

# Gnathostomulida from Australia and Papua New Guinea

Wolfgang STERRER

Bermuda Natural History Museum - PO Box FL 145

Flatts FLBX, Bermuda

Fax: (1) 441 293 8944 - E-mail: wsterrer@sargasso.bbsr.edu

**Abstract:** This is the first record of the phylum Gnathostomulida from Australia and Papua New Guinea. Of twenty species encountered, five are new. One also represents a new genus (*Goannagnathia susannae* gen. et sp. nov.), and four are new species (*Pterognathia sica* sp. nov., *Agnathiella nominata* sp. nov., *Vampyrognathia varanus* sp. nov., and *Austrognathia australiensis* sp. nov.); two others are not identified to species (*Gnathostomula* sp. 1 and *G.* sp. 2). The remaining species have been identified, some tentatively, with species previously recorded only in the Atlantic (*Haplognathia gubbarnorum*, *Labidognathia longicollis*, *Tenuignathia rikerae*, *Austrognathia* cf. *christianae*, and *Austrognatharia* cf. *kirsteueri*), or species already known from the Pacific (*Haplognathia asymmetrica*, *H. rosea*, *H. ruberrima*, *Cosmognathia arcus*, *C. bastillae*, *Pterognathia ctenifera*, *Gnathostomula* cf. *maorica*, and *Austrognathia nannulifera*). At least nine of the 20 species encountered (45%), all belonging to Filospermoidea and lower Bursovaginoidea-Scleroperalia, are cosmopolitan.

**Résumé :** *Gnathostomulides d'Australie et de Papouasie-Nouvelle Guinée.* Le phylum des Gnathostomulida est signalé pour la première fois en Australie et en Papouasie-Nouvelle Guinée. Parmi les vingt espèces trouvées, cinq sont nouvelles (*Pterognathia sica* sp. nov., *Agnathiella nominata* sp. nov., *Vampyrognathia varanus* sp. nov., et *Austrognathia australiensis* sp. nov.) et un genre est nouveau (*Goannagnathia susannae* gen. et sp. nov.) ; deux autres espèces n'ont pas été identifiées (*Gnathostomula* sp. 1 et *G.* sp. 2 ). Le reste du matériel a été identifié à des espèces connues seulement de l'Atlantique (*Haplognathia gubbarnorum*, *Labidognathia longicollis*, *Tenuignathia rikerae*, *Austrognathia* cf. *christianae*, et *Austrognatharia* cf. *kirsteueri*), ou à des espèces trouvées déjà dans l'Océan Pacifique (*Haplognathia asymmetrica*, *H. rosea*, *H. ruberrima*, *Cosmognathia arcus*, *C. bastillae*, *Pterognathia ctenifera*, *Gnathostomula* cf. *maorica*, et *Austrognathia nannulifera*). Au moins neuf des vingt espèces (45 %), toutes appartenant aux Filospermoidea et aux Bursovaginoidea-Scleroperalia inférieurs, sont cosmopolites.

**Keywords:** Gnathostomulida, taxonomy, new taxa, biogeography.

## Introduction

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Gnathostomulida are microscopic, freeliving, non-segmented marine worms of enigmatic phylogenetic affiliation. Initially described as aberrant flatworms (Ax,

1956), they were recognized as a separate phylum by Riedl (1969). Gnathostomulida now appear most closely related to Syndermata (Rotifera and Acanthocephala), as recently suggested on the basis of ultrastructural evidence (Rieger & Tyler, 1995) and strengthened by 18S rDNA analysis (Giribet et al., 2000). The 89 species described to date (Sterrer, 1998) are grouped in two orders (Sterrer, 1972), Filospemoidea (with three genera and 25 species) and Bursovaginoidea; the latter with two suborders, Scleroperalia (with 18 genera and 42 species) and Conophoralia (with three genera and 22 species). The main distinguishing characteristics of the phylum are an exclusively monociliated epidermis (i.e., each cell carries only a single cilium), and a bilaterally symmetric muscular pharynx that usually contains complex cuticular mouth parts.

As members of the meiobenthos, Gnathostomulida are remarkable because they occur almost exclusively, often in large numbers, in sand enriched with organic detritus, as is typically found on sheltered beaches and intertidal sand flats, coastal ponds, leeward of coral reefs, and near sea grasses and mangroves (Sterrer, 1998). Our scant knowledge of their biology suggests that they feed by grazing on the microflora (bacteria and fungal hyphae) coating sand grains, and that they have extremely low oxygen requirements (Schiemer, 1973), in addition to mechanisms for sulphide detoxification (Powell et al., 1979).

While most early species descriptions were from European shores (Sterrer, 1969), collecting emphasis in the 1970s shifted to the (sub)tropical northwestern Atlantic where 45 species have now been recorded (Sterrer, 1998). With a total of six species in three genera (Gerlach, 1958; Riedl, 1971b; Ehlers & Ehlers, 1973), the Pacific remained largely unexplored until I recorded 18 species from Fiji, Tonga and New Zealand (Sterrer, 1991a), eight species from Hawaii (Sterrer, 1991b), and nine species from Tahiti (Sterrer, 1991c). This paper reports 20 species from northeastern Australia and northern Papua New Guinea, including five new species and a new genus. This brings the total number of described gnathostomulid species to 94, and of genera to 25.

## Materials and methods

During the summer of 1996, 41 sediment samples were collected, at three sites, with the specific objective of finding Gnathostomulida (Table 1): 1. Stradbroke Island at Moreton Bay off Brisbane, 27° 35'S, 153° 28'E (August 12-17); 2. Lizard Island, NE of Cairns, 14° 40'S, 145° 28'E (August 25-September 8), and 3. Madang, on the north coast of Papua New Guinea, 5° 15'S, 145° 50'E (September 22-October 2). At Stradbroke Island, five out of 10 samples (50%) yielded Gnathostomulida; on Lizard Island, the

**Table 1.** Localities and samples yielding Gnathostomulida in Australia and Papua New Guinea.

**Tableau 1.** Localités et échantillons ayant fourni des Gnathostomulides en Australie et Papouasie-Nouvelle Guinée.

Sample	# Locality	Detail	Date	Sediment	Depth	Species	Specimens
AUSTRALIA							
W3	Stradbroke Island	Amity Point	13-Aug-96	fine sand in sparse seagrass	upper tidal pond	1	1
W4	Stradbroke Island	Amity Point	13-Aug-96	fine gray sand	mid-tide level	2	2
W5	Stradbroke Island	in front of Dunwich Lab	14-Aug-96	fine sand with detritus & sparse seagrass	low-tide level	2	2
W6	Stradbroke Island	in front of Dunwich Lab	14-Aug-96	fine sand with detritus & sparse seagrass	mid-tide level	1	1
R6	Stradbroke Island	in front of Dunwich Lab	14-Aug-96	fine sand with detritus & sparse seagrass	mid-tide level	3	4
LZ1	Lizard Island	beach off research station	26-Aug-96	fine sand between patch reefs	lower intertidal	5	20
LZ3	Lizard Island	beach off research station	26-Aug-96	fine sand with seagrass between patch reefs	lower intertidal	4	4
LZ5	Lizard Island	Watson's Bay, north end	27-Aug-96	fine sand in fine grass patches	lower intertidal	1	
LZ9	Lizard Island	Watson's Bay, south end	27-Aug-96	fine sand with fine seagrass	mid-tide level	12	48
LZ11	Lizard Island	beach off research station	27-Aug-96	fine sand between patch reefs	lower intertidal	4	
PAPUA N. GUINEA							
PNG6	Madang	Wongat Island, steep slope	25-Sep-96	mostly Halimeda debris	8 m	2	6
PNG9	Madang	Tab Island, reef inside passage	26-Sep-96	sand with Halimeda debris	3 m	3	8
					Samples	12	
					Species	20	
					Specimens		96

success rate was five out of 17 samples (29%), and at Madang it was two out of 14 samples (14%). Of more than 100 specimens extracted, 96 were studied live in squeeze preparation, and recorded in detail for this paper.

Methods of sample collection, specimen extraction, analysis, and data presentation are as described previously (Sterrer, 1991a, 1998). This includes the use of a drawing tube for tracing to scale and recording up to 72 morphometric variables for each specimen examined. The dimensions of many of the features that distinguish species, such as teeth on the cuticular mouth parts, lie at the lower limit of light microscopy (Sørensen & Sterrer, in press). Because the detailed study of a specimen in squeeze preparation almost invariably brings about its destruction by reducing it to a flat 'pancake', type material – while necessary – is inferior in the long run to camera-lucida scale drawings and photographs. Data presentation includes a relative scale of 100 units (U) for the body length, various indices for length-width ratios, and the mean (X), standard deviation (S), maximum (Max), minimum (Min), and number (n) of measurements. Individual measurements, with the exception of sperm width, were made (and are given) to the nearest micrometer whereas calculated numbers (means, indices etc.) are expressed with two decimals, not only to distinguish them from actual measurements but also to record the frequently surprising consistency even of 'soft' characters. As I have shown earlier (Sterrer, 1977), salient characteristics of the 'hard' pharyngeal structures (such as length and width, and number of teeth) are independent of specimen size or maturity, and thus provide a practical tool for population analysis. Measurements and indices are defined as follows:

Body length = from anterior to posterior tip, including a tail when present;

Body width = maximum diameter;

Body index = body length divided by body width;

Rostrum length = from anterior tip to anterior edge of jaws;

Rostrum width = maximum diameter of rostrum;

Rostrum index = rostrum length divided by rostrum width;

Basal plate length = from anterior-most to posterior-most contour;

Basal plate width = maximum width (including lateral wings but excluding muscles);

Basal plate index = basal plate length divided by basal plate width;

Jaw length = from anterior tip to posterior edge of symphysis (but excluding caudal appendages);

Pharynx bulb length = from caudal edge of jaw symphysis to caudal edge of pharynx bulb;

Sperm length = total length of sperm (including tail) or conulus (excluding the surrounding matrix); in the case of conuli this measurement is taken of the three largest conuli per specimen;

Sperm width = maximum diameter (in filiform sperm measured to the nearest 0.3  $\mu\text{m}$ );

Sperm index = sperm length divided by sperm width.

Whenever more than one specimen was measured, a Table provides morphometric data (in  $\mu\text{m}$ ) in a standard format, leaving out S, Max and Min where not applicable. Species are presented in a standard narrative consisting of a *Description* (with *Organization and behaviour*, *Digestive tract*, *Male system* and *Female system*) and a *Discussion*. This format is reduced to *Description* and *Discussion* wherever material was too scarce to provide much new or detailed information. Figure 1 gives a general overview of gnathostomulid anatomy and terminology. Scales are given for all drawings but not for photographs, which were taken at variable (zoom) magnifications. All type material has been deposited in the Queensland Museum in Brisbane (QM). Other type material referred to is in the American Museum of Natural History in New York (AMNH), and the U. S. National Museum of Natural History in Washington, DC (USNMNH).

## Taxonomy

Order Filospermoidea Sterrer, 1972

Family Haplognathiidae Sterrer, 1972

Genus *Haplognathia* Sterrer, 1970

### Diagnosis

Haplognathiidae with simple, not horizontally bipartite jaws without or with very few (usually not more than 5) teeth.

Testes paired.

Type species: *H. simplex* (Sterrer, 1966). No type material deposited.

*Haplognathia asymmetrica* Sterrer, 1991

(Figs 2. 1-2, 3. 1; Table 2)

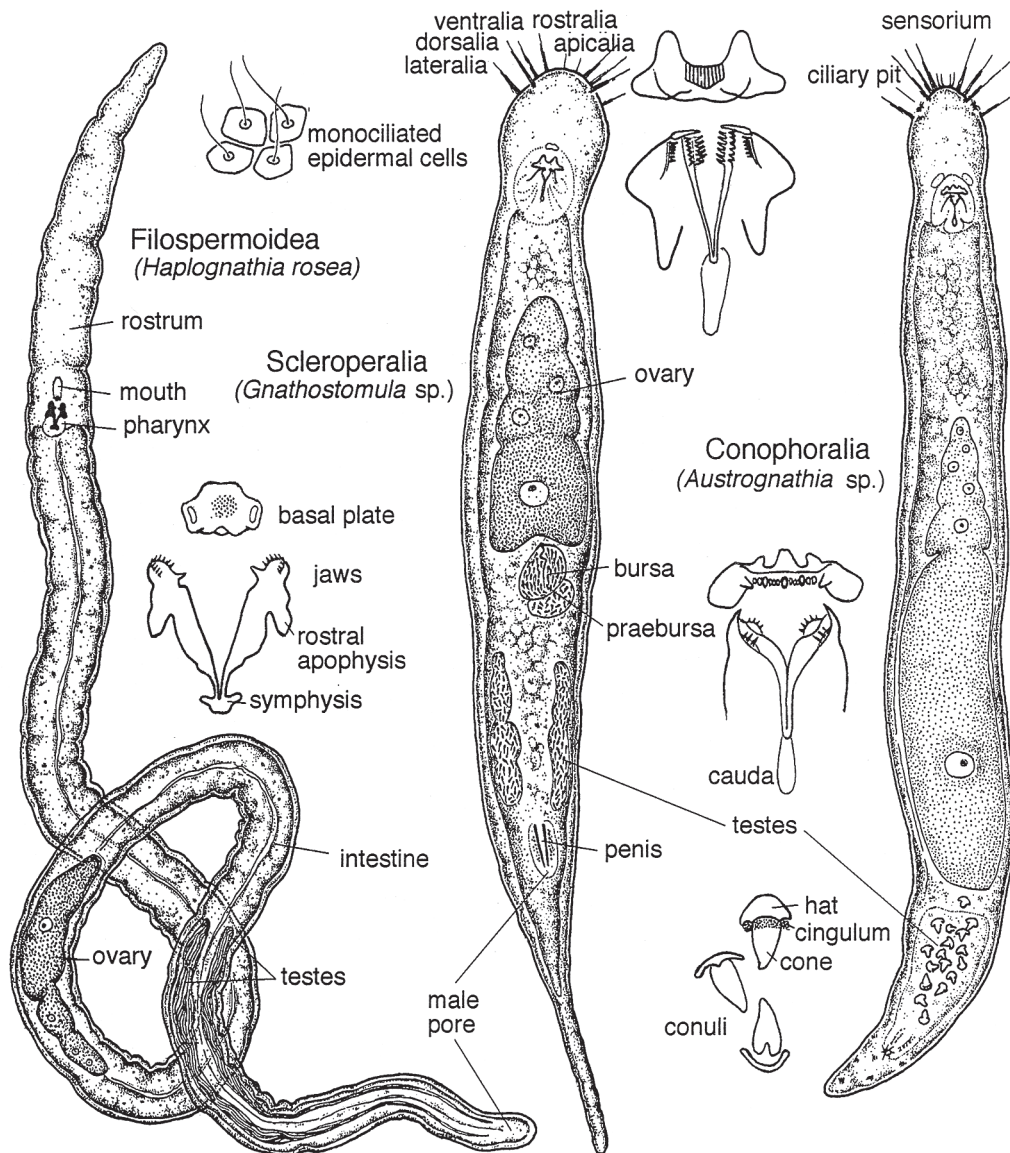
Holotype USNMNH #132187.

