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Descriptions of species of *Stegelleta* Thorne, 1938 (Nematoda, Rhabditida, Cephalobidae) from California, New Zealand and Senegal, and a revision of the genus

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Abstract. Populations of *Stegelleta* are described from California, New Zealand and Senegal. An amphimictic population from California is identified as belonging to *S. incisa* and compared with type specimens from Utah and an amphimictic population from Italy. One population from New Zealand is close to *S. incisa* but considered to represent a new species, *Stegelleta laterocornuta* sp. nov. It is particularly characterised by a 379–512 µm long body in females and 365–476 µm in males; cuticle divided into 16 rows of blocks at midbody (excluding lateral field); lateral field with four incisures; three pairs of asymmetrical lips, U-shaped primary axils without guarding processes, each lip asymmetrically rectangular with a smooth margin, only lateral lips have slender acute tines; three labial probolae, bifurcated at half of their length; vulva without flap; spermatheca 17–31 µm long; postuterine sac 7–24 µm long; spicules 21.5–23.5 µm long. Other specimens from New Zealand are identified as belonging to *S. tuarua*. A parthenogenetic population from Senegal is identified as belonging to *S. ophioglossa* and compared with type specimens from Mongolia and records of several other populations of *S. ophioglossa*. The generic diagnosis is emended and a key to the species of *Stegelleta* is provided.

Keywords. Morphology, new species, SEM, *Stegelleta*, taxonomy.

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Introduction

The genus *Stegella* was erected by Thorne (1937) with *Stegella incisa* Thorne, 1937 as type species, for cephalobids having: cuticle divided into plate-like segments over entire body; labial probolae furcate, prongs simple or with few branches; cephalic probolae variable, rounded axil borders or flap-like with membranes; and wing area unusually broad with a medial line and crenate borders.

Due to a homonomy with a hydroid, *Stegella* Stechow, 1919, it was later renamed and became *Stegelleta* Thorne, 1938. *Stegelleta* currently includes six valid species of which the most recent one, *S. arenaria* Boström & Holovachov, 2012, was described from Kelso Dunes, Mojave National Preserve, California. Specimens of *S. incisa* were also found in the samples from Kelso Dunes. This population is here described from studies by light (LM) and scanning electron microscope (SEM) and compared with type specimens from Utah and an amphimictic population from Italy described under the name *S. ophioglossa* Andrássy, 1967 (Thorne 1937; Orselli & Vinciguerra 2002). Another population from New Zealand, described here from studies by light and scanning electron microscope, is close to *S. incisa* but considered to represent a new species. Some specimens of *S. tuarua* Yeates, 1967 from New Zealand are also described and compared with the original description (Yeates 1967). A recent parthenogenetic population of *S. ophioglossa* from Senegal is described and compared with the original description of *S. ophioglossa* from Mongolia and records of populations from Uzbekistan, Senegal, Iran and Spain (Andrássy 1967; Mavljanov 1978; De Ley *et al.* 1990; Shokoohi *et al.* 2008; Abolafia *et al.* 2011). The generic diagnosis is emended and a key to the species of *Stegelleta* is provided.

Material and methods

During a tour in the Kelso Dunes area, Mojave National Preserve, southern California, the junior author collected several samples of sand underneath different species of desert plants. Nematodes were recovered from sand samples using a modified Baermann funnel extraction. For LM, specimens were relaxed by gentle heat, fixed in cold 4% formaldehyde solution, transferred to pure glycerine by a slow evaporation method and mounted on permanent slides in glycerine with paraffin wax as support for the coverslip. After measuring and observations, some specimens were removed from slides and rehydrated by first gradually adding drops of S1 (1% glycerine, 20% ethanol and 79% distilled water) to glycerine in an embryo-dish until the volume tripled and then gradually adding distilled water until the volume tripled again. The specimens were then washed in distilled water before resuspension in formaldehyde. For SEM, specimens were post-fixed in 1% osmium tetroxide (OsO_4) and transferred to pure acetone through an acetone/distilled water series. Specimens were critical point dried in liquid CO_2, mounted on stubs, gold-plated under vacuum to a thickness of 200 Å in an Agar High Resolution Sputter Coater Model 20, and examined in a Hitachi S-4300 SEM at an accelerating voltage of 5 kV.

Specimens from New Zealand were collected by Christine (Gamble) Powell in the Abel Tasman National Park and subsequently cultured as the strain *Stegelleta* sp. JB-75, which was sequenced and included in a phylogenetic study on Cephalobina (Nadler *et al.* 2006). Additional material from the Castlecliff beach in New Zealand was supplied by Dieter Sturhan and Gregor Yeates. This is one of the localities where the original populations of *S. iketaia* Yeates, 1967 were collected. Specimens from Senegal were collected in the Kaolack region, Thyssé-Kaymor by Cécile Villenave. For LM, the specimens from New Zealand and Senegal were processed using different modifications of a slow evaporation method. Specimens from the strain *Stegelleta* sp. JB-75 were processed to SEM by Dan Bumbarger and photographs were put at our disposal.

Morphometric characters applied herein and their abbreviations are as defined for Cephalobidae in De Ley *et al.* (1999); terminology of the labial and cephalic region and stoma terminology follows Holovachov *et al.* (2009). Type and other specimens are deposited in the invertebrate collections of the Department of Zoology, Swedish Museum of Natural History, Stockholm, Sweden (SMNH).

Results

Class Chromadorea Inglis, 1983
Order Rhabditida Chitwood, 1933
Family Cephalobidae Filipjev, 1934

Genus ***Stegelleta*** Thorne, 1938

Stegella Thorne, 1937: 4 [junior homonym of *Stegella* Stechow, 1919].
Stegelleta Thorne, 1938: 64–65.

Type species

Stegella incisa Thorne, 1937.

Diagnosis (emended after Holovachov *et al.* 2009)

Cuticle annulated, without distinctly annulated internal layer; annuli with longitudinal incisures (tessellated). Lateral field with two or four wings (appearing as three, four or five incisures); ending at tail terminus in females and in males. Lip region weakly offset, consisting of six globular lips arranged in three pairs: one dorsal and two subventral. Pairs of lips separated by primary axils; guarding processes absent; secondary axils undeveloped. Cephalic probolae absent or in the shape of one acute tine extending along the primary axil occurring only on lateral lips or on all six lips. Labial probolae elongate-conoid with broad basis, bifurcated about halfway forming two slender prongs, in some species further bifurcated apically. Six labial and four cephalic papilliform sensilla arranged in a cephaloboid manner. Amphidial aperture slit-shaped, located on lateral lips. Stoma divided into cheilo-, gymno- and stegostom: cheilostom barrel-shaped with strongly sclerotized bacilliform cheilorhabdia; gymnostom weakly developed, as wide as stegostom, with weak gymnorhabdia; stegostom consists of a funnel-shaped prostegostom and variably shaped mesostego-, metastego- and telostegostom parts. Metastegostom denticle present. Pharynx cephaloboid: pharyngeal procorpus and metacorpus cylindrical, lining of procorpus and metacorpus are of same thickness; isthmus narrower than metacorpus; basal pharyngeal bulb oval, with strongly developed valves. Nerve ring encircling posterior part of metacorpus or anterior part of isthmus. Excretory pore opens at level of nerve ring, at posterior part of metacorpus or anterior part of isthmus. Deirids present. Female reproductive system cephaloboid; posterior part of ovary straight; spermatheca present; postvulval uterine sac present; vagina straight; vulva flat, vulval flap absent or present. Male reproductive system cephaloboid; spicules cephaloboid with manubrium and corpus of approximately equal width; gubernaculum plate-like or wedge-shaped; cornua crurum present. Male genital papillae: at least one ventrosublateral pair located anterior to cloaca; one ventrosublateral pair located at the level of cloacal opening; two pairs located at middle of tail length; and three pairs (lateral, subventral and subdorsal) near tail terminus; there is a midventral papilla on anterior cloacal lip. Rectum short (1–2 times longer than anal body diameter). Phasmids located at about one-third to half of tail length in both sexes. Female tail conoid or subcylindrical, straight, tail terminus bluntly rounded or truncate; male tail conoid, arcuate ventrad, tail terminus bluntly rounded.

