *A. lanai* and *A. elegantissima* **n. sp.** have external glands associated with the dorsal bases of the parapodia: in *A. lanai* a single gland is reported near the insertion of the dorsal cirrus whereas in *A. elegantissima* **n. sp.** there are glands at both the anterior and posterior bases of the parapodium.

The strikingly uneven heterogomph shaft of *A. elegantissima* **n. sp.** is not present in *A. lanai*, although Fig. 13G in Barroso *et al.* (2017) suggests that one side may be longer than illustrated in Fig. 14C–D.

Although indistinct and difficult to count, the number of muscle rows in the barrel-shaped proventricle were reported as ca. 12 for *A. lanai* compared with 30–35 in *A. elegantissima* **n. sp.** Especially when Shirlastain A is used, *A. elegantissima* **n. sp.** is clearly seen to have biannulate and triannulate (and possibly quadriannulate) setigers, whereas *A. lanai* does not. *Anguillosyllis lanai* has many fewer setae than *A. elegantissima* **n. sp.**, which has up to 50 setae in the first setiger, with several curved anteriorly in a graceful arc, and 35–40 setae in mid-body setigers; whereas, *A. lanai* has only up to 15 setae in anterior setigers. *Anguillosyllis elegantissima* **n. sp.** has up to five aciculae per parapodium; *A. lanai* has only two aciculae per parapodium.

Etymology. The species name *elegantissima* is derived from the Latin word *elegans*, and refers to the graceful, Bali-dancer-like appearance of this species.

Records. South China Sea, off Brunei, 1050–2162 m.

Anguillosyllis enneapoda n. sp.

Figures 27–28

urn:lsid:zoobank.org:act:8D0BDCAC-9CCE-4726-A212-96B0DD303627

Material examined. *(40 specimens from 27 stations)* **South China Sea, off Brunei.** Coll. J.A. Blake: Sta. 12, 6 Jun 2011, 5°49′20.73816″N, 114°09′45.51185″E, 1469 m, 1 specimen (MCZ 147963); Sta. 15, 6 Jun 2011, 5°44′32.59263″N, 114°04′34.13854″E, 1721 m, 2 specimens (MCZ 147964); Sta. 16, 5 Jun 2011, 5°43′02.93420″N, 114°04′33.77977″E, 1649 m, 2 specimens (MCZ 147965); Sta. 20, 5 Jun 2011, 5°48′57.17939″N, 114°10′54.28492″E, 1435 m, 2 specimens (MCZ 147966); Sta. 25, 5 Jun 2011, 5°47′23.69441″N, 114°10′48.45326″E, 1402 m, 1 specimen (MCZ 147967); Sta. 29, 4 Jun 2011, 5°43′01.15997″N, 114°06′07.18190″E, 1537 m, 1 specimen (MCZ 147968); Sta. 32, 4 Jun 2011, 5°44′28.60071″N, 114°09′16.86792″E, 1415 m, 2 specimens (MCZ 147969); Sta. 35, 3 Jun 2011, 5°47′37.12906″N, 114°14′10.75153″E, 1329 m, 1 specimen (MCZ 148500); Sta. 47, 2 Jun 2011, 5°47′21.86444″N, 114°17′10.72194″E, 1242 m, 1 specimen (MCZ 148501); Sta. WH_Jokit-SW, 5 Jun 2011, 5°46′27.76503″N, 114°07′33.98027″E, 1487 m, 1 specimen (MCZ 148502). Coll. P. Neubert: Sta. AN2, 27 Jun 2011, 5°25′43.52552″N, 113°47′34.41444″E, 1568 m, 1 specimen (MCZ 148503); Sta. AN3, 28 Jun 2011, 5°28′16.43794″N, 113°49′34.34518″E, 1540 m, 1 specimen (MCZ 148504); Sta. AN5, 27 Jun 2011, 5°26′51.39448″N, 113°46′41.57612″E, 1632 m, **holotype** (MCZ 148506), 6 **paratypes** (MCZ 148505); Sta. AN8, 27 Jun 2011, 5°27′56.15653″N, 113°45′42.93641″E, 1783 m, 2 specimens (MCZ 148507); Sta. AN9, 28 Jun 2011, 5°30′30.14745″N, 113°47′38.56098″E, 1820 m, 1 specimen (MCZ 148508); Sta. DA3, 3 Jul 2011, 5°25′15.03011″N, 113°29′30.52872″E, 1772 m, 1 specimen (MCZ 148509); Sta. JA1, 30 Jun 2011, 5°28′22.57522″N, 113°36′38.54386″E, 1888 m, 2 specimens (MCZ

148510); Sta. JA4, 30 Jun 2011, 5°30′54.36931″N, 113°37′21.11932″E, 1967 m, 1 specimen (MCZ 148511); Sta. JA6, 30 Jun 2011, 5°31′02.11247″N, 113°36′27.60639″E, 1999 m, 1 specimen (MCZ 148512); Sta. ME14, 26 Jun 2011, 5°25′20.73778″N, 113°39′02.48164″E, 1792 m, 1 specimen (MCZ 148513); Sta. ME16, 26 Jun 2011, 5°24′24.44585″N, 113°35′28.03023″E, 1805 m, 2 specimens (MCZ 148514); Sta. SA3, 3 Jul 2011, 5°35′09.05425″N, 113°38′49.25754″E, 2117 m, 1 specimen (NJM); Sta. SE1, 28 Jun 2011, 5°33′07.24983″N, 113°46′11.03389″E, 1894 m, 1 specimen (MCZ 148515); Sta. SE5, 28 Jun 2011, 5°35′44.35485″N, 113°47′09.29726″E, 1947 m, 1 specimen (MCZ 148516); Sta. SE6, 28 Jun 2011, 5°35′12.78573″N, 113°44′06.06326″E, 2095 m, 1 specimen (MCZ 148517); Sta. TA5, 2 Jul 2011, 5°27′50.62360″N, 113°26′34.31837″E, 2008 m, 1 specimen (MCZ 148518); Sta. TU4, 25 Jun 2011, 5°12′34.01837″N, 113°42′17.60077″E, 1439 m, 1 specimen (MCZ 148519).

Description. Body with 9 setigers, colorless, more-or-less linear in shape (Figs. 27A, 28A–B); most specimens including holotype 1.0 mm long without anal cirri, 0.2 mm wide without parapodia, 0.5–0.6 mm wide with parapodia but excluding setae. Palps completely fused, narrowing to slightly rounded anterior tip, without medial notch (Figs. 27A, 28A–B); eyes lacking; prostomium oval with anterior border slightly dome-shaped, three club-shaped antennae in transverse row; peristomium well-defined, nearly as long as prostomium, with two small, oval tentacular cirri. Nuchal area oval lateral patches between prostomium and peristomium. Pharynx distally surrounded by 10–12 soft papillae, tooth absent. Proventricle in 2–3 setigers, barrel-shaped, tapered posteriorly (Figs. 27A, 28A–B); ca. 13–18 rows of muscle cells; post-ventricle with dorsal circlet of cells retaining MG stain (Fig. 28C).

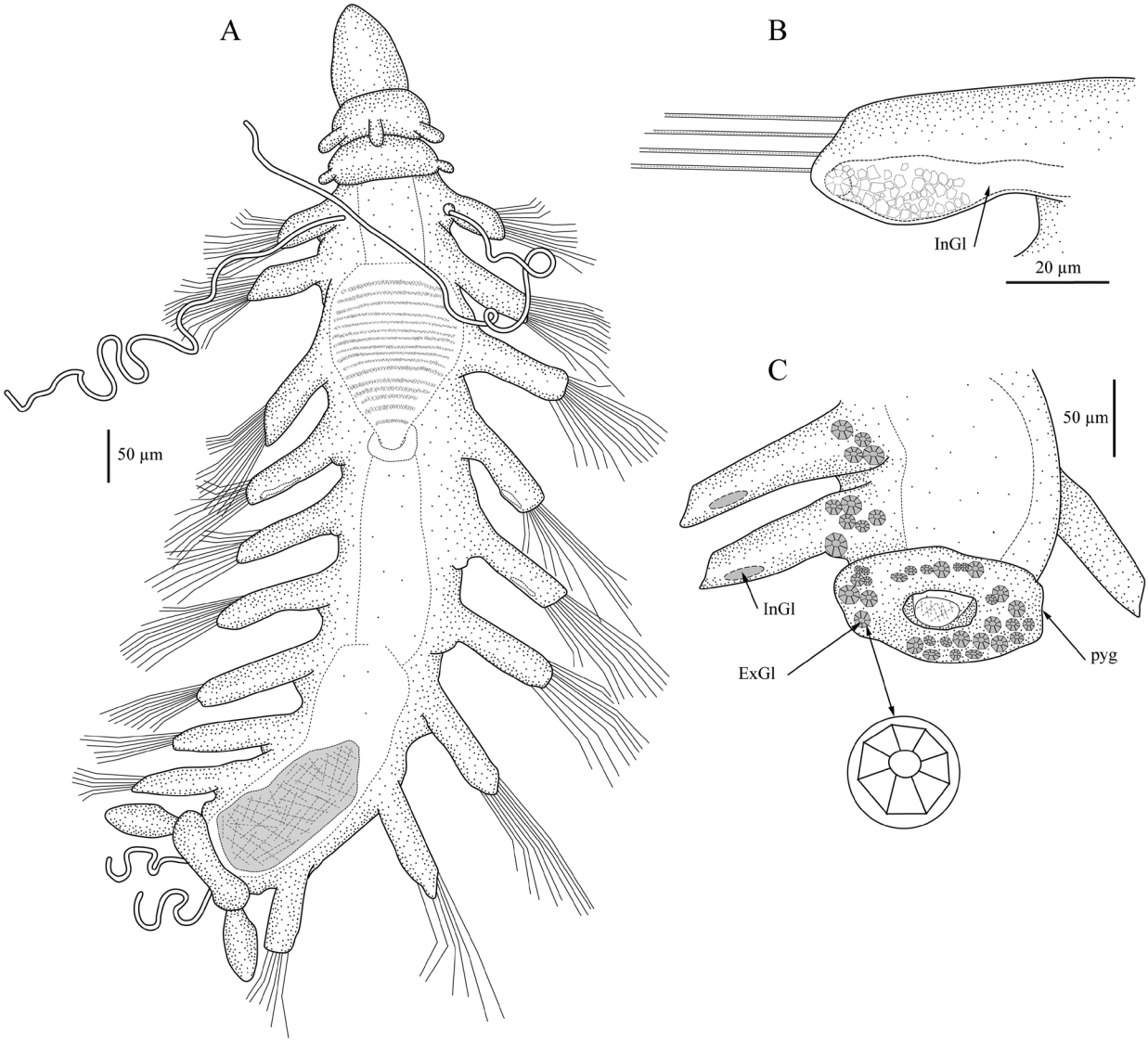

FIGURE 27. ***Anguillosyllis enneapoda*** **n. sp.** Holotype (MCZ 148506): A, entire specimen, dorsal view; B, setiger 8, dorso-lateral view; C, setigers 8–9 and pygidium, dorso-posterior view, anal cirri removed, inset not to scale. Abbreviations: ExGl—external gland, InGl—internal gland, pyg—pygidium.