*Material examined.* One anterior fragment and one juvenile from Lizard I. (sample LZ9); one anterior fragment from Stradbroke I. (sample W5).

*Distribution.* Hawaii (Sterrer, 1991b); (sub)tropical NW Atlantic (Sterrer, 1998).

### Description

Juveniles are colourless-translucent; adults more opaque. This species is readily identified by the roughly triangular but invariably asymmetric basal plate which is longitudinally traversed by a pair of ridges, and whose corners usually end in conspicuous, often elongated knobs. The toothless jaws are rounded, giving a solid, 'cartilaginous' impression.



**Figure 1.** General overview of gnathostomulid anatomy and terminology, showing representatives of the order Filospermoidea, and the suborders Bursovaginoidea-Scleroperalia and Bursovaginoidea-Conophoralia.

**Figure 1.** Organisation des Gnathostomulida, représentant l'ordre des Filospermoidea, et les sous-ordres des Bursovaginoidea-Scleroperalia et Bursovaginoidea-Conophoralia.

*Discussion.* The new records agree well with those from the Atlantic (jaws 21.93  $\mu\text{m}$  long; basal plate 9.86  $\mu\text{m}$  by 8.14  $\mu\text{m}$ , index 1.21). The asymmetric basal plate and the smaller jaws (22.67  $\mu\text{m}$  vs. 30.0  $\mu\text{m}$ ) distinguish this species from the otherwise very similar *H. simplex* (Sterr, 1966).

*Haplognathia gubbarnorum* (Sterr, 1969)

(Figs 2. 3-4, 3. 2; Table 3)

*Pterognathia gubbarnorum* Sterr, 1969: 68-75, figs 208-241. No type material deposited.

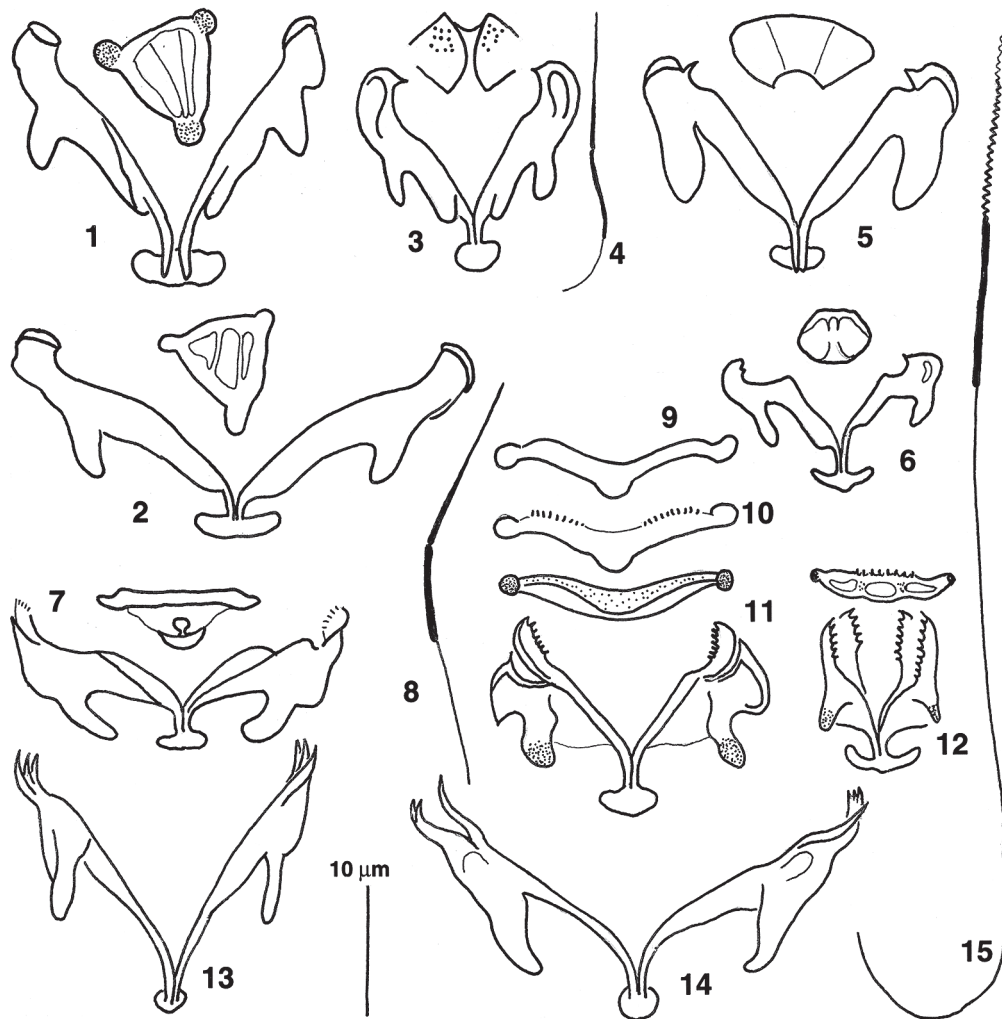
*Haplognathia lyra* Sterr, 1970: 377-379, figs. 15-21, 22-23. No type material deposited.

*Material examined.* One adult and one anterior fragment from Lizard I. (sample LZ9).

*Distribution.* North Sea, Irish Sea (Sterr, 1969); (sub)tropical NW Atlantic (Sterr, 1998).

#### *Description*

Colourless and very translucent. The only adult was particularly slender (body index 36.50, rostrum index 8.00)



**Figure 2.** Filospermoidea, all from Lizard Island; mouth parts and sperm. 1.-2. *Haplognathia asymmetrica*, basal plate and jaws of two specimens; 3.-4. *Haplognathia gubbarnorum*; 3. basal plate and jaws; 4. sperm; 5. *Haplognathia ruberrima* basal plate and jaws; 6. *Haplognathia rosea* basal plate and jaws; 7. *Cosmognathia arcus*, basal plate and jaws; 8.-11. *Cosmognathia bastillae*; 8. sperm; 9. and 10. basal plates 11. basal plate and jaws of a third specimen; 12. *Pterognathia ctenifera*, basal plate and jaws; 13.-15. *Pterognathia sica* sp. nov., 13.-14 jaws of two specimens; 15. sperm. All to the same scale.

**Figure 2.** Filospermoidea de Lizard Island ; pièces buccales et spermatozoïdes. 1.-2. *Haplognathia asymmetrica*, pièce basale et mâchoire de deux spécimens ; 3.-4. *Haplognathia gubbarnorum* ; 3. pièce basale et mâchoire ; 4. spermatozoïde ; 5. *Haplognathia ruberrima* pièce basale et mâchoire ; 6. *Haplognathia rosea* pièce basale et mâchoire ; 7. *Cosmognathia arcus*, pièce basale et mâchoire ; 8.-11. *Cosmognathia bastillae* ; 8. spermatozoïde ; 9. et 10. pièces basales de deux spécimens ; 11. pièce basale et mâchoire d'un troisième spécimen ; 12. *Pterognathia ctenifera*, pièce basale et mâchoire ; 13.-15. *Pterognathia sica* sp. nov., 13.-14 mâchoires de deux spécimens ; 15. spermatozoïde. Tous à la même échelle.

when compared with N. Carolina specimens (29.43 and 5.75, respectively), and especially with Swedish specimens (about 25, and about 4). The largest egg, 150 µm long, was located between U 37.67 and U 47.97. Jaw length lies between that of N. Carolina (16.6 µm) and Swedish specimens (20.6 µm), as do the dimensions of the eyeglass-shaped basal plate (5.17 µm by 10.17 µm in N. Carolina, and 6.0 µm by 11.5 µm in Sweden). The delicate sperm (Fig.

1.4) is identical, with the same length of about 24 µm, in all three localities.

**Discussion.** Sterrer (1998) made *H. lyra* from N. Carolina a junior synonym of *H. gubbarnorum* f. *typica* (Sterrer, 1969) from Sweden and the Irish Sea, acknowledging the small differences in jaw length as insufficient for species distinction. The Australian specimens, which most closely

**Table 2.** Morphometric data for *Haplognathia asymmetrica*.**Tableau 2.** Données morphométriques sur *Haplognathia asymmetrica*.

<b>Lizard Island</b>	Mean	S	Max	Min	n
Jaw length	22.50		23	22	2
Basal plate length	10.00		10	10	2
Basal plate width	8.00		8	8	2
Basal plate index	1.25		1.25	1.25	2
<b>Stradbroke Island</b>	Mean	S	Max	Min	n
Jaw length	23				1
Basal plate length	10				1
Basal plate width	10				1
Basal plate index	1.00				1
<b>ALL DATA</b>	Mean	S	Max	Min	n
Jaw length	22.67	0.58	23	22	3
Basal plate length	10.00	0.00	10	10	3
Basal plate width	8.67	1.15	10	8	3
Basal plate index	1.17	0.14	1.25	1.00	3

**Table 3.** Morphometric data for *Haplognathia gubbarnorum*.**Tableau 3.** Données morphométriques sur *Haplognathia gubbarnorum*.

<b>Lizard Island</b>	Mean	S	Max	Min	n
Body length of adults	1460				1
Body width of adults	40				1
Body index of adults	36.50				1
Rostrum index of adults	8.00				1
Jaw length	18.00		18	18	2
Basal plate length	6.50		7	6	2
Basal plate width	11.50		13	10	2
Basal plate index	0.58		0.70	0.46	2
Sperm length	24.00	3.00	27	21	3
Sperm width	0.50	0.00	0.50	0.50	3
Sperm index	48.00	6.00	54.00	42.00	3

resemble *H. gubbarnorum* f. *typica*, reaffirm the similarity of all measurable morphological parameters over this vast geographic and climatic range, as exemplified in jaw length, basal plate length and width, and sperm length.

*Haplognathia rosea* (Sterrer, 1969)

(Fig. 2. 6)

*Pterognathia rosea* Sterrer, 1969: 63-67, figs 182-207. No type material deposited.

*Haplognathia rosacea* Sterrer, 1970: 379-382, figs 22-34. No type material deposited.

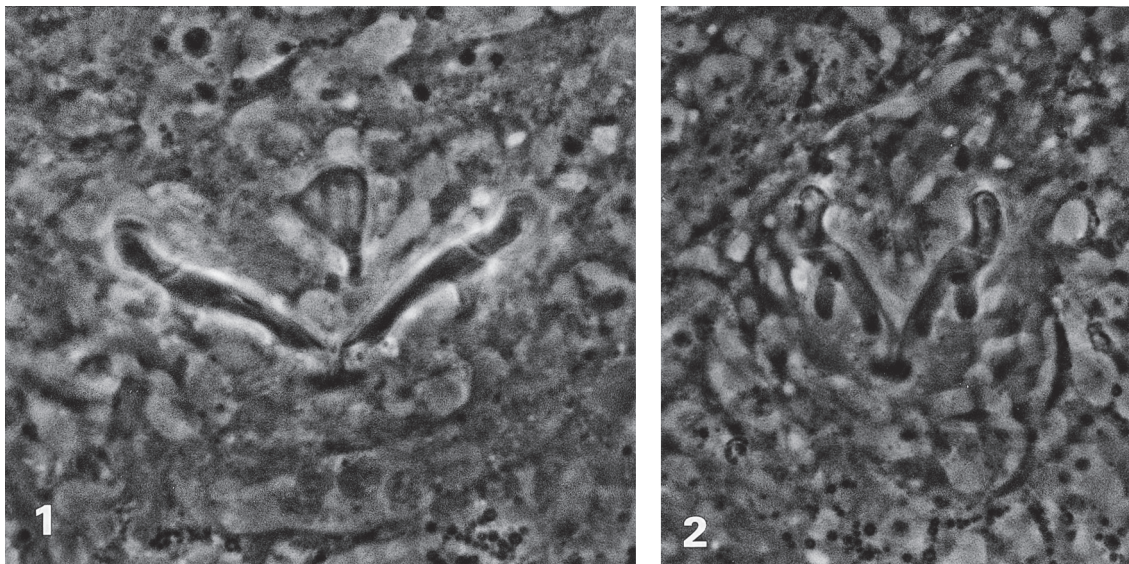
*Material examined.* One anterior fragment from Lizard I. (sample LZ3).

*Distribution.* North Sea, Irish Sea (Sterrer, 1969); Canary Islands (Sterrer, 1997); (sub)tropical NW Atlantic (Sterrer, 1998); Fiji (Sterrer, 1991a); Tahiti (Sterrer, 1991c).

#### Description

The single specimen was uniformly red. The delicate basal plate was 4  $\mu\text{m}$  long and 6  $\mu\text{m}$  wide (index 0.67), hexagonal, with a pair of longitudinal ridges connecting the reinforced anterior to the fainter posterior edge. Jaw length was 14  $\mu\text{m}$ . Anterior jaw apophyses are less than half as long as the jaws (index 0.43).

*Discussion.* Among the most widely distributed of all gnathostomulid species, *H. rosea* has been re-diagnosed by Sterrer (1998) as having horn-like rostral jaw apophyses that are less than half as long as the jaws (index 0.50 or



**Figure 3.** *Haplognathia* spp. from Lizard I. 1. *Haplognathia asymmetrica*, basal plate and jaws; 2. *Haplognathia gubbarnorum*, basal plate and jaws. Phase contrast micrographs of live specimens.

**Figure 3.** *Haplognathia* spp. de Lizard Island. 1. *Haplognathia asymmetrica*, pièce basale et mâchoire ; 2. *Haplognathia gubbarnorum*, pièce basale et mâchoire. Microphotos d'exemplaires vivants, en contraste de phase.

smaller), and a vertically sculpted basal plate with longitudinal ridges but without thorns. The Australian worm falls within these criteria.

*Haplognathia ruberrima* (Sterrer, 1966)

(Fig. 2. 5)

*Pterognathia ruberrima* Sterrer, 1966: 408-409,

figs 2a-d. No type material deposited.

*Pterognathia ruberrima* Sterrer, 1969: 53-61, figs 150-179.

*Material examined.* One adult and four juveniles and fragments from Lizard I. (sample LZ9).

*Distribution.* North Sea, Adriatic (Sterrer, 1969); Canary Islands (Sterrer, 1997); (sub)tropical NW Atlantic (Sterrer, 1998); Fiji (Sterrer, 1991a); Hawaii (Sterrer, 1991b).