Valid species

Stegelleta arenaria Boström & Holovachov, 2012
Stegelleta georgica Bagaturija, 1973
Stegelleta iketaia Yeates, 1967
Stegelleta incisa (Thorne, 1937)
Stegelleta ophioglossa Andrássy, 1967
= *Stegelleta cylindrica* Mavljanov, 1978: 1889, figs 1–6
Stegelleta tuarua Yeates, 1967

Stegelleta incisa (Thorne, 1937)
Figs 1A–E, 2, Table 1

Stegella incisa Thorne, 1937: 14–15, fig. 4G–I.

Stegelleta incisa – Thorne 1938: 65.
Stegelleta ophioglossa – Orselli & Vinciguerra 2002: 216–219, figs 5, 6A–C.

Diagnosis

Stegelleta incisa is characterised by a 465–580 µm long body in females and 428–600 µm in males; cuticle divided by regular longitudinal striations into 16 rows of blocks at midbody (excluding lateral field); lateral field with four incisures extending almost to tail terminus in females and to midtail papillae in males, two outer incisures extend to tail terminus in males; three pairs of asymmetrical lips, pairs of lips separated by U-shaped primary axils without guarding processes, secondary axils demarcated by a shallow incisure, each lip asymmetrically rectangular with a smooth margin and without tines; three labial probolae, bifurcated at half of their length, prongs bent toward one another apically, "snake-tongue"-shaped; pharyngeal corpus 2.1–2.9 times isthmus length; nerve ring and excretory pore at level of metacorpus to metacorpus-isthmus junction, deirids at level of metacorpus-isthmus junction to isthmus; vulva with anterior flap; spermatheca 24–43 µm long; postuterine sac 22–36 µm long; spicules 22–36 µm long.

Material examined

USA: 13 ♀♀, 9 ♂♂, SMNH 135940–135942, 28 Mar. 2010, California, Mojave National Preserve, Kelso Dunes, soil around roots of desert plants (34°53.698' N, 115° 42.155' W and 34° 53.754' N, 115° 42.248' W), *legit* O. Holovachov & P. De Ley.

Description

Adult

Body slightly arcuate in different ways when killed by heat, males often strongly arcuate ventrad in tail end. Cuticle coarsely annulated, annuli 2.4–3.4 µm wide at midbody and 2.2–3.0 µm wide in pharyngeal region. Cuticle tessellated: longitudinal striae giving it a tiled appearance, each block often with a central indentation as seen under SEM. Anteriorly, 9–10 first annuli, the longitudinal striation is irregular and blocks rounded, followed by a more regular striation creating rectangular blocks, 16 rows of blocks at midbody (excluding lateral field). Lateral field consisting of two wings separated by a broad groove, appearing as four incisures under LM, occupying about 20–25% of body diameter, extending almost to tail terminus in females and to midtail papillae in males, two outer incisures extend to tail terminus in males. Lip region slightly offset, carrying 6 + 4 papillae and two round amphids. Three pairs of asymmetrical lips, one dorsal and two ventrolateral. Pairs of lips separated by U-shaped primary axils without guarding processes. Each pair with a shallow incisure demarcating a secondary axil. Each lip asymmetrically rectangular with a smooth margin, without any tines. Three labial probolae, 8.0–9.5 µm high, bifurcated at half of their length, prongs bent toward one another apically ("snake-tongue"-shaped). Stoma somewhat longer than lip region diameter. Stomatal parts not clearly discernible. Cheilorhabdia bacilliform in lateromedian view; metastegostom with a dorsal denticle. Pharynx cephaloboid. Pharyngeal corpus cylindrical; isthmus narrow, often folded, and not clearly demarcated from corpus; bulb oval, with valves. Nerve ring at level of metacorpus to metacorpus-isthmus junction. Excretory pore and deirids at level of metacorpus-isthmus junction to isthmus.

Female

Reproductive system monodelphic, prodelphic, in dextral position in relation to intestine. Ovary reflexed posteriorly at oviduct, ovary straight posterior to vulva. Spermatheca well developed. Postvulval uterine

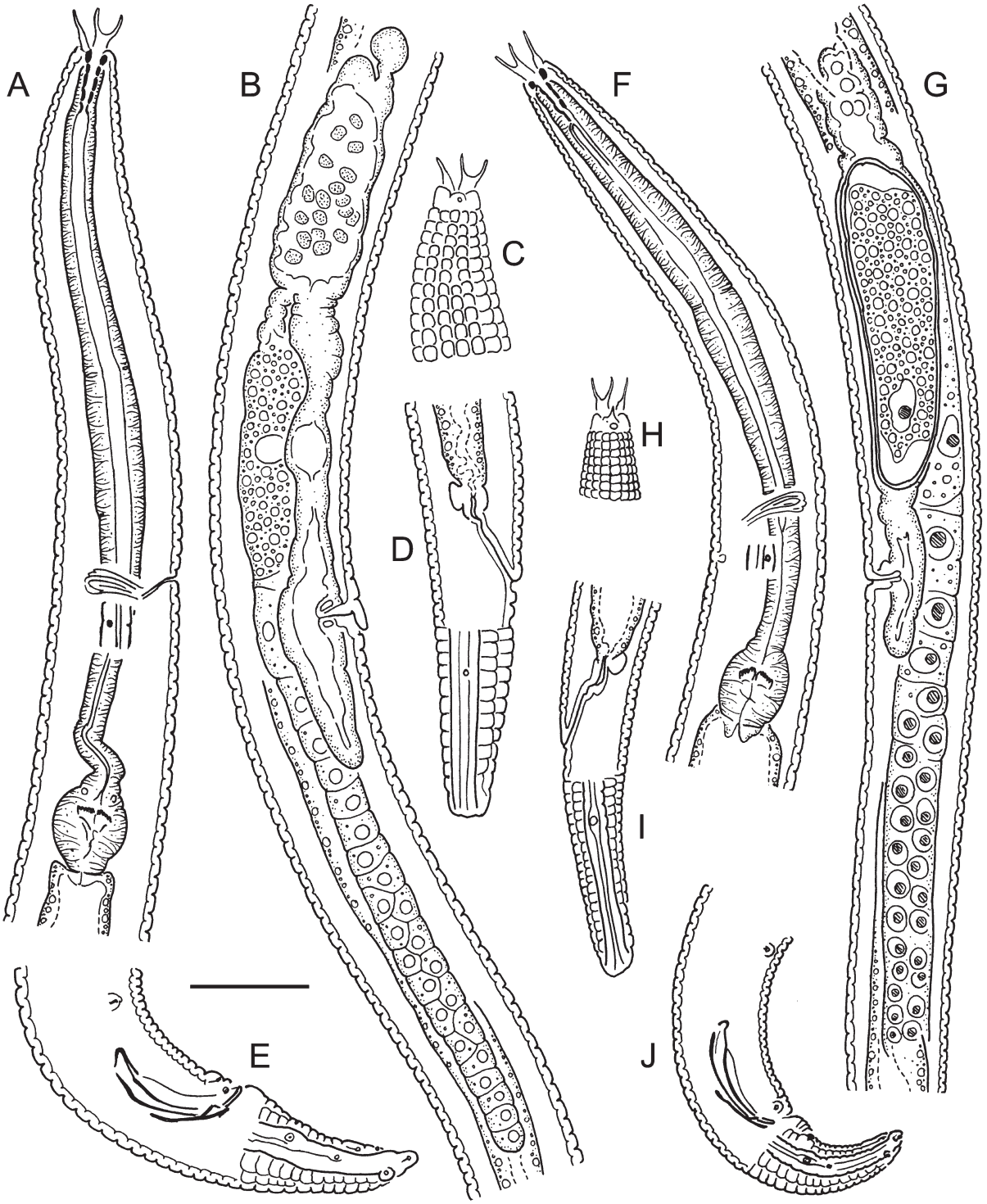

Fig. 1. A–E. *Stegelleta incisa* (Thorne, 1937). **A**. Pharyngeal region. **B**. Female gonad. **C**. Anterior end, surface view. **D**. Female tail. **E**. Male tail. **F–J**. *Stegelleta laterocornuta* sp. nov. **F**. Pharyngeal region. **G**. Female gonad. **H**. Anterior end, surface view. **I**. Female tail. **J**. Male tail. Scale bar = 20 μm.

sac one to one-and-a-half times vulval body diameter long. Vagina about one-third of vulval body diameter. Vulval lips not or slightly protruding, anterior lip with cuticular flap directed posteriad and partly covering vulval opening. Vulva covered by genital plug in some specimens. Tail conoid with 13–15 ventral annuli, terminus truncate. One specimen has a tail with only 10–11 annuli and broadly rounded terminus. Phasmids located at about one-third to half of tail length.

