



## Taking a closer look: an SEM review of *Levinsenia* species (Polychaeta: Paraonidae) reported from California

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### Abstract

Scanning electron (SEM) and light microscope examinations of members of *Levinsenia* Mesnil, 1897, species from California yielded a new species, new characters, emended name and range extension for *L. kirbyorum* Lovell, 2002. Specimens of *L. gracilis* (Tauber, 1879) from Sweden, Iceland, and California were compared and could not be distinguished on the basis of morphology. Two other Californian species, *L. multibranchiata* (Hartman, 1957) and *L. oculata* (Hartman, 1957), were also examined. SEM revealed features previously undescribed for the genus. Additional prostomial ciliary bundles, dorsal transverse ciliary branchial connections, notopodial sensory pores, and neurochaetal fascicle configurations. *Levinsenia barwicki* **n.sp.** possessing a terminal sensory organ, 4-8 leaf-like ciliate branchiae, and recurved neurochaete with distal hood is described. More SEM work is necessary to confirm if these features are present among other members of *Levinsenia* and other Paraonidae genera. The status of *Levinsenia* according to the phylogenetic analysis performed by Langeneck *et al.* (2019, *Molecular Phylogenetics and Evolution*, 136, 1-13) is discussed.

**Key words:** Annelida, new species, range extension, neurochaetae, new characters, notopodial sensory pores

### Introduction

The type species of *Levinsenia* Mesnil, 1897, was designated as *Aonides gracilis* Tauber, 1879, by Melville (1979). In the same paper, *Tauberia* Strelzov, 1973, was placed into synonymy with *Levinsenia*. *Periqueta* Brito & Núñez, 2002, was placed into synonymy with *Levinsenia* by Giere *et al.* (2007). The World Polychaete Database (Read & Bellan, 2013) currently lists 22 valid species in *Levinsenia* while Blake (2016) lists two additional species *L. japonica* Imajima, 1973 (as a subspecies of *L. gracilis*) and *L. pycnbranchiata* (Fauchald, 1972), a new combination (Table 1).

The present study reviews five species of *Levinsenia* reported from the Southern California Bight (SCB) in the Southern California Association of Marine Invertebrate Taxonomists (SCAMIT) Species List (Edition 11, 2016 <https://scamit.org/publications/SCAMIT%20Ed%2011-2016.pdf>): *L. gracilis*, *L. sp. B* SCAMIT 2007 §, *L. multibranchiata* (Hartman, 1957), *L. oculata* (Hartman, 1957), and *L. sp. SD1* Barwick 2000 § (<https://www.scamit.org/tools/#>). A review of these species using scanning electron microscopy (SEM) revealed new characters, confirmed a broad geographic range for *L. gracilis*, reported a new geographic distribution for *L. kirbyorum* and contributed to the description of a new species, *L. barwicki* **n. sp.**, with terminal sensory organ, 4-8 leaf-like branchiae, neurochaetae with recurved tip and distal hood. Specimens of *Levinsenia gracilis* collected from the Baltic Sea near the type locality were compared with specimens from Iceland, Puget Sound, and California, and are morphologically indistinguishable from one another. *Levinsenia* sp B SCAMIT 2007 § is confirmed to be *L. kirbyorum* Lovell, 2002, emended, reported previously from the Andaman Sea and now Southern California.

### Material and methods

For examination using SEM, specimens were first dehydrated in an ethanol series. Ethanol was subsequently re-

moved through transfers to increasing concentrations of hexamethyldisilazane (HMDS). Specimens in HMDS were allowed to air dry, then mounted on aluminum stubs and coated with gold-palladium. Specimens were observed using a Hitachi S-3000N scanning electron microscope at the Natural History Museum of Los Angeles County (NHMLAC).

The following institutional abbreviations are used: LACM-AHF, Allan Hancock Foundation Polychaete Collection, Natural History Museum of Los Angeles County; USNM, National Museum of Natural History, Smithsonian Institution; ZMUC, Zoological Museum, University of Copenhagen, MBARI, Monterey Bay Aquarium Research Institute. Use of § following an undescribed taxon, e.g. *Levinsenia* sp B SCAMIT 2007 §, indicates an accepted provisional identification within the SCAMIT Edition 11 (<https://scamit.org/publications/SCAMIT%20Ed%2011-2016.pdf>) species list, with accepted voucher sheet distinguishing characters documenting the taxon's validity and standardizing identification in the Southern California Bight.

**TABLE 1. List of *Levinsenia* species in World Register of Marine Species (WoRMS; except *L. barwicki* n. sp.)\***

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<i>L. acutibranchiata</i> (Strelzov, 1973),
<i>L. antarctica</i> (Strelzov, 1973)
<i>L. barwicki</i> n. sp. (described herein)
<i>L. brevibranchiata</i> (Strelzov, 1973)
<i>L. canariensis</i> (Brito & Núñez, 2002)
<i>L. demiri</i> Çinar, Dagli & Acik, 2011
<i>L. duodecimbranchiata</i> Cantone, 1995
<i>L. flava</i> (Strelzov, 1973)
<i>L. gracilis</i> (Tauber, 1879)
<i>L. hawaiiensis</i> Giere, Ebbe & Erséus, 2007
<i>L. kantauriensis</i> Aguirrezabalaga & Gil, 2008
<i>L. kirbyorum</i> Lovell, 2002
<i>L. kosswigi</i> Çinar, Dagli & Acik, 2011
<i>L. marmarensis</i> Çinar, Dagli & Acik, 2011
<i>L. materi</i> Çinar & Dagli, 2013
<i>L. multibranchiata</i> (Hartman, 1957)
<i>L. oculata</i> (Hartman, 1957)
<i>L. oligobranchiata</i> (Strelzov, 1973)
<i>L. reducta</i> (Hartman, 1965)
<i>L. tribranchiata</i> Çinar, Dagli & Acik, 2011
<i>L. uncinata</i> (Hartman, 1965)

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\*Two additional species listed in Blake, (2016) not appearing in WoRMS are *Levinsenia japonica* Imajima, 1973) and *L. pycnibranchiata* (Fauchald, 1972).

## Results

### Systematics account

#### Family PARAONIDAE Cerruti, 1909

#### Genus *Levinsenia* Mesnil, 1897

*Tauberia* Strelzov, 1973. *Fide* Melville (1979).

*Periquesta* Brito & Núñez, 2002. *Fide* Giere *et al.* (2007).

**Type Species.** *Aonides gracilis* Tauber, 1879, designated by ICZN (Melville 1979).

**Description.** Body threadlike, 16–30 mm long, 0.15–0.35 mm wide, sometimes with spiral or corkscrew shape.

Prostomium without median antenna; lateral, dorsal, and ventral ciliary patches present; terminal sensory organ or palpode present. Nuchal organs on peristomium. Four to seven prebranchial chaetigers, 4–22+ branchial pairs. Notopodial postchaetal lobes present; neuropodial postchaetal lobes absent. Capillary chaetae only in notopodia; neuropodia with capillary chaetae only in pre-branchial and branchial chaetigers, post-branchial chaetigers mixed, with capillary chaetae and apically curved acicular spines with fringe on convex side or with hooded apex. Pygidium tapered, with two anal cirri.

### *Levinsenia gracilis* (Tauber, 1879)

Figures 1A–D; 2A–D, 7A, B

*Aonides gracilis* Tauber, 1879: 115.

*Levinsenia gracilis*.—Mesnil & Caullery, 1898: 136–138, Pl. 6, Fig. 10.—Blake 1996: 33–44, Fig. 2.1.

*Paraonis (Paraonis) gracilis*. Cerruti, 1909: 468, 498, 504.—Pettibone, 1963: 301–302, Fig. 79a–d.

*Paraonis gracilis*.—Eliason, 1920: 55–56, Fig. 16a–e. Wesenberg-Lund, 1950: 32, Pl. 7, Fig. 34.—Ushakov, 1955: 286, Fig. 103a–b. Hartman, 1957: 330–331, Pl. 22, Figs 4–5 (synonymy); 1969: 75–76, Figs 1–3.

*Paraonis gracilis gracilis*.—Day, 1967: 566, Fig. 24.4a–b.

*Paraonis gracilis minuta*. Hartmann-Schröder, 1965: 197–198, Figs 181–182. *Fide* Strelzov, 1973.

*Paraonis (Paraonides) gracilis*.—Monro, 1930: 150–152, Fig. 58.