#### *Description*

Most specimens were uniformly crimson; a few were blotched crimson and colourless. The only intact adult had a large egg but no male organs. That same specimen also carried many irregularly rod-shaped, orange-coloured epidermal inclusions throughout the pre-ovary part of the body. The delicate basal plate, whose outline is difficult to ascertain and changes with the degree of squeezing, is flat buckle-shaped, 3 µm long and 8 µm wide (index 0.38); none of the three basal plates recorded was dorsally set with thorns. Mean jaw length was 19.50 µm (S 2.88, Max 22 µm, Min 19 µm, n 5). Anterior jaw apophyses are more than half as long as the jaws (index 0.52).

*Discussion.* *H. ruberrima* is as wide-spread as *H. rosea* with which it may occur sympatrically, and possibly hybridize (see Sterrer, 1998 for a discussion of 'red' *Haplognathia* species). It has been re-diagnosed by Sterrer (1998) as having 16-30 µm long jaws with shovel-like rostral apophyses that are at least half as long as the jaws (index 0.50 or greater), and a flat, transverse-oval basal plate with longitudinal rows of dorsocaudally pointing thorns on the dorsal surface. While the Australian specimens lacked thorns I assign them to this species on the strength of jaw dimensions and proportions.

Family Pterognathiidae Sterrer, 1972

Genus *Cosmognathia* Sterrer, 1991

#### *Diagnosis*

Pterognathiidae with few to many, usually very delicate jaw teeth arranged in two groups but not equally divided between dorsal and ventral part of jaw nor forming an arc or basket. Rostral edge of basal plate without or with very delicate teeth or ridges; caudal edge usually convex and enclosing a spherical knob.

Type species: *C. arcus* Sterrer, 1991.

*Cosmognathia arcus* Sterrer, 1991

(Figs 2. 7, 4. 1)

Holotype USNMNH #132173.

*Material examined.* One juvenile from Lizard I. (sample LZ1).

*Distribution.* Fiji (Sterrer, 1991a); Hawaii (Sterrer, 1991b); (sub)tropical NW Atlantic (Sterrer, 1998).

#### *Description*

The only specimen, a juvenile, was 1450 µm long and 60 µm wide at U 69.0 (body index 24.17), and colourless-opaque. The pharynx bulb, which measured 18 µm behind the jaw symphysis, contained two pairs of glands: a finely granular rostral pair situated on either side of the mouth opening, and a more coarsely granular caudal pair behind the jaw symphysis. Jaws are 19 µm long, with 8 very delicate teeth. The basal plate, in the shape of an upside-down coat hanger, is 4 µm long and 13 µm wide (index 0.31).

*Discussion.* Biometric data for this specimen are within the range of other Pacific and Atlantic localities.

*Cosmognathia bastillae* Sterrer, 1991

(Figs 2. 8-11, 4. 2-3; Table 4)

Holotype USNMNH #132174.

*Material examined.* Four adults and nine juveniles from Lizard I. (sample LZ9).

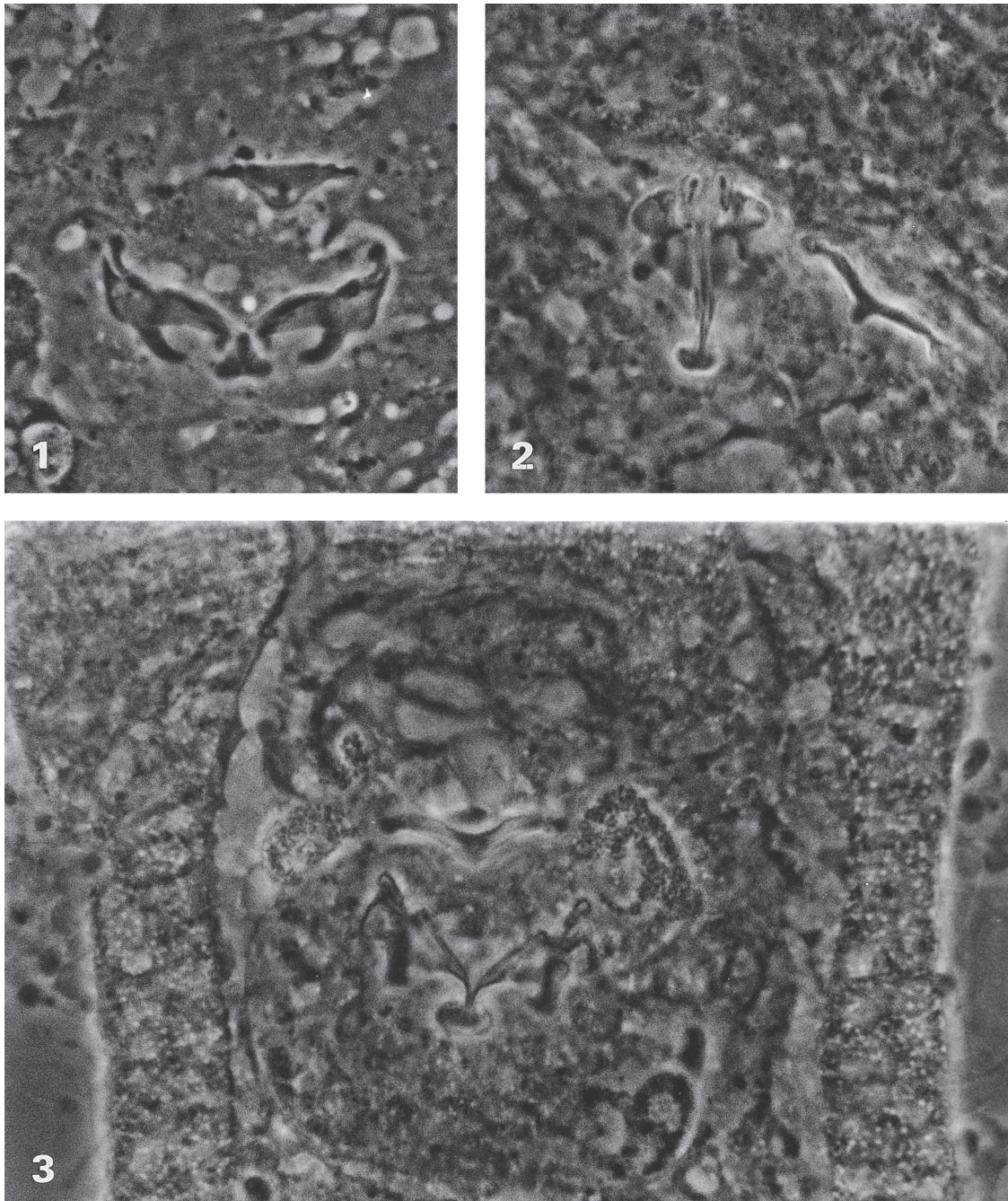
*Distribution.* Fiji (Sterrer, 1991a).

#### *Description*

*Organization and behaviour.* Colourless-translucent to yellowish-opaque, the latter owing to many round inclusions in the intestine. The largest adult was 2230 µm long and 80 µm wide at U 53.8 (body index 27.88). Rostrum pointed, slender (index 4.89), 250 µm long.

*Digestive tract.* The basal plate has the shape of a hunting bow, with knobs at each end, and frequently also at the posterior apex. It is 3.64 µm long and 18.00 µm wide. Its latero-anterior edge may be set with very fine teeth or ridges (Fig. 2. 10). Jaws are 18.43 µm long, with semicircular cristae and plump rostral apophyses. The delicate teeth appear as two groups: a ventral row of 7-9 teeth which overlaps (and usually obscures) a dorsal row of 4-5 teeth. The pharynx extends 9 µm behind the jaws. One pair of pharyngeal glands, with coarser granules, flanks the mouth opening whereas another, with somewhat finer granules, is located behind the jaws.

*Male system.* The testis is probably unpaired, extending from U 75.49 to U 85.83 at which point it empties into two vasa deferentia. A male pore is located ventrally at the posterior end (about U 99). Sperm is 33.00 µm long,



**Figure 4.** *Cosmognathia* spp. from Lizard I. 1. *Cosmognathia arcus*, basal plate and jaws; 2.-3. *Cosmognathia bastillae*, 2. basal plate and jaws; 3. pharynx with basal plate and jaws of another specimen. Phase contrast micrographs of live specimens.

**Figure 4.** *Cosmognathia* spp. de Lizard Island. 1. *Cosmognathia arcus*, pièce basale et mâchoire ; 2-3. *Cosmognathia bastillae*, 2. pièce basale et mâchoire ; 3. pharynx avec pièce basale et mâchoire d'un autre spécimen. Microphotos d'exemplaires vivants, en contraste de phase.

delicate, three-partite, consisting of a pointed but unspiralled head 13  $\mu\text{m}$  long, a middle piece of 7-10  $\mu\text{m}$ , and a tail of 10-15  $\mu\text{m}$ . Whereas the head is always stiff, and thus clearly demarcated from the middle piece, both middle

piece and tail make writhing motions when squeezed out of the body, and are thus not always set off against one another.

*Female system.* The ovary extends from U 24.30 to U 71.19; the largest egg may reach 520  $\mu\text{m}$  in length.



**Table 4.** Morphometric data for *Cosmognathia bastillae*.**Tableau 4.** Données morphométriques sur *Cosmognathia bastillae*.

Lizard Island	Mean	SD	Max	Min	n
Body length of adults	1726.67	608.80	2230	1050	3
Body width of adults	63.33	20.82	80	40	3
Body index of adults	27.09	0.81	27.88	26.25	3
Rostrum index of adults	4.89	1.23	6.25	3.83	3
Jaw length	18.43	0.51	19	18	14
Basal plate length	3.64	0.84	6	3	14
Basal plate width	18.00	1.04	19	15	14
Basal plate index	0.20	0.04	0.32	0.16	14
Sperm length	33.00	1.41	35	31	6
Sperm width	0.50	0.00	0.50	0.50	6
Sperm index	66.00	2.83	70.00	62.00	6

**Discussion.** Described from only two juvenile specimens found in Fiji, this species is well characterized by its slender, transverse basal plate. The Fijian morphometric data are somewhat below those from Australia, as apparent in jaw length (16.50  $\mu\text{m}$ ), and basal plate length (3.00  $\mu\text{m}$ ) and width (12.50  $\mu\text{m}$ ).

Genus *Pterognathia* Sterrer, 1966  
(emend. Sterrer, 1991a)

#### Diagnosis

Pterognathiidae with many, usually fairly robust jaw teeth (usually more than five) arranged in a rostro-ventral arc or

ventro-rostro-dorsal basket and more or less equally divided between the dorsal and the ventral part of the jaw. Rostral edge of basal plate set with teeth which usually correspond in number and structure to those of a jaw. Testis usually unpaired and situated dorsally.

Type species: *P. swedmarki* Sterrer, 1966. No type material deposited.

*Pterognathia ctenifera* Sterrer, 1970

(Figs 2, 12, 5, 1)

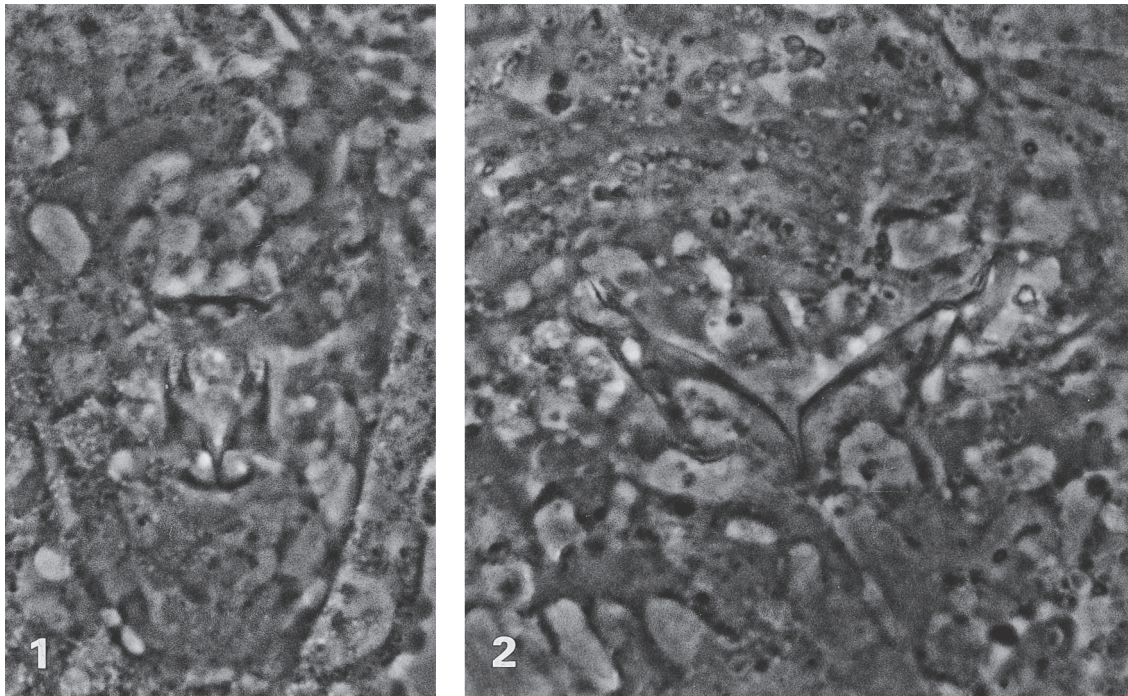
No type material deposited.

**Material examined.** One juvenile from Lizard I. (sample LZ3).

**Distribution.** Fiji (Sterrer, 1991a); Hawaii (Sterrer, 1991b); (sub)tropical NW Atlantic (Sterrer, 1998).

#### Description

The juvenile measured 1080  $\mu\text{m}$  in length and 30  $\mu\text{m}$  in width at U 21.3 (body index 36.00; rostrum index 6.00). The basal plate, 3  $\mu\text{m}$  long and 12  $\mu\text{m}$  wide, is tripartite, and ends laterally in small knobs. Its antero-median edge is set with 7 fine teeth. The jaws are 13  $\mu\text{m}$  long, bipartite, with 7 teeth in the dorsal and 8 teeth in the ventral part. The pharynx bulb is 14  $\mu\text{m}$  long.



**Figure 5.** *Pterognathia* spp. from Lizard I. 1. *Pterognathia ctenifera*, basal plate and jaws; 2. *Pterognathia sica* sp. nov., jaws. Phase contrast micrographs of live specimens.

**Figure 5.** *Pterognathia* spp. de Lizard Island. 1. *Pterognathia ctenifera*, pièce basale et mâchoire; 2. *Pterognathia sica* sp. nov., mâchoire. Microphotos d'exemplaires vivants, en contraste de phase.