Male

Reproductive system monorchic, dextral in position; testis reflexed ventrad anteriorly. Spicules paired and symmetrical, curved ventrad; with oval manubrium and subcylindrical, gradually narrowing shaft. Gubernaculum plate-like, cornua crurum present. Tail strongly arcuate ventrad, conoid with rounded terminus. The two outer lateral lines extend posterior to the phasmid, transforming into a cuticular ridge that reaches tail terminus. Genital papillae arranged as follows: two pairs subventral precloacal (at 24–33 µm and at 42–58 µm anterior to cloaca), one pair subventral adcloacal, a single midventral papilla

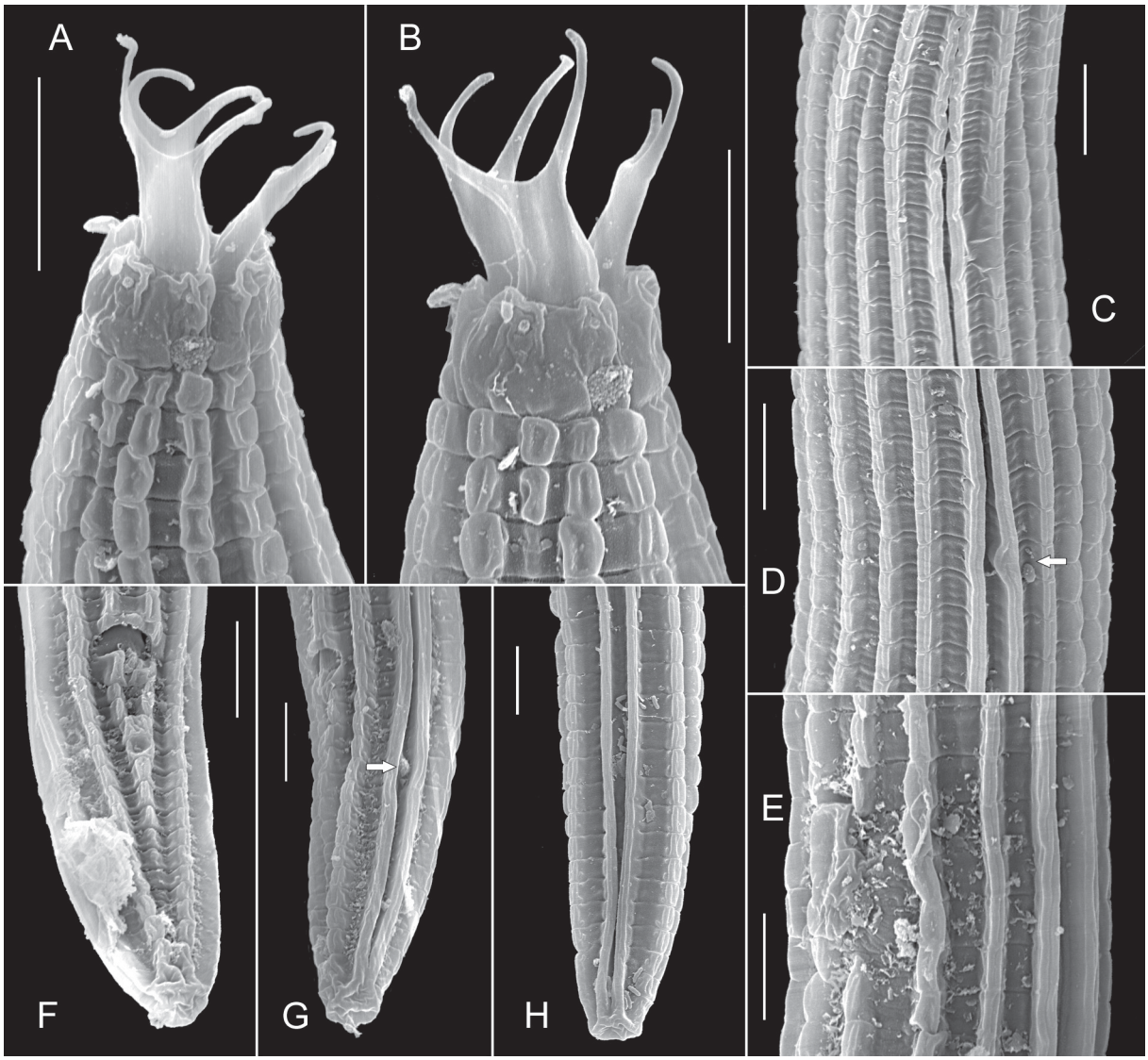

Fig. 2. *Stegelleta incisa* (Thorne, 1937), SEM micrographs. **A–B**. Anterior end, left lateral view. **C**. Anterior part of lateral field. **D**. Deirid (arrow). **E**. Vulval region. **F**. Female tail, subventral view. **G**. Female tail, left sublateral view (arrow points at phasmid). **H**. Female tail, lateral view. Scale bars = 5 µm.

Table 1. Measurements (in µm) of *Stegelleta incisa* (Thorne, 1937) from Kelso Dunes, California compared with the type population of *S. incisa* from Utah and a bisexual population described by Orselli & Vinciguerra (2002) from Italy under the name *S. ophioglossa* Andrássy, 1967 (presented as mean ± s.d. and (range) or only range). * Calculated from data in original publication; ** number of annuli from anterior end to nerve ring, excretory pore and deirid, respectively; ¤ estimated from drawings in original publication; - indicates that data is not available or not applicable; figures within [ ] indicate the number of specimens measured.