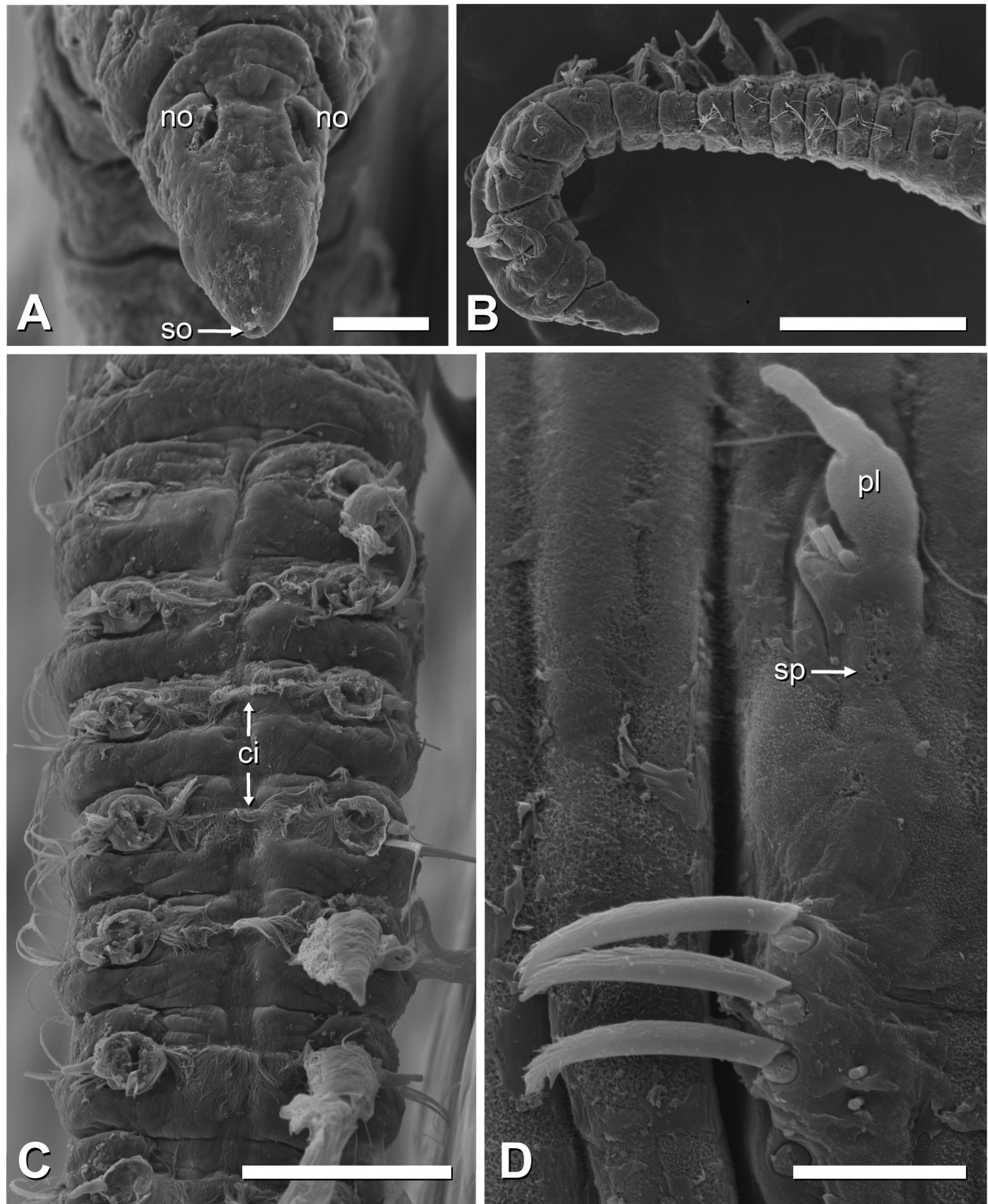
*Paraonis filiformis*.—Hartman, 1953: 39–40, Fig. 12B–C. *Fide* Hartman, 1957.

*Paraonis (Paraonis) ivanovi*.—Banse & Hobson, 1968: 23, Fig. 5f. *Fide* Strelzov, 1973.

*Tauberia gracilis*.—Strelzov, 1973: 127–133, Figs 14, 54–57 (synonymy).

**Material examined.** **Denmark**, Samsø, Kattegat, coll. Winther, **syntype** (NHMD 108749 (prev. ZMUC CRU-966)), as *Aonides gracilis* Tauber; Kattegat, Frederikshavn, Hirsholmene, July 23, 1949, coll. P.L. Kramp, det. E. Wesenberg-Lund, 1 specimen (LACM-AHF 12549).—**Sweden**, Kattegat, Värö, Ringhals Sund, 19 m depth, Sta. L7, 57°16.1'N, 12°4.8'E, 0.1 m<sup>2</sup> Smith-McIntyre grab, 11 March 1975, coll. KMS Kristineberg, sample 2, det. M.E. Petersen, 1 specimen on SEM stub (LACM-AHF 12548), 9 specimens in ethanol (NHMD 644302).—**Iceland**, Danish *Ingolf* Expedition, Sta. 138, 63°26'N, 7°56'W, 887 m depth, 10 August 1896, det. E. Wesenberg-Lund, 2 specimens (1 in ethanol, 1 mounted on SEM stub) (LACM-AHF 12550); NE of Iceland, 65°45'N, 12°10'W, 107 m depth, 13 June 1925, coll. Fisheries Board of Scotland, det. E. Wesenberg-Lund, 1 specimen (NHMD 644303).—**Greenland**, SW Greenland, Bankeundersøgelse, Sta. 37 B, April 1975, 1 specimen (NHMD 644314); SW Greenland, Bankeundersøgelse, Sta. 31-B, April 1975, 1 specimen (NHMD 644315); SW Greenland, Bankeundersøgelse, Sta. 3C, April 1975, 5 specimens (NHMD 644316); SW Greenland, Bankeundersøgelse, Sta. 81A, April 1975, 1 specimen (NHMD 644318).—**USA, California, Santa Barbara County**, Santa Barbara Channel, 12.7 miles bearing 86.6° True from Pt. Conception Light, 34°27'25"N, 120°12'55"W, 17.4 m depth, Hayward orange peel grab, R/V *Velero IV*, Sta. 4938-57, coll. Allan Hancock Foundation, 09 April 1957, 25+ specimens (1 specimen on SEM stub, other specimens in ethanol (LACM-AHF 12551); Northern Channel Islands, north of Santa Cruz Island, Bight 2008, Sta. 7556, 92 m depth, 34.08°N, 119.71°W, 0.1 m<sup>2</sup> Van Veen, 1.0 mm sieve, 09 September 2008, 2 specimens (LACM-AHF 12560).—**San Diego County**, Carlsbad, Encina, National Pollution Discharge Elimination System (NPDES) 9232, Sta. G1, replicate 4, 45 m depth, 33°06.42'N, 117°20.75'W, 0.1 m<sup>2</sup> Van Veen grab, February 1992, 3 specimens (1 specimen on SEM stub, 2 in ethanol) (LACM-AHF 12552); San Onofre, San Onofre Nuclear Generating Station (SONGS) D6700-60, Sta. XXXI, replicate 1, 33.32°N, 117.51°W, 18.3 m deep, 0.008 m<sup>2</sup> diver core, 0.5 mm sieve, 16 September 1981, 1 specimen (LACM-AHF 12553)—**Orange County**, Huntington Beach, Orange County Sanitation District (OCSD) Survey 8501, Sta. 13, rep. 3, 33°35.31'N, 118°2.94'W, 60 m depth, 0.1 m<sup>2</sup> Van Veen grab, 18 August 1985, 1.0 mm sieve, 1 specimen (LACM-AHF 12554); Huntington Beach, OCSD Survey 8501, Sta. 30, rep. 1, 33°35.49'N, 118°2.89'W, 30 m depth, 0.1 m<sup>2</sup> Van Veen grab, 20 August 1985, 1.0 mm sieve, 1 specimen (LACM-AHF 12555); Huntington Beach, OCSD Survey 9276, Sta. Control, rep. 5, 33°36.04'N, 118°5.39'W, 60 m depth, 0.1 m<sup>2</sup> box core, 1 specimen (LACM-AHF 12556); Huntington Beach, OCSD Survey 9382, Sta. LA3, rep. 1, 33°31.72'N, 117°54.73'W, 436 m depth, 0.3mm sieve, 25 January 1993, 0.1m<sup>2</sup> Van Veen grab, 4 specimens (LACM-AHF 12557); Dana Point, SCWD NPDES Sta. A, rep. 3, ~33.45°N, 117.68°W, 39.6 m depth, 0.1m<sup>2</sup> Van Veen grab, 1.0 mm sieve, 16 December 1981, 1 specimen (LACM-AHF12558).—**Los Angeles County**, Southern California Coastal Water Research Project (SCCWRP) Los Angeles County Stormwater, survey 1914, Sta. MBD25, rep. 1, Van Veen grab, 1 specimen (LACM-AHF 12559)—**Monterey County**, Monterey Canyon, MBARI sample V3147–C17, 1004 m depth, 7 January 2008, 36.74°N, 122.28°W, ROV *Ventana*, 1 specimen

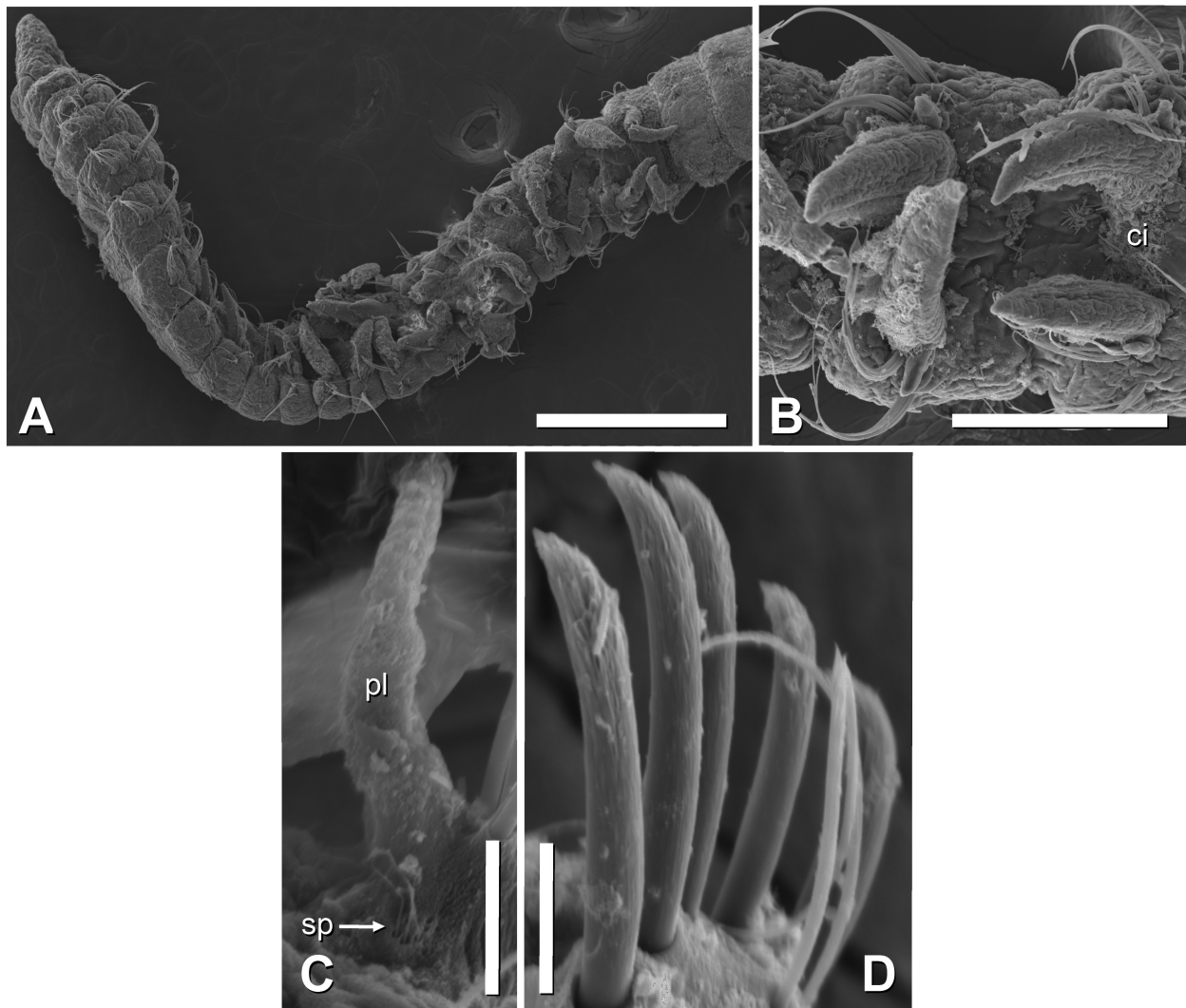
(LACM-AHF 12561); MBARI sample V3124–C24, 1004 m depth, 7 January 2008, 36.74°N, 122.28°W, ROV *Ventana*, 1 specimen (LACM-AHF 12562); MBARI sample V3147–C27, 1004 m depth, 7 January 2008, 36.74°N, 122.28°W, ROV *Ventana*, 1 specimen (LACM-AHF 12563).—Washington, Puget Sound, Seattle Metro, Publically Owned Treatment Works (POTW), West Point, METRO/TPPS Sta. XIII-100, 47.66°N, 122.46°W, 30.5 m depth, 28 September 1981, 0.1 m<sup>2</sup> Van Veen grab, 1.0 mm sieve, 7 specimens (LACM-AHF 12564).