*Discussion.* This is yet another species that combines circumtropical distribution with remarkable constancy in pharyngeal structures, as evidenced by jaw length, basal plate length and width from Fiji (12  $\mu\text{m}$ , 3  $\mu\text{m}$ , 10  $\mu\text{m}$ ), Hawaii (12  $\mu\text{m}$ , 3  $\mu\text{m}$ , 11  $\mu\text{m}$ ), and the (sub)tropical NW Atlantic (13.00  $\mu\text{m}$ , 3.39  $\mu\text{m}$ , 10.91  $\mu\text{m}$ ).

*Pterognathia sica* sp. nov.  
(Figs 2. 13-15, 5. 2; Table 5)

*Type material.* Holotype is one adult, in squeeze preparation, from Lizard I. (sample LZ9), 14° 40'S, 145° 28'-E (QM G 218272).

*Further material.* An anterior fragment from the same sample.

*Etymology.* *Sica* means *dagger* in Latin, in reference to the shape of the dorsal jaw tooth.

*Diagnosis.* *Pterognathia* with long jaws (length 26.00  $\mu\text{m}$ ) with only one dagger-like tooth dorsally and three teeth ventrally; basal plate lacking. Sperm 85-95  $\mu\text{m}$  long, with distinctly spiralised head.

**Table 5.** Morphometric data for *Pterognathia sica* sp. nov.

**Tableau 5.** Données morphométriques sur *Pterognathia sica* sp. nov.

Lizard Island	Mean	S	Max	Min	n
Body length of adults	26.80				1
Body width of adults	100				1
Body index of adults	26.80				1
Rostrum index of adults	3.07				1
Jaw length	26.00		27	25	2
Sperm length	90.00		95	85	2
Sperm width	0.50		0.50	0.50	2
Sperm index	180.00		190.00	170.00	2

### Description

*Organization and behaviour.* Colourless-opaque. The adult was 2680  $\mu\text{m}$  long and 100  $\mu\text{m}$  wide at U 61.6 (body index 26.80), with a rostrum 215  $\mu\text{m}$  long and 70  $\mu\text{m}$  wide (rostrum index 3.07).

*Digestive tract.* Neither of the two specimens seemed to have a basal plate. The jaws are slender, 26.00  $\mu\text{m}$  long, bipartite, with a crista, and with only one dagger-like tooth in the dorsal and 3 teeth in the ventral part. Rostral apophyses are slender, and their tips curve inward. The pharynx bulb is 15  $\mu\text{m}$  long.

*Male system.* The paired testes are 480  $\mu\text{m}$  long, extending from U 60.4 to U 78.4 where they empty into paired vasa deferentia. The simple male pore is located ventrally at U 95. Sperm (Fig. 1. 15) is 85-95  $\mu\text{m}$  long, consisting of a delicate but conspicuously spiralised, 16  $\mu\text{m}$  long head, a plain, 15  $\mu\text{m}$  long middle piece, and a 54-64  $\mu\text{m}$  long tail.

*Discussion.* The apparent absence of a basal plate, whose shape generally distinguishes the genera *Haplognathia* and *Pterognathia*, makes it somewhat difficult to assign this species to the latter genus. However, the bipartition of the jaws and possession of a crista as well as the long pharynx bulb are characteristics of *Pterognathia*. This is the only species in the genus in which a basal plate seems to be lacking. However, the absence of a basal plate appears to be the rule in some other genera (e.g., *Clausognathia suicauda* Sterrer, 1992; *Tenuignathia rikerae* Sterrer, 1976), whereas in several species (e.g., *Nanognathia exigua* Sterrer, 1973a), the presence of a delicate basal plate can only be ascertained in a small fraction of the specimens studied. In terms of jaw structure and length, *P. sica* most resembles *P. meixneri* Sterrer, 1969 (jaw length 25.3  $\mu\text{m}$ ) and *P. hawaiiensis* Sterrer, 1991b (jaw length 24  $\mu\text{m}$ ). *P. sica*, however, is the only species in this genus with a single tooth in the dorsal part of the jaw. Sperm most resembles that of *P. sorex* Sterrer, 1969. *P. sica* brings the number of described species in this genus to 13.

Order Bursovaginoidea Sterrer, 1972

Suborder Scleroperalia Sterrer, 1972

Family Agnathiellidae Sterrer, 1972

Genus *Agnathiella* Sterrer, 1971

### Diagnosis

Agnathiellidae without a basal plate or jaws. Usually with a clover-shaped rostrum; often with a dorsal protrusion in the posterior body region.

Type species: *A. beckeri* Sterrer, 1971. No type material deposited.

*Agnathiella nominata* sp. nov.

(Figs 6. 1-5, 7. 1; Table 6)

*Agnathiella beckeri* Sterrer, 1971 (pro parte): 216, fig. 4.

*Agnathiella* sp. Sterrer, 1991a: 114-115, figs 9A-D.

*Agnathiella* sp. Sterrer, 1998: 64, figs 29.2-3, 30.2.

*Type material.* Holotype is one adult from Lizard I. (sample LZ3), in squeeze preparation (QM G 218273).

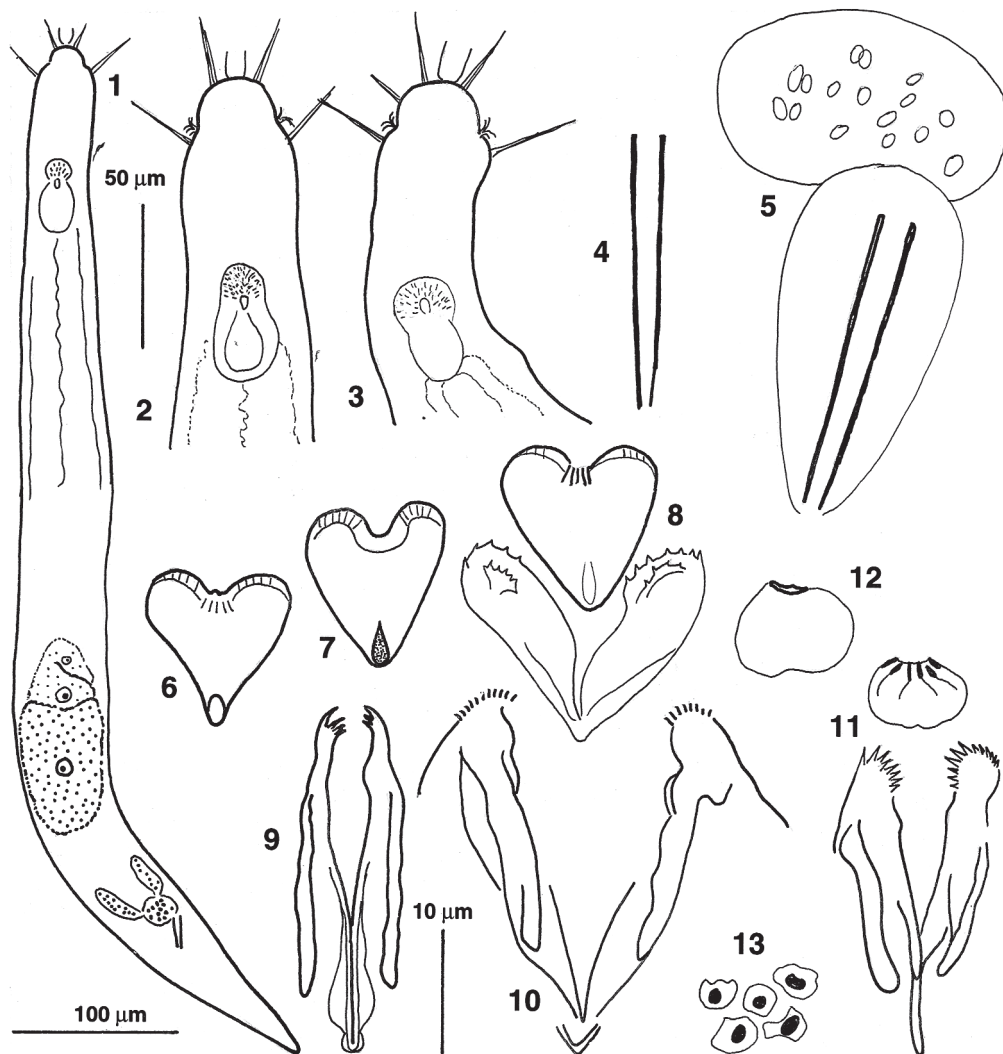
*Further material.* Another adult from Lizard I. (sample LZ9).

*Etymology.* The species was first misidentified as *A. beckeri* by Sterrer (1971) but is only now being named (from Latin *nominare* = to name).

*Distribution.* (Sub)tropical NW Atlantic, N. Carolina (Sterrer, 1971), Fiji (Sterrer, 1991a).

### Description

*Organization and behaviour.* Animals are colourless, slow-moving. Adults are 695.00  $\mu\text{m}$  long and 57.50  $\mu\text{m}$  wide at U 39.39, with a fairly slender body that tapers to a blunt tail (body index 12.24). The rostrum is 87.50  $\mu\text{m}$  long and



**Figure 6.** Bursovaginoidea. 1-5. *Agnathiella nominata* sp. nov. from Lizard I; 1. habitus of adult; 2-3. rostrum of two adults; 4-5. copulatory stylets of two adults; 6-8. *Labidognathia longicollis* from Lizard I; 6. and 7. basal plates of two specimens; 8. basal plate and jaws of a third specimen; 9-12. *Tenuignathia rikerae*; 9. jaws of a Lizard I. specimen, unsqueezed; 10. the same, strongly squeezed; 11. basal plate and jaws of another Lizard I. specimen; 12. basal plate of a Stradbroke I. specimen; 13. sperm of a Lizard I. specimen. Scale on lower left applies to 1., on upper left to 2.-3., and on lower middle to the remaining figures.

**Figure 6.** Bursovaginoidea. 1-5. *Agnathiella nominata* sp. nov. de Lizard I.; 1. habitus d'un adulte; 2.-3. rostrum de deux adultes; 4.-5. stylet copulateur de deux adultes; 6.-8. *Labidognathia longicollis* de Lizard I.; 6. et 7. pièce basale de deux spécimens; 8. pièce basale et mâchoire d'un troisième spécimen; 9.-12. *Tenuignathia rikerae*; 9. mâchoire d'un exemplaire de Lizard I., non comprimé; 10. le même, très comprimé; 11. pièce basale et mâchoire d'un autre spécimen de Lizard I.; 12. pièce basale d'un spécimen de Stradbroke I.; 13. spermatozoïde d'un spécimen de Lizard I. L'échelle en bas à gauche s'applique à 1., en haut à gauche à 2.-3., et en bas, au milieu, aux autres figures.

39.00  $\mu\text{m}$  wide, slender yet somewhat clover-shaped owing to the ciliary pits located at U 2.52 (rostrum index 2.25). The sensorium consists of one pair of single apicalia (to 11  $\mu\text{m}$  long), and one pair each of compound frontalia (to 26  $\mu\text{m}$ ), ventralia, dorsalia (to 12  $\mu\text{m}$ ), and lateralialia (to 31  $\mu\text{m}$ ). No postlateralialia were seen.

**Digestive tract.** The oval mouth, located between U 11.45

and U 12.59, opens into a pharynx devoid of a basal plate or jaws. The preoral mouth epithelium contains granular inclusions. The muscular pharynx, measured from the posterior edge of the mouth, is 20-25  $\mu\text{m}$  long. The intestine is strongly vacuolised, and there is a 'lateral system', i.e., paired strands of tissue filled with needle-like granules which line the gut for its entire length.

**Male system.** The paired, tubular testes are only 20 µm long and 7 µm in diameter, extending from U 79.1 to U 82.1. They empty into a seminal vesicle which in turn connects to a copulatory organ with a stylet. Located between U 87.65 and U 89.81, the conical stylet is 22.50 µm long and 3 µm wide proximally.

**Female system.** Neither of the two specimens had a bursa, and only the holotype had an ovary. The largest egg was 70 µm long.

**Table 6.** Morphometric data for *Agnathiella nominata* sp. nov.

**Tableau 6.** Données morphométriques sur *Agnathiella nominata* sp. nov.

Lizard Island	Mean	S	Max	Min	n
Body length of adults	695.00		720	670	2
Body width of adults	57.50		65	50	2
Body index of adults	12.24		13.40	11.08	2
Rostrum index of adults	2.25		2.37	2.13	2
Penis stylet length	22.50		23	22	2

**Discussion.** In my original description of *Agnathiella beckeri* (see Sterrer, 1971: fig. 4) I included a juvenile which, as I realized later (Sterrer, 1991a: 115), had actually come from a different NW Atlantic locality, and probably belonged to a different species. I assigned three juveniles from Fiji to this same species but, for lack of type material, continued listing it as *A. sp.* The find of two adults now makes it possible to name it, and split it from *A. beckeri* on the basis of its smaller body (length 695.00 µm vs. 1033.33 µm in *A. beckeri*), more slender rostrum (index 2.25, vs. 2.15 in *A. beckeri*), the absence of postlateralia, and the much shorter penis stylet (22.50 µm vs. 44.00 µm in *A. beckeri*).

Family Mesognathariidae Sterrer, 1972

Genus *Labidognathia* Riedl, 1970

#### Diagnosis

Mesognathariidae with lamellar jaws with long shoulder lamella; teeth arranged in two arcs. Basal plate shield-like, much longer than wide.

Type species: *L. longicollis* Riedl, 1970. Holotype AMNH #595, paratypes AMNH #596.1-596.7.

*Labidognathia longicollis* Riedl, 1970

(Figs 6. 6-8, 7. 2; Table 7)

Holotype AMNH #595, paratypes AMNH #596.1-596.7.