Population	**Utah**		**Kelso Dunes, California**		**Italy**	
No. & sex	**1** ♀	**1** ♂	**10** ♀♀	**11** ♂♂	**5** ♀♀	**5** ♂♂
Body length	500	460	490 ± 23 (465–534)	463 ± 28 (428–526)	550 ± 30 (510–580)	550 ± 30 (510–600)
Body diameter (BD)	24*	20*	23.2 ± 1.0 (22–25)	21.2 ± 1.7 (18–24)	29 ± 1.4 (27.5–30.8)	25.3 ± 2.6 (20.9–27.5)
Pharynx length	139*	115*	130.6 ± 1.0 (115–141)	123.9 ± 7.9 (107–135)	181.4 ± 6.1 (177–192)	184.8 ± 24.2 (161–225)
Tail length	34*	34*	38.8 ± 1.7 (32–41)	32.2 ± 2.5 (29–36)	50.1 ± 3.6 (44–53.9)	48.6 ± 3.6 (45.1–53.9)
Anal or cloacal diam. (ABD)	-	-	14.4 ± 0.2 (14.0–14.5)	16.1 ± 1.0 (14.5–18.0)	18.4 ± 0.4 (17.6–18.7)	22 ± 1.1 (20.9–23.1)
Vulva or Testis	-	-	307 ± 14 (291–335)	269 ± 23 (223–300)	-	-
V-A/T	-	-	3.8 ± 0.2 (3.4–4.1)	-	-	-
a	21	23	21.2 ± 0.9 (19.6–22.5)	21.9 ± 1.3 (19.5–24.2)	19 ± 2 (17–21)	22 ± 2.2 (15–25)
b	3.6	4	3.8 ± 0.2 (3.5–4.2)	3.7 ± 0.2 (3.4–4.3)	3 ± 0.1 (2.8–3.2)	2.9 ± 0.2 (2.6–3.3)
c	15.0	13.5	12.7 ± 0.6 (11.8–13.4)	14.4 ± 1.0 (12.7–15.5)	11 ± 0.5 (10.4–11.5)	11.3 ± 0.6 (10.9–12.2)
c'	-	-	2.7 ± 0.1 (2.5–2.8)	2.0 ± 0.2 (1.8–2.3)	2.6 ± 0.2 (2.3–2.9)	2.1 ± 0.1 (1.9–2.3)
V or T (%)	66	41	62.7 ± 1.1 (61–65)	58.1 ± 3.4 (52–64)	62.5 ± 0.6 (61.4–63)	-
Lip region diameter	-	-	8.3 ± 0.3 (7.5–8.5)	8.0 ± 0.6 (7.0–8.5)	-	-
Stoma length	-	-	9.8 ± 0.9 (8.5–11.0)	9.7 ± 0.6 (9–11)	13.2 ± 2 (11–15.4)	13.5 ± 0.4 (13.2–14.3)
Corpus length	-	-	83.2 ± 2.8 (78–86) [5]	81.2 ± 3.9 (76–87) [5]	123 ± 5.4 (117–129)	123.6 ± 21.5 (102–159)
Isthmus length	-	-	34.2 ± 2.7 (29–36) [5]	31.8 ± 2.4 (30–36) [5]	30.3 ± 7.5 (17.6–36.3)	32.7 ± 4.6 (25.3–37.4)
Bulb length	-	-	16.6 ± 0.7 (16–18)	15.7 ± 0.9 (14.5–17.0) [6]	20.2 ± 2.1 (17.6–23.1)	18.8 ± 0.6 (18.1–19.8)
Bulb diameter	-	-	12.2 ± 0.7 (11–13)	11.8 ± 0.7 (11–13) [6]	-	-
Corpus/isthmus ratio	3	-	2.4 ± 0.2 (2.3–2.9) [5]	2.6 ± 0.2 (2.1–2.8) [5]	-	-
Nerve ring from ant. end	-	-	88.5 ± 4.5 (78–94)	90.2 ± 7.1 (78–102)	137.5 ± 6.3 (129–144)	141.8 ± 23.1 (118–179)

Population	Utah		Kelso Dunes, California		Italy	
No. & sex	**1** ♀	**1** ♂	**10** ♀♀	**11** ♂♂	**5** ♀♀	**5** ♂♂
Excretory pore from ant. end	-	-	93.8 ± 2.9 (88–99)	95.6 ± 7.0 (84–108)	122–147	-
Deirid from ant. end	-	-	101.1 ± 3.4 (94–107)	101.5 ± 8.3 (82–114)	-	-
R_{NR}**	-	-	32 ± 1.5 (30–35)	32 ± 2 (30–36)	-	-
R_{EP}**	-	-	34 ± 2 (32–38)	34 ± 2 (31–38)	-	-
R_{DEI}**	-	-	37 ± 2 (35–41)	37 ± 2 (34–41)	-	-
Annuli width at midbody	-	-	2.4–3.4	2.4–3.0	2.0–2.5	-
Annuli width anteriorly	-	-	2.4–2.7	2.2–3.0	-	-
Vagina or Testis flexure length	-	-	7.3 ± 0.4 (7–8)	39.5 ± 6.7 (27–48)	7–8	-
Spermatheca or Spicule length	-	-	30.9 ± 6.7 (24–43)	24.0 ± 1.3 (22–27)	24–26.5	34.5 ± 1.6 (31.9–36.3)
PUS or Gubernaculum length	-	-	27.3 ± 2.3 (24–31)	13.2 ± 1.1 (12–16)	30.6 ± 5.9 (22.5–36.3)	20.4 ± 1.4 (19.8–23.1)
PUS/VBD	-	-	1.3 ± 0.1 (1.1–1.4)	-	0.7–1.3	-
Rectum	-	-	16.0 ± 1.6 (13–18)	-	21.6 ± 0.3 (16.5–24.7)	-
Rectum/ABD	-	-	1.1 ± 0.1 (0.9–1.2)	-	-	-
Phasmid	-	-	14.9 ± 2.2 (12–20)	14.1 ± 1.8 (11–18)	-	-
Phasmid (% of tail)	30 ¤	47 ¤	38.3 ± 4.6 (32–49)	43.8 ± 4.7 (37–50)	15–30	25–35

on anterior cloacal lip; two pairs (one ventrosublateral and one lateral) at midtail; three pairs (one lateral, one subventral and one dorsosublateral) closer to tail terminus. Phasmids located at about two-fifths to half of tail length.

Remarks

The population collected from sand in the Kelso Dunes area, Mojave Desert, California and described here, agrees in many respects with the type specimens of *Stegelleta incisa* described from Utah by Thorne (1937) and a bisexual population described from Italy by Orselli & Vinciguerra (2002) under the name *S. ophioglossa*. One major difference is the presence of a cuticular flap on the anterior vulval lip directed posteriad and partly covering the vulval opening, as seen by SEM in the present specimens. This feature is not easily seen with light microscopy, which probably explains why it was not mentioned by Thorne (1937) in his original description. Orselli & Vinciguerra (2002) also did not mention or illustrate it in their specimens, presumably for the same reason.

Stegelleta laterocornuta sp. nov.
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Figs 1F–J, 3, Table 2

Stegelleta sp. JB-75 – Nadler *et al.* 2006: 701, table 1.

Diagnosis

Stegelleta laterocornuta sp. nov. is characterised by a 379–512 µm long body in females and 365–476 µm in males; cuticle divided by regular longitudinal striations into 16 rows of blocks at midbody (excluding lateral field); lateral field with four incisures extending almost to tail terminus in females and to midtail papillae in males, two outer incisures extend to tail terminus in males; three pairs of asymmetrical lips, pairs of lips separated by U-shaped primary axils without guarding processes, secondary axils demarcated by a shallow incisure, each lip asymmetrically rectangular with a smooth margin, only lateral lips have slender acute tines; three labial probolae, bifurcated at half of their length, prongs bent toward one another apically, "snake-tongue"-shaped; pharyngeal corpus 2.3–3.0 times isthmus length; nerve ring and excretory pore at level of metacorpus to metacorpus-isthmus junction, deirids at level of isthmus; vulva without flap; spermatheca 17–31 µm long; postuterine sac 7–24 µm long; spicules 21.5–23.5 µm long.

Etymology

The species name is derived from the Latin *lateris* (= side) and *cornu* (= horn), referring to the long acute tine extending along the primary axil on the lateral lips.

Material examined

NEW ZEALAND: holotype ♀, paratypes 13 ♀♀ and 9 ♂♂, SMNH Type-8602, 1999, South Island, Tasman District, Abel Tasman National Park, *legit* Christine (Gamble) Powell, cultured as the strain *Stegelleta* sp. JB-75.