**FIGURE 1.** *Levinsenia gracilis* (Tauber, 1879), adult, California specimen: (A) prostomium with palpode, nuchal organs, dorsal view; (B) anterior body with branchiae, lateral view; (C) transverse ciliary bands between branchiae, dorsal view; (D) notopodial glandular pores, acicular neurochaetae with fibrils, lateral view. Abbreviations: ci, cilia; no, nuchal organ; pl, post-chaetal lobe; so, palpode sensory organ; sp, sensory pores. Scale bars: A, 50  $\mu$ m; B, 300  $\mu$ m; C, 100  $\mu$ m; D, 15  $\mu$ m.

**Description.** Specimens up to 30 mm long, 0.2–0.3 mm wide. Body thin, dorsally flattened in prebranchial region, thereafter round in cross section, uniformly wide. Body tan, gut visible in posterior chaetigers. Prostomium triangular, slightly longer than wide; terminal sensory organ present; eyes absent; nuchal organs ciliated slits; median antenna absent (Fig. 1A). Prebranchial region 5–7 segments, followed by 7–16 branchial pairs (size dependent) (Figs 1B, 2A); branchiae distally tapered, blunt tipped, ciliated laterally, with dorsal transverse ciliary bands between branchiae (Figs 1C, 2B). Notopodial post-chaetal lobes as low mounds in prebranchial chaetigers, digitate in branchial region, shorter in post-branchial region; neuropodial post-chaetal lobes absent. Notopodial sensory pores present along entire body (Figs 1D, 2C), may have projecting filament (mucous strand?). Notochaetae capillary throughout; neurochaetae capillary only for anterior segments, post-branchially an anterior capillary row and posterior row of slightly curved, tapering acicular chaetae with fringe of fibrils along distal convex side, usually 3–7 acicular chaetae per fascicle (Figs 1D, 2D). Pygidium with pair of anal cirri.

**Methyl green stain.** Ventral banding in branchial region, no MG spots in post-branchial region (Fig. 7A–B). Specimens from Sweden and California with similar staining patterns.



**FIGURE 2.** *Levensenia gracilis* (Tauber, 1879), adult, Sweden specimen: (A) anterior body with branchiae, lateral view; (B) transverse ciliary bands between branchiae, dorsal view; (C) notopodial glandular pores, lateral view; (D) acicular neurochaetae with fibrils, lateral view. Abbreviations: ci, cilia; pl, post-chaetal lobe; sp, sensory pores. Scale bars: A, 500  $\mu$ m; B, 100  $\mu$ m; C, 10  $\mu$ m; D, 10  $\mu$ m.

**Remarks.** Several species of Paraonidae are reported with broad geographic and depth ranges. SEM images of *Levensenia gracilis* from near the type locality (Baltic Sea) and Southern California Bight were compared and found to be indistinguishable morphologically. Ciliary bands dorsally connecting the branchiae are newly described for the species and consistent in material from both locations. Methyl green staining has not been previously published

with paraonid specimens, but the same pattern is present in all *L. gracilis* specimens stained. For information on diagnostic character differences, see the dichotomous key below and table of character distributions (Table 2).

*Levinsenia gracilis* has a reported cosmopolitan distribution with a broad bathymetric range (Strelzov 1973, Blake 1996). Material examined from Denmark, Sweden, Iceland, Greenland, Washington, USA, and California, USA, were all collected within the reported (very wide) depth range, are morphologically similar, and represent occurrences indicating a broad geographic distribution. The specimen from the Zoological Museum, Natural History Museum of Denmark, is noted as the only surviving syntype and is in four pieces, but the characters match the published description of *L. gracilis*.

It cannot be assumed that all literature reports of *Levinsenia gracilis* from other locations are correctly identified. Nine species of *Levinsenia* (Table 1) have been described since Strelzov (1973) reviewed the family. Several of these new species were originally identified as *L. gracilis*, but later re-examined and determined to be new (see WoRMS).

**Type locality.** Denmark.

**Distribution.** Cosmopolitan, subtidal to 3000+ m.

### *Levinsenia kirbyorum* Lovell, 2002, emended

Figures 3A–D, 7C, H

*Levinsenia kirbyae* Lovell, 2002: 49–51, Fig. 9A–D.

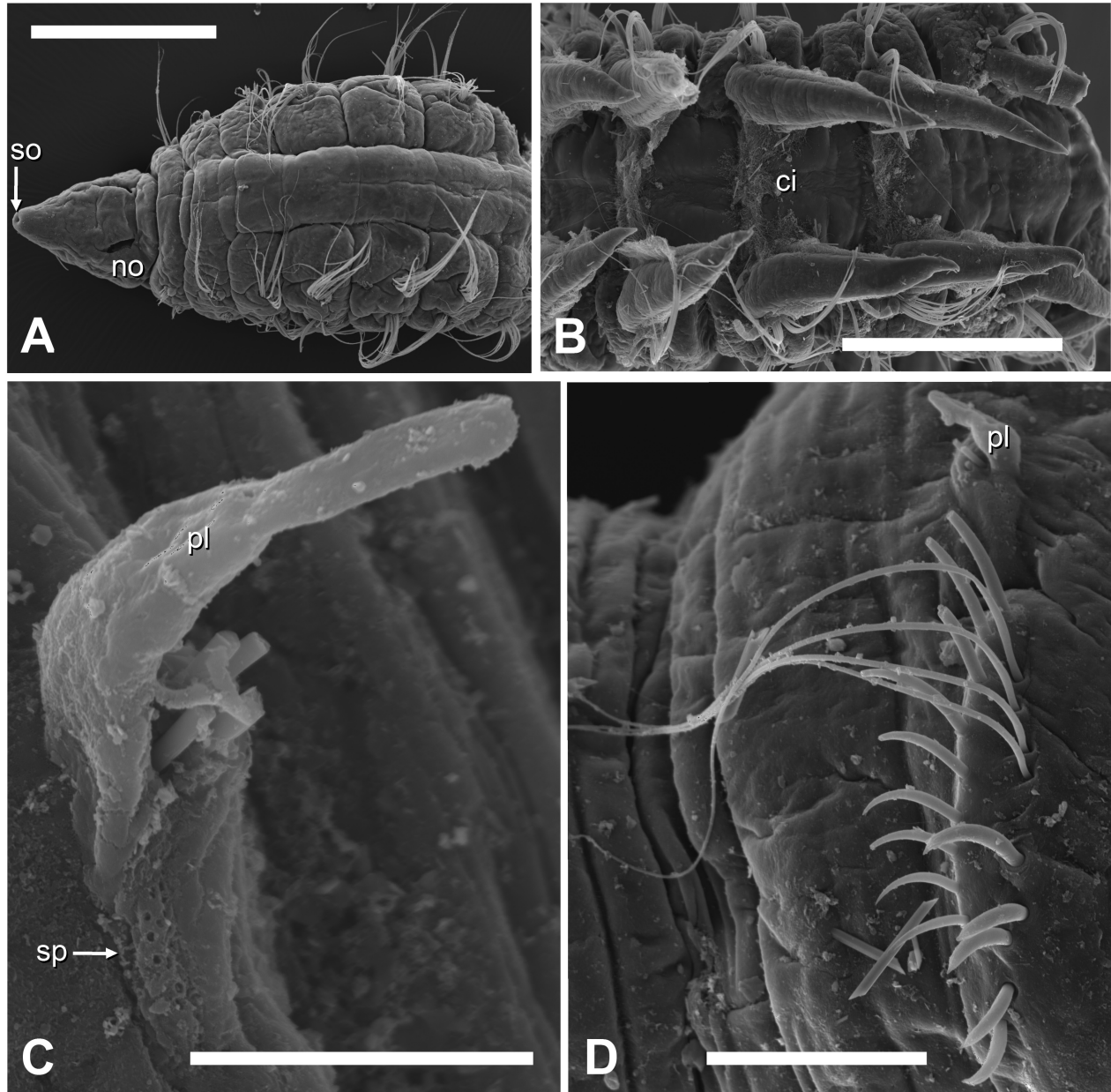
*Levinsenia* sp B SCAMIT 2007 §: SCAMIT 2007, Vol 25, No. 5, 1–12.