**Material examined.** Seven adults and one juvenile from Lizard I. (LZ3 and LZ9); (QM G 218274).

**Distribution.** (Sub)tropical NW Atlantic (Sterrer, 1998); Canary Islands (Sterrer, 1997).

**Table 7.** Morphometric data for *Labidognathia longicollis*.

**Tableau 7.** Données morphométriques sur *Labidognathia longicollis*.

Lizard Island	Mean	Si	Max	Min	n
Body length of adults	435.71	58.70	495	335	7
Body width of adults	47.86	2.67	50	45	7
Body index of adults	9.12	1.28	10.89	7.44	7
Rostrum index of adults	1.69	0.25	2.07	1.36	6
Jaw length	17.13	1.25	19	15	8
Basal plate length	12.57	0.53	13	12	7
Basal plate width	11.14	0.90	12	10	7
Basal plate index	1.13	0.10	1.30	1.00	7
Penis stylet length	19.50	3.73	24	15	6
Sperm length	3.00		3	3	2
Sperm width	2.00		2	2	2
Sperm index	1.50		1.50	1.50	2

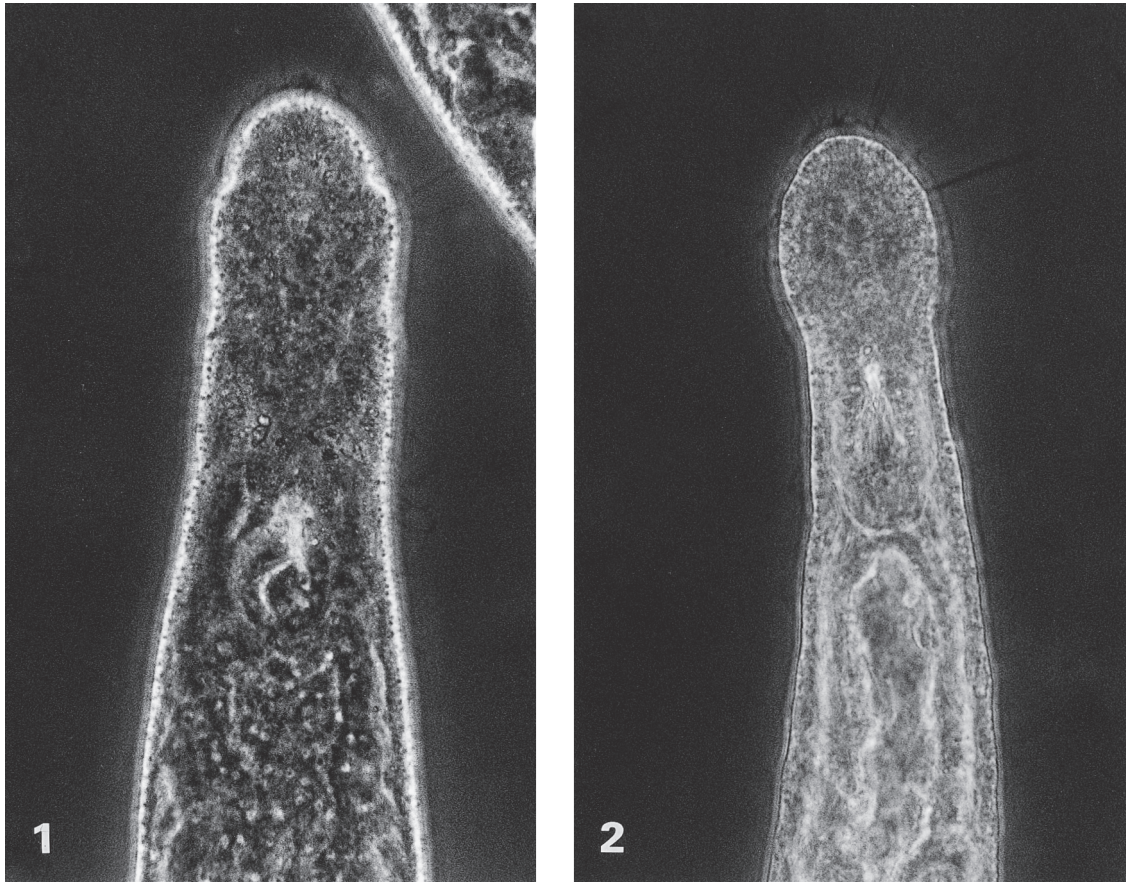
#### Description

**Organization and behaviour.** Colourless to yellow. Adults are slender, 435.71 µm long and 47.86 µm wide at U 46.87 (body index 9.12). The rostrum is set off from the body by a shallow sulcus at about U 11 (rostrum index 1.69). The body tapers into a slender tail. The sensorium consists of one pair each of frontalia (to 11 µm), ventralia (19 µm), dorsalia, and lateralialia (25 µm), as well as a row of occipitalia (18 µm), and ciliary pits. The epidermis contains numerous dark, round to elliptic inclusions of 1 µm diameter; these are slightly larger in the preoral ventral epidermis (2-3 µm). The animal is able to swim backwards.

**Digestive tract.** The basal plate is shield-shaped, 12.57 µm long and 11.14 µm wide (index 1.13). Its media-rostral edge is set with five caudally diverging ridges whereas each latero-rostral edge is set with 4-6 ridges or teeth. Caudally the basal plate ends in an elongated knob. Jaws are 17.13 µm long, and provided with two rows of teeth: a distal one of 6-12 teeth arranged along a rostro-dorsal arc, and a shorter proximal one of only 3-5 teeth. Teeth are frequently unequal in size. The pharynx bulb is 10.00 µm long.

**Male system.** Paired tubular testes are 15-35 (24.17) µm long; they extend from U 77.01 to U 82.90, and empty into a round seminal vesicle 15 µm in diameter. Located between U 82.09 and U 86.71, the penis stylet is 19.50 µm long and proximally 3.00 µm wide. Sperm is irregularly angular, 2-3 µm in diameter.

**Female system.** The ovary extends from U 33.77 to U 60.36; the largest egg may be 110 µm long. One adult contained a mature egg 80 µm long by 55 µm wide, bulging the otherwise only 35 µm wide body; the egg membrane was densely yellow-brown whereas the egg plasma was colourless. A bursa system is located behind the mature egg, between U 61.24 and U 66.57. It usually consists of an ovoid-conical bursa, 20 µm long and 10 µm wide, with an anterior mouthpiece; and a spherical prebursa.



**Figure 7.** 1. *Agnathiella nominata* sp. nov. from Lizard I., anterior body region; 2. *Labidognathia longicollis* from Lizard I., anterior body region. Phase contrast micrographs of live specimens.

**Figure 7.** 1. *Agnathiella nominata* sp. nov. de Lizard I., partie antérieure ; 2. *Labidognathia longicollis* de Lizard I., partie antérieure. Microphotos d'exemplaires vivants, en contraste de phase.

*Discussion.* This is the first record of this monotypic genus outside the Atlantic. Australian specimens differ from Atlantic ones in their smaller body length (335-495  $\mu\text{m}$  vs. 560-1070  $\mu\text{m}$ ), body index (9.12 vs. 14.63), and stylet length (15-24  $\mu\text{m}$  vs. 23-35  $\mu\text{m}$ ). All other morphometric data are virtually identical, including the seeming absence of apicalia. Australian specimens also show pronounced teeth on the rostral edge of the basal plate, which had been previously noted only on specimens from Puerto Rico (Sterrer, 1998) and the Canary Islands (Sterrer, 1997).

#### Genus *Tenuignathia* Sterrer, 1976

##### *Diagnosis*

Mesognathariidae with lamellar jaws with long ventro-lateral apophyses; teeth arranged in one ventro-rostral arc. Basal plate very delicate or lacking.

Type species: *T. rikeræ* Sterrer, 1976. No type material deposited.

#### *Tenuignathia rikeræ* Sterrer, 1976

(Figs 6. 9-13; Table 8)

No type material deposited.

*Material examined.* Three adults and one juvenile from Lizard I. (sample LZ9); two adults from Stradbroke I. (samples R6 and W4), (QM 218275).

*Distribution.* (Sub)tropical NW Atlantic (Sterrer, 1998).

##### *Description*

*Organization and behaviour.* Colourless to yellow, often giving a somewhat 'wrinkled' appearance. Adults are 691.00  $\mu\text{m}$  long and 79.00  $\mu\text{m}$  wide at U 43.79 (body index 8.84). The rostrum is delimited by a deep sulcus at about U 6.5 (index 1.30); the posterior end tapers to a blunt tail. Of the sensorium, one pair each of apicalia (to 13  $\mu\text{m}$ ), frontalia (26  $\mu\text{m}$ ), ventralia, dorsalia, and lateralialia (to 28  $\mu\text{m}$ ) were recorded.

**Table 8.** Morphometric data for *Tenuignathia rikeræ*.  
**Tableau 8.** Données Morphométriques sur *Tenuignathia rikeræ*.

<b>Lizard Island</b>	Mean	S	Max	Min	n
Body length of adults	635.00	126.19	770	520	3
Body width of adults	80.00	10.00	90	70	3
Body index of adults	8.06	2.02	9.63	5.78	3
Rostrum index of adults	1.29		1.53	1.05	2
Jaw length	28.20	0.84	29	27	5
Basal plate length	7				1
Basal plate width	9				1
Basal plate index	0.78				1
Penis stylet length	42.67	12.66	57	33	3
Sperm length	3.00		3	3	2
Sperm width	3.00		3	3	2
Sperm index	1.00		1.00	1.00	2

<b>Stradbroke Island</b>	Mean	S	Max	Min	n
Body length of adults	775.00		850	700	2
Body width of adults	77.50		85	70	2
Body index of adults	10.00		10	10	2
Rostrum index of adults	1.31		1.38	1.24	2
Jaw length	25.50		27	24	2
Basal plate length	5				1
Basal plate width	8				1
Basal plate index	0.63				1
Penis stylet length	56.00		56	56	2
Sperm length	3.00	0.00	3	3	3
Sperm width	2.00	0.00	2	2	3
Sperm index	1.50	0.00	1.50	1.50	3

<b>ALL DATA</b>	Mean	S	Max	Min	n
Body length of adults	691.00	129.05	850	520	5
Body width of adults	79.00	8.94	90	70	5
Body index of adults	8.84	1.78	10.00	5.78	5
Rostrum index of adults	1.30	0.20	1.53	1.05	4
Jaw length	27.43	1.72	29	24	7
Basal plate length	6.00		7	5	2
Basal plate width	8.50		9	8	2
Basal plate index	0.70		0.78	0.63	2
Penis stylet length	48.00	11.55	57	33	5
Sperm length	3.00	0.00	3	3	5
Sperm width	2.40	0.55	3	2	5
Sperm index	1.30	0.27	1.50	1.00	5

**Digestive tract.** An extremely delicate basal plate was noted in one Lizard I. and one Stradbroke I. specimen, but not confirmed in any of the other specimens. The basal plate is lens-shaped, 6.00 µm long and 8.50 µm wide (index 0.70), with a concave, enforced medio-rostral contour which, in the Stradbroke I. specimen (Fig. 5. 11), carried six teeth. Four of these (the inner- and outermost pairs) were on the dorsal surface of the basal plate whereas the intermediate pair were somewhat more ventrally located. All six teeth were rooted. The jaws are lamellar, 27.43 µm long, with long rostral apophyses, and with 10-12 teeth forming a rostro-ventral arc. The pharynx bulb is 4.67 µm long. The gut usually appears strongly vacuolised.

**Male system.** The testes extend from U 77.41 to U 84.36; they are 15-90 (52.50) µm long. There is no conspicuous seminal vesicle. The penis stylet, which may be slightly curved, is 48.00 µm long, and proximally 5.40 µm wide. It extends from U 84.66 to U 92.33. Sperm (Fig. 5. 13) is irregularly angular, to 3 µm in diameter.

**Female system.** The ovary extends from U 31.10 to U 65.73; a terminal egg may be 190 µm long. The bursa system lies between U 67.54 and U 70.28. It consists of an ovoid bursa with two cristae, and a prominent mouthpiece. A prebursa was not observed.

**Discussion.** This is the first record of this species outside the Atlantic. A second species, *T. vitiensis* described from Fiji (Sterrer, 1991a), has shorter and much plumper jaws. The Australian specimens of *T. rikeræ* fall within the exceptionally broad range of morphometric data recorded from the Atlantic (Sterrer, 1998), particularly with regard to jaw length (24-40 µm). The possession of a basal plate of at least two Australian specimens confirms my earlier observation (Sterrer, 1976: fig 18) of a basal plate contour, and again demonstrates that at least the degree of basal plate cuticularization, and hence its visibility under the phase contrast microscope, may vary widely among conspecifics.

Family Onychognathiidae Sterrer, 1972

Genus *Vampyrognathia* Sterrer, 1998

#### Diagnosis

Slender Onychognathiidae (body index 9-13) with a long rostrum (index 1.5-2) and a long mouth opening. Basal plate very delicate, buckle-shaped. Jaws with very long teeth in a ventral and a rostral group; no terminal tooth developed. Type species: *V. horribilis* Sterrer, 1998. Holotype USNMNH 178349.

*Vampyrognathia varanus* sp. nov.

(Figs 8. 1-6, 9. 1-4)

**Type material.** Holotype one adult, in squeeze preparation, from Lizard Island, NE of Cairns, 14° 40'S 145° 28'E (sample LZ9), (QM G 218276).

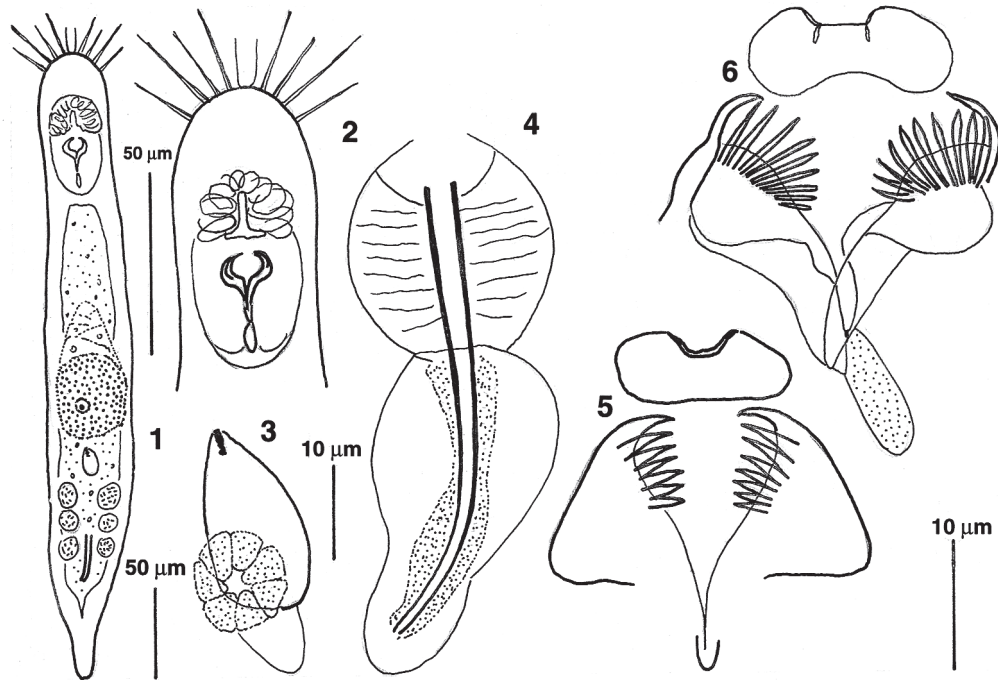
**Etymology.** After Gould's Goanna (*Varanus gouldii*), which gave Lizard Island its name.

#### Diagnosis

*Vampyrognathia* with body index 6.98, rostrum index 1.26. Basal plate 6 µm long, 13 µm wide (index 0.46). Jaws 22 µm long, with 8-10 teeth in ventral and 3-4 teeth in dorsal group. Penis stylet 48 µm long.