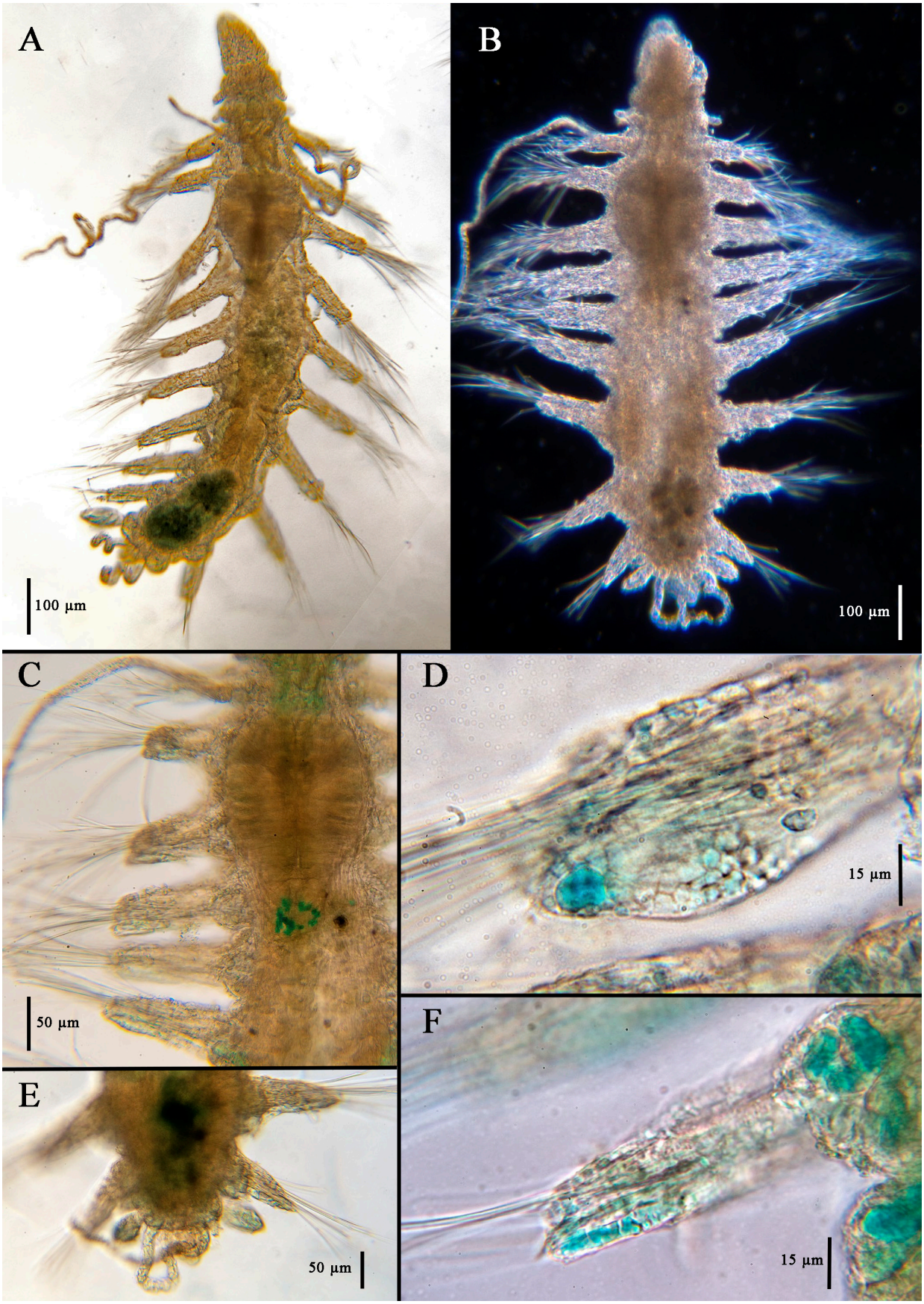

FIGURE 28. ***Anguillosyllis enneapoda*** **n. sp.** Holotype (MCZ 148506): A, entire specimen. Paratype (MCZ 148505): B, entire specimen. Holotype (MCZ 148506): C, setigers 1–6, post-ventricle caeca with dorsal ring of stained cells; D, setiger 8; E, setigers 8–9 and pygidium with anal cirri; F, setiger 9. A–F, dorsal view; C–F stained with MG.

Parapodia uniramous, obliquely truncate, usually swollen along posterior edge anterior and posterior lobes lacking (Figs. 27B, 28C–D, F), dorsal lobe small; parapodia of setiger 1 shortest, becoming slightly longer over setigers 2–5, then slightly shorter through setiger 9. Elongated internal gland with deeply staining distal tip visible in parapodia of some but not all specimens (Figs. 27B–C, 28D, F); some specimens with faintly staining cells along posterior edge of parapodium, likely associated with and obscuring long gland; small glands that stain deeply with MG on surface of parapodia and pygidium, these in a range of sizes from tiny to large (Fig. 27C). Dorsal cirri long, thin, retained only on setiger 1, never observed on other setigers. Ventral parapodial cirri slim, slightly wider at base, inserted in middle of parapodium, not exceeding length of parapodium.

All setae compound with long heterogomph shafts, up to 2.5 times length of blade. Setiger 1 with ca. 10–16 setae per parapodium, setigers 2–3 with 14, setigers 4–9 with up to 10 setae; some setae emerging from distal tip of parapodium, remaining setae emerging from ventral face of parapodium between insertion of ventral cirrus and distal tip. Ventral-most blades shortest, 25–75 µm, serrated on proximal portion, serrations clearly visible at 1000x; longer blades up to 300 µm, with very long, fine, drawn-out tips, possibly serrated at base. Parapodia each with up to four aciculae, these with heavy, thick, pointed, or knobby tip, often appearing golden in color, not protruding from parapodia but forming anterior and posterior bumps at distal end.

Pygidium with two ventromedial thin, filiform cirri and two lateral oval cirri, with glandular areas as seen on parapodia (Figs. 27A, 28E).

Reproductive specimens with oocytes in setigers 6–9, measuring 50–60 µm in greatest diameter, some squeezing into and filling half of parapodium, others in coelom near parapodia.

Remarks. *Anguillosyllis enneapoda* **n. sp.** is most similar to *Anguillosyllis inornata* **n. sp.** from offshore California: both species have nine setigers, fused palps, and lack any development of anterior or posterior lobes on the parapodia**.** However, the pharynx of *A. enneapoda* **n. sp.** lacks the deep golden-brown color seen in *Anguillosyllis inornata* **n. sp.** *Anguillosyllis enneapoda* **n. sp.** has four aciculae per parapodium and these are golden in color and heavier compared with the two aciculae per parapodium of *A. inornata* **n. sp.** Some aciculae appear to have a bent or knobby tip, others are clearly straight and pointed but this depends on the angle of view. In some specimens only two or three aciculae could be seen, but in specimens where the tissue was torn or decomposed, four were clearly visible, two each in the anterior and posterior parts of each parapodium. The setal blades of *A. enneapoda* **n. sp.** are clearly and more deeply serrated rather than appearing plain or only minimally serrated at very high magnifications as in *A. inornata* **n. sp.** The remaining species with nine setigers and fused palps, *A. pupa*, has large posterior parapodial lobes, which *A. enneapoda* **n. sp.** lacks.

Two other species, *A. blakei* **n. sp.** and *A. sepula* **n. sp.**, also have large tubular glands in the parapodia, but those two species have 10 setigers whereas *A. enneapoda* **n. sp.** has nine. In *A. enneapoda* **n. sp.**, the distal tip of the internal parapodial glands has a large-diameter opening that stains deeply with MG whereas in *A. blakei* **n. sp**. there is a narrow, nipple-like tip on the gland.

In addition to the deeply staining external glands associated with the parapodia, there are glands in the pygidial segment of *A. enneapoda* **n. sp.** that also stain; these glands appear to have a rosette structure similar to that seen in other species such as *A. aciculata* **n. sp.** and *A. hadra* **n. sp.**

Etymology. From the Greek *ennea*, meaning nine and *podos*, meaning foot; in reference to the nine setigers of this species.

Records. South China Sea, off Brunei, 1242–2117 m.

Anguillosyllis hessleri n. sp.

Figures 29–30A

urn:lsid:zoobank.org:act:04177057-7E4B-49C7-91DD-14A880E9BB1D

Material examined. *(3 specimens from 3 stations, 3 samples)* **Abyssal Pacific Ocean, Clarion-Clipperton Fracture Zone**. NOAA DOMES Site C, coll. R.R. Hessler, ECHO I, sample H353, Sandia box corer, 18 June 1983, 14°42.09′N, 125°24.27′W, 4516 m, 1 specimen, damaged (LACM-AHF Poly 10171); sample H356, Sandia box corer, 21 June 1983, 14°42.45′N, 125°24.27′W, 4518 m, **holotype** (LACM-AHF Poly 10169); sample H362, Sandia box corer, 18 June 1983, 14°42.08′N, 125°25.86′W, 4480 m, **paratype (**LACM-AHF Poly 10170).

Description. Body with 11 setigers (holotype and paratype) (Figs. 29A, 30A), third specimen smaller, damaged, with 10 setigers, colorless, opaque; holotype complete, 3.8 mm long without anal cirri, 0.5 mm wide without

parapodia, 1.2 mm wide with parapodia but excluding setae; paratype 2 mm long, appearing linear or rectangular in overall shape. Palps elongated, completely fused, anterior margin bluntly rounded with small medial indentation, median furrow faintly visible (Figs. 29A, 30A); prostomium dome-shaped, demarcation with peristomium indistinguishable, both appearing as one large dome-shaped unit (Figs. 29A, 30A); one antenna present, others presumably lost; eyes lacking; peristomium with two oval tentacular cirri. Small nuchal patches between prostomium and peristomium seen with Shirlastain A and MG as area staining darker than surrounding tissue. Proventricle in two setigers, blocky and bluntly barrel-shaped, occupying width of body (Figs. 29A, 30A), rows of muscle cells at least 10, but mostly obscured by opaque body wall; post-ventricle caeca with dorsal circlet of cells retaining MG stain (Fig. 30A).

Parapodia uniramous, shortest on setigers 1 and 2, longer, rectangular, with truncate distal margin on setigers 3–10, becoming slightly shorter on setiger 11; anterior lobe from setiger 1, obvious in anterior setigers, becoming reduced or absent in posterior setigers (Fig. 29B–G); posterior lobe absent; dorsal lobe or hood low, not obvious. Internal parapodial glands noticeable from setiger 2, elongated, sac-like, becoming larger, through setiger 9, numbering 3–5 per parapodium, wrapped around posterior aciculae (Fig. 29C–G). Dorsal cirri filiform, retained only on setiger 1 (Fig. 30A). Ventral cirri slim, digitiform, inserted in middle of parapodium, may extend beyond parapodium (Fig. 29E). Small, rounded external structures, possibly glands, on anterior and posterior margins of parapodia near body wall; tiny on setiger 1–5, larger on setiger 6, largest on setiger 8.

All setae compound with heterogomph shafts, those with shortest blades emerging from ventral face of parapodium between insertion of ventral cirrus and distal tip, remaining setae emerging from distal tip of parapodium; all blades with fine proximal serrations, short falcigers terminating in narrow pointed tips (Fig. 29H), longer spiniger-like setae terminating in fine elongated tips. Setigers 1–3 with ca. 26 setae, blades ranging from 30–120 µm long in setigers 1–2, setiger 3 with longest blades reaching 240–300 µm. Setigers 4–10 with 14–16 setae, shortest blades 38–50 µm, longest blades 240–360 µm. Setiger 11 with slightly fewer setae (ca. 12), with slightly shorter blades ranging from 50 µm to 195 µm. Parapodia with four aciculae, two anterior and two posterior; posteriormost acicula heaviest, golden, pointed; upper posterior acicula slimmer, may move to middle of parapodium in posterior setigers (Fig. 29E); aciculae in anterior of each parapodium slimmer, pointed, less obvious and sometimes not seen; tips of posterior aciculae emergent (Fig. 29B–G), those of anterior aciculae usually not emergent.

Pygidium with two ventromedial, filiform cirri and two lateral cirri with stalk or base measuring ca. 35 µm long, ending in very large (0.2 mm long), distal oval portion (Figs. 29H, 30A).

Remarks. *Anguillosyllis hessleri* **n. sp.** is one of several species that have 11 setigers, most of which have palps that are entirely or at least dorsally free (i.e., *A. aciculata* **n. sp.**, *A. hadra* **n. sp.**, *A. hampsoni* **n. sp.**, *A. palpata*, and *A. truebloodi* **n. sp.**) unlike *A. hessleri* **n. sp.**, which has bulky palps that are fused for their entire length with only a small medial dimple on a wide anterior margin. *Anguillosyllis capensis*, which most likely also has 11 setigers, has palps that are not completely fused, but have a clear separation of the tips (*fide* Day 1963; Aguado & San Martín 2008).