Description

Adult

Body slightly arcuate in different ways when killed by heat, males often strongly arcuate ventrad in tail end. Cuticle coarsely annulated, annuli 1.9–2.7 µm wide at midbody and 2.0–2.4 µm wide in pharyngeal region. Cuticle tessellated: longitudinal striae giving it a tiled appearance, 16 rows of blocks at midbody (excluding lateral field). Lateral field consisting of two wings separated by a broad groove, appearing as four incisures under LM, occupying about 20–25% of body diameter, extending almost to tail terminus in females and in males. Lip region slightly offset, carrying 6 + 4 papillae and two round amphids. Three pairs of asymmetrical lips, one dorsal and two ventrolateral. Pairs of lips separated by U-shaped primary axils without guarding processes. Each pair with a shallow incisure demarcating a secondary axil. Each lip asymmetrically rectangular with a smooth margin. Lateral lips only with long, slender, acute tine extending along the primary axil. Three labial probolae, 7.0–8.5 µm high, bifurcated at half of their length, prongs bent toward one another apically ("snake-tongue"-shaped). Stoma somewhat longer than lip region diameter. Stomatal parts not clearly discernible. Cheilorhabdia bacilliform in lateromedian view; metastegostom with a dorsal denticle. Pharynx cephaloboid. Pharyngeal corpus cylindrical; isthmus narrow, often wrinkled, and not clearly demarcated from corpus; bulb oval, with valves. Nerve ring and excretory pore at level of metacorpus-isthmus junction to isthmus. Deirids generally at level of isthmus.

Female

Reproductive system monodelphic, prodelphic, in dextral position in relation to intestine. Ovary reflexed posteriorly at oviduct, ovary straight posterior to vulva. Spermatheca well developed. Postvulval uterine

sac about half to one-and-a-half times vulval body diameter long. Vagina about one-third of vulval body diameter. Vulval lips not or slightly protruding, without flaps. Vulva with genital plug seen in one specimen. In four females one intrauterine egg each was found, measuring 36–57 x 14.5–15.5 µm. Tail conoid with 16–22 ventral annuli, terminus broadly rounded or truncate. Phasmids located at about one-third to two-fifths of tail length.

Male

Reproductive system monorchic, dextral in position; testis reflexed ventrad anteriorly. Spicules paired and symmetrical, curved ventrad; with oval manubrium and subcylindrical, gradually narrowing shaft. Gubernaculum plate-like, cornua crurum present. Tail strongly arcuate ventrad, conoid with rounded terminus. The two outer lateral lines extend posterior to the phasmid, transforming into a cuticular ridge that reaches tail terminus. Genital papillae arranged as follows: two pairs subventral precloacal (at 4–6 µm and at 23–28 µm anterior to cloaca), one pair subventral adcloacal, a single midventral papilla on anterior cloacal lip; two pairs (one ventrosublateral and one lateral) at midtail; three pairs (one lateral, one subventral and one dorsosublateral) closer to tail terminus. Phasmids located at about two-fifths to half of tail length.

Remarks

The population of *Stegelleta laterocornuta* sp. nov. from New Zealand described here agrees in many respects with the descriptions of *S. incisa*. One major difference is the presence of a long, slender and

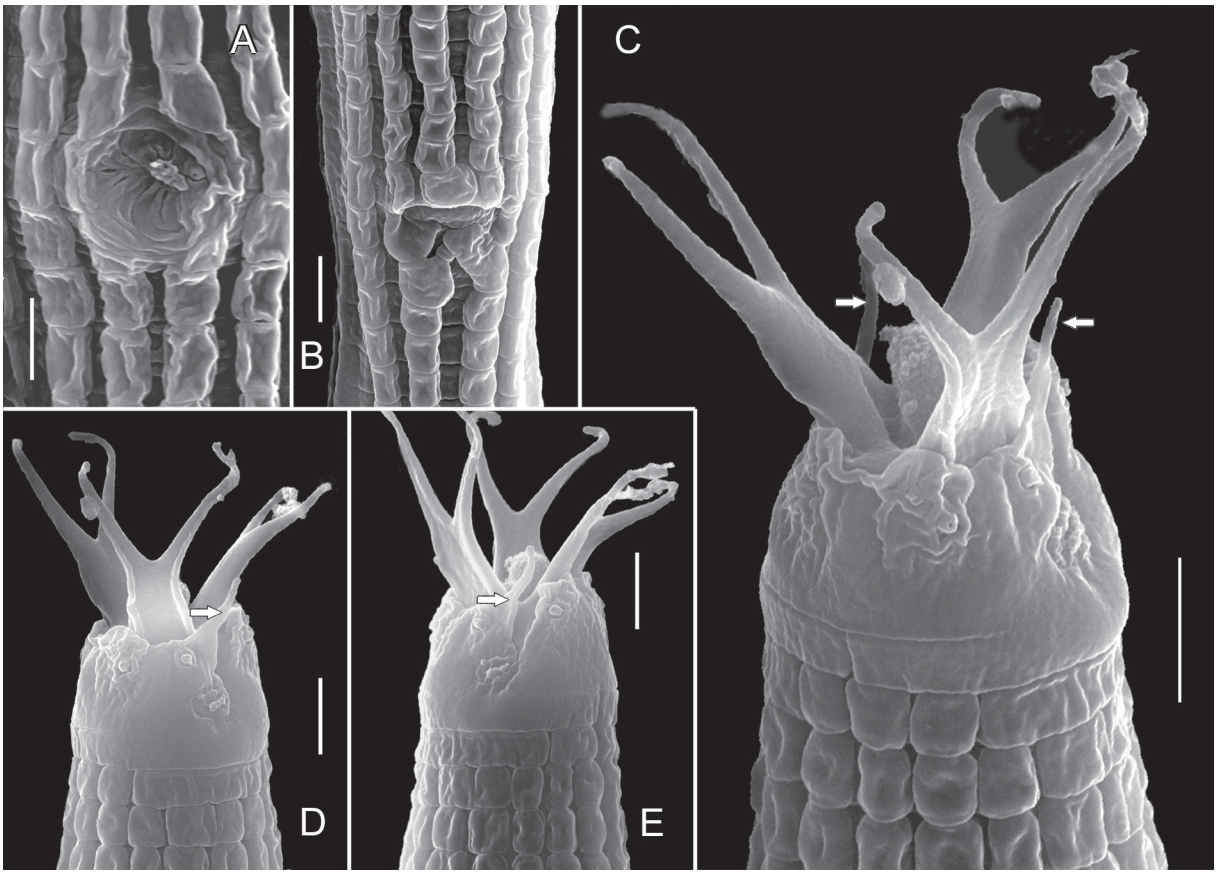

Fig. 3. *Stegelleta laterocornuta* sp. nov., SEM micrographs. **A**. Vulval opening. **B**. Anal opening. **C–D**. Anterior end, left subventral view. **E**. Anterior end, left lateral view (arrows in C–E point at the long acute tine extending along the primary axil on the lateral lips). Scale bars = 2 µm.

Table 2. Measurements (in µm) of *Stegelleta laterocornuta* sp. nov. and *S. tuarua* Yeates, 1967 from Castlecliff, New Zealand, the latter compared to the type population (presented as mean ± s.d. and (range) or only range).* Number of annuli from anterior end to nerve ring, excretory pore and deirid, respectively; - indicates that data is not available or not applicable.