#### Description

**Organization and behaviour.** The only specimen, an adult, was colourless, 335 µm long and 48 µm wide at U 49.25 (body index 6.98). The rounded rostrum is 44 µm long, 35 µm wide at U 7.5 (rostrum index 1.26). The sensorium is made up of one pair each of apicalia (to 14 µm long), frontalia (23 µm), ventralia (20 µm), dorsalia (21 µm), and lateralia (20 µm). Posteriorly the body narrows abruptly into a 30 µm long tail.



**Figure 8.** *Vampyrognathia varanus* sp. nov. from Lizard Island. 1. habitus; 2. head and sensorium; 3. bursa and vagina; 4. male copulatory organ; 5. basal plate and jaws, slightly squeezed; 6. the same, strongly squeezed. Scale on lower left applies to 1., on upper left to 2., on lower middle to 3.-4., and on lower right to 5.-6.

**Figure 8.** *Vampyrognathia varanus* sp. nov. de Lizard Island. 1. habitus ; 2. rostrum et sensorium ; 3. bursa et vagin ; 4. organe copulateur mâle ; 5. pièce basale et mâchoire, peu comprimées ; 6. les mêmes, très comprimées. L'échelle en bas à gauche s'applique à 1., en haut à gauche à 2., en bas, au milieu, à 3.-4., et en bas à droite à 5.-6.

**Digestive tract.** Extending from U 7.8 to U 12.5, the mouth is slit-like, 16 µm long, and surrounded by a massive preoral gland. The basal plate is 6 µm long and 13 µm wide (index 0.46). Its lateral and caudal contours are very faint; only the trough-shaped medio-rostral contour is sufficiently defined to be traced with certainty. The jaws, 22 µm long, are forceps-shaped, with a long, narrow symphysis which extends into a 7 µm long cauda. Teeth are long, scythe-like, and arranged in two groups: a rostral group of 3-4 (of which one, the terminal tooth, is especially sharp and curved), and a rostro-ventral group of 8-10. All teeth originate quite close together, opposite short, curved rostral apophyses. The pharynx bulb is 10 µm long. The gut is very opaque in transmitted light.

**Male system.** The paired testes are follicular, 40 µm long, extending from U 73.73 to U 85.67. The penis stylet, slender and curved, is composed of about 10 rods. It is 48 µm long and 3 µm wide proximally, extending from U 77.61 to U 92.54. It is embedded in a penis made up of an anterior, muscular, globe of 20 µm diameter, and a posterior, bulbous glandular part 35 µm long and 20 µm wide.

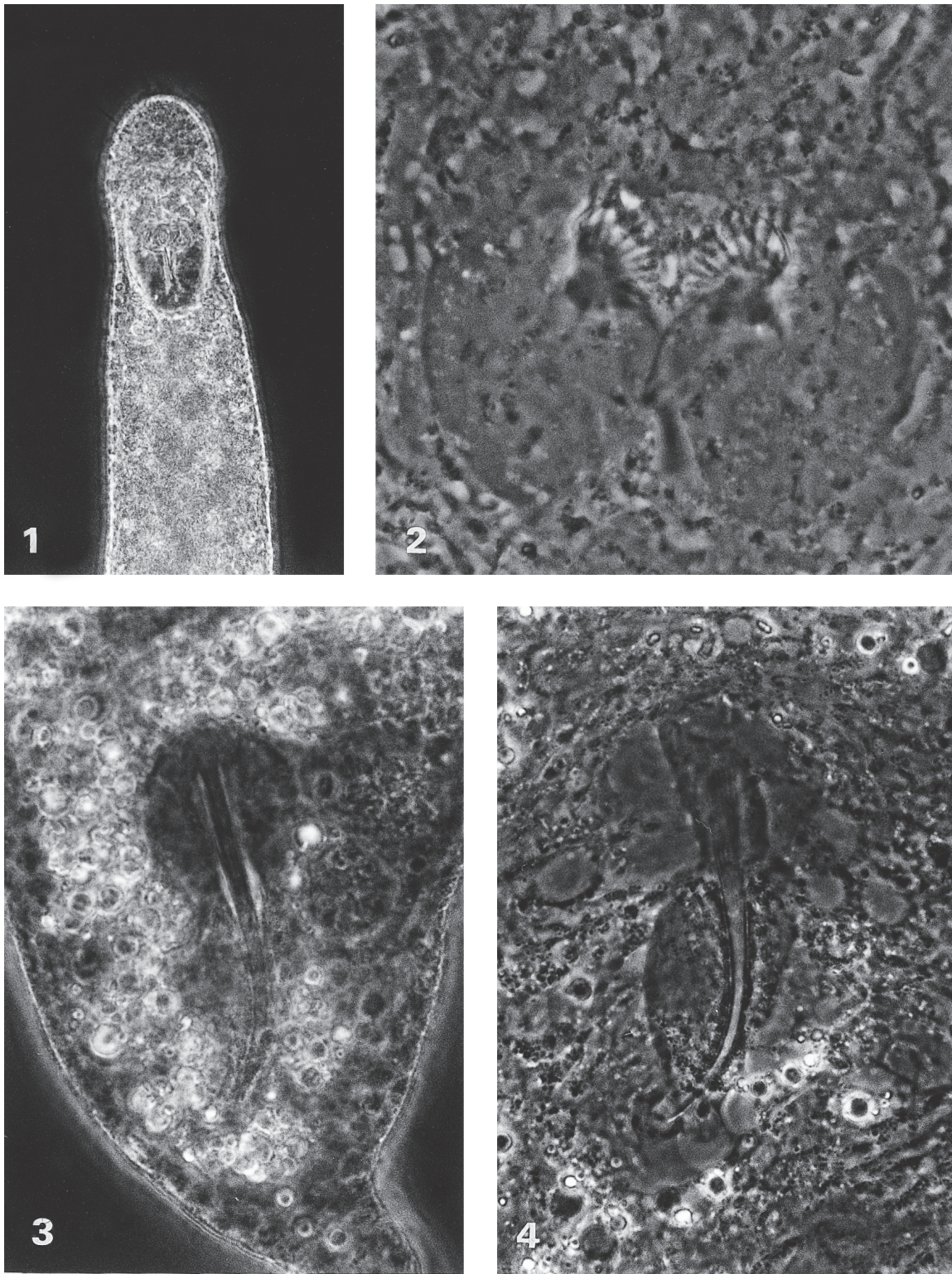
**Female system.** Located immediately behind the mature egg, the bursa copulatrix is pear-shaped, 20 µm long and 10 µm wide, with a 3 µm long mouthpiece. Posteriorly it opens into a short canal which surfaces dorsally as a rosette-shaped vagina.

**Discussion.** The presence and shape of the basal plate make this species the third in the genus *Vampyrognathia*. It most resembles *V. minor*, the smaller of the two described species (Sterrer, 1998), but differs by its shorter, stouter body and much longer stylet (48 µm vs. 29.33 µm). Within the family Onychognathiidae, only *Onychognathia filifera* has been reported to have a vagina (Riedl 1971a). *V. varanus* is the first member of the family Onychognathiidae reported from the Pacific.

Genus *Goannagnathia* gen. nov.

#### Diagnosis

Slender Onychognathiidae with a very slender rostrum (index >2.0) and long tail. Basal plate very delicate, buckle-shaped. Jaws with few teeth on a strong double rim.



**Figure 9.** *Vampyrognathia varanus* sp. nov. from Lizard Island. 1. anterior body region; 2. basal plate and jaws, strongly squeezed; 3. posterior body region with male copulatory organ; 4. the same, more strongly squeezed. Phase contrast micrographs of live specimens.

**Figure 9.** *Vampyrognathia varanus* sp. nov. de Lizard Island. 1. partie antérieure ; 2. pièce basale et mâchoire, très comprimées ; 3. partie postérieure avec organe copulateur mâle ; 4. le même, plus comprimé. Microphotos d'exemplaires vivants, en contraste de phase.



Type species: *Goannagnathia susannae* sp. nov.

*Goannagnathia susannae* gen. nov., sp. nov.  
(Figs 10. 1-14, 11. 1-5; Table 9)

*Type material.* One adult specimen from Lizard Island, NE of Cairns, 14° 40'S 145° 28'E (sample LZ9) in squeeze preparation (QM G 218277).

*Further material.* Seven adults and one juvenile from Lizard I. (samples LZ1 and LZ9); two juveniles from Stradbroke Island, Moreton Bay off Brisbane, 27° 35'S 153° 28'E (sample R6); and two adults from Madang, N coast of Papua New Guinea, 5° 15'S 145° 50'E (sample PNG9), (QM G 218278).

*Etymology.* The genus name refers to 'goanna', the common name of *Varanus gouldii* from which Lizard Island derives its name. I dedicate the species to my wife, Susan K. Young, in gratitude for her help as dive buddy and sample collector.

#### Diagnosis

*Goannagnathia* with body index 9.99, rostrum index 2.26. Basal plate 7.11 µm long, 15.44 µm wide, with 8-14 teeth in semi-circular arrangement. Jaws 17.17 µm long, with claw-shaped dorsal tooth and 3-4 ventral teeth of which the first is largest, the second and third are of equal but smaller size, and the third if present is very delicate. Penis stylet 24.67 µm long.

#### Description

*Organization and behaviour.* Colourless, except for the intestine which is usually yellow to orange-purple. Adults are 604.44 µm long and 62.56 µm wide at U 39.66 (body index 9.99). The slender rostrum is 74.00 µm long and 34.33 µm wide at U 6.79 (rostrum index 2.26); it is fairly blunt to nearly squared anteriorly. Posteriorly, at about U 71, the body tapers to a distinct tail. The sensorium contains at least one pair of single apicalia (to 14 µm long); a second pair was seen in one Stradbroke I. specimen but could not be verified in any other specimen. There is also one pair each of compound frontalia (to 29 µm), ventralia (to 24 µm), dorsalia (to 20 µm), and lateralia (to 27 µm). Dorsally on the rostrum, a row of single occipitalia (to 18 µm) extends from about U 7 to U 13. A pair of ciliary pits is found at U 4.12, behind the lateralia. The epidermis contains rows of oval rhabdoids (Fig. 9. 10), 3 µm long and 1 µm wide, but epidermal cells are not conspicuously arranged in stripes. The tail is adhesive, and may stretch to take up a third of the total length of the animal. In anesthetized specimens the tail is often curled ventrally, which makes the animal usually come to rest on its side. None of the specimens were ever observed to swim backwards.

*Digestive tract.* The elongated, oval mouth (length 10-13 µm) lies between U 13.45 and U 15.80. It opens into a

**Table 9.** Morphometric data for *Goannagnathia susannae* sp. nov.

**Tableau 9.** Données morphométriques sur *Goannagnathia susannae* sp. nov.

<b>Lizard Island</b>	Mean	S	Max	Min	n
Body length of adults	575.71	87.01	710	435	7
Body width of adults	54.71	5.53	60	45	7
Body index of adults	10.60	1.74	12.56	7.25	7
Rostrum index of adults	2.42	0.29	2.57	1.91	5
Jaw length	17.33	0.87	19	16	9
Basal plate length	7.17	0.41	8	7	6
Basal plate width	15.17	1.47	17	14	6
Basal plate index	0.48	0.06	0.57	0.41	6
Penis stylet length	24.67	6.43	32	20	3
Sperm length	2.67	0.58	3	2	3
Sperm width	1.67	0.58	2	1	3
Sperm index	1.83	1.04	3.00	1.00	3

<b>Stradbroke Island</b>	Mean	S	Max	Min	n
Jaw length	16.50		17	16	2
Basal plate length	7.50		8	7	2
Basal plate width	16.50		19	14	2
Basal plate index	0.47		0.57	0.37	2

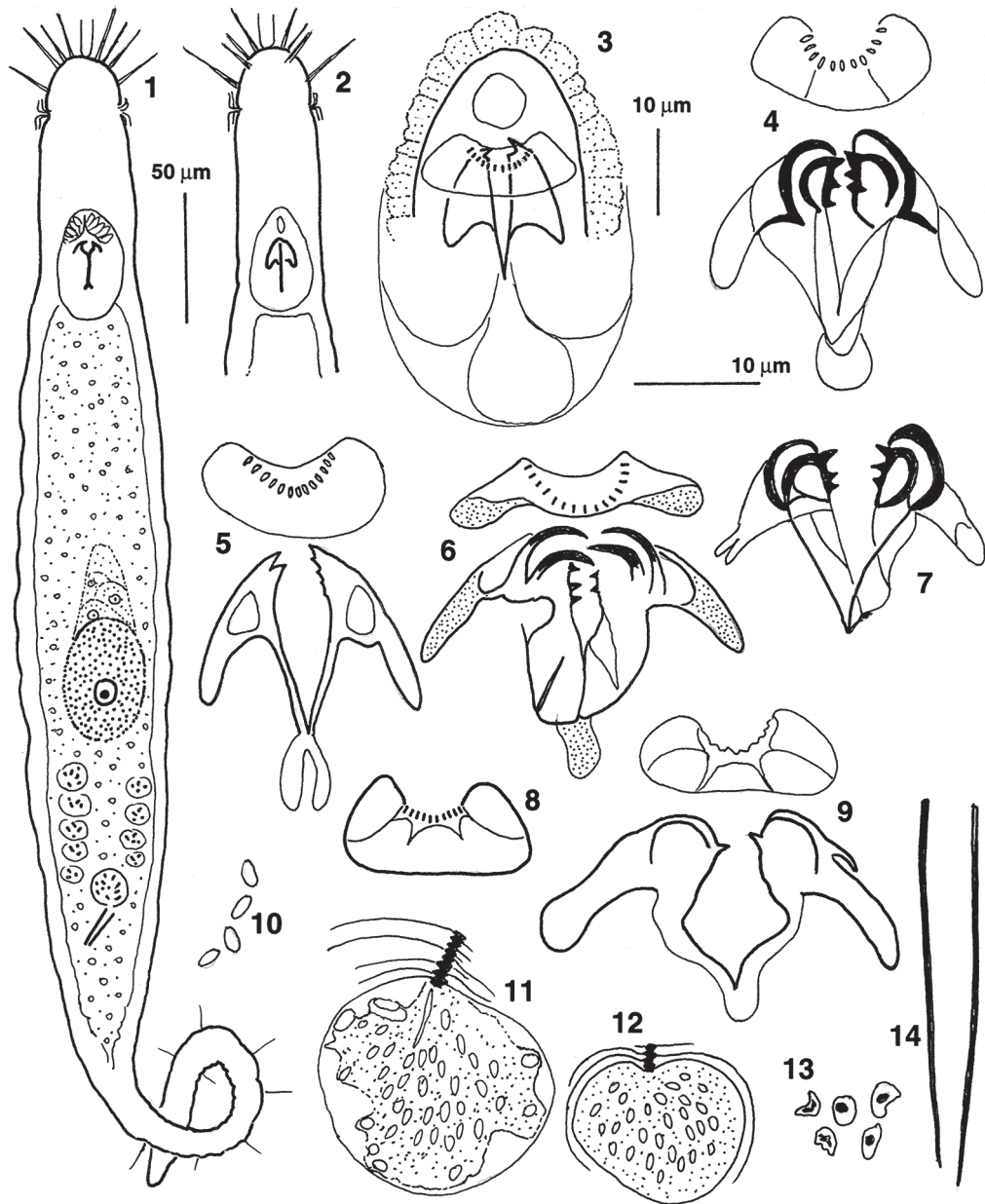
  

<b>Madang</b>	Mean	S	Max	Min	n
Body length of adults	705.00		850	560	2
Body width of adults	90.00		90	90	2
Body index of adults	7.83		9	6	2
Rostrum index of adults	1.45				1
Jaw length	17				1
Basal plate length	6				1
Basal plate width	15				1
Basal plate index	0.40		0.40	0.40	1