**Material examined.** **Indian Ocean, Andaman Sea**, Sta. G-2/OS, 23 April 1996, 63 m depth, **paratype** (LACM-AHF 2091).—**USA. California. Orange County**, Huntington Beach, OCS D Survey 97130, 1997, Sta. 37, rep. 4, 56 m depth, 0.1 m<sup>2</sup> Van Veen grab, 07 January 1997, 1.0 mm sieve, 1 specimen, SEM stub (LACM-AHF 12565); OCS D Survey 9276, Sta. Control, replicate 5, 60 m depth, 0.1 m<sup>2</sup> Van Veen grab, 23 July 1992, 1.0 mm sieve, 1 specimen, SEM stub (LACM-AHF 12566).—**San Diego County**, Carlsbad, Encina Treatment Plant, NPDES 9126, Sta. R2, rep. 4, 33°07.566'N, 117°20.694'W, 45 m depth, 0.1 m<sup>2</sup> Van Veen grab, 1991, 1.0 mm sieve, 1 specimen, SEM stub (LACM-AHF 12567); Southern California Bight Project (SCBP), Bight 2003, Sta. A2, 29 m deep, 6 Aug 2003, North San Diego Shelf, 33.165°N 117.391°W, 0.1 m<sup>2</sup> Van Veen grab, 1.0 mm sieve, coll. Weston Solutions 1 specimen, SEM stub (LACM-AHF 12568); SCCWRP, Southern California Bight Project (SCBP), Bight 2008, Sta. 7556, 92 m deep, 09 September 2008, Channel Islands, 34.0790°N 119.7008°W, 0.1 m<sup>2</sup> Van Veen grab, 1.0 mm sieve, 3 specimens (LACM-AHF 12569); Carlsbad, Encina Treatment Plant NPDES 9232, Sta. G1, replicate 3, 33°06.42'N 117°20.74'W, 45 m depth, 0.1 m<sup>2</sup> Van Veen grab, 1992, 1.0 mm sieve, 1 specimen (LACM-AHF 12570); NPDES 9344, Sta. G2, rep. 3, 33°06.73'N, 117°20.85'W, 45 m depth, Van Veen grab, 1993, 1.0 mm sieve, 1 specimen (LACM-AHF 12571); NPDES 9232, Sta. R2, rep. 1, 33°07.566'N, 117°20.694'W, 45 m depth, 0.1 m<sup>2</sup> Van Veen grab, 1992, 1.0 m sieve, 1 specimen (LACM-AHF 12572); Cardiff by the Sea, San Elijo Treatment Plant NPDES, sta. A-2-5, replicate 2, ~33.07°N, 117.25°W, 45(?) m depth, 9 March 2004, 0.1 m<sup>2</sup> Van Veen grab, 1.0 mm sieve, 1 specimen (LACM-AHF 12573); San Onofre, SONGS D400-175 XXII, rep. 2, ~33.36°N, 117.57°W, 53.34 m depth, 6 April 1980, 0.1 m<sup>2</sup> Van Veen grab, 1.0 mm sieve, 1 specimen (USNM 1604269); Carlsbad, Encina Treatment Plant NPDES: 9344, Sta. R2, rep. 3, 33°07.566'N, 117°20.694'W, 46 m depth, 0.1 m<sup>2</sup> Van Veen grab, 1993, 1.0 mm sieve, 1 specimen (USNM 1604270).—**Orange County**, Huntington Beach, OCS D NPDES Survey 97139, Sta. ZB, rep. 3, 33°34.54'N, 118°0.00'W, 56 m depth, 0.1 m<sup>2</sup> Van Veen grab, 22 October 1997, 1.0 mm sieve, 1 specimen (LACM-AHF 12574); OCS D NPDES Survey 9276, Sta. 37, rep. 2, 33°34.83'N, 117°57.37'W, 56 m depth, 0.1 m<sup>2</sup> box core, 24 July 1992, 1.0 mm sieve, 1 specimen (LACM-AHF 12575); OCS D NPDES Survey 9276, Sta. Control, replicate 4, 33°36.04'N, 118°5.39'W, 60 m depth, 0.1 m<sup>2</sup> box core, 23 July 1992, 1.0 mm sieve, 2 specimens (LACM-AHF 12576); OCS D NPDES Survey 98151, Sta. 5, rep. 1, 33°34.74'N, 118°01.61'W, 59 m depth, 0.1 m<sup>2</sup> Van Veen, 21 October 1998, 1.0 mm sieve, 1 specimen (LACM-AHF 12577)

**Description.** Specimens up to 39 mm long, 0.15–0.35 mm wide. Body inflated, dorsally flattened in prebranchial region, thereafter round in cross section. Tan color. Prostomium triangular, longer than wide; terminal sensory organ present; median antenna absent; ciliated peristomial nuchal slits. Prebranchial segments slightly inflated (Fig. 3A), with two longitudinal dorsal grooves. Branchiae begin on chaetigers 7–8, 13–20 pairs, conical; cilia present on lateral branchiae margins, continue as transverse bands across dorsum (Fig. 3B). Notopodial post-chaetal lobes

short, conical in pre-branchial chaetigers, digitate in branchial region, shorter post-branchial. Notopodial sensory pores present along entire body (Fig. 3C), immediately below notochaetae, may have projecting filament. Neuro-podial post-chaetal lobes absent. Notopodia with capillary chaetae only. Neuropodia with capillary chaetae and up to 13 concave, fringed acicular spines in post-branchial segments. Neuropodial spines thinner, straighter (superior) and thicker, more recurved (inferior), double rows in far posterior chaetigers (Figs 3E, 7H). Abdominal segments with deep, transverse dorsal intersegmental furrows. Pygidium unknown.

**Methyl green stain.** Branchial region with ventral bands, and distinct notopodial post-branchial spots (Fig. 7C).



**FIGURE 3.** *Levisensia kirbyorum* Lovell, 2002, adult: (A) prostomium with palpode, nuchal organs, dorsal view; (B) transverse ciliary bands between branchiae, dorsal view; (C) notopodial glandular pores, lateral view; (D) posterior chaetal fascicle showing multiple rows of acicular spines, lateral view. Abbreviations: ci, cilia; no, nuchal organ; pl, post-chaetal lobe; so, palpode sensory organ; sp, sensory pores. Scale bars: A, 200  $\mu$ m; B, 200  $\mu$ m; C, 20  $\mu$ m; D, 50  $\mu$ m.

**Remarks.** SEM images of *Levisensia* sp B SCAMIT 2007 § confirmed that it is the same as *L. kirbyorum*, described from the Andaman Sea, as noted in the voucher sheet. The unusual dorsal longitudinal furrows on the California material, which are very clearly visible with SEM (Fig. 3A), were not described for *L. kirbyorum* are confirmed. The paratype of *L. kirbyorum* (LACM-AHF 2091) was reviewed and dorsal furrows were confirmed. The original description of *L. kirbyorum* Lovell 2002 is emended to include these furrows. The California material

examined also has the unique double-rowed neurochaetal fascicle arrangement described for *L. kirbyorum*. Identical methyl green staining spots are present in post-branchial notopodial areas in both Andaman Sea and California specimens. This is a range extension from the Andaman Sea into Southern California. For information on diagnostic character differences, see the dichotomous key below and table of character distributions (Table 2). The specific epithet is emended to acknowledge that the species was named in honor of three persons; Jacqueline Kirby Lovell, Andrew Kirby Lovell, and Robin Kirby Lovell. The name *L. kirbyae* is emended to *Levinsenia kirbyorum*.

**Type locality.** Andaman Sea.

**Distribution.** Andaman Sea, Indian Ocean; Southern California, 42–60 m depth.

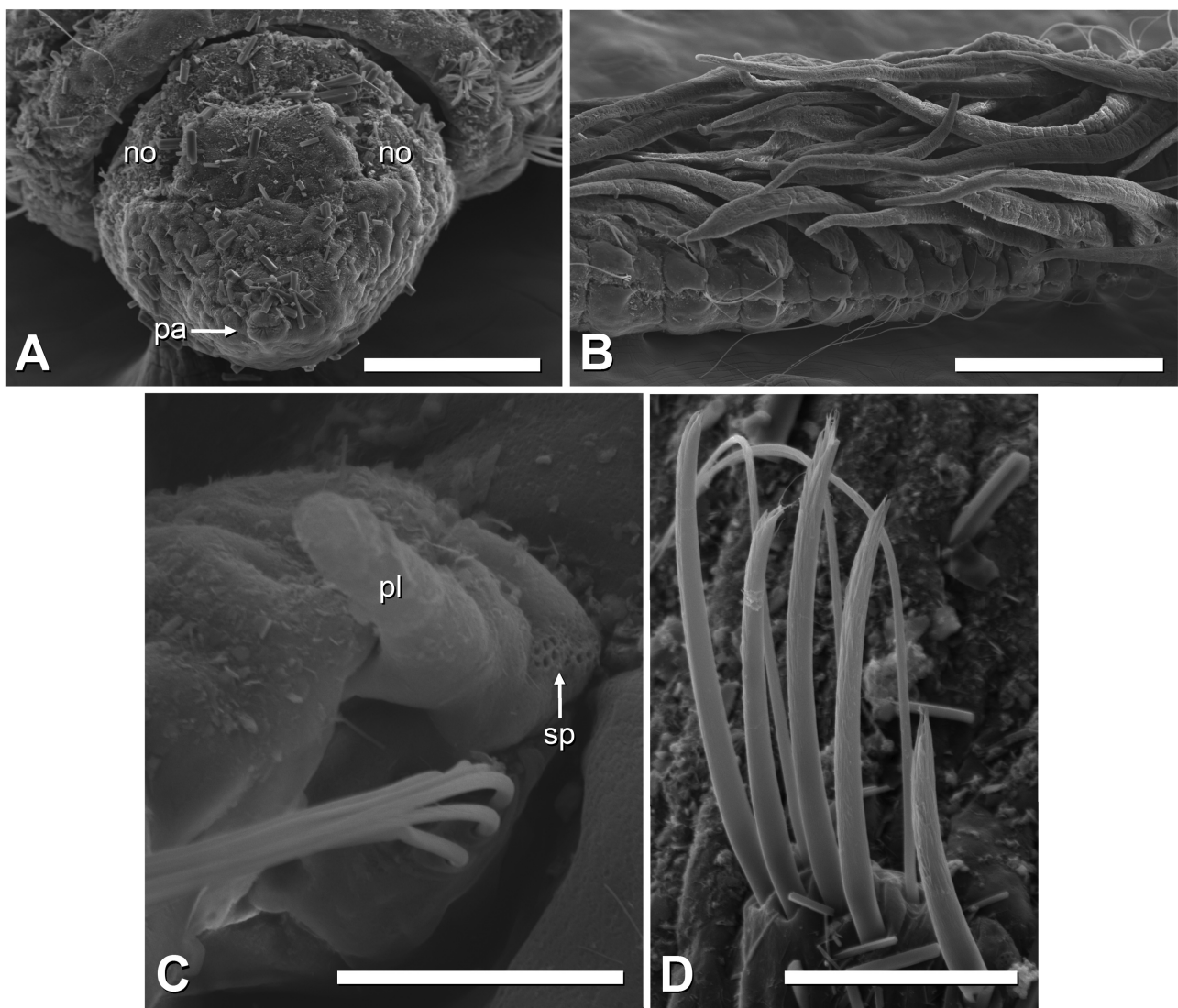
***Levinsenia multibranchiata* (Hartman, 1957)**

Figures 4A–D, 7D

*Paraonis multibranchiata* Hartman, 1957: 332–333; 1969: 79–80, Fig. 1.