The prostomium and peristomium of *A. hessleri* **n. sp.** appear completely fused from the dorsal side. Staining with Shirlastain A and examination at 1000x revealed only the faintest suggestion of demarcation between the two, with the peristomium appearing as long as the prostomium. Two small patches that stain more deeply than the surrounding tissue may represent nuchal patches just at the line between prostomium and peristomium, but no separate cilia could be seen, even at 1000x (SEM may reveal cilia in this area).

The aciculae in the posterior part of the parapodia of *A. hessleri* **n. sp.** also appear to differ from those of most other species in being much heftier and of a darker golden color, and especially in having protruding pointed tips rather than being fully enclosed in tissue. *A. aciculata* **n. sp.** has four emergent aciculae in each parapodium, but that species has palps that are not fused.

The small external structures on the margins of the parapodia of *A. hessleri* **n. sp.** are similar to those seen on *A. elegantissima* **n. sp.** and described for *A. lanai*; in *A. hessleri* **n. sp.** they are larger on the posterior rather than the anterior edges of the parapodia.

The lateral anal cirri differ from those seen in the other *Anguillosyllis* species in that they are much larger and have a base or stalk connecting the expanded oval portion to the pygidium. The stalk measured one-quarter the length of the expanded oval portion, which appears to have some internal structure but does not stain with MG.

Etymology. This species is named for Dr. Robert R. Hessler, Scripps Institute of Oceanography, Co-Chief Scientist on the survey to the Clarion-Clipperton Fracture Zone in 1983 on which these specimens were collected, in recognition of his considerable contributions to the study and understanding of deep-sea benthos.

Records. Abyssal Pacific, Clarion-Clipperton Fracture Zone, 4480–4518 m.

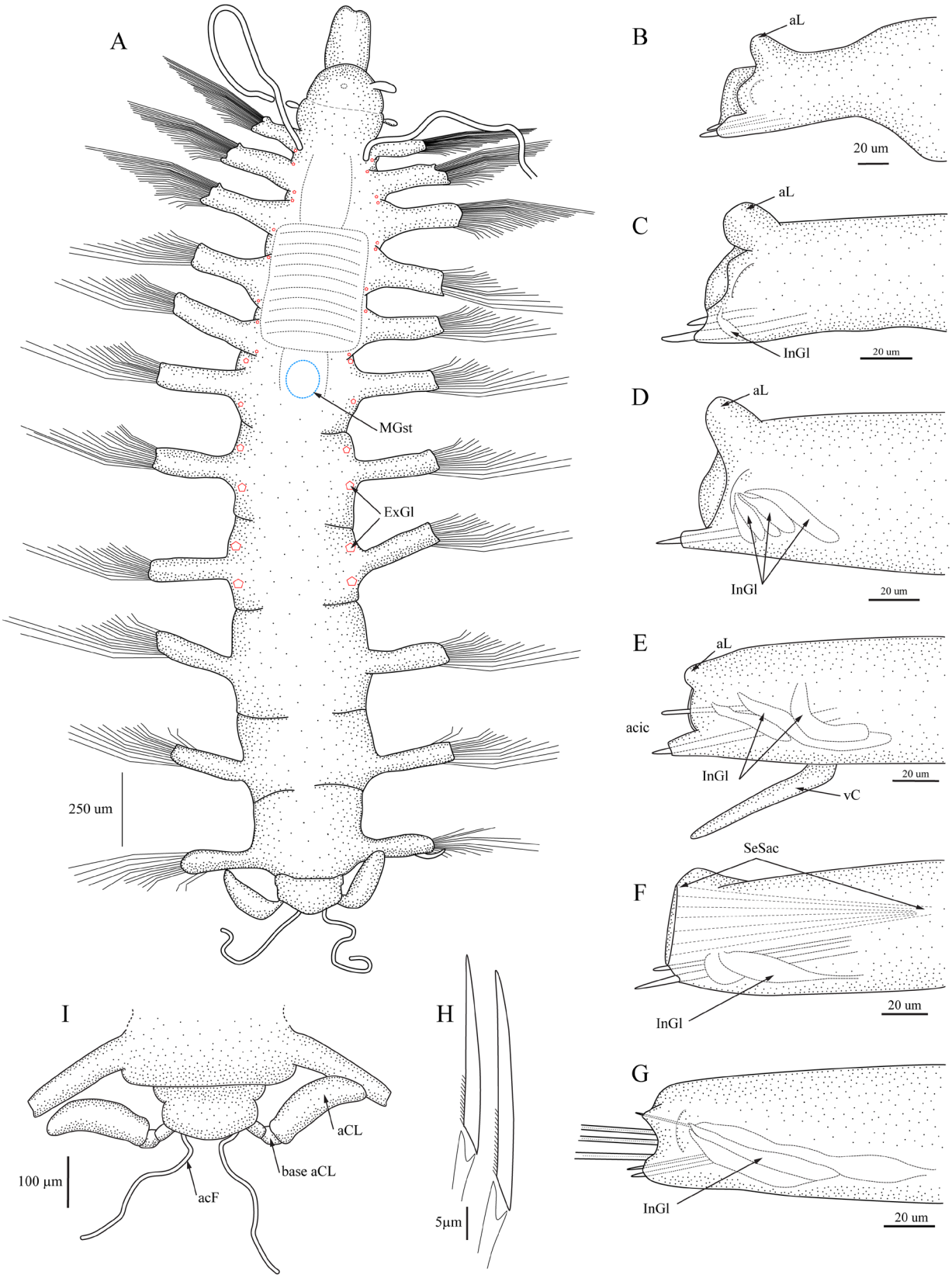

FIGURE 29. ***Anguillosyllis hessleri*** **n. sp.** Holotype (LACM-AHF Poly 110169): A, entire specimen, dorsal view. Paratype (LACM-AHF Poly 110170): B, setiger 1; C, setiger 2; D, setiger 3; E, setiger 5; F, setiger 7; G, setiger 9; H, falcigers from setiger 1; I, pygidium and anal cirri. A–G, I, dorsal view. Abbreviations: aCF—filiform anal cirrus, aCL— lateral anal cirrus, aL—anterior lobe, base aCL—basal portion of lateral anal cirrus, ExGl—external glands, InGl—internal gland, MGst—cells stained with Methyl Green, SeSac—setal sac, vC—ventral cirrus.

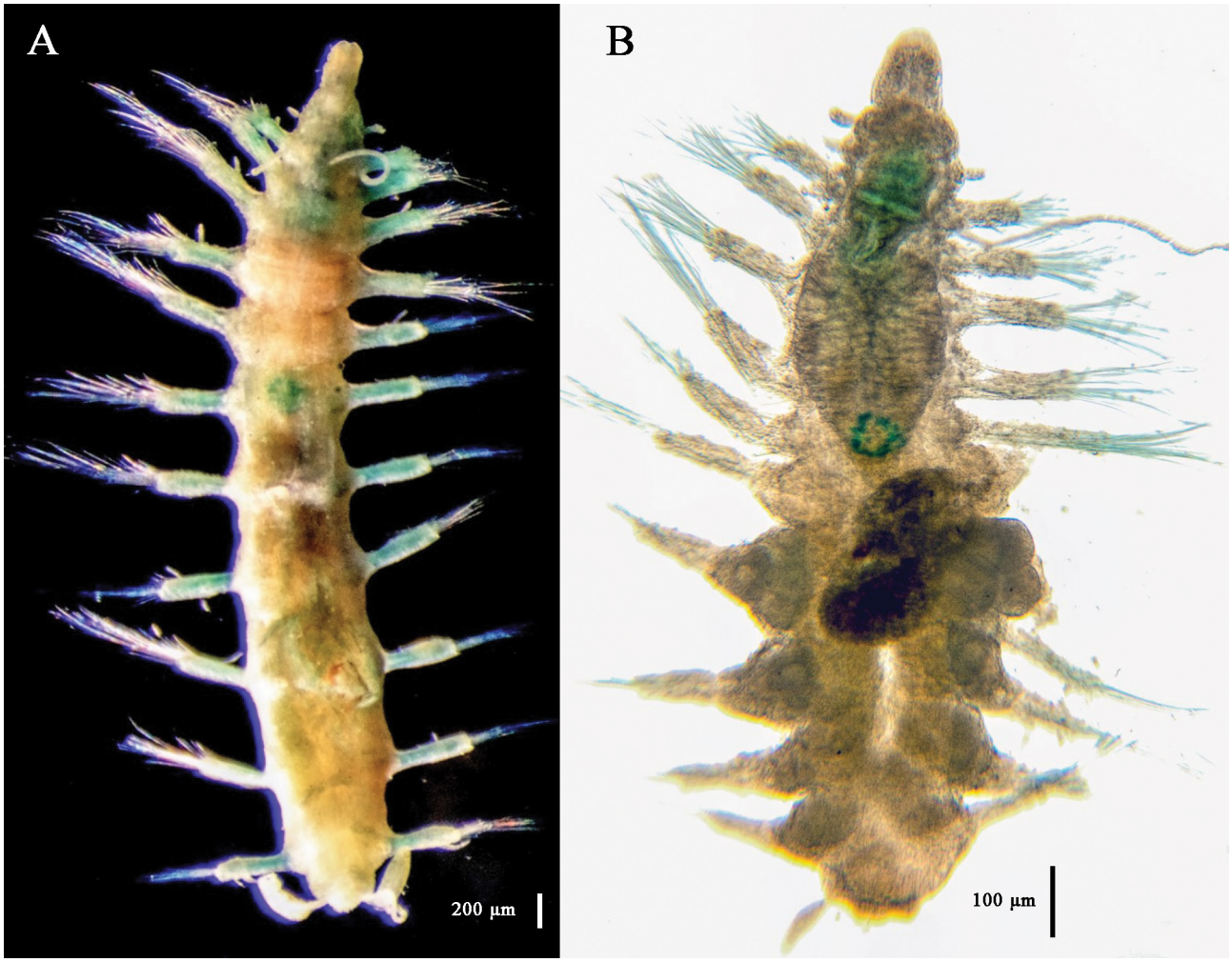

FIGURE 30. ***Anguillosyllis hessleri*** **n. sp**. Holotype (LACM-AHF Poly 110169): A, entire specimen, dorsal view.—***Anguillosyllis sepula*** **n. sp.** Holotype (MCZ 150582): B, entire specimen, dorsal view.

Anguillosyllis inornata n. sp.

Figures 31–32

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Braniella sp. 1: Blake *et al.* 2009: 1797.