<b>ALL DATA</b>	Mean	S	Max	Min	n
Body length of adults	604.44	119.10	850	435	9
Body width of adults	62.56	16.28	90	45	9
Body index of adults	9.99	2.10	12.56	6.22	9
Rostrum index of adults	2.26	0.47	2.57	1.45	6
Jaw length	17.17	0.83	19	16	12
Basal plate length	7.11	0.60	8	6	9
Basal plate width	15.44	1.81	19	14	9
Basal plate index	0.47	0.07	0.57	0.37	9
Penis stylet length	24.67	6.43	32	20	3
Sperm length	2.67	0.58	3	2	3
Sperm width	1.67	0.58	2	1	3
Sperm index	1.83	1.04	3.00	1.00	3

dome-shaped buccal cavity which is anteriorly lined by a diffuse preoral gland. The basal plate is delicate, and its lateral and posterior contour changes with squeezing under the coverslip. The most distinctive feature of the basal plate is a semi-circular set of about 8-14 (11.13) teeth. The basal plate outline appears broadly buckle-shaped, posteriorly convex or flattened, or more saddle-shaped (Fig. 10. 6). It is 7.11 µm long and 15.44 µm wide on average (index 0.47). The jaws are 17.17 µm long, and complex-lamellar. Their most salient feature is a 'double rim', i.e., a pair of strongly curved, reinforced ridges which diverge from a point 6-7 µm behind the tip, then converge again at the tip of the jaws. The outer, dorsal ridge seems to end anteriorly in a prominent, claw-shaped dorsal tooth whereas the inner, more ventral ridge descends ventrally to a row of 3-4 teeth. Tooth #1 is large, #2-3 are significantly smaller, and #4 if present is barely visible. Wing-shaped rostral apophyses extend latero-caudally, to 13-16 µm from the tip of the jaws. The



**Figure 10.** *Goannagnathia susanna* gen. nov., sp. nov. 1. habitus of a specimen from Lizard I.; 2. rostrum of another Lizard I. specimen; 3. pharynx of a Stradbroke I. specimen; 4. basal plate and jaws of a Lizard I. specimen; 5. basal plate and jaws of a Stradbroke I. specimen, unsqueezed; 6. the same specimen, squeezed; 7. jaws of a Lizard I. specimen; 8. basal plate of another Lizard I. specimen; 9. basal plate and jaws of a Madang specimen, drawn from a strongly squeezed wholmount; 10. row of epidermal rhabdoids; 11. and 12. bursae of two Lizard I. specimens; 13. sperm of a Lizard I. specimen; 14. copulatory stylet of a Lizard I. specimen. Scale on upper left applies to 1.-2., on upper right to 3., and the third scale to the remaining figures.

**Figure 10.** *Goannagnathia susanna* gen. nov., sp. nov. 1. habitus d'un spécimen de Lizard I. ; 2. rostrum d'un autre spécimen de Lizard I. ; 3. pharynx d'un spécimen de Stradbroke I. ; 4. pièce basale et mâchoire d'un spécimen de Lizard I. ; 5. pièce basale et mâchoire d'un spécimen de Stradbroke I., non comprimé ; 6. le même spécimen, comprimé ; 7. mâchoire d'un spécimen de Lizard I. ; 8. pièce basale d'un autre spécimen de Lizard I. ; 9. pièce basale et mâchoire d'un spécimen de Madang, d'après un spécimen fixé et très comprimé ; 10. série de rhabdoïdes épidermiques ; 11. et 12. bursae de deux spécimens de Lizard I. ; 13. spermatozoïde d'un spécimen de Lizard I. ; 14. stylet copulateur d'un spécimen de Lizard I. L'échelle en haut à gauche s'applique à 1.-2., en haut à droite à 3., et la troisième aux autres figures.

symphysis is forceps-shaped, and embedded in a bulbous cauda. The pharynx bulb is 13.88  $\mu\text{m}$  long behind the symphysis, and only inconspicuously tripartite. The intestine is usually packed with granular inclusions that are mainly orange to purple in the foregut, and yellow in the hindgut.

*Male system.* Of ten adults with a mature female reproductive system, only three also had male organs. The paired, follicular testes are 61.67  $\mu\text{m}$  long and 15  $\mu\text{m}$  wide, extending from U 51.03 to U 61.87. They empty into an inconspicuous seminal vesicle which in turn connects to the copulatory organ. Made up of about eight rods, the penis stylet lies between U 66.01 and U 69.17; it is 24.67  $\mu\text{m}$  long and 2.67  $\mu\text{m}$  wide proximally. Sperm is irregularly lumpy, 2-3  $\mu\text{m}$  in diameter.

*Female system.* Of ten adults with an ovary, only six had a bursa copulatrix as well. The ovary extends from U 30.75 to U 52.58; the single mature egg is 43-118 (82.89)  $\mu\text{m}$  long and 22-50 (36.71)  $\mu\text{m}$  wide. A bursa is located between U 59.17 and U 61.31; it is more or less spherical, with a diameter of 10-20 (16.50)  $\mu\text{m}$ . The mouthpiece, 3-5  $\mu\text{m}$  long, often protrudes from the sperm-filled bursa.

*Discussion.* Possession of paired testes, a cuticular penis stylet, aflagellate sperm and a cuticular bursa place this species in Bursovaginoidea-Scleroperalia. The mouth parts alone, however, are unusual enough to warrant a new genus. The basal plate resembles that of *Problognathia minima* Sterrer & Farris, 1975 in its semicircular dentition, and of Onychognathiidae (especially *Nanognathia exigua* Sterrer, 1973a) in its broad outline. The jaws, lamellar yet compact, also most resemble those of *Nanognathia* but have far fewer teeth, and in only one row. Body proportions, especially the long, narrow rostrum and possession of a tail, stand out among Bursovaginoidea, being only similar to those of *Semaeognathia sterreri* Riedl, 1970b (body index 10.38, rostrum index 2.70), but not as extreme as of *Clausognathia suicauda* Sterrer, 1992 (body index 13.54, rostrum index 4.47). A small, spherical bursa is also typical of *Semaeognathia sterreri*. Yet in spite of its long rostrum, *Semaeognathia* has the mouth parts (including a jugum) typical of the family Gnathostomulidae, whereas the mouth parts of *G. susannae* conform with those of *Nanognathia* and other Onychognathiidae.

Family Gnathostomulidae Sterrer

Genus *Gnathostomula* Ax, 1956

#### Diagnosis

Fairly plump Gnathostomulidae with a fairly short rostrum and short mouth opening. Ciliary pits lacking. With or without a permanent vagina. Sperm usually droplet-shaped, or round with a bunch of short filaments. Usually with a well-delimited tail region.

Type species: *G. paradoxa* Ax, 1956. No type material deposited.

*Gnathostomula* cf. *maorica* Sterrer, 1991

(Figs 12. 1-5, 13; Table 10)

Holotype USNMNH #132181.

*Material examined.* Two adults from Stradbroke I. (sample W3 and W5).

*Distribution.* New Zealand (Sterrer, 1991a).

#### Description

*Organization and behaviour.* Animals very slender, 775.00  $\mu\text{m}$  long and 80.00  $\mu\text{m}$  wide at U 31.80 (body index 9.69). Rostrum 75  $\mu\text{m}$  long, 60  $\mu\text{m}$  wide at U 4.7 (index 1.25). Posteriorly to the male stylet the body tapers to a 250  $\mu\text{m}$  long tail.

*Digestive tract.* The basal plate is 7.50  $\mu\text{m}$  long and 24.00  $\mu\text{m}$  wide. Jaws are 16.00  $\mu\text{m}$  long, with three rows of teeth; there are 4-8 teeth in the dorsal, 6-8 in the median, and 8-11 teeth in the ventral row. The log-shaped jugum is 87-10  $\mu\text{m}$  long and 19-28  $\mu\text{m}$  wide.

*Male system.* The paired follicular testes, 70  $\mu\text{m}$  long, extend from U 49.21 to U 60.32, and the penis stylet, 68.50  $\mu\text{m}$  long and 3  $\mu\text{m}$  wide proximally, extends between U 62.37 and U 71.19. The penis stylet was somewhat curved in both specimens. Sperm is bowling pin-shaped, 3-4  $\mu\text{m}$  long and 1  $\mu\text{m}$  wide.

*Female system.* The ovary in one specimen was exceptionally long, extending 265  $\mu\text{m}$ , from U16.8 (i.e., shortly behind the pharynx) to U 45.7. A bell-shaped bursa is located between U 41.18 and U 46.11.

*Discussion.* Slender body and rostrum dimensions and possession of a tail are characteristics of *G. maorica*, with which the Australian specimens also share details of the mouth parts. The major obstacle to assigning them to this species outright is the twice-as-large stylet of Stradbroke specimens (65-72  $\mu\text{m}$  vs. only 26-33  $\mu\text{m}$  in New Zealand specimens).

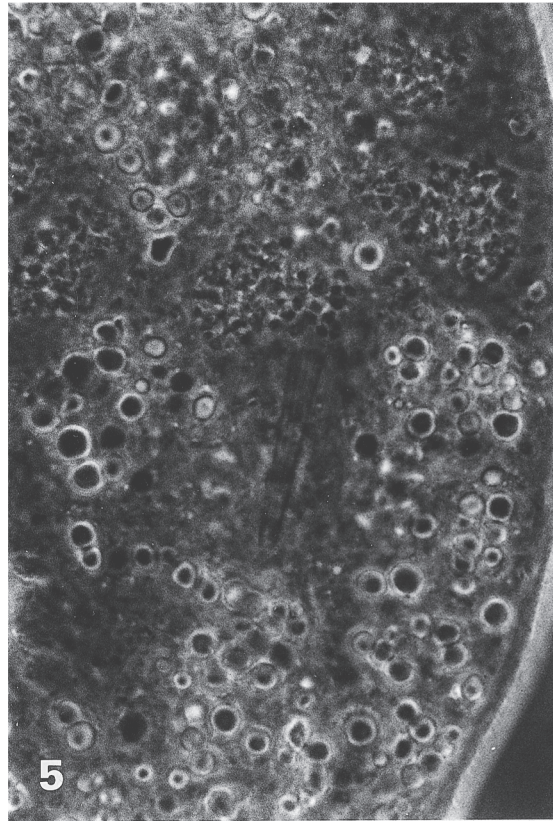
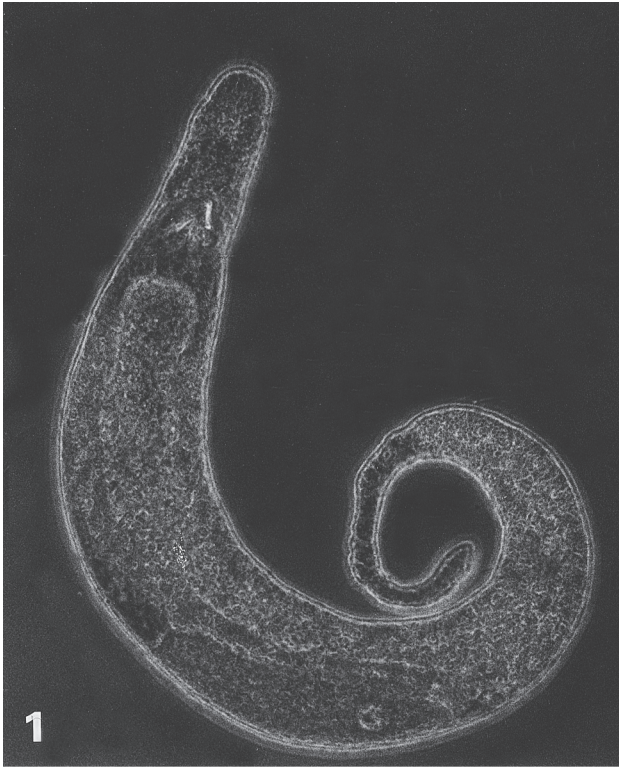
*Gnathostomula* sp. 1

(Figs 12. 6-8; Table 11)

*Material examined.* Five adults and one juvenile from Lizard I. (samples LZ1 and LZ9).