*Tauberia multibranchiata*.—Strelzov, 1973: 135–136, Figs 11(1), 59.

*Levinsenia multibranchiata*.—Blake, 1996: 36, Fig. 2.3.



**FIGURE 4.** *Levinsenia multibranchiata* (Hartman, 1957), paratype AHF-LACM POLY 648, adult: (A) prostomium with palpode, nuchal organs, dorsal view; (B) branchial region, dorsal view; (C) notopodial glandular pores, lateral view; (D) acicular neurochaetae with fibrils, lateral view. Abbreviations: no, nuchal organ; pa, palpode; pl, post-chaetal lobe; sp, sensory pores. Scale bars: A, 100  $\mu$ m; B, 300  $\mu$ m; C, 20  $\mu$ m; D, 30  $\mu$ m.



**Material examined.** USA, California, Santa Barbara County, Santa Barbara Channel Basin, 18.0 miles bearing 135° True from Point Conception Light, 34°14'10"N, 120°12'45"W, 502.9 m depth, green mud, Hayward orange peel grab, R/V *Velero IV*, Sta. 3731-55, coll. Allan Hancock Foundation, 12 December 1955, 14 **paratypes** (one specimen mounted on SEM stub) (LACM-AHF POLY 648).—**Orange County**, Huntington Beach, OCS D NPDES Survey 9270, Sta. C2, rep. 5, 33°36.12'N, 117°56.02'W, 56 m depth, 0.1 m<sup>2</sup> Van Veen grab, 1.0 mm sieve, 1 specimen (LACM-AHF 12578); survey 9382, Sta. C2, rep. 1, 33°36.12'N, 117°56.02'W, 56 m depth, 0.1 m<sup>2</sup> Van Veen grab, 1.0 mm sieve, 12 specimens (LACM-AHF 12579); survey 9279, Sta. C2, rep. 3, 33°36.12'N, 117°56.02'W, 56 m depth, 0.1 m<sup>2</sup> Van Veen grab, 1.0 mm sieve, 20 specimens (LACM-AHF 12580); survey 9279, Sta. C2, rep. 5, 33°36.12'N, 117°56.02'W, 56 m depth, 0.1 m<sup>2</sup> Van Veen grab, 1.0 mm sieve, 2 specimens (LACM-AHF 12581); survey 95109, Sta. C2, rep. 1, 33°36.12'N, 117°56.02'W, 56 m depth, 0.1 m<sup>2</sup> Van Veen grab, 1.0 mm sieve, 1 specimen (LACM-AHF 12582).—**San Diego County**, Carlsbad, Encina Treatment Plant NPDES Survey 9344, Sta. R2, rep. 1, ~33°07.57'N, 117°20.69'W, 46 m depth, 0.1 m<sup>2</sup> Van Veen grab, 1.0 mm sieve, 1 specimen (LACM-AHF 12583); survey 9344, Sta. R2, rep. 3, ~33°07.57'N, 117°20.69'W, 46 m depth, 0.1 m<sup>2</sup> Van Veen grab, 1.0 mm sieve, 1 specimen (LACM-AHF 12584).

**Description.** Specimens up to 30 mm long, 0.15–0.25 mm wide. Thorax slightly inflated in prebranchial chaetigers, rounded in cross section thereafter. Body tan. Prostomium conical, wider than long; poorly-developed terminal sensory organ; pair of ciliated peristomial nuchal organs; median antenna absent (Fig. 4A). Branchiae begin on chaetigers 7–8, 20–36 pairs; thin, tapering, five times longer than wide (Fig. 4B); cilia present on lateral edges, with connecting transverse dorsal bands of short cilia. Notopodial post-chaetal lobes papilla-like on chaetiger 1, digitate in branchiate region, shorter post-branchial. Notopodial sensory pores (Fig. 4C) present on all segments. Neuro-podial post-chaetal lobes absent. Noto- and neuropodial capillary chaetae from chaetiger 1. Acicular neurochaetae, 5–7 per fascicle, begin post-branchial; each spine slightly curved, tapering and thinner distally, with fringe of fibrils on convex margin; spines alternating with capillary chaetae (Fig. 4D). Pygidium with dorsal anal pore, mid-ventral lobe, two short anal cirri.

**Methyl green stain.** None present (Fig. 7D).

**Type locality.** Southern California, Santa Barbara Basin.

**Distribution.** Southern and Central California, 45–540 m deep.

**Remarks.** *Levinsenia multibranchiata* is readily distinguished from other SCB species by the more numerous and elongate branchiae. For information on diagnostic character differences, see the dichotomous key and Table 2.

### *Levinsenia oculata* (Hartman, 1957)

Figures 5A–E, 7E, F

*Paraonis gracilis oculata* Hartman, 1957: 331–332, Pl. 44, Figs 1–3; 1963: 77–78, 3 Figs 1–3.

*Tauberia oculata*.—Strelzov, 1973: 133–135, Figs 16(10), 58 (Synonymy).—Smith, 1985: 186.

*Levinsenia oculata*.—Blake, 1996: 34–36, Fig. 2.2.

*Levinsenia kirbyorum*.—of authors SCB not Lovell 2002.

**Material examined.** USA, California, Southern California Bight, Bight 2008, Sta. 7168, 822 m depth, 33.2748°N, 118.0861°W, 18 September 2008, 0.1 m<sup>2</sup> Van Veen, 1.0 mm sieve, 1 specimen (LACM-AHF 12585); station 7251, 696 m depth, 33.5793°N, 118.3287°W, 16 July 2008, 0.1 m<sup>2</sup> Van Veen grab, 1.0 mm sieve, 1 specimen (LACM-AHF 12586); Sta. 5925, 1 specimen, SEM stub (LACM-AHF 12587). OCS D 97130, Sta. 37, rep. 4, 56 m, 0.1 m<sup>2</sup> Van Veen grab, 1.0 mm sieve, 1 specimen, SEM stub (LACM-AHF 12588). Bight 2013, Sta. 9132, 82.6 m, 9 September 2013 (OCS D voucher 2436), 1 specimen, SEM stub (LACM-AHF 12589).

**Description.** Specimens up to 20 mm long, 0.25 mm wide. Body slightly inflated in prebranchial region, thereafter cylindrical in cross section. Body cream colored, brownish 'ocular' pigment on lateral margins of prostomium. Prostomium triangular, as long as wide, with terminal sensory organ, nuchal organs and lateral ciliary patches; pigmented 'eyespot' (Fig. 7E, F); median antenna absent; peristomium with ciliated nuchal organs. Five to eight prebranchial segments followed by 8–11 pairs of tapering branchiae, 6–7 times longer than wide, distally blunt, sparsely ciliated, connected dorsally by bands of cilia (Fig. 5B, C). Prebranchial notopodial post-chaetal lobes as low mounds, cirriform in branchial region, shorter post-branchial. Neuro-podial post-chaetal lobes absent. Noto-podial sensory pores present on all segments (Fig. 5D). Notochaetae capillary throughout. Neuro-podial capillary

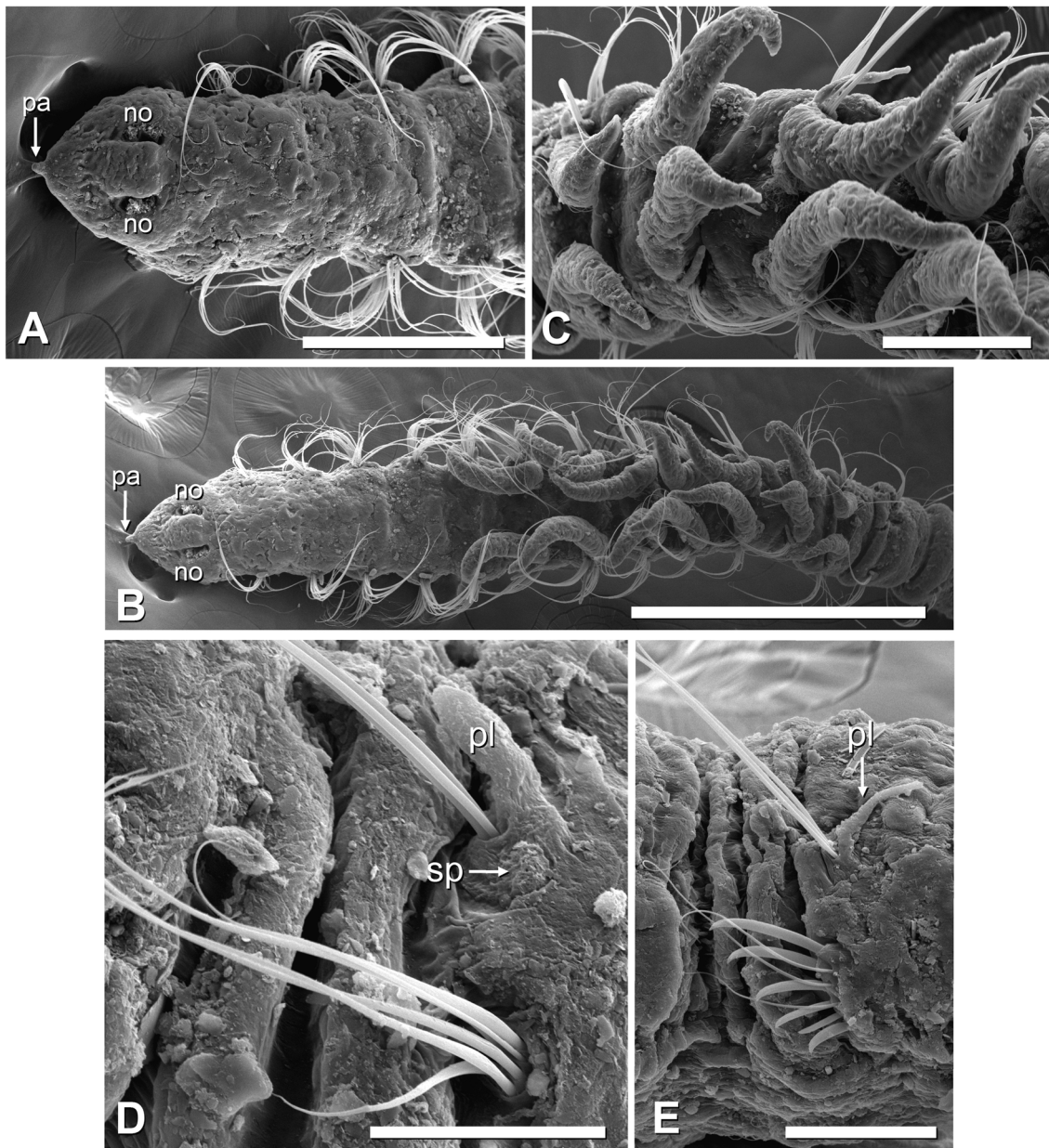
chaetae throughout; post-branchial chaetigers include distally curved acicular spines with convex fringe of fibrils, up to seven per fascicle, alternating with long capillaries (Fig. 5E). Pygidium narrow, two anal cirri.