Material examined. *(424 specimens from 25 stations, 100 samples).* **Gulf of the Farallones, California continental slope. US Navy Survey**, **103 Site Selection Survey, west of the Farallon Islands,** coll. J.A. Blake, Sta. B1, 18 Jul 1991, 37°39.64′N, 123°30.02′W, 2955 m, 3 specimens (CASIZ 229826); Sta. B2, 19 Jul 1991, 37°40.36′N,123°27.96′W, 2701 m, 2 specimens (CASIZ 229822); Sta. B3, 20 Jul 1991, 37°40.06′N, 123°23.69′W, 2385 m, 4 specimens (CASIZ 229828); Sta. B4, 20 Jul 1991, 37°38.46′N, 123°30.07′W, 3055 m, 2 specimens (CASIZ 229823); Sta. B5, 20 Jul 1991, 37°38.94′N, 123°28.81′W, 2925 m, 1 specimen (CASIZ 229824); Sta. B6, 21 July1991, 37°38.78′N, 123°25.21′W, 2720 m, 1 specimen (CASIZ 229825); Sta. B8, 24 Jul 1991, 37°38.58′N, 123°29.86′W, 2985 m, 2 specimens (CASIZ 229829); Sta. B-10, 24 Jul 1991, 37°37.84′N, 123°26.0′W, 2400 m, 1 specimen (CASIZ 229827).—**EPA 102 Site Selection Survey,** coll. J.A. Blake. north of Pioneer Canyon, Sta. 3-8, 13 Sep 1991, 37°27.13′N, 123°23.02′W, 1990 m, 3 **paratypes** (CASIZ 229816); south side of Pioneer Canyon, Sta. DS1A, 23 Sep 1991, 37°10.97′N, 123°19.10′W, 2205 m, 2 specimens (CASIZ 229821); Sta. DS2A, 23 Sep 1991, 37°10.50′N, 123°20.52′W, 2394 m, 10 specimens (CASIZ 229814); Sta. DS3A, 24 Sep 1991, 37°09.86′N, 123°22.71′W, 2755 m, 4 specimens (CASIZ 229815).—**San Francisco Deep Ocean Disposal Site (SF-DODS),**

west of the Farallon Islands, coll. JA Blake. Sta. 23, 21 Jan 1996, 37°37.00′N, 123°28.99′W, ~2875 m, 1 specimen (CASIZ 229831); 10 Dec 1996, 37°37.13′N, 123°29.08′W, ~2950 m, 4 specimens (LACM-AHF Poly 10465); 3 Nov 1997, 37°37.06′N, 123°29.15′W, 3093 m, 6 specimens (LACM-AHF Poly 10464); 6 Oct 1998, 37°37.23′N, 123°29.18′W, 2970 m, 19 specimens (NJM); 9 Oct 1999, 37°36.96′N, 123°28.93′W, 2970 m, 5 **paratypes** (LACM-AHF Poly 10454), 5 specimens (NJM); 26 Sep 2002, 37°36.95′N, 123°29.02′W, 2954 m, **holotype** (LACM-AHF Poly 10453), 8 **paratypes** (LACM-AHF Poly 10455); 24 Sep 2003, 37°36.86′N, 123°28.85′W, 2821 m, 3 specimens (CASIZ 229832);13 July 2007, 37°37.170′N, 123°29.222′W, 2995 m, 3 specimens (CASIZ 229830). Sta. 1, 11 Dec 1996, 37° 41.10′N, 123°31.03′W, 2799 m, 4 specimens (CASIZ 229789); Sta. 2, 11 Dec 1996, 37°41.01′N, 123°29.90′W, 2600 m, 4 specimens (CASIZ 229793); 29 Oct 1997, 37°41.01′N, 123°29.97′W, 2603 m, 1 specimen (CASIZ 229790); 12 Oct 1998, 37°40.96′N, 123°29.93′W, 2592 m, 8 specimens (CASIZ 229791); Sta. 3, 21 Jan 1996, 37°41.01′N, 123°29.03′W, ~2500 m, 1 specimen (CASIZ 229792); Sta. 8, 5 Dec 1996, 37°40.11′N, 123°28.98′W, ~2850 m, 1 specimen (NJM); 29 Oct 1997, 37°40.05′N, 123°28.98′W, 2843 m, 1 specimen (CASIZ 229842). Sta. 9, 5 Dec 1996, 37 °40.01′N, 123°30.00′W, 2906 m, 1 specimen (CASIZ 229840). Sta. 10, 11 Dec 1996, 37°40.02′N, 123°30.97′W, 2954 m, 6 specimens (CASIZ 229801); 30 Oct 1997, 37°40.04′N, 123 °30.96′W, 2920 m, 5 specimens (CASIZ 229799); 8 Oct 1999, 37°39.96′N, 123°31.06′W, 3015 m, 7 specimens (CASIZ 229800); 16 Oct 2000, 37°40.01′N, 123°31.03′W, 3065 m, 2 specimens (LACM-AHF Poly 10456); 23 Oct 2001, 37°40.02′N, 123°31.00′W, 2985 m, 4 specimens (LACM-AHF Poly 10457); 22 Sep 2002, 37°40.00′N, 123°31.00′W, 2739 m, 7 specimens (LACM-AHF Poly 10458); 14 Sep 2005, 37°39.970′N, 123°31.997′W, 2750 m, 3 specimens (CASIZ 229798); 26 Sep 2006, 37°40.197′N, 123°30.834′W, 2760 m, 2 specimens (CASIZ 229802). Sta. 11, 23 Jan 1996, 37°39.00′N, 123°30.99′W, ~3070 m, 3 specimens (CASIZ 229841); 11 Dec 1996, 37°39.09′N, 123°30.99′W, 2990 m, 9 specimens (CASIZ 229843); 3 Nov 1997, 37°39.10′N, 123°31.03′W, 2955 m, 4 specimens (CASIZ 229839). Sta. 12, 21 Jan 1996, 37°39.00′N, 123°30.00′W, ~3015 m, 4 specimens (CASIZ 229812); 5 Dec 1996, 37°38.92′N, 123°29.85′W, 3097 m, 3 specimens (CASIZ 229811); 29 Oct 1997, 37°39.05′N, 123°29.92′W, 3025 m, 3 specimens (CASIZ 229813); 8 Oct 1999, 37°38.91′N, 123°29.89′W, 2989 m, 2 specimens (CASIZ 229820). Sta. 16, 3 Nov 1997, 37°38.07′N, 123°27.05’W, 2690 m, 3 specimens (CASIZ 229818); 8 Oct 1998, 37°38.04′N, 123°26.88′W, 2749 m, 1 specimen (CASIZ 229819); 21 Sep 2002, 37°38.02′N, 123°26.95′W, 2693 m, 10 specimens (LACM-AHF Poly 10459); 15 Sep 2005, 37°37.990′N, 123°26.976′W, 2610 m, 9 specimens (LACM-AHF Poly 10460); 27 Sep 2006, 37°38.190′N, 123°26.974′W, 2676 m, 4 specimens (CASIZ 229817). Sta. 17, 3 Nov 1997, 37°37.97′N, 123°27.95′W, 2795 m, 4 specimens (NJM); 7 Oct 1998, 37°38.00′N, 123°27.99′W, 2830 m, 2 specimens (CASIZ 229806); 13 Oct 1999, 37°38.02′N, 123°20.00′W, 2770 m, 1 specimen (CASIZ 229804); 15 Oct 2000, 37°37.94′N, 123°27.91′W, 2780 m, 4 specimens (CASIZ 229803); 21 Oct 2001, 37°38.00′N, 123°28.03′W, 2862 m, 1 specimen (CASIZ 229807); 15 Sep 2005, 37°37.998′N, 123°27.995′W, 2750 m, 3 specimens (CASIZ 229805). Sta. 18, 30 Oct 1997, 37°37.95′N, 123°28.89′W, 2905 m, 1 specimen (CASIZ 229856); 8 Oct 1999, 37°37.86′N, 123°28.86′W, 2900 m, 2 specimens (CASIZ 229855). Sta. 19, 20 Jan 1996, 37°38.00′N, 123°30.00′W, 2947 m, 5 specimens (CASIZ 229849); 7 Oct 1998, 37°38.04′N, 123°30.02′W, 3030 m, 10 specimens (CASIZ 229850); 9 Oct 1999, 37°37.94′N, 123°29.94′W, 3020 m, 15 specimens (LACM-AHF Poly 10461); 15 Oct 2000, 37°37.95′N, 123° 29.95′W, 2940 m, 3 specimens (NJM); 22 Oct 2001, 37°37.98′N, 123°30.03′W, 3123 m, 4 specimens (NJM); 22 Sep 2002, 37°38.01′N, 123°30.00′W, 3000 m, 1 specimen (CASIZ 229851); 15 Sep 2005, 37°37.909′N, 123°29.662′W, 2900 m, 2 specimens (CASIZ 229848); 11 July 2007, 37°38.166′N, 123°30.213′W, 3100 m, 2 specimens (CASIZ 229852). Sta. 20, 15 Oct 2000, 37°37.96′N, 123°31.06′W, 3060 m, 10 specimens (LACM-AHF Poly 10462); 23 Oct 2001, 37°38.04′N, 123°31.01′W, 3142 m, 8 specimens (CASIZ 229810); 22 Sep 2002, 37°38.06′N, 123°31.01′W, 3050 m, 2 specimens (CASIZ 229809); 15 Sep 2005, 37°37.987′N, 123°30.989′W, 3037 m, 3 specimens (CASIZ 229808); 25 Sep 2006, 37°37.960′N, 123°30.996′W, 3052 m, 4 specimens (LACM-AHF Poly 10463); 11 July 2007, 37°38.163′N, 123°31.265′W, 2980 m, 4 specimens (NJM). Sta. 24, 8 Oct 1999, 37°36.90′N, 123°27.92′W, 2900 m, 2 specimens (CASIZ 229794); 19 Oct 2000, 37°36.97′N, 123°27.92′W, 2650 m, 5 specimens (CASIZ 229786); 22 Oct 2001, 37°36.94′N, 123°27.93′W, 2680 m, 8 specimens (LACM-AHF Poly 10466). Sta. 27, 8 Oct 1999, 37°41.00′N, 123°32.00′W, 2929 m, 3 specimens (CASIZ 229846); 16 Oct 2000, 37°40.97′N, 123°31.98′W, 2740 m, 4 specimens (CASIZ 229845); 22 Oct 2001, 37°40.98′N, 123°31.95′W, 2770 m, 4 specimens (CASIZ 229847); 23 Sep 2002, 37°40.96′N, 123°31.94′W, 2825 m, 7 specimens (CASIZ 229844). Sta. 33, 20 Oct 2000, 37°42.01′N, 123°27.01′W, 2400 m, 1 specimen (CASIZ 229853). Sta. 53, 12 Dec 1996, 37°39.57′N, 123°29.45′W, 3084 m, 3 specimens (CASIZ 229854). Sta. 57, 13 Oct 1999, 37°43.00′N, 123°33.00′W, 2668 m, 3 specimens (CASIZ 229797); 16 Oct 2000, 37°42.99′N, 123°32.99′W, 2650 m, 5 specimens (LACM-AHF Poly 10467); 22 Oct 2001, 37°42.96′N, 123°32.97′W,

2750 m, 6 specimens (LACM-AHF Poly 10468); 23 Sep 2002, 37°42.97′N, 123°32.94′W, 2709 m, 5 specimens (LACM-AHF Poly 10469); 14 Sep 2005, 37°42.982′N, 123°32.919′W, 2629 m, 4 specimens (LACM-AHF Poly 10470); 24 Sep 2006, 37°42.946′N, 123°32.947′W, 2637 m, 1 specimen (CASIZ 229796); 9 Jul 2007, 37°43.021′N, 123°33.013′W, 2658 m, 1 specimen (CASIZ 229795). Sta. 64, 25 Sep 2002, 37°36.01′N, 123°33.01′W, 3136 m, 2 specimens (CASIZ 229838); 14 Sep 2005, 37°36.079′N, 123°32.954′W, 3120 m, 4 specimens (LACM-AHF Poly 10471); 13 Jul 2007, 37°36.028′N, 123°33.078′W, 3115 m, 3 specimens (LACM-AHF Poly 10472). Sta. 92, 24 Sep 2002, 37°45.00′N, 123°35.00′W, 2850 m, 3 specimens (CASIZ 229837); 24 Sep 2006, 37°45.080′N, 123°35.134′W, 2800–2815 m, 4 specimens (CASIZ 229836). Sta. 114, 27 Sep 2002, 37°35.08′N, 123°26.96′W, 2420 m, 2 specimens (CASIZ 229834). Sta.116, 25 Sep 2002, 37°34.99′N, 123°28.98′W, 2975 m, 6 specimens (CASIZ 229835); 14 Sep 2005, 37°34.927′N, 123°28.935′W, 2733 m, 2 specimens (CASIZ 229833); 13 July 2007, 37°35.080′N, 123°29.039′W, 2908 m. 8 specimens (LACM-AHF Poly 10473). Sta. DR1, 29 Sep 2006, 37°27.846′N, 123°55.437′W, 3666 m, 14 specimens (LACM-AHF Poly 10474); Sta. DR2A+B, 29 Sep 2006, 37°22.924′N, 124°01.001′W, 3775 m, 20 specimens (LACM-AHF Poly 10475); Sta. DR3B, 13 Jul 2007, 37°17.537′N, 124°09.192′W, 3864 m, 2 specimens (LACM-AHF Poly 10476).—Off Central California, abyssal plain, HOV *Alvin* Dive 4227, M. Spear (Pilot), Station M, core 23, 14 Aug 2006, 34°39.167′N, 123°05.190′W, 4119 m, 1 specimen (NJM).