	***Stegelleta laterocornuta* sp. nov.**			***Stegelleta tuarua***		
Population	**New Zealand JB-75**			**Type population**		**Castlecliff**
No. & sex	**Holotype**	**14 ♀♀ (incl. holotype)**	**9 ♂♂ {1 aberr.}**	**1 ♀**	**3 ♂♂**	**2 ♂♂**
Body length	447	433 ± 41 (379–512)	428 ± 35 (365–476)	635	563–739	650; 688
Body diameter (BD)	20.5	19.1 ± 1.7 (15.5–21.5)	17.4 ± 1.1 (15–19)	-	-	45; 46
Pharynx length	118	116.7 ± 5.2 (109–126)	117.8 ± 4.6 (109–123) {138}	-	-	144; 165
Tail length	38	35.9 ± 2.9 (30–42)	24.2 ± 0.9 (22–25) {36}	-	-	43; 48
Anal or cloacal diam. (ABD)	11	11.1 ± 0.8 (9.5–12.5)	11.9 ± 0.4 (11.0–12.5) {13}	-	-	30; 30
Vulva or Testis	273	270 ± 22 (235–315)	223 ± 15 (200–235)	-	-	432; 476
V-A/T	3.6	3.6 ± 0.3 (3.0–3.9)	-	-	-	-
a	21.8	22.7 ± 1.7 (18.6–26.0)	24.6 ± 1.3 (21.5–26.5)	21.2	17.2–18.8	14.4; 15.0
b	3.8	3.7 ± 0.3 (3.4–4.3)	3.6 ± 0.2 (3.3–4.0)	3.8	3.9–4.8	4.5; 4.2
c	11.8	12.1 ± 0.7 (10.5–13.0)	17.7 ± 1.4 (15.2–19.8) {13.1}	25.4	14.1–16.0	15.1; 14.3
c'	3.5	3.2 ± 0.2 (2.7–3.6)	2.0 ± 0.1 (1.8–2.2) {2.8}	1.6	1.6–1.9	1.4; 1.6
V or T (%)	61	62.3 ± 1.2 (60–65)	54.2 ± 3.7 (49–60)	69.2	56.8–62.7	66; 69
Lip region diameter	7.0	6.8 ± 0.4 (6.5–8.0)	6.7 ± 0.4 (6–7)	-	-	11; 12
Stoma length	9.0	8.9 ± 0.3 (8.5–9.5)	8.7 ± 0.5 (8.0–9.5)	-	-	14.5; 19
Corpus length	70	69.6 ± 4.1 (63–75)	69.6 ± 1.9 (66–72) {81}	-	-	92; 110
Isthmus length	26	26.7 ± 2.3 (24–30)	27.1 ± 1.7 (24–29) {36}	-	-	22; 20.5
Bulb length	14.5	14.8 ± 1.0 (13–17)	14.3 ± 0.7 (13.0–15.5) {17}	-	-	23; 24
Bulb diameter	11	11.5 ± 0.7 (10–13)	11.0 ± 0.7 (10–12)	-	-	19; 20.5
Corpus/isthmus ratio	2.7	2.6 ± 0.2 (2.3–3.0)	2.6 ± 0.2 (2.4–2.9) {2.3}	-	-	4.2; 5.4
Nerve ring from ant. end	92	83.0 ± 7.7 (70–96)	86.6 ± 6.4 (77–96) {102}	-	-	108; 121

	***Stegelleta laterocornuta* sp. nov.**			***Stegelleta tuarua***		
Population	**New Zealand JB-75**			**Type population**		**Castlecliff**
No. & sex	**Holotype**	**14 ♀♀ (incl. holotype)**	**9 ♂♂ {1 aberr.}**	**1 ♀**	**3 ♂♂**	**2 ♂♂**
Excretory pore from ant. end	94	86.3 ± 8.1 (72–97)	92.0 ± 6.6 (81–99) {106}	-	-	?; 130
Deirid from ant. end	100	92.9 ± 7.2 (81–104)	100.2 ± 5.6 (89–105) {107}	-	-	141; 171
R_{NR}*	42	35 ± 4 (28–42)	35 ± 2 (32–39) {47}	-	-	35; 38
R_{EP}*	43	37 ± 4 (32–43)	37 ± 2 (33–39) {49}	-	-	?; 41
R_{DEI}*	46	40 ± 4 (35–48)	42 ± 2 (37–44) {50}	-	-	46; 55
Annuli width at midbody	2.7	2.0–2.7	2.0–2.7	-	-	2.4; 2.4
Annuli width anteriorly	2.0	2.0–2.4	2.0–2.4	-	-	3.0–3.4; 3.0–3.4
Vagina or Testis flexure length	6.0	6.0 ± 0.6 (5–7)	39.8 ± 3.9 (35–46)	-	-	90 (dors); 82
Spermatheca or Spicule length	18	20.6 ± 4.6 (17–31)	22.5 ± 0.7 (21.5–23.5)	-	36–40	43; 42
PUS or Gubernaculum length	17	18.1 ± 5.9 (7–24)	11.4 ± 0.5 (11–12)	-	21–24	25; 24
PUS/VBD	0.9	1.0 ± 0.3 (0.6–1.3)	-	-	-	-
Rectum	17	16.6 ± 1.1 (15.5–19.0)	-	-	-	-
Rectum/ABD	1.5	1.5 ± 0.1 (1.4–1.6)	-	-	-	-
Phasmid	12	11.6 ± 0.7 (10–13)	10.6 ± 1.1 (8.5–12.0) {18}	-	-	18; 18
Phasmid (% of tail)	32	32.2 ± 1.7 (30–37)	44.0 ± 3.6 (38–50)	-	~40	42; 38

acute tine extending along the primary axil on the lateral lips. This is a somewhat intermediate stage between *S. incisa*, which has no tines, and *S. arenaria*, in which each lip has one acute tine extending along the primary axil. Another difference is the absence of a cuticular flap on the anterior vulval lip, as seen by SEM in the specimens of *S. incisa* from California.

Stegelleta ophioglossa Andrássy, 1967
Fig. 4A–D, Table 3

Stegelleta ophioglossa Andrássy, 1967: 208–210, fig. 3.

Diagnosis

Stegelleta ophioglossa is characterised by a 315–490 µm long body in females; cuticle divided by regular longitudinal striations into 12–16 rows of blocks at midbody (excluding lateral field); lateral field with four incisures extending almost to tail terminus in females; three pairs of asymmetrical lips, pairs of lips separated by U-shaped primary axils without guarding processes, secondary axils demarcated by

a shallow incisure, each lip asymmetrically rectangular with a smooth margin and without tines; three labial probolae, bifurcated at half of their length, prongs bent toward one another apically, "snake-tongue"-shaped; pharyngeal corpus 3–5 times isthmus length; nerve ring, excretory pore and deirids at level of isthmus; vulva without flap; spermatheca 7–13 µm long; postuterine sac 7–17 µm long.