**Methyl green stain.** Thorax staining in pre- and post-chaetal areas, speckled in pre-branchial chaetigers, a solid band in branchial and 2–3 post-branchial chaetigers, with similar lighter staining in abdominal chaetigers (Fig. 7E).

**Type locality.** USA, Southern California, outer Los Angeles Harbor.

**Distribution.** Central California to Gulf of California, shallow subtidal to 1272 m.

**Remarks.** This species is rarely encountered on the Southern California Bight shelf and more typically collected in slope and basin depths. Reports of shallow subtidal collections need to be verified. For information on diagnostic species differences see the dichotomous key below and table of character distributions (Table 2). The presence of ‘ocular’ pigment separates *L. oculata* from *L. gracilis*, but can fade over time in preserved specimens. The first author has seen freshly collected specimens from off Angola West Africa with ‘ocular’ pigment similar to *L. oculata*, but differs in having shorter, curved neurochaetal spines.



**FIGURE 5.** *Levinsenia oculata* (Hartman, 1957), adult: (A) prostomium with palpode, nuchal organs, dorsal view; (B) anterior body with branchiae, dorso-lateral view; (C) low transverse ciliary bands between branchiae, dorso-lateral view; (D) notopodial glandular pores, lateral view; (E) posterior chaetal fascicle showing capillary and acicular spines, lateral view. Abbreviations: no, nuchal organ; sp, sensory pores. Scale bars: A, 200  $\mu\text{m}$ ; B, 300  $\mu\text{m}$ ; C, 50  $\mu\text{m}$ ; D, 10  $\mu\text{m}$ ; E, 20  $\mu\text{m}$ .

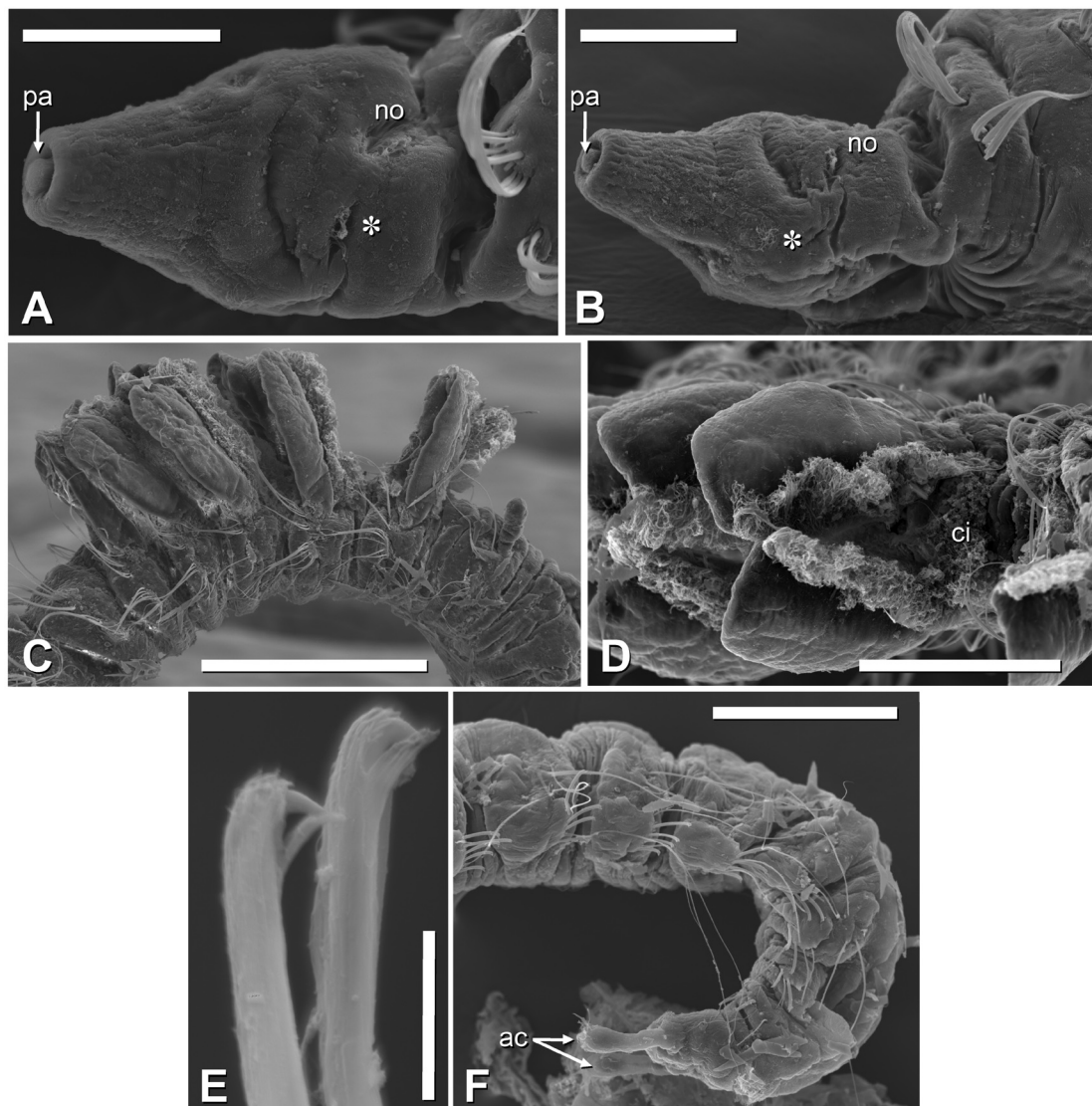
*Levinsenia barwicki* n. sp.

Figures 6A–F, 7G

*Levinsenia* sp SD1 Barwick 2000§

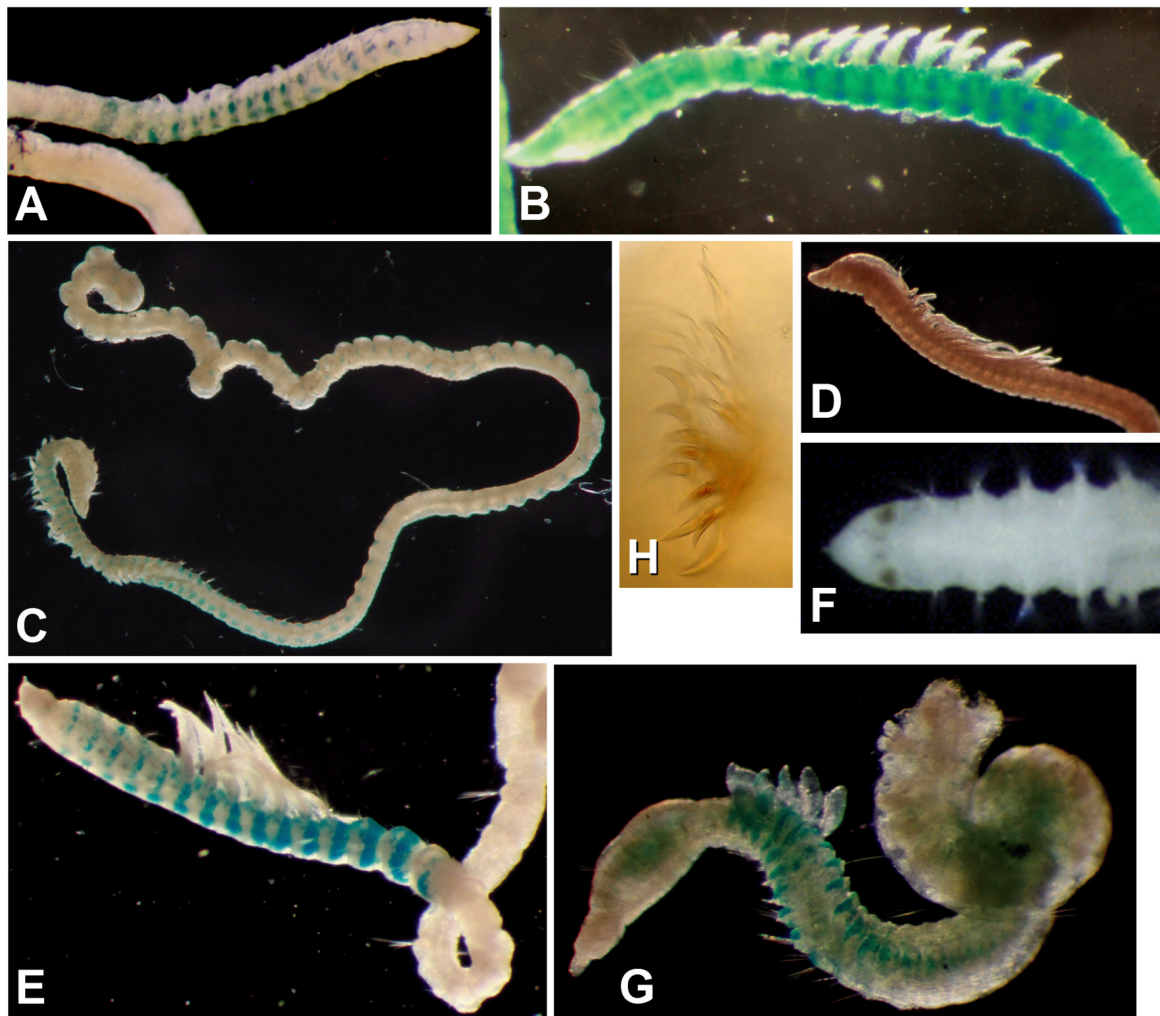
*Levinsenia* sp A Phillips (unpublished)