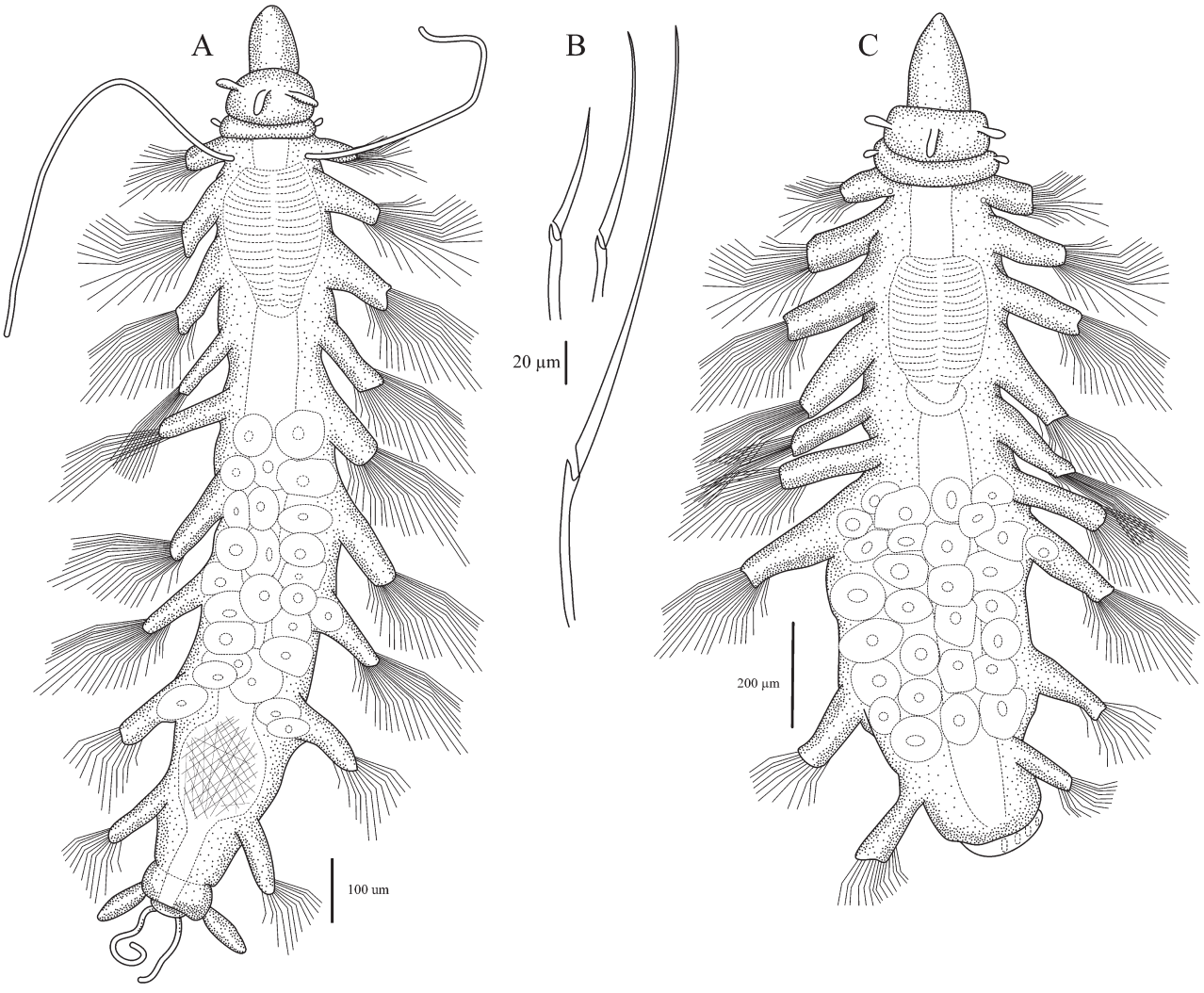

FIGURE 31. ***Anguillosyllis inornata*** **n. sp.** Paratype (LACM-AHF Poly 10455): A, entire specimen, dorsal view; B, setae from setiger 1. Paratype (CASIZ 229816): C, entire specimen, dorsal view.

Description. Body with 9 setigers (Figs. 31A, C; 32A); holotype complete, 1.4 mm long without anal cirri, 0.2 mm wide without parapodia, 0.45 mm wide with parapodia but excluding setae; maximum length 2 mm, maximum width 0.75 mm. Body colorless except dark golden-brown eversible pharynx (Fig. 32A–B). Palps elongated, completely fused, narrowing anteriorly to softly pointed tip; prostomium oval to slightly rectangular, eyes lacking; three

antennae in transverse row; peristomium shorter than prostomium, not clearly demarcated, with two short, oval tentacular cirri. Nuchal cilia visible when stained with Shirlastain A, in small oval lateral patches between prostomium and peristomium. Pharynx distally surrounded by 10 soft papillae, tooth absent. Proventricle in 2.5–3 setigers, barrel-shaped anteriorly, tapered posteriorly (Fig. 32A–B); with ca. 20 (18–22) rows of muscle cells; post-ventricle with dorsal circlet of cells retaining faint MG stain.

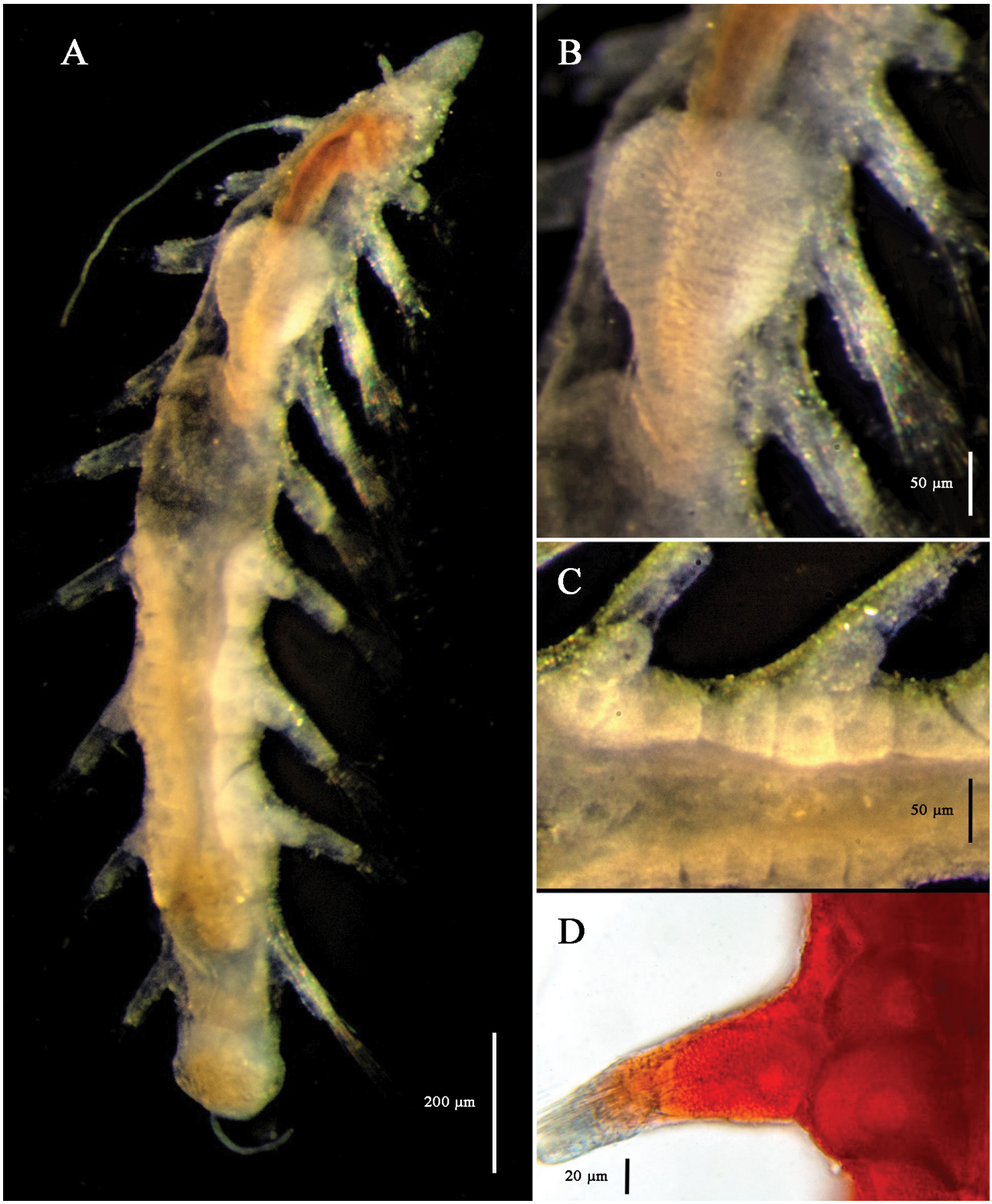

FIGURE 32. ***Anguillosyllis inornata*** **n. sp.** Paratypes (LACM-AHF 10455): A, entire specimen, dorsal view; B, proventricle, dorsal view; C, setigers 6–7, eggs in coelom and entering parapodia. D, another specimen with Shirlastain A, setiger 8, egg in parapodium.

Parapodia uniramous, short, nearly square on setiger 1, becoming elongated, rectangular over next few setigers, slightly shorter on setiger 9; anterior and posterior lobes not developed; dorsal lobe small but obvious; posterior edge of parapodium with pad of large cells that stain faintly with MG. Dorsal cirri long, thin, retained only on setiger 1 (Figs. 31A, 32A), never observed on other setigers. Ventral parapodial cirri slim, slightly wider at base, inserted in middle of parapodium, not exceeding length of parapodium.

Setiger 1 with 14–18 setae per parapodium, setigers 2–7 with 20–24 setae, setigers 8 and 9 with 10–14 setae; about half emerging from ventral face of parapodium between insertion of ventral cirrus and distal tip, remaining setae emerging from distal tip of parapodium. Ventral falcigers with blunt-tipped blades measuring 20–40 µm, spiniger-like blades with long, thin, tapering tips measuring 70–80 µm long in setiger 1 (Fig. 31B), becoming longer in subsequent setigers, up to ca. 125 µm. Blades with minute proximal serrations seen only at 1500x. Parapodia each with two aciculae, not protruding but forming anterior and posterior bumps at distal end of parapodia.

Pygidium with four cirri: two ventromedial thin, filiform and two lateral, oval (Fig. 31A); cirri often lost.

Reproductive specimens collected in July and September/October; eggs measuring 70–85 µm greatest diameter, about 28 eggs visible in setigers 6–9, some entering and filling parapodia (Figs. 31A, C; 32A, C–D).

Remarks. Of the 424 specimens of *Anguillosyllis inornata* **n. sp.** examined, all but three had nine setigers; of those three, one with eight setigers was damaged posteriorly, another with eight setigers was complete but only about half the length of adults with eggs, and a third very small (0.5 mm long) specimen had seven setigers. Because all other characters were the same, it is likely that the two small specimens were juveniles. In some samples, the larger specimens with eggs were twice the length of other specimens that lacked eggs, but all specimens in those samples had nine setigers.

Although the dorsal cirri on setiger one were attached in nearly all specimens, dorsal cirri were not seen on any other setigers. While it is possible that additional cirri might have been lost, no indication of attachments such as basal cirrophores were seen, even on setiger 1, with the exception of a few darker cells where cirri might have been inserted. Also, the fact that over 400 specimens were examined suggests that, while it would be unusual for syllids, perhaps only one pair of dorsal cirri is the norm for this species. As with all other species of *Anguillosyllis*, the anal cirri were often lost; a few specimens retained all four cirri while most retained only one, two, or three, including the holotype, which retained three cirri.