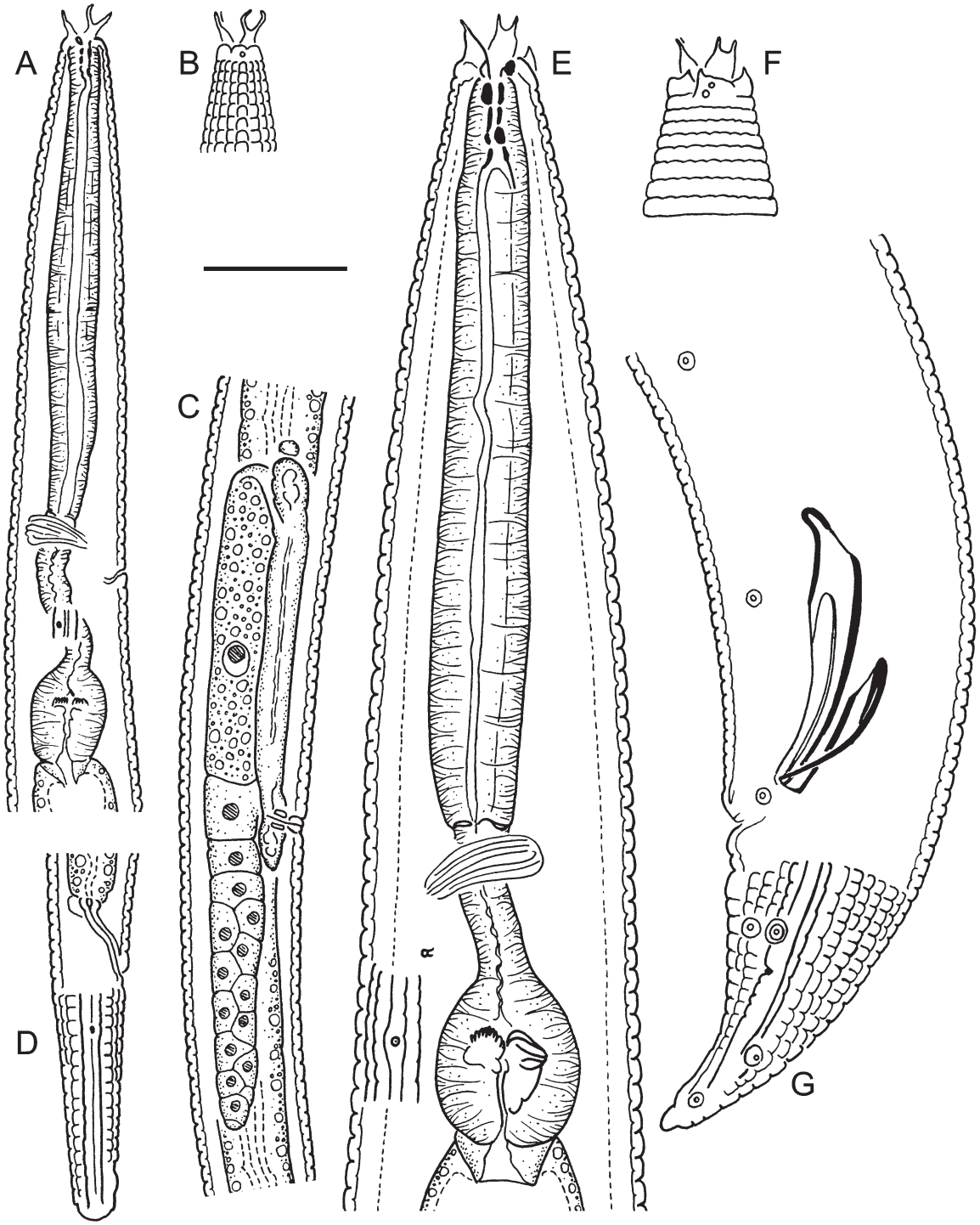

Fig. 4. A–D. *Stegelleta ophioglossa* Andrássy, 1967. **A**. Pharyngeal region. **B**. Anterior end, surface view. **C**. Female gonad. **D**. Female tail. **E–G**. *Stegelleta tuarua* Yeates, 1967. **E**. Pharyngeal region. **F**. Anterior end, surface view. **G**. Male tail. Scale bar = 20 µm.

Table 3. Measurements of females of *Stegelleta ophioglossa* Andrássy, 1967 from Senegal compared with other populations of the same species (presented as mean ± s.d. and (range) or only range). * Calculated from data in original publication. ** Number of annuli from anterior end to nerve ring, excretory pore and deirid, respectively; - indicates that data is not available or not applicable.

Population	**Mongolia**	**Uzbekistan**	**Senegal**	**Iran**	**Spain**	**Senegal**
Reference	Andrássy 1967	Mavljanov 1978	De Ley *et al.* 1990	Shokoohi *et al.* 2008	Abolafia *et al.* 2011	This paper
No. & sex	? ♀♀	19 ♀♀	8 ♀♀	4 ♀♀	? ♀♀	6 ♀♀
Body length	470–490	335–390	347 ± 16 (324–356)	347 ± 17.5 (324–356)	330–420	353 ± 22 (315–382)
Body diameter (BD)	-	17.7*	15–18	16.1 ± 1.2 (15–18)	-	17.9 ± 1.5 (15.5–20.5)
Pharynx length	-	114.7*	104 ± 5 (99–111)	93.9 ± 3.2 (90–98)	-	102.7 ± 3.8 (97–107)
Tail length	-	34.8*	31 ± 2 (28–33)	30.0 ± 1.5 (29–32)	27–32	31.6 ± 1.8 (29–34)
Anal body diam. (ABD)	-	10	9–10	9.6 ± 0.7 (9–10)	-	10.8 ± 0.6 (9.5–11.5)
Vulva	-	253*	-	219.7 ± 12.6 (209–238)	-	224 ± 13 (200–243)
V-A/T	-	-	-	-	-	3.1 ± 0.1 (2.8–3.2)
a	20–21	18.1–22.9	21.3 ± 1.2 (19.7–23.1)	21.6 ± 0.6 (20.8–21.9)	19–23	19.8 ± 0.8 (18.6–20.4)
b	3.3–3.4	3.1–3.6	3.3 ± 0.1 (3.2–3.5)	3.7 ± 0.1 (3.7–3.8)	3.2–3.6	3.4 ± 0.2 (3.2–3.7)
c	11–12	10.4–11.8	11.2 ± 0.6 (10.4–12.9)	11.6 ± 0.2 (11.3–11.8)	12–13	11.2 ± 0.4 (10.5–11.6)
c'	3.0–3.5		3.3 ± 0.2 (3.0–3.6)	3.1 ± 0.3 (2.9–3.4)	2.3–2.7	2.9 ± 0.2 (2.6–3.2)
V (%)	60–62	63.0–66.8	61–63	63.2 ± 0.6 (63–64)	62–63	63.5 ± 0.8 (63–65)
Lip region diameter	-	-	-	4.9 ± 0.7 (4–6)	-	6.6 ± 0.3 (6–7)
Stoma length	-	-	7–9	7.8 ± 1.2 (6–8)	-	8.8 ± 0.3 (8.5–9.0)
Corpus length	-	-	67 ± 3 (63–71)	63.5 ± 3.6 (60–68)	-	65.9 ± 2.9 (61.5–69.0)
Isthmus length	-	-	22 ± 2 (18–25)	14.7 ± 2.8 (12–18)	-	15.9 ± 1.1 (14.5–17.0)
Bulb length	-	-	13–14	16.0 ± 0.9 (16–17)	-	14.1 ± 0.9 (12.0–14.5)
Bulb diameter	-	-	-	-	-	11.3 ± 0.9 (9.5–12.0)
Corpus/isthmus ratio	-	-	3	3.8–5.0	3	4.2 ± 0.2 (4.0–4.4)
Nerve ring from ant. end	-	-	68 ± 4 (60–71)	67.7 ± 2.9 (64–71)	-	76 ± 3.6 (69–81)

Population	Mongolia	Uzbekistan	Senegal	Iran	Spain	Senegal
Excr. pore from ant. end	-	-	66 ± 3 (61–71)	69.4 ± 3.6 (70–74)	-	79.5 ± 3.5 (72–83)
Deirid from ant. end	-	-	75 ± 2 (72–78)	73.6 ± 3.3 (70–78)	-	82.3 ± 4.0 (75–87)
R_{NR}**	-	-	-	-	-	36 ± 1 (35–37)
R_{EP}**	-	-	-	36–39	-	37 ± 1 (36–38)
R_{DEI}**	-	-	-	43	-	39 ± 1 (37–40)
Annuli width at midbody	1.7–2.0	2.1	1.5–2.1	1.7–2.3	-	1.6–2.2
Annuli width anteriorly	-	1.5	-	-	-	1.7–2.0
Vagina length	-	-	3–5	6.2 ± 0.6 (6–7)	-	5.8 ± 0.3 (5.5–6.0)
Spermatheca length	-	-	≤ 13	8.1 (n=1)	13	8.9 ± 1.7 (7–12)
PUS length	-	-	11–14	13.6 ± 4.9 (8–17)	10	7.0–8.5
PUS/VBD	~1	-	1.1–1.4	0.5–0.9	-	0.4–0.5
Rectum	-	-	13 ± 2 (10–16)	12.7 ± 0.8 (12–14)	-	12.7 ± 1.5 (9.5–14.5)
Rectum/ABD	1.7–2.0	-	-	1.3–1.4	> 1	1.2 ± 0.1 (1.0–1.3)
Phasmid	-	-	-	-	-	8.8 ± 0.4 (8.5–9.5)
Phasmid (% of tail)	~30	-	21–29	24–31	33–46	27.5 ± 2.4 (25–32)
Rows of cuticle blocks	14	16	16	-	12	16

Material examined

SENEGAL: 6 ♀♀, SMNH 135943–135944, Kaolack region, Thyssé-Kaymor, *legit* C. Villenave.