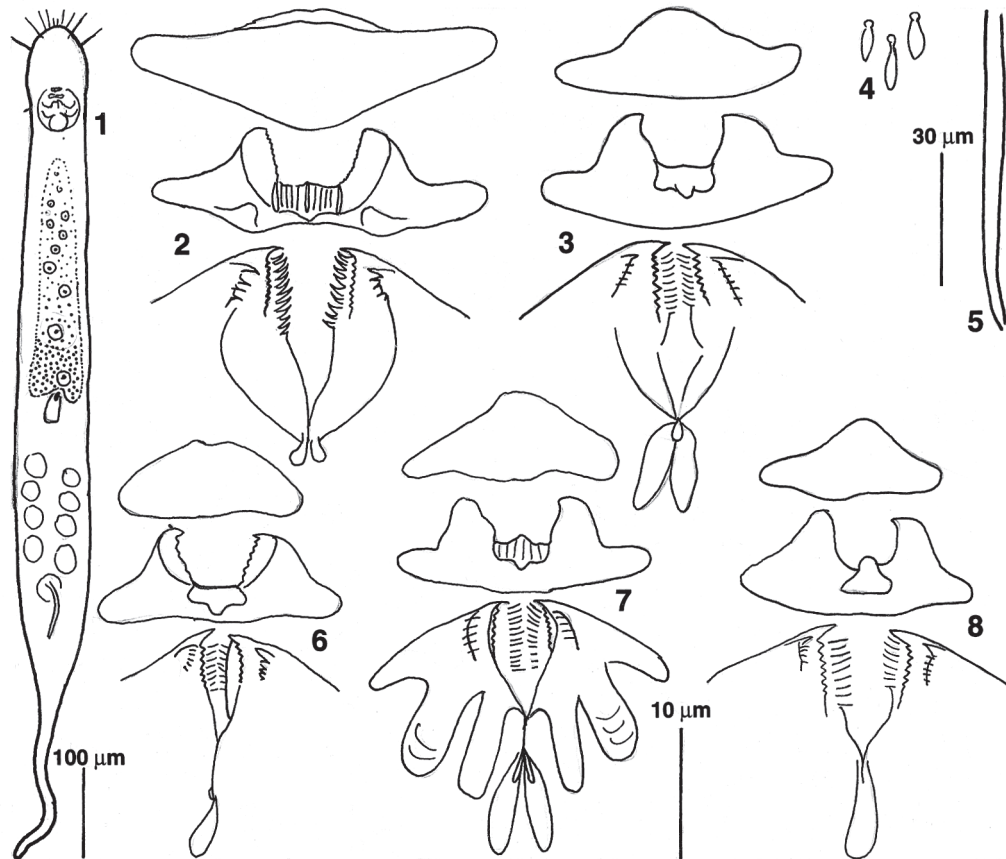
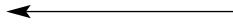
#### Description

*Organization and behaviour.* Adults are 391.00  $\mu\text{m}$  long and 44.60  $\mu\text{m}$  wide at U 42.96 (body index 8.81). Rostrum 41.00  $\mu\text{m}$  long and 42.67  $\mu\text{m}$  wide at U 7.56 (rostrum index 0.96). Posteriorly there is a short, not conspicuously delimited tail. Epidermal rhabdoids, which are arranged in



**Figure 11.** *Goannagnathia susannae* gen. nov., sp. nov. from Lizard I. 1. habitus; 2. anterior body region; 3.-4. jaws of the same specimen, strongly squeezed, at different focal planes; 5. posterior body region showing testes, seminal vesicle and penis stylet. Phase contrast micrographs of live specimens.

**Figure 11.** *Goannagnathia susannae* gen. nov., sp. nov. de Lizard Island. 1. habitus; 2. partie antérieure; 3.-4. mâchoire du même spécimen, très comprimé, mise au point à différents niveaux; 5. partie postérieure avec testicules, vésicule séminale et stylet copulateur. Microphotos d'exemplaires vivants, en contraste de phase.



**Figure 12.** *Gnathostomula* spp. 1.-5. *Gnathostomula* cf. *maorica* from Stradbroke I. 1. habitus; 2. and 3. jugum, basal plate and jaws of two specimens from Stradbroke I.; 4. sperm; 5. copulatory stylet; 6.-8. *Gnathostomula* sp. 1 from Lizard I., jugum, basal plate and jaws of three specimens. Scale on lower left applies to 1., on upper right to 5., and the third scale to the remaining figures.

**Figure 12.** *Gnathostomula* spp., 1.-5. *Gnathostomula* cf. *maorica* de Stradbroke I. 1. habitus; 2. et 3. jugum, pièce basale et mâchoire de deux spécimens de Stradbroke I.; 4. spermatozoïde; 5. stylet copulateur; 6.-8. *Gnathostomula* sp. 1 de Lizard I., jugum, pièce basale et mâchoire de trois spécimens. L'échelle en bas à gauche s'applique à 1., en haut à droite à 5., et la troisième aux autres figures.

loose rows, may be up to 6 µm long and 2 µm wide. When isolated in a bowl this species swims fast and elegantly.

**Digestive tract.** Basal plate 7.40 µm long, 18.60 µm wide (index 0.40). Jaws 14.00 µm long, with 4-5 teeth in dorsal, 5-7 poorly defined teeth in median, and 8-12 teeth in ventral row. Jugum (the "stiff upper lip" which is typical of the

family Gnathostomulida) crescent-shaped, 7.00 µm long and 14.75 µm wide.

**Male system.** Made up of up to nine follicles, each testis is 65-130 µm long, extending from U 56.34 to U 78.73. The penis stylet, 42.20 µm long and 3 µm wide proximally, extends from U 76.24 to U 85.76. It is slightly curved, and



**Figure 13.** *Gnathostomula cf. maorica* from Stradbroke I.; basal plate and jaw, strongly squeezed. Phase contrast micrographs of live specimen.

**Figure 13.** *Gnathostomula cf. maorica* de Stradbroke I. ; pièce basale et mâchoire, très comprimées. Microphotos d'exemplaires vivants, en contraste de phase.

**Table 10.** Morphometric data for *Gnathostomula cf. maorica*.

**Tableau 10.** Données morphométriques sur *Gnathostomula cf. maorica*.

Stradbroke Island	Mean	S	Max	Min	n
Body length of adults	775.00		920	630	2
Body width of adults	80.00		80	80	2
Body index of adults	9.69		12	8	2
Rostrum index of adults	1.25				1
Jaw length	16.00		16	16	2
Basal plate length	7.50		8	7	2
Basal plate width	24.00		25	23	2
Basal plate index	0.31		0.35	0.28	2
Penis stylet length	68.50		72	65	2
Sperm length	3.67	0.58	4	3	3
Sperm width	1.00	0.00	1	1	3
Sperm index	3.67	0.58	4.00	3.00	3

**Table 11.** Morphometric data for *Gnathostomula* sp. 1.

**Tableau 11.** Données morphométriques sur *Gnathostomula* sp. 1.

Lizard Island	Mean	S	Max	Min	n
Body length of adults	391.00	65.52	450	315	5
Body width of adults	44.60	5.32	53	40	5
Body index of adults	8.81	1.47	11.00	7.22	5
Rostrum index of adults	0.96	0.14	1.11	0.83	3
Jaw length	14.00	1.26	16	12	6
Basal plate length	7.40	0.89	8	6	5
Basal plate width	18.60	1.14	20	17	5
Basal plate index	0.40	0.07	0.47	0.32	5
Penis stylet length	42.20	4.55	47	36	5
Sperm length	2.67	0.52	3	2	6
Sperm width	1.00	0.00	1	1	6
Sperm index	2.67	0.52	3.00	2.00	6

may be rather soft since it bent easily in several squeeze preparations. Sperm is bowling pin-shaped, 2-3  $\mu\text{m}$  long and 1  $\mu\text{m}$  wide.

*Female system.* The ovary extends between U 33.33 and U 50.79; largest egg to 85  $\mu\text{m}$  long. Bursa system between U 45.29 and U 54.10; the largest egg is often partially wrapped around it. The bursa is bell-shaped, 33  $\mu\text{m}$  long and 25  $\mu\text{m}$  wide, with four cristae. The prebursa is short and narrow.

*Discussion.* *Gnathostomula* is probably the most cosmopolitan and eurytopic genus, occurring from arctic to tropical waters, from the intertidal to 400 metres depth, and straying from detritus-rich sand into clean sand, mud, and mangrove debris. It is also taxonomically the most elusive of all genera, with each locality presenting specimens with a slightly different combination of characters most of which approach the lower limit of light microscopy (Sterrer, 1991a). Farris (1977) summarized the 16 species known to him; I have since added five new species (Sterrer, 1991a, c; 1998) and synonymized one (*G. tuckeri* Farris is a junior synonym of *G. peregrina* Kirsteuer). Of currently 20 valid species, few are well enough characterized to be instantly recognizable. In the interest of careful documentation and biogeography I will continue, therefore, to describe new species rather than prematurely lump new finds, but resort to 'sp.' whenever there is not enough evidence for diagnosing and naming a distinct species.

*Gnathostomula* sp. 2

*Material examined.* One juvenile from Big Bay, Heron Island (R. M. Kristensen coll., 12 Dec. 1986), in squeeze preparation, (QM #000000).

Little information can be extracted from the wholemount of this 300 µm long juvenile except that it clearly was a *Gnathostomula*, had a jugum 5 µm long and 14 µm wide, and jaws 9 µm long.

Suborder Conophoralia Sterrer, 1972

Family Austrognathiidae Sterrer, 1971

Genus *Austrognathia* Sterrer, 1965 (emend. Sterrer, 1991a)

*Diagnosis*

Austrognathiidae with two rows of jaw teeth, the dorsal row consisting of three or more teeth. Median lobe of basal plate usually prominent, rarely flattened or absent; lateral lobes usually prominent. Teeth of basal plate of more or less equal size.

Type species: *A. riedli* Sterrer, 1965. No type material deposited.

*Austrognathia australiensis* sp. nov.

(Figs 14. 1-16, 15. 1-3, 16. 1-5; Table 12)

*Type material.* Holotype one adult from Lizard Island, NE of Cairns, 14° 40'S, 145° 28'E (sample LZ1) in squeeze preparation (QM G 218279).

*Further material.* Seven adults and one juvenile from Lizard I. (samples LZ1 and LZ9), (QM G 218280), and photomicrographs of one adult from a sand flat in Hinchinbrook Channel (coll. by Sabine Dittmann, 19 Nov 1988).

*Etymology.* Discovered in Australia.

*Diagnosis*

Slender *Austrognathia* (body index 10.48) with slender rostrum (index 1.03), and abundant adhesive papillae in the tail region. Basal plate 5.75 µm long, 18.88 µm wide (index 0.30), with pronounced median lobe. Jaws 17.50 µm long, delicate, with 3.00 teeth in dorsal and 5.33 teeth in ventral row. Conuli to 50 µm long and 21 µm wide (index 2.79), with faint, net-like cingulum; hat with parallel sides, covering 30-50% of the cone. Bursa conuli with S-shaped hats.

*Description*

*Organization and behaviour.* The slender adults are 679.00 µm long and 68.75 µm wide at U 42.02 (body index 10.48). The rostrum measures 50.75 µm in length and 49.50 µm in width at U 4.82 (rostrum index 1.03). Sensorium as for the genus, including 13 µm long occipitalia. The tail may appear somewhat triangular, and its ventral and lateral

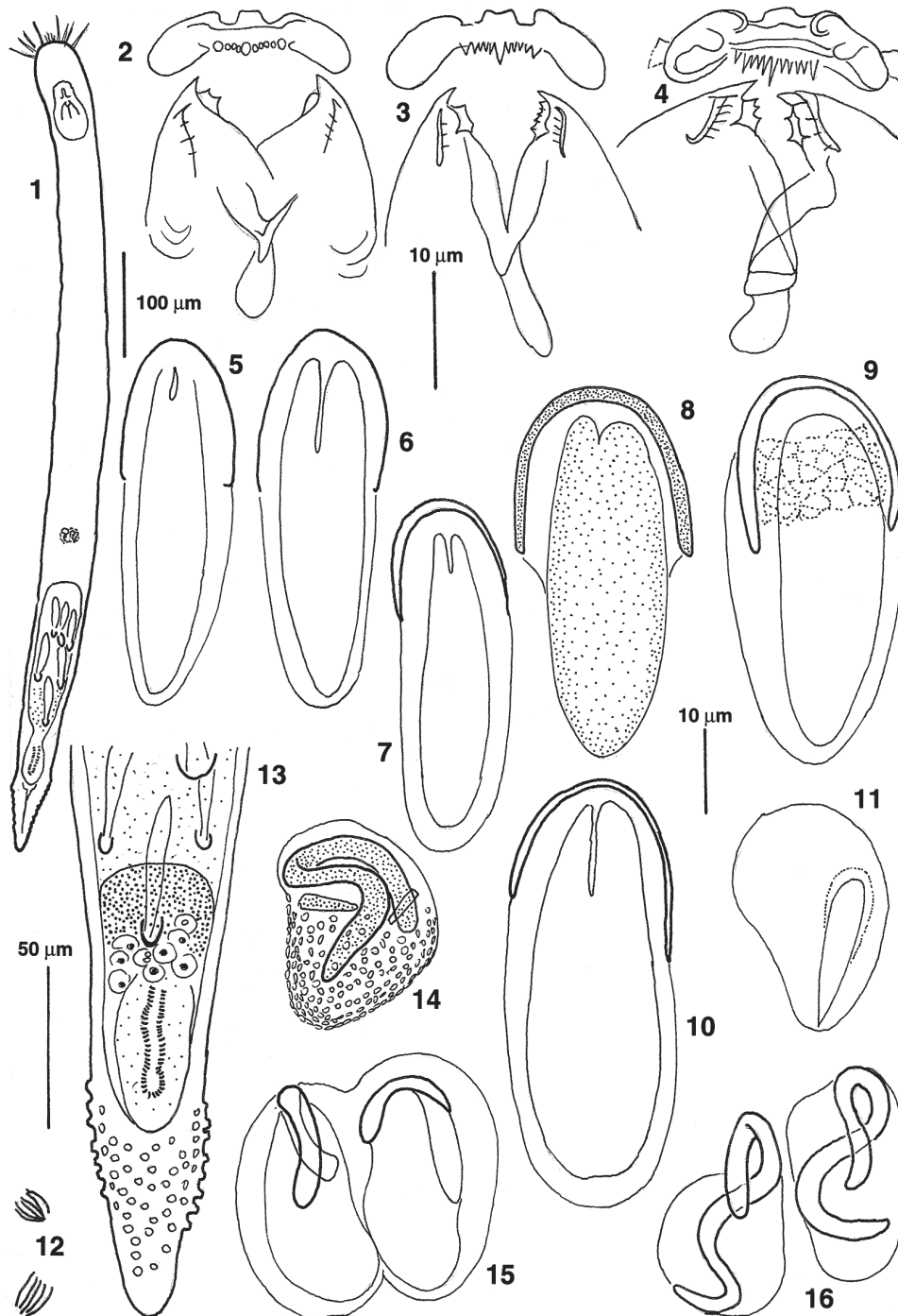
surfaces are studded with adhesive papillae, i.e., bundles of 5 µm long, rod-shaped rhabdoids (Fig. 14. 12).

*Digestive tract.* The oval mouth, 10-17 µm long, opens between U 6.69 and U 8.68. The basal plate is 5.75 µm long and 18.88 µm wide (index 0.30). Its antero-lateral lobes are well developed, and the median lobe is square in most specimens, sometimes even slightly concave at the apex. The 9-11 (10.40) basal plate teeth are of rather uniform size, except for the median tooth and the lateral-most pair which are larger. The jaws, 17.50 µm long, are extremely delicate, with a longer, ventral row of 4-7 (5.33) thin but long teeth, and a shorter, dorsal row of 2-5 (3.00) short teeth. The cauda is 5 µm long. The pharynx bulb is 18.75 µm long behind the symphysis. The gut may contain refractile inclusions.

*Male system.* The unpaired testis extends from U 67.96 to U 82.56; it is 110-120 µm long. It opens into a tripartite copulatory organ (Fig 14. 13) consisting of an anterior, finely granular part, a second, coarsely granular part, and a third part that seems muscular and