Anguillosyllis inornata **n. sp.** is most similar to *A. enneapoda* **n. sp.** from the South China Sea: both species have nine setigers and fused palps and lack any development of anterior or posterior lobes on the parapodia**.** The pharynx of *Anguillosyllis inornata* **n. sp**., however, has a characteristic deep golden-brown color that is not seen in *A. enneapoda* **n. sp.** or any other *Anguillosyllis* species. The setae also differ between the two species, with *A. inornata* **n. sp.** having fewer aciculae that *A. enneapoda* **n. sp.** and setal blades that are much less distinctly serrated. The internal parapodial glands seen in *A. enneapoda* **n. sp.** were not seen in *A. inornata* **n. sp.** *Anguillosyllis pupa* also has nine setigers, but *A. inornata* **n. sp.** has narrower, anteriorly pointed fused palps rather than palps that are softly rounded on the anterior margin and lacks the large posterior parapodial lobes seen in *A. pupa*.

Etymology. From the Latin *inornatus*, meaning plain or unadorned, in reference to the lack of anterior or posterior lobes on the parapodia.

Records. California, continental shelf off San Francisco; 2005–4119 m.

Anguillosyllis pupa (Hartman, 1965)

Figure 33

Braniella pupa Hartman, 1965: 72–73, pl. 8; Hartman & Fauchald, 1971: 51.
Anguillosyllis pupa: Aguado & San Martín, 2008: 38, Figure 2; Lucas *et al.* 2018: 773.

Material examined. *(holotype plus 109 specimens in 15 samples from 2 stations)* **Western Atlantic Slope, off Georges Bank south of Cape Cod. Holotype** (AHF Poly 0168), Sta. SL4, 39°56′30″N, 70°39′54″W, 400 m, Aug 1962, coll. H.L. Sanders, WHOI.—**US North Atlantic ACSAR Program**, **Sta. 12**, coll. G. Hampson, WHOI, Chief Scientist, Cruise North-1, R/V *Cape Hatteras*, 15 Nov 1984, Rep. 2, 39°54.35′N, 70°55.18′W, 558 m, 15 specimens (USNM 1480245); Rep. 3, 39°54.37′N, 70°55.18′W, 553 m, 9 specimens (USNM 1480246); Cruise North-2, R/V *Oceanus*, 4 May 1985, Rep. 1, 39°54.31′N, 70°55.04′W, 551 m, 10 specimens (USNM 1480247); Rep. 2, 39°54.26′N, 70°55.07′W, 555 m, 7 specimens (USNM 1480248); Rep. 3, 39°54.29′N, 70°55.04′W, 554

m, 8 specimens (USNM 1480249); Cruise North-4, R/V *Gyre*, 30 Nov 1985, Rep. 1, 39°54.28′N, 70°55.12′W, 560 m, 2 specimens (USNM 1480250), 1 (NJM); Rep. 2, 39°54.28′N, 70°55.12′W, 559 m, 9 specimens (USNM 1480251); Rep. 3, 39°54.32′N, 70°55.12′W, 544 m, 3 specimens (USNM 1480252); Cruise North-5, R/V *Cape Hatteras*, 06 May 1986, Rep. 1, 39°54.17′N, 70°55.22′W, 560 m, 2 specimens (USNM 1480253); Rep. 2, 39°54.27′N, 70°55.17′W, 548 m, 11 specimens (USNM 1480254); Rep. 3, 39°54.28′N, 70°55.09′W, 552 m, 2 specimens (USNM 1480255); Cruise North-6, R/V *Cape Hatteras*, 30 July 1986, Rep. 1, 39°54.25′N, 70°55.04′W, 563 m, 10 specimens (USNM 1480256); Rep. 2, 39°54.26′N, 70°55.07′W, 559 m, 7 specimens (USNM 1480257); Rep. 3, 39°54.24′N, 70°55.09′W, 563 m, 9 specimens (USNM 1480258) (2, NJM). **Gulf of Maine**, coll. G. Hampson, WHOI, Chief Scientist, BIMP Sta. 14A, 41°57.5′N, 68°31.0′W, 165 m, Jul 1982, 2 specimens (USNM 1480244).

Description. Body with 9 setigers; maximal length 2 mm without anal cirri, width 0.3–0.4 mm without parapodia, 0.6–0.75 mm including parapodia but without setae, most specimens 1 mm long, 0.5 mm wide. Palps completely fused, short, broad, anterior margin wide and gently rounded (Fig. 33A), occasionally slightly pointed, sometimes with tiny medial notch. Prostomium elliptical, wider than long; eyes lacking; three oval antennae in transverse row on posterior half of prostomium; peristomium shorter than prostomium, clearly demarcated, with two short tentacular cirri. Nuchal cilia not visible even when stained with Shirlastain A. Eversible pharynx distally surrounded by 10 long, soft papillae, tooth absent. Proventricle in three setigers, spherical in two setigers and usually tapered in third; rows of muscle cells difficult to discern, ca. 20–25 (*fide* Aguado & San Martín 2008); post-ventricle with dorsal circlet of cells retaining MG stain.

Parapodia uniramous, elongated, rectangular; with very small anterior lobe present in anterior setigers, essentially absent in posterior setigers (Fig. 33B–K); posterior lobe small in anterior setigers, becoming much larger over subsequent setigers (Fig. 33B–K); dorsal lobe small, difficult to observe; parapodial glands not observed except in the large posterior lobes. Dorsal cirri with basal cirrophore (Fig. 33A–B), cirri extremely long, thin, tightly coiled into corkscrew or relaxed, absent on setiger 2. Ventral cirri slender, inserted in middle of parapodium (Fig. 33I).

Anterior setigers with ca. 12–18 setae, setiger 1 with slightly fewer setae than setigers 2–5; number of setae after setiger 5 up to 6–10 per parapodium. All setae composite with heterogomph shafts, blades include ventral falcigers and dorsal spiniger-like setae; all blades with fine to medium serrations on proximal part of blade, these most obvious at 1000x. Falcigers with blunt, slightly hooked tips, emerging in two rows from ventral face of parapodium between insertion of ventral cirrus and distal tip of parapodium; blades measuring 30–85 µm. Spiniger-like setae with fine, sinuous tips, emerging from distal end of parapodium; blades measuring 75–95 µm in setiger 1, 110–140 µm in setigers 2–6, 110–120 µm in setigers 7–9. Parapodia each with two aciculae, not protruding but forming anterior and posterior bumps (e.g., Fig. 33F).

Pygidium with four anal cirri: two ventromedial, filiform, coiled and two lateral, oval, glandular (Fig. 33L–M); anus surrounded by fine cilia.

Reproductive specimens collected in November 1984; oocytes present from setiger 6 onward, on either side of midline, pressed up against parapodia, measuring 70–95 µm greatest diameter. Specimens collected in May 1985 without eggs but included one very small 8-setiger specimen that may be a juvenile.

Remarks. *Anguillosyllis pupa* was described by Hartman (1965) from collections made by Dr. Howard L. Sanders of the Woods Hole Oceanographic Institution (WHOI) in the early 1960s during his pioneering investigations of deep-sea benthic fauna retained by fine 300-µm-mesh screens. Most of the new material examined here was collected at a station (ACSAR North 12) close to the type locality (Sanders' Sta. SL4). Lucas *et al.* (2018) referred 41 specimens of *Anguillosyllis* collected from five stations off Norway to *A. pupa*; these specimens were collected mostly from Rijpfjord in 128–366 m.

The new materials agree well with the holotype, with the following additions to the original description, some of which were also noted by Aguado & San Martín (2008): (1) the distal end of the pharynx is surrounded by soft papillae rather than lacking papillae, (2) both falcigers and spiniger-like setae are present, rather than only spinigers, (3) the setae are finely serrated rather than smooth, (4) the ventral cirri are inserted halfway along the parapodia rather than at the base, and (5) the pygidium has four anal cirri rather than two.

Aguado & San Martín (2008) refer to the holotype in their redescription, but their material examined does not include any type material: the holotype is deposited in the Allan Hancock Foundation, LA County Museum, and is the only designated type specimen for this species. They noted the serrations on the blades of the setae and the presence of falcigers as well as spiniger-like setae but reported shorter blades than measured here (spinigers 95 µm vs. 140 µm and falcigers 10 µm vs. 30 µm).

In her description of the genus (as *Braniella*), Hartman (1965: 274) wrote that the ventral cirri are "similar *(to the dorsal cirri)* but much shorter and slenderer" and were "inserted at the base" of the parapodia; the illustration of a median parapodium (Hartman 1965: Plate 8b, p. 275) shows the ventral cirrus inserted at the base of the parapodium, but thicker than the dorsal cirrus. In my examination of the holotype and new material, the ventral cirri were noted to be as slender as the dorsal cirri but inserted halfway along the parapodia on all setigers; occasionally, the ventral cirrus on setiger 1 appeared to be at the base of the parapodium, but this is possibly an artifact due to the parapodium being pulled in toward the body of some specimens at the time of fixation.

Only a few specimens of *A. pupa* had a full complement of four anal cirri, with 0–3 usually being noted on any one individual. The arrangement of two slender, usually coiled, cirri in a ventromedial position and two lateral, oval, glandular-appearing cirri as figured here for *A. pupa* is also typical for all other members of the genus.

Other *Anguillosyllis* species with nine setigers include *A. enneapoda* **n. sp.** from the South China Sea and *A. inornata* **n. sp.** from off California. These species differ from *A. pupa* in: (1) having narrower, anteriorly pointed fused palps rather than palps softly rounded on the anterior margin and (2) lacking the large posterior parapodial lobes seen in *A. pupa*. The depth distribution of the three species also differs, with *A. pupa* occurring in shallower shelf and upper slope depths than almost all other species of *Anguillosyllis*.

Records. Gulf of Maine, 168 m; off New England, 400–550 m; off Delaware, 183 m (USNM 56762); off northeast South America, 770–805 m (*fide* Hartman 1965); off Norway, 128–366 m (*fide* Lucas *et al.* (2018).

Anguillosyllis sepula n. sp.

Figures 30B, 34

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Material examined. South China Sea, off Brunei. *(7 specimens from 6 stations)*. Coll. J.A. Blake. Sta. 33, 4 Jun 2011, 5°48′54.28228″N, 114°14′02.81573″E, 1370 m, 1 specimen (MCZ 150581); Sta. 45, 2 Jun 2011, 5°48′57.88185″N, 114°17′18.08262″E, 1260 m, **holotype** (MCZ 150582); Sta. 46, 2 Jun 2011, 5°48′02.68476″N, 114°18′10.00693″E, 1234 m, **paratype** (MCZ 150583); Sta. 61, 31 May 11, 5°40′32.90422″N, 114°13′15.64893″E, 1050 m, 1 specimen (NJM); Sta. WH-Jokit-SW, 5 Jun 2011, 5°46′27.76503″N, 114°07′33.98027″E, 1487 m, 1 specimen (MCZ 150584). Coll. P. Neubert. Sta. TU7, 4 Jul 2011, 5°19′24.21956″N, 113°47′15.61845″E, 1327 m, 1 specimen (MCZ 150585); Sta. TU10, 23 Jun 2011, 5°24′42.72532″N, 113°51′35.81868″E, 1354 m, 1 specimen (MCZ 150586).

Description. Body with 10 setigers (Figs. 30B, 34A), colorless; holotype 1.2 mm long without anal cirri, 0.25 mm wide without parapodia, 0.5 mm wide with parapodia but excluding setae. Palps completely fused, slightly wider at base, narrowing to somewhat pointed anterior margin; prostomium oval, with three long antennae, eyes lacking; peristomium short, with two oval tentacular cirri. Nuchal cilia not noticeable even when specimen stained with Shirlastain A. Proventricle in 3–4, setigers, bluntly barrel-shaped anteriorly, gently tapered posteriorly; rows of muscle cells indistinct anterior and posterior, ca. 10 rows in middle section (Figs. 30B, 34A); post-ventricle with dorsal circlet of cells retaining MG stain (Fig. 30B).