Description

Adult

Body slightly arcuate ventrad when killed by heat. Cuticle annulated, annuli 1.6–2.2 µm wide at midbody and 1.7–2.0 µm wide in pharyngeal region. Cuticle tessellated: longitudinal striae giving it a tiled appearance, 16 rows of blocks at midbody (excluding lateral field). Lateral field consisting of two wings separated by a narrow groove, appearing as four incisures under LM, occupying about 20% of body diameter, extending almost to tail terminus in females. Lip region slightly offset, carrying 6 + 4 papillae and two round amphids. Three pairs of asymmetrical lips, one dorsal and two ventrolateral. Pairs of lips separated by U-shaped primary axils without guarding processes. Each pair with a shallow incisure demarcating a secondary axil. Each lip asymmetrically rectangular with a smooth margin. Three labial probolae, 6–7 µm high, bifurcated at half of their length, prongs bent toward one another apically ("snake-tongue"-shaped). Stoma somewhat longer than lip region diameter. Stomatal parts not clearly discernible. Cheilorhabdia bacilliform in lateromedian view; metastegostom with a dorsal denticle. Pharynx cephaloboid. Pharyngeal corpus cylindrical; isthmus narrow, not clearly demarcated from corpus; bulb oval, with valves. Nerve ring, excretory pore and deirids at level of isthmus.

Female

Reproductive system monodelphic, prodelphic, in dextral position in relation to intestine. Ovary reflexed posteriorly at oviduct, ovary straight posterior to vulva. Spermatheca small, not developed. Postvulval uterine sac short, about one-half of vulval body diameter long. Vagina about one-third of vulval body diameter. Vulval lips not protruding. Tail conoid with 12–20 ventral annuli, terminus truncate. Phasmids located at about one-fourth to one-third of tail length.

Male

Not found.

Remarks

The specimens described here agree in many respects with the population of *Stegelleta ophioglossa* from Senegal described by De Ley *et al.* (1990) and several other populations of *S. ophioglossa* (Andrássy 1967; Mavljanov 1978; Shokoohi *et al.* 2008; Abolafia *et al.* 2011).

Stegelleta tuarua Yeates, 1967
Fig. 4E–G, Table 2

Stegelleta tuarua Yeates, 1967: 536–538, fig. 5.

Diagnosis

Stegelleta tuarua is characterised by a 635 µm long body in females and 563–739 µm in males; cuticle divided by regular longitudinal striations into 40–44 rows of blocks at midbody; lateral field with five incisures extending almost to tail terminus in females and in males; three pairs of asymmetrical lips, pairs of lips separated by U-shaped primary axils without guarding processes, secondary axils demarcated by a shallow incisure, each lip asymmetrically rectangular with a smooth margin and one tine; three labial probolae, bifurcated at about 1/5 of their length; pharyngeal corpus 4.2–5.4 times isthmus length; nerve ring and excretory pore at level of isthmus and deirids at level of bulb; vulva and spermatheca undescribed, postuterine sac about 1 vulval body diameter long; spicules 21–25 µm long.

Material examined

NEW ZEALAND: 2 ♂♂, SMNH 135945–135946, 18 May 2008, North Island, Wanganui, Castlecliff beach, partly stabilized coastal sand dunes with *Ammophila arenaria*, 50 cm deep, *legit* G. Yeates.

Description

Adult

Body slightly arcuate ventrad when killed by heat. Cuticle annulated, annuli 2.4 µm wide at midbody and 3.0–3.4 µm wide in pharyngeal region. Cuticle tessellated: longitudinal striae giving it a tiled appearance, tiles are not equal in size and are not arranged in straight rows, approximately 40–44 rows of blocks at midbody. Lateral field with five incisures occupying about 20% of body diameter, extending almost to tail terminus in females. Lip region slightly offset, carrying 6 + 4 papillae and two round amphids. Three pairs of asymmetrical lips, one dorsal and two ventrolateral. Pairs of lips separated by U-shaped primary axils without guarding processes. Each pair with a shallow incisure demarcating a secondary axil. Each lip asymmetrically rectangular with a smooth margin and one acute tine extending along the primary axil. Three labial probolae, 7.0–8.5 µm high, bifurcated at about 1/5 of their length. Stoma somewhat longer than lip region diameter. Stomatal parts not clearly discernible. Cheilorhabdia bacilliform in lateromedian view; metastegostom with a dorsal denticle. Pharynx cephaloboid. Pharyngeal corpus cylindrical; isthmus narrow, not clearly demarcated from corpus; bulb oval, with valves. Nerve ring and excretory pore at level of isthmus and deirids at level of bulb.

Male

Reproductive system monorchic, dextral in position; testis reflexed ventrad anteriorly. Spicules paired and symmetrical, curved ventrad; with oval manubrium and subcylindrical, gradually narrowing shaft. Gubernaculum wedge-shaped, cornua crurum present. Tail strongly arcuate ventrad, conoid with rounded terminus. The two outer lateral lines extend posterior to the subdorsal papilla close to tail terminus, transforming into a cuticular ridge that reaches tail terminus. Genital papillae arranged as follows: two pairs subventral precloacal (at 36 µm and at 74 µm anterior to cloaca), one pair subventral adcloacal, a single midventral papilla on anterior cloacal lip; two pairs (one ventrosublateral and one lateral) at midtail; three pairs (one lateral, one subventral and one dorsosublateral) closer to tail terminus. Phasmids located at about two-fifths to half of tail length.

Female

Not found in our study.

Remarks

The specimens described here agree well in main morphological and morphometric features with the original description by Yeates (1967) of the males of *S. tuarua* from New Zealand.

Key to species

1. Lateral field with five incisures; cuticle with over 40 longitudinal rows of blocks; labial probolae biacute apically ..... ***S. tuarua*** Yeates, 1967
– Lateral field with three-four incisures; cuticle with 12–26 longitudinal rows of blocks; labial probolae bifurcate half of length 2

2. Labial probolae with minute secondary bifurcations at tips ..... ***S. iketaia*** Yeates, 1967
– Labial probolae without minute secondary bifurcations at tips 3

3. Cephalic probolae in shape of acute tines present on all six lips along the primary axils; cuticle with 24–26 longitudinal rows of blocks ..... ***S. arenaria*** Boström & Holovachov, 2012
– Cephalic probolae absent, or present only on lateral lips along the primary axils; cuticle with 12–22 longitudinal rows of blocks 4

4. Cuticle with 22 longitudinal rows of blocks ..... ***S. georgica*** Bagaturija, 1973
– Cuticle with 12–16 longitudinal rows of blocks 5

5. Parthenogenetic species; spermatheca 7–13 µm long; postuterine sac about 7–17 µm long .... ***S. ophioglossa*** Andrássy, 1967
– Amphimictic species; spermatheca 24–43 µm long; postuterine sac about 22–36 µm long 6

6. Cephalic probolae absent ..... ***S. incisa*** (Thorne, 1937)
– Cephalic probolae setose, present on lateral lips only ..... ***S. laterocornuta*** sp. nov.

Discussion

Representatives of the family Cephalobidae Filipjev, 1934 are mostly terrestrial and bacteria-consuming nematodes with a worldwide distribution, including Antarctica. They occur in tropical and temperate regions as well as in hot and cold arid areas globally. They seem to be especially diverse and abundant in deserts and many species have been described from warm and dry habitats like the Namib Desert in southern Africa (see, e.g., Rashid & Heyns 1990a, b; Rashid *et al.* 1990a, b) and the Mojave Desert in southern California (see, e.g., De Ley *et al.* 1999; Taylor *et al.* 2004; Waceke *et al.* 2005). Sand dunes

appear to be another suitable habitat for cephalobids, as evidenced by several studies (see, e.g., Boström & Holovachov 2012, 2013a, b; Bussau 1991; Orselli & Vinciguerra 2002; Yeates 1967). Species of the genus *Stegelleta* are rather rare inhabitants of terrestrial habitats, although they occur on all continents except Antarctica. In the present study, a new species of *Stegelleta*, *S. laterocornuta* sp. nov., is described from New Zealand, which brings the total number of species in this genus to seven. Descriptions of new material of some already known species from dry areas in California and Senegal are also included. This leads to an addition of morphological data which broadens the diagnosis of *Stegelleta* and increases the number of character combinations useful for species identification in the genus.

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