**Material examined.** USA, California. Santa Barbara County, Gaviota, GAVBIOCORE, 28 October 1993, Sta. C, rep. 1, ~34°27'29"N, 120°12'43"W, 27 m depth, 0.008m<sup>2</sup> hand core, 0.5 mm sieve, **holotype** (LACM-AHF 12590). Western Santa Barbara Channel, Chevron Platform Gail, Sta. 6, rep. 1, ~34.28°N, 119.59°W, March 1984, 0.1 m<sup>2</sup> Smith-McIntyre grab, 1.0 mm sieve, 1 **paratype** (LACM-AHF 12591).—San Diego County, City of San Diego Regional Survey 2010, Sta. 8032, 32.56°N, 117.19°W, 6 July 2010, 33 m depth, 0.1 m<sup>2</sup> Van Veen grab, 1.0 mm sieve, 1 **paratype** (USNM 1548300); South San Diego Shelf, City of San Diego, SCCWRP Bight 2013, Sta. 9007, 15 July 2013, 35 m depth, 32.5515°N, 117.1995°W, 0.1 m<sup>2</sup> Van Veen grab, 1.0 mm sieve, 1 **paratype** (LACM-AHF 12593).—Los Angeles County, Outer Los Angeles Harbor, Catalina Sea Ranch, Sta. 1, 22 February 2016, 45 m depth, 33.61260°N, 118.10437°W, 0.1m<sup>2</sup> Van Veen grab, 1.0 mm sieve, R/V *Yellowfin*, 1 **paratype** (LACM-AHF 12596).



**FIGURE 6.** *Levinsenia barwicki* n. sp., adult, holotype (AHF-LACM POLY 12590): (A) prostomium, lateral view; (B) prostomium, ventro-lateral view; (C) truncate, ciliated branchiae, lateral view; (D) transverse ciliary bands between branchiae, dorsal view; (E) hooded acicular spines, lateral view; (F) posterior fascicles with pygidium showing long capillary chaetae and acicular spines, lateral view. Abbreviations: \*, lateral peristomial cilia patches; ac, anal cirri; ci, cilia; no, nuchal organ; pa, palpode. Scale bars: A, 50 µm; B, 50 µm; C, 200 µm; D, 100 µm; E, 5 µm; F, 100 µm.

**Additional material. USA, California.** Santa Barbara County, Gaviota, GAVBIOCORE Sta. Ni, rep. 1, ~34°27'29"N, 120°12'43"W, 27 m depth, 13 August 1992, 0.008 m<sup>2</sup> hand core, 0.5 mm sieve, id. L. Lovell, 1 specimen mounted on SEM stub (LACM-AHF 12597); Monterey County, Monterey Bay, MBARI sample T387C76, 36.20°N, 122.62°W, 5 December 2001, 3322 m depth, 6.9 cm diameter tube core, top 5 cm, 0.3 mm sieve, ROV *Tiburon*, 1 specimen (LACM-AHF 12594); Monterey Bay, MBARI sample T387C80, 36.20°N, 122.62°W, 5 December 2001, 3322 m depth, 6.9 cm diameter tube core, top 5 cm, 0.3 mm sieve, ROV *Tiburon*, 1 specimen (LACM-AHF 12595); Monterey Bay, MBARI MARS sample D703-PC45, 36.71°N, 122.19°W, 17 December 2014, 889 m depth, 6.9 cm diameter tube core, top 5 cm, 0.3 mm sieve, ROV *Doc Ricketts*, determined by T. Phillips, 2 specimens (USNM 1604268); MBARI MARS sample D702-PC49, 36.75°N, 122.28°W, 17 December 2014, 1001 m depth, 6.9 cm diameter tube core, top 5 cm, 0.3 mm sieve, ROV *Doc Ricketts*, id. T. Phillips, specimen labelled as *Levinsenia* sp SD1, 1 specimen mounted on SEM stub (LACM-AHF 12598); labelled as SD1; Monterey Bay, MBARI sample T387C57, 36.20°N, 122.62°W, 5 December 2001, 3322 m depth, 6.9 cm diameter tube core, top 5 cm, 0.3 mm sieve, ROV *Tiburon*, 1 specimen; Southern California Bight, South of Imperial Beach, City of San Diego South Plant Ocean Outfall, I15 rep. 1, 32.54°N, 117.19°W, 6 July 2015, 33 m depth, Van Veen grab, 1.0 mm sieve; City of San Diego South Plant Ocean Outfall, Sta. I16, rep. 1, 32.54°N, 117.18°W, 13 July 2006, 28 m depth, 0.1 m<sup>2</sup> Van Veen grab, 1.0 mm sieve.



**FIGURE 7.** A–G, *Levinsenia* spp. methyl green staining patterns: A, *L. gracilis* California specimen; B, *L. gracilis* Sweden specimen; C, *L. kirbyorum*; D, *L. multibranchiata*; E, F, *L. oculata*; G, *L. barwicki* n. sp.; H, *L. kirbyorum*, posterior neuropodial fascicle.

**Description.** Holotype 4 mm long, 0.10 mm wide, complete, damaged mid-body. Body slightly inflated in pre-branchial region, thereafter cylindrical in cross section. Body cream colored. Prostomium conical; terminal sensory organ well developed, mid-prostomial ciliary recessed area (Fig. 6A); peristomial ciliated nuchal organs; lateral ciliary patches, dorsal and ventral ciliary patches (Fig. 6B); median antenna absent. Six prebranchial segments, followed by 5 (6<sup>th</sup> developing on one side) pairs of heavily ciliated, truncate, leaf-like, branchiae (Fig. 6C), mid-dorsal transverse ciliary bands continuous with branchiae (Fig. 6D). Notopodial glandular pores absent. Post-branchial neurochaetae acicular, up to 5 acicular spines with sharply bent tip and thick surrounding sheath (Fig. 6E), alternating with capillary chaetae. Far posterior chaetigers with pad-like chaetal fascicles, capillary notochaetae extremely long. Anal cirri distally inflated with cilia at tips (Fig. 6F).

**Methyl green stain.** Staining limited to pre-chaetal areas of notopodia in branchial and 7–8 post-branchial chaetigers (Fig. 7G).

**Type locality.** USA, Santa Barbara County, Gaviota, California, 27 m depth.

**Distribution.** Central to southern California, 27–3322 m depth.

**Variations.** Paratypes: body up to 15 mm long. Branchiae up to 8 pairs, heavily ciliated.

**Remarks.** *Levinsenia barwicki* n. sp. is distinct by way of the several patches of cilia on the prostomium, especially on the mid-prostomial recessed area where a median antenna is found in other Paraonidae. Lateral ‘cheek’ and ventral ciliary patches are noted and have not been previously described. Branchiae are heavily ciliated, flattened and leaf-like, similar to *Paraonis pygoenigmatica* (Jones, 1968) (formerly *Levinsenia pygoenigmatica*, reassigned to *Paraonis*, see Blake 2016). Neurochaetae are unidentate, sharply bent, with a thick sheath, ‘appearing’ bidentate using light microscopy; unlike *L. canariensis* and *L. hawaiianensis*, which are truly bidentate. J. Blake (pers. comm.) reports that other very small, shelf and slope *Levinsenia* with similar branchial and neurochaetal features are known to exist in the North Atlantic. *Levinsenia barwicki* is a very small species and is usually collected on a 0.5 mm (or finer) sieve, occasionally on a 1.0 mm sieve.

The reported depth range for *L. barwicki* is very broad. However, other *Levinsenia* species present such broad depth ranges. Blake (1996) reports *Levinsenia gracilis* occurring from “shallow subtidal to 3000+ m”. This species is named in honor of Kelvin Barwick, SCAMIT President.

## Discussion

New characters were revealed during this SEM study of Southern California Bight *Levinsenia*. Patches of cilia were observed in new locations on the prostomium of *L. barwicki* n. sp. (Fig. 6 A–B). Transverse, dorsal ciliary bands connecting branchiae were observed on most species reviewed (Figs 1C, 2B; 3B, 5C, 6D), however they are best developed in posterior branchial segments and can be difficult to observe. Ciliary bands were not observed using SEM on the specimen of *L. multibranchiata*, although because the branchiae are long and numerous the view of the dorsum between branchiae was obscured.

Clusters of notopodial ‘glandular’ pores were observed in four of the five *Levinsenia* species reviewed (Figs 1D, 2C, 3C, 4C, 5D); they were not seen in *L. barwicki*. These pores occur on all chaetigerous segments, next to or just ventral to notopodial fascicles. Some pores have emergent filaments. These presumptive glandular pore areas have not been previously noted for other *Levinsenia* species. They can, however, be seen in SEM images of *Aricidea* (*Strelzovia*) *roberti* (Aguirrezabalaga & Gil, 2008). They are reported as secretory among Spionidae (V. Radaševsky, pers. com.) and may occur among members of other polychaete families. Notopodial pores are not readily observable with light microscopy, the primary tool of taxonomists, and thus are of little use in general identification work.

*Levinsenia barwicki* is a very small species collected primarily on a 0.5 mm sieve (only once on a 1.0 mm sieve), has unique flattened, leaf-like branchiae, and acicular spines that appear bidentate with light microscopy. *Levinsenia kirbyorum* has double overlapping rows of more numerous acicular spines; while all other local species have single rows of 3–7 acicular spines. *Levinsenia multibranchiata* is distinguished from other California *Levinsenia* species by the large number of pairs and length of branchiae. *Levinsenia oculata* has a conical prostomium and ‘ocular’ pigment that separates it from *L. gracilis* with a triangular prostomium and no prostomial pigment. However, the ‘ocular’ pigment can fade over time and should not be relied upon with older material.