Parapodia uniramous, shortest on setiger 1, becoming longer, rectangular over next few setigers, then shorter again on setigers 9–10. Anterior and posterior parapodial lobes absent; dorsal lobe round, curled up or back on some setigers, most obvious on setigers 3–6 (Fig. 34C–F); pad of cells that retain MG stain on posterior portion of parapodia, surrounding smooth gland that opens at tip of parapodium (Fig. 34D–E). Dorsal cirri long, filamentous, observed only on setiger 1, possibly lost on other setigers. Ventral parapodial cirri digitiform, inserted in middle of parapodium.

All setae compound, heterogomph; setiger 1 with ca. 24 setae, setigers 8–10 with 8–10 setae; several setae emerge from ventral face of parapodium between insertion of ventral cirrus and distal tip, remaining setae emerge from distal tip of parapodium. Ventral falcigers with blunt-tipped blades measuring 20–40 µm (Fig. 34B), blades of distal setae long, thin, measuring up to ca. 120 µm in middle setigers. All blades with fine proximal serrations, difficult to see even at 1500x. Parapodia each with at least two aciculae, not protruding but forming anterior and posterior bumps at distal end of parapodia; aciculae with straight or angled tips.

Anal cirri fragile, mostly lost, holotype with one long filiform ventromedial cirrus, another specimen with oval lateral cirrus (lost during examination).

Reproductive specimens with oocytes in coelom of setigers 6–10, oocytes crowded against or entering para-

podia (Figs. 30B, 34A); oocytes appear especially large in relation to body size, measuring 85–120 µm greatest diameter (ave. =102.9 µm, median = 107.5 µm).

Remarks. *Anguillosyllis sepula* **n. sp.** is most similar to *A. blakei* **n. sp.** from offshore California, but lacks the biannulation on the dorsum of the first one or two setigers and also lacks the small anterior and posterior parapodial lobes seen in *A. blakei* **n. sp.** The large clear golden tubular gland seen in *A. blakei* **n. sp.** is not as obvious in *A. sepula* **n. sp.**, being more-or-less hidden behind the pad of cells on the posterior part of the parapodium. *Anguillosyllis sepula* **n. sp.** is more robust than *A. blakei* **n. sp.**: the parapodia are slightly wider and longer when two specimens of a similar size are compared side-by-side, and *A. sepula* **n. sp.** has more setae in the first few setigers than *A. blakei* **n. sp.** The eggs are also fewer and much larger in *A. sepula* **n. sp.** than in other *Anguillosyllis* species examined.

Etymology. From the Malay word *sepuluh*, meaning ten; referring to the ten setigers of this species.

Records. South China Sea, off Brunei, 1234–1487 m.

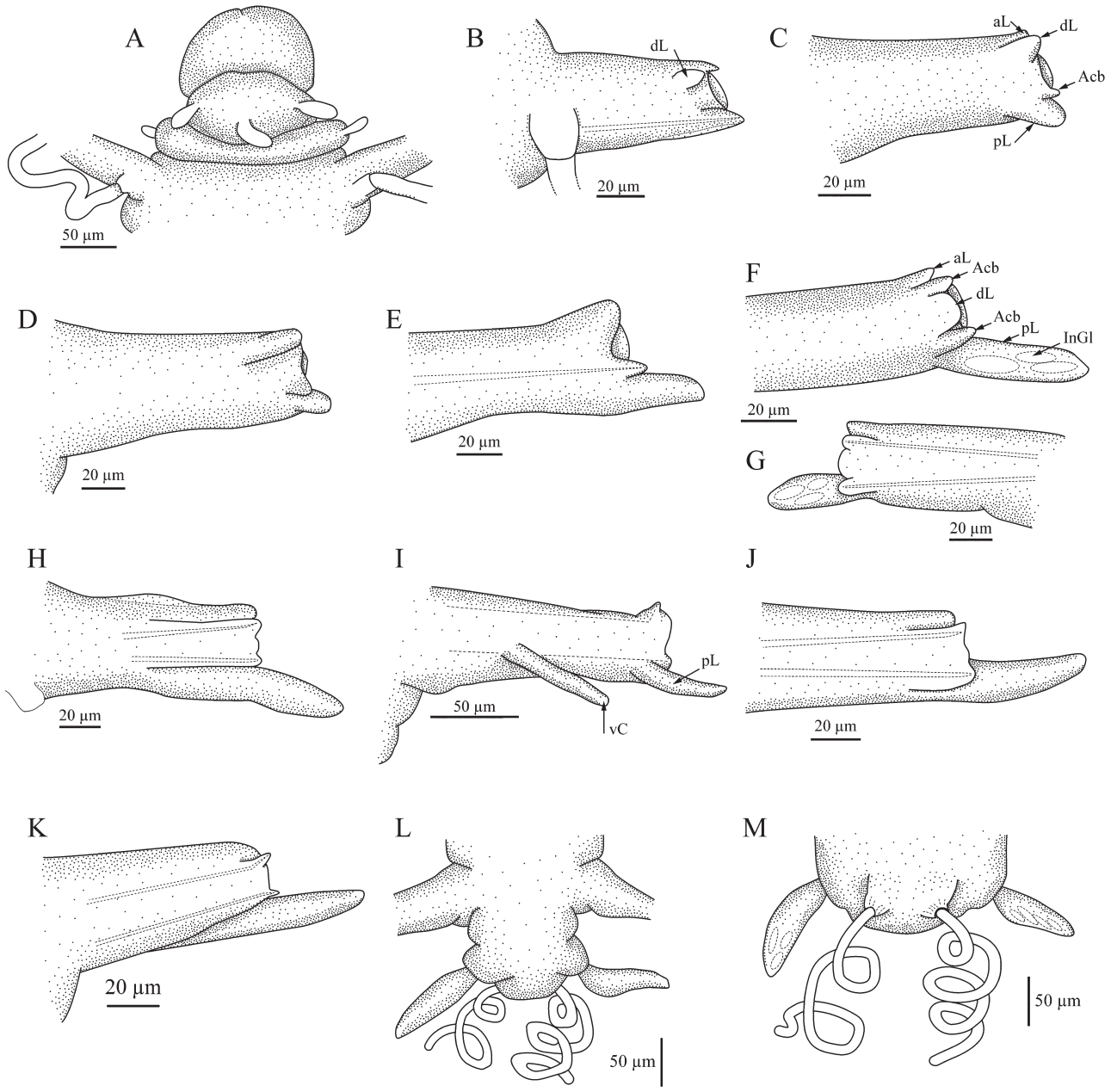

FIGURE 33. ***Anguillosyllis pupa*** **(Hartman, 1965).** Specimen from USNM 1480249: A, anterior end; B, setiger 1; C, setiger 2; D, setiger 3; E, setiger 4; F–G, setiger 5 from right and left sides; H, setiger 6; I, setiger 7; J, setiger 8; K, setiger 9; L, pygidium and anal cirri. A–H, J–L: dorsal view, I: ventral view. Another specimen from USNM 1480249: M, pygidium and anal cirri, ventral view. Abbreviations: Acb—acicular bump, aL—anterior lobe, dL—dorsal lobe, InGl—internal gland, pL—posterior lobe, vC—ventral cirrus.

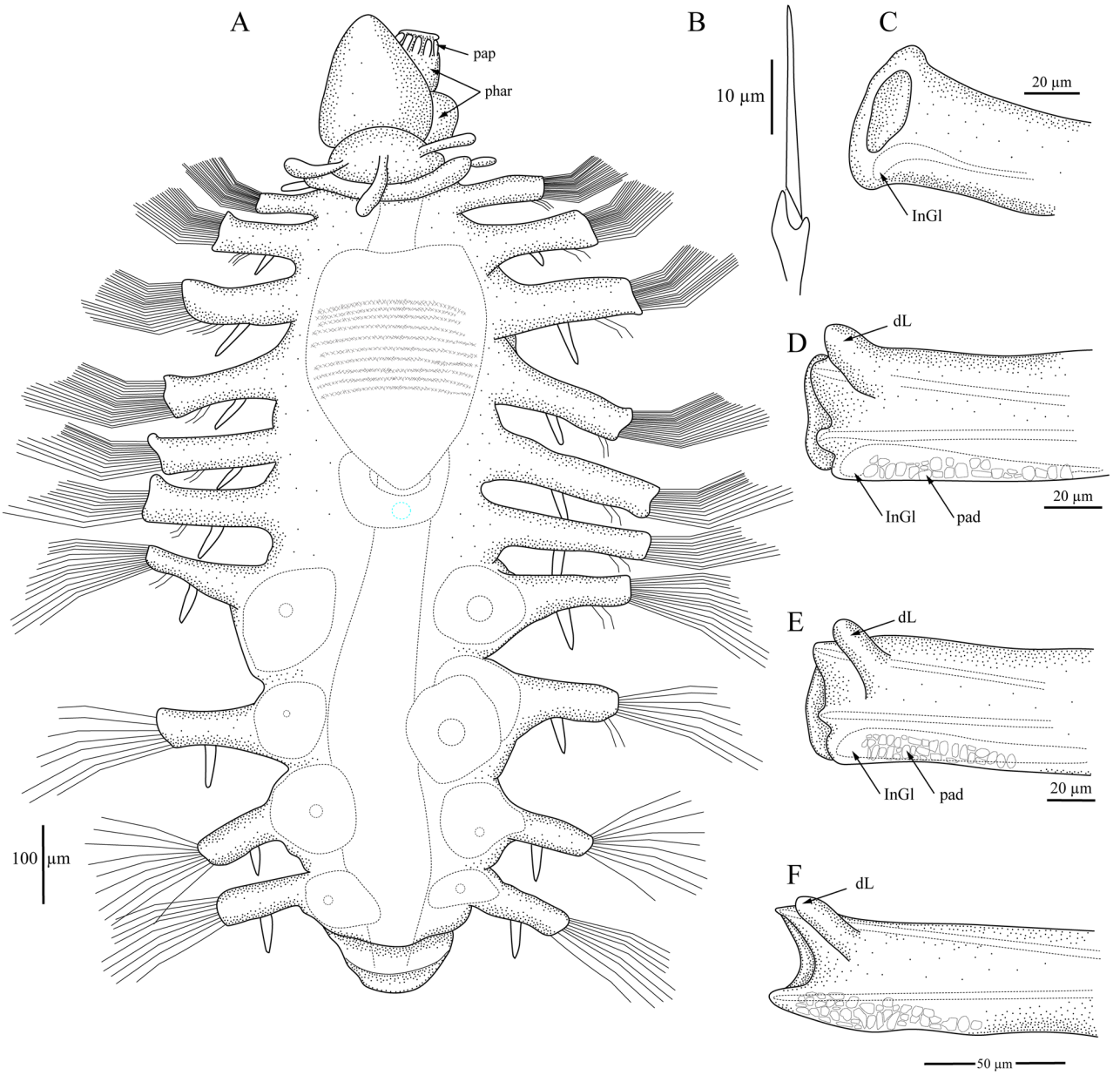

FIGURE 34. ***Anguillosyllis sepula*** **n. sp.** Holotype (MCZ 150582): A, entire specimen; B, ventral falciger, setiger 1; C, setiger 2; D, setiger 4; E, setiger 5; F, setiger 7. A, C–F: dorsal view. Abbreviations: dL—dorsal lobe, pap—papillae, phar—pharynx, InGl—internal gland.

Anguillosyllis sp.

Material examined. Abyssal Pacific, Clarion-Clipperton Fracture Zone. Coll. Dwight D. Trueblood for NOAA. Sta. 4-94, 12°55.967′N, 128°35.758′W, 4851 m, 1 specimen (USNM 1480276).

Remarks. This single nine-setiger specimen is in poor condition, with significantly decomposed tissue that precludes a full description. However, it is recognized as unique because of the combination of characters that distinguish it from other *Anguillosyllis* species with nine setigers (i.e., *A. enneapoda* **n. sp.**, *A. inornata* **n. sp.**, and *A. pupa*). It has large posterior lobes that are lacking in *A. enneapoda* **n. sp.** and *A. inornata* **n. sp.** and differs from *A. pupa* in having more obviously pointed fused palps and other details of the parapodial lobes. Large eggs are present in setigers 6 and 7. It is also found in very deep water (4851 m) compared with the other three species.

General remarks

Although limited to continental shelf, slope, and abyssal depths, the syllid genus *Anguillosyllis* is much more common in marine benthic environments than previously recognized. The 300-µm-mesh screens used in the surveys from which the present material was obtained probably undersampled this tiny meiofaunal genus, with only the very largest specimens being retained; careful elutriation of small subcores in some studies was likely the reason that so many were caught on the relatively coarse mesh. In those studies in which a species of *Anguillosyllis* was found to represent a significant proportion of the sampled community (Blake & Grassle 1994; Fiege *et al.* 2010; Gunton *et al.* 2015), the number of individuals would have been even higher and the percentage of the community greater if finer-mesh screens had been used. Certainly, any benthic or newly settled juveniles of the many species seen to have eggs and specimens measuring less than the 0.5-mm minimum length recorded in this study would pass through a 300-µm-mesh sieve.

Additional species are certain to be found. Widespread species such as *A. palpata* and *A. pupa* might ultimately be determined to represent more than one species. *Anguillosyllis* has been reported in the ecological literature either as unknown species (Aguado *et al.* 2012) or as *A.* (cf.) *capensis*; if not one of the new species described in this paper, these are most likely undescribed species. Böggemann & Purschke's (2005) and Böggemann's (2009) specimens from deep water off the west coast of Africa are most likely two new species rather than *A. capensis,* differing from *A. capensis* and from each other in palp structure and number of setigers. Gunton *et al.* (2015) recorded *A. capensis* as a dominant in samples from Whittard Canyon off the coast of Ireland, but as with Böggemann & Purschke's (2005) specimens, these deep-water forms are unlikely to be the shelf species *A. capensis*. Langeneck *et al.* (2018) recorded a syllid that had 14 setigers at 2 mm length as *Anguillosyllis* sp.; this specimen was also illustrated as having very long, thin tentacular cirri. Both the number of setigers and the long tentacular cirri are unusual for *Anguillosyllis*; although the tentacular cirri might possibly be dorsal cirri on setiger 1, the overall appearance of the illustrated specimen suggests that it might be a *Parexogone* rather than *Anguillosyllis*. In this study, additional material (LACM-AHF Poly 10175–10180) from the CCFZ that might represent additional species was too limited or damaged to allow complete descriptions to be made.

The reproductive strategy of *Anguillosyllis* is still unclear. Reproduction is considered to be by epigamy (Aguado & San Martín 2008, 2009), but the morphological and behavioral modifications (e.g., enlarged eyes, natatory setae, modification of the posterior body, and/or brooding) common to other syllids that exhibit this mode of reproduction were not seen on any of the ca. 1400 specimens examined. In every specimen that had eggs, the eggs were seen to fill the coelom posterior to the proventricle, usually setiger 6 to the end of the body. Eggs generally measured 50–85 µm across the largest diameter, with one species, *A. sepula* **n. sp.**, having larger eggs with a median diameter of 107.5 µm. In many species, larger eggs were seen entering the parapodia, but none were seen exiting. Only one specimen (*A. palpata*, Fig. 3D) had an attached dorsal mass, but the contents of this mass were not clear and may or may not be related to reproduction. A recent paper by Fukuda & Barroso (2019) documented dorsal brooding of eggs in *A. lanai* and it is possible, although undemonstrated, that the large eggs entering the parapodia of specimens in this study may exit and attach to the dorsal surface of the animal, perhaps to the glandular structures at the base of the parapodia. Fukuda & Barroso (2019) point out that given the sister-group position of *Anguillosyllis* relative to other genera of syllids (Aguado *et al.* 2012), dorsal brooding in this genus implies a very early development of this trait.

The division of species into two groups based on the full or only partial fusion of the palps was done for practical reasons in dealing with several new species and is not suggested to represent a real phylogenetic division. The degree of fusion of the palps of the species reported herein appears to be on a continuum from totally free to completely fused. It is expected that future work using additional techniques will reveal additional species as well as other characters of *Anguillosyllis* palps and structure that will refine the practical categorization used in this study.

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References

Aguado, M.T. & San Martín, G. (2008) Re-description of some enigmatic genera of Syllidae (Phyllodocida: Polychaeta). *Journal of the Marine Biological Association of the United Kingdom*, 88, 35–56.
https://doi.org/10.1017/S002531540800026X

Aguado, M.T. & San Martín, G. (2009) Phylogeny of Syllidae (Polychaeta) based on morphological data. *Zoologica Scripta*, 38, 379–402.
https://doi.org/10.1111/j.1463-6409.2008.00380.x

Aguado, M.T., San Martín, G. & Siddall, M.E. (2012) Systematics and evolution of syllids (Annelida, Syllidae). *Cladistics*, 28, 234–250.
https://doi.org/10.1111/j.1096-0031.2011.00377.x

Aguado, M.T., Helm, C., Weidhase, M. & Bleidorn, C. (2015) Description of a new syllid species as a model for evolutionary research of reproduction and regeneration in annelids. *Organisms Diversity & Evolution*, 15, 1–21.
https://doi.org/10.1007/s13127-014-0183-5

Aguado M.T., Capa, M., Lago-Barcia, D., Gil, J., Pleijel, F. & Nygren, A. (2019) Species delimitation in *Amblyosyllis* (Annelida, Syllidae). PLoS ONE, 14 (4), e0214211.
https://doi.org/10.1371/journal.pone.0214211

Barroso, R., Paiva, P.C., Nogueira, J.M.M. & Fukuda, M.V. (2017) Deep sea Syllidae (Annelida, Phyllodocida) from Southwestern Atlantic. *Zootaxa*, 4221 (4), 401–430.
https://doi.org/10.11646/zootaxa.4221.4.1

Blake, J.A. & Grassle, J.F. (1994) Benthic community structure on the U.S. South Atlantic slope off the Carolinas: Spatial heterogeneity in a current-dominated system. *Deep Sea Research Part II*, 41 (4–6), 835–874.
https://doi.org/10.1016/0967-0645(94)90051-5

Blake, J.A., Maciolek, N.J., Ota, A.Y. & Williams, I.P. (2009) Long-term benthic infaunal monitoring at a deep-ocean dredged material disposal site off North California. *Deep-Sea Research II*, 56, 1775–1803.
https://doi.org/10.1016/j.dsr2.2009.05.021

Böggemann, M. (2009) Polychaetes (Annelida) of the abyssal SE Atlantic. *Organisms Diversity & Evolution*, 9, 251–428.

Böggemann, M. & Purschke, G. (2005) Abyssal benthic Syllidae (Annelida: Polychaeta) from the Angola Basin. *Organisms Diversity & Evolution*, 5, 221–226.
https://doi.org/10.1016/j.ode.2004.11.006

Day, J.H. (1963) The Polychaete fauna of South Africa. Part 8: New Species and records from grab samples and dredgings. *Bulletin of the British Museum (Natural History). Zoology*, 10, 381–445, 12 figs.
https://doi.org/10.5962/bhl.part.20530

Day, J.H. (1967) *A Monograph on the Polychaeta of Southern Africa. Part I. Errantia. Publication No. 656*. British Museum (Natural History), London, 458 pp.
https://doi.org/10.5962/bhl.title.8596

Fiege, D., Ramey, P. & Ebbe, B. (2010) Diversity and distributional patterns of Polychaeta in the deep South Atlantic. *Deep-Sea Research I*, 57, 1329–1344.
https://doi.org/10.1016/j.dsr.2010.06.012

Fukuda, M.V. & Barroso R. (2019) First report of brooding of eggs in the deep-sea genus *Anguillosyllis* (Annelida: Syllidae). *Journal of the Marine Biological Association of the United Kingdom*, 99 (8), 1775–1778.
https://doi.org/10.1017/S0025315419000754

Gunton, L.M., Neal, L., Gooday, A.J., Bett, B.J. & Glover, A.G. (2015) Benthic polychaete diversity patterns and community structure in the Whittard Canyon system and adjacent slope (NE Atlantic). *Deep Sea Research Part I*: *Oceanographic Research Papers*, 106, 42–54.
https://doi.org/10.1016/j.dsr.2015.07.004

Haswell, W.A. (1921) The proboscis of the Syllidea. Part 1. *Quarterly Journal of Microscopical Science*, 65, 323–337.

Hartman, O. (1965) Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. *Allan Hancock Foundation Publications,* Occasional Paper No. 28, 1–378 pp., 52 pls. [http://digitallibrary.usc.edu/cdm/compoundobject/collection/p15799coll82/id/20299/rec/2]

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, 51 pls.

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. [https://repository.si.edu/handle/10088/3458?show=full]

Hilbig, B. (1994) Faunistic and zoogeographical characterization of the benthic infauna on the Carolina continental slope. *Deep-Sea Research II*, 41, 929–950.
https://doi.org/10.1016/0967-0645(94)90055-8

Hilbig, B. & Blake, J.A. (2006) Deep-sea polychaete communities in the northeast Pacific Ocean off the Gulf of the Farallones, California. *Bulletin of Marine Science*, 78 (2), 243–269. [https://www.ingentaconnect.com/content/umrsmas/bullmar/2006/00000078/00000002/art00002]

Jeuniaux, C. (1969) Nutrition and digestion. *In:* Florkin, M. & Scheer, B T. (Eds.), *Chemical Zoology (Annelida, Echiura, and Sipuncula. Vol. IV*. Academic Press, New York, pp. 69–91.
https://doi.org/10.1016/B978-0-12-395537-1.50008-7

Langeneck, J., Musco, L., Busoni, G., Conese, I., Aliani, S. & Castelli, A. (2018) Syllidae (Annelida: Phyllodocida) from the deep Mediterranean Sea, with the description of three new species. *Zootaxa*, 4369 (2), 197–220.
https://doi.org/10.11646/zootaxa.4369.2.3

Lucas, Y., Sikorski, A. & San Martín, G. (2018) Syllidae (Annelida) from the Boreal and sub-Arctic seas off Norway (North Sea, Norwegian Sea, Barents Sea). *Journal of the Marine Biological Association of the United Kingdom*, 98 (4), 755–775.
https://doi.org/10.1017/S002531541600182X

Maciolek-Blake, N, Grassle, J.F. & Neff, J.M. (Eds.) (1985) *Georges Bank Benthic Infauna Monitoring Program. Final Report for Third Year of Sampling. Vol. 2 & 3.* U.S. Department of the Interior, Minerals Management Service, Performed under Contract No. 14-12-0001-29192 by Battelle New England Marine Research Laboratory, Duxbury, Massachusetts, 333 pp. & Appendices A–K.

Trueblood, D.D. & Ozturgut, E. (1997) The Benthic Impact Experiment: A Study of the Ecological Impacts of Deep Seabed Mining on Abyssal Benthic Communities. International Society of Offshore and Polar Engineers. *Proceedings of the Seventh International Offshore and Polar Engineering Conference, Honolulu, Hawaii, USA,* 25–30 May, 1–7.

Weidhase, M., Beckers, P., Bleidorn, C. & Aguado, M.T. (2016) On the role of the proventricle region in reproduction and regeneration in *Typosyllis antoni* (Annelida: Syllidae). *BMC Evolutionary Biology*, 16 (196), 1–16.
https://doi.org/10.1186/s12862-016-0770-5

Wilson, G. (2017) Macrofauna abundance, species diversity and turnover at three sites in the Clipperton-Clarion Fracture Zone. *Marine Biodiversity*, 47, 323–347.
https://doi.org/10.1007/s12526-016-0609-8