Methyl green staining patterns have been used as additional diagnostic tools in several polychaete families:

Capitellidae, Cirratulidae and Sabellidae in papers by Banse (1972), Blake (2015), Green (2002), and Tovar-Hernandez *et al.* (2007). Staining pattern results in other Paraonidae genera may provide an additional diagnostic tool to separate genera or species. Table 2 presents differentiating characters for the *Levinsenia* species reported from California.

### Remarks on the status of *Levinsenia sensu* Langeneck *et al.* (2019)

While the present paper is primarily descriptive in scope, we want to take this opportunity to comment on some of the results reported by Langeneck *et al.* (2019) for recognizing Paraonidae genera, including *Levinsenia*, as well as more inclusive phylogenetic hypotheses. This study is the most extensive phylogenetic analysis of Paraonidae. Only one previous analysis, by Reuscher (2013), has been performed but was limited to addressing monophyly of *Cirrophorus* Ehlers, 1908, and *Paradoneis* Hartman, 1965. The hypotheses inferred by Langeneck *et al.* (2019) were based on sequence data, although they proceeded to ‘map’ several morphological characters onto the cladograms in an effort to claim particular explanatory hypotheses for those characters. *Levinsenia* was shown to be monophyletic (Langeneck *et al.* 2019: figs 1–2), albeit the specific nucleotides serving as synapomorphies were not mentioned. As a result of character mapping, Langeneck *et al.* (2019) suggested that the absence, explained as a loss, of the median antenna among members of *Levinsenia* is a synapomorphy for the genus (Langeneck *et al.* 2019: fig. 3c).

There are two fundamental epistemic problems that compromise the results of Langeneck *et al.*'s (2019) study. The first problem, identified by Fitzhugh (2016a; see also Nogueira *et al.* 2017: 683–684), is that causally accounting for differentially-shared nucleotides by way of available phylogenetics algorithms do not, at a minimum, make a distinction between explanations by means of natural selection or genetic drift with regard to causal mechanisms leading to fixation of characters among members of ancestral populations when explaining non-sequence characters, i.e. ‘morphological’ characters. This agnostic approach does not seem to present a problem for non-sequence characters since such features are amenable to being explained by either drift or selection (Fitzhugh 2016a), and phylogenetic hypotheses implied by cladograms are notoriously lacking in causal details in relation to novel character origin/fixation and population splitting events (‘speciation’) (Fitzhugh 2006a, 2006b, 2008b, 2013, 2014, 2016a, 2016b, 2016c, 2016d). The situation is, however, different for sequence data, since selection does not operate at the level of individual nucleotides or amino acids in consequence of the fact that these molecules exhibit no emergent properties upon which fitness differences are directly manifested. Selection can occur at higher organizational levels of phenotypes, and it is by way of downward causation (*sensu* Campbell 1974; Okasha 2006, 2012; Auletta *et al.* 2008; Ellis 2008, 2012, 2013; Martínez & Moya 2011; Davies 2012; Ellis *et al.* 2012; Jaeger & Calkins 2012; Walker *et al.* 2012; Griffiths & Stotz 2013; Martínez & Esposito 2014; Walker 2014; Fitzhugh 2016a; Paoletti & Orilia 2017) that sequence data can be indirectly affected. Differentially-shared nucleotides or amino acids can be readily explained by drift, but it would be unrealistic to assume that all sequence data can be accounted for by that cause, since selection at higher levels is known to occur. The consequence is that in order to explain sequence data by way of phylogenetic hypotheses it first would be necessary to segregate those nucleotides or amino acids to be explained by drift from those sequence data to be explained via downward causation, such that the latter would be excluded from the data matrix since those characters would be explained in association with phenotypic characters. The difficulty then faced is determining whether or not empirical criteria are available for filtering out those sequence data to be explained by downward causation. In the absence of such criteria, the only option would be to exclude sequence data altogether from causal consideration. This is a difficulty that severely limits the integrity of phylogenetic hypotheses that attempt to causally account for sequence data. As such, the monophyly of *Levinsenia* and other paraonid genera considered in Langeneck *et al.*'s (2019) study lack epistemic justification.

The second problem manifested in Langeneck *et al.* (2019) is that of character mapping, wherein a set of characters, usually morphological, are ‘mapped’ or ‘optimized’ onto a phylogenetic tree diagram that was originally inferred to explain other characters, usually sequence data. This approach has grown in popularity, yet relies on an invalid inferential process, offering results that fail to be interpretable as explanatory hypotheses (Fitzhugh 2014, 2016b). The inferences of phylogenetic hypotheses occur by a form of non-deductive reasoning known as abduction (Peirce 1878, 1902, 1931, 1932, 1933a, 1933b, 1934, 1935, 1958a, 1958b; Hanson 1958; Achinstein 1970; Fann 1970; Reilly 1970; Curd 1980; Nickles 1980; Thagard 1988; Josephson and Josephson 1994; Baker 1996; Hacking 2001; Magnani 2001, 2009, 2017; Psillos 2002, 2007, 2011; Godfrey-Smith 2003; Norton 2003; Walton 2004; Gab-

bay & Woods 2005; Aliseda 2006; Schurz 2008; Park 2017; for abductive reasoning in systematics, cf. Fitzhugh 2005a, 2005b, 2006a, 2006b, 2008a, 2008b, 2008c, 2009, 2010, 2013, 2014, 2015, 2016a, 2016b, 2016c, 2016d). In relation to systematics, abductive reasoning involves conjoining an explicit or implied theory(ies) with effects to be explained, to conclude a set of explanatory hypotheses, diagrammatically represented by cladograms (e.g. Fitzhugh 2006a, 2012, 2014, 2016a). Mapping additional characters onto cladograms cannot lead to those characters being explained since mapped characters played no role in the inferences of the explanatory hypotheses accounting for those characters. There are no forms of inference that can warrant mapping as a valid scientific process. As a consequence, the absence of a median antenna among members of *Levinsenia* cannot at this time be claimed as evidence of monophyly.

**TABLE 2. Differentiating characters for *Levinsenia* species from California. Characters in bold are diagnostic. MG, methyl green; L, length; W, width.**

Species/Character	Prostomium shape	Terminal sensory organ (palode)	No. pre-branchial chaetigers	No. branchial pairs
<i>Levinsenia gracilis</i> (Tauber, 1879)	Triangular L>W	Present	5–7	7–16, size dependent
<i>Levinsenia kirbyorum</i> Lovell, 2002	Triangular L>W	Present	6–7, body inflated	13–20
<i>Levinsenia multibranchiata</i> (Hartman, 1957)	Conical W>L	Poorly developed	6–7, body inflated	<b>28–36</b>
<i>Levinsenia oculata</i> (Hartman, 1957)	Conical W>L, w/ocular pigment (eyes)	<b>Well developed</b>	5–8	8–11
<i>Levinsenia barwicki</i> n. sp.	Conical L>W	<b>Well developed</b>	6, body inflated	4–8

**TABLE 2. (Continued)**

Species/Character	Branchial shape	No. acicular neuro (spines)	MG staining
<i>Levinsenia gracilis</i> (Tauber, 1879)	Tapered, blunt-tipped	3–7, single row, recurved distally	Branchial region ventral bands
<i>Levinsenia kirbyorum</i> Lovell, 2002	Conical	<b>Up to 13, double rows, recurved shape not uniform</b>	Ventral bands branchial region, <b>notopodial spots post-branchial</b>
<i>Levinsenia multibranchiata</i> (Hartman, 1957)	<b>Thin, long tapering</b>	5–7, thin nearly straight distally	No stain
<i>Levinsenia oculata</i> (Hartman, 1957)	Tapering, blunt tipped, L 6-7X- W	Up to 7, recurved distally	Branchial region, 2–3 post-branchial chaetigers solid bands
<i>Levinsenia barwicki</i> n. sp.	<b>Leaf-like, margin ciliated</b>	<b>Up to 5, recurved tip with distal hood</b>	Branchial region, 7–8 post-branchial chaetigers segmental stain

### Key to the species of *Levinsenia* reported from California

1. 1A. Body very small (10–15 mm long, 0.10 mm wide), terminal sensory organ well developed, 4–8 pairs of truncate, heavily ciliated branchiae, acicular spines bent tipped with thick hoods . . . . . *L. barwicki* n. sp.
- 1B. Body small to moderate size (15–30 mm long, 0.15–0.35 mm wide), terminal sensory organ not well developed, 5–36 branchial pairs, acicular spines not bent tipped, with fringe on convex side . . . . . 2
2. 2A. Posterior acicular neurochaetae in multiple overlapping rows; vary in shape from longer, thinner, straighter to shorter, thicker more recurved; post-branchial notopodial with methyl green staining spots . . . . . *L. kirbyorum*
- 2B. Posterior acicular neurochaetae in single rows, uniformly shaped; post-branchial notopodia without methyl green staining spots . . . . . 3
3. 3A. More than 25 pairs of long, thin, tapering branchiae; posterior acicular neurochaetae thin, nearly straight distally; methyl green staining absent on any part of the body . . . . . *L. multibranchiata*
- 3B. Fewer than 25 pairs of tapering, blunt-tipped branchiae; posterior acicular neurochaetae, thicker, recurved distally . . . . . 4

4. 4A. Prostomium conical, with ‘ocular’ pigment (may fade); 5–9, and up to 20 branchial pairs; methyl green stain pre- and post-chaetal areas, speckled in prebranchial chaetigers; solid methyl green band in branchial region and 2–3 post-branchial chaetigers ..... *L. oculata*
- 4B. Prostomium triangular, longer than wide, without “ocular” pigment; 7–16 branchial pairs; ventral methyl green staining in branchial region ..... *L. gracilis*

## Acknowledgements

We would like to thank the Southern California Association of Marine Invertebrate Taxonomists (SCAMIT), Leslie Harris (NHMLAC), Danny Eibye-Jacobsen (ZUMC), and Linda Kuntz (MBARI) for providing specimens for this study. Use of and access to the SEM and the AHF-LACM polychaete collection was provided by the Natural History Museum of Los Angeles County. This research was supported by the County Sanitation Districts of Los Angeles County. The paper benefitted from comments offered by Jim Blake and Leslie Harris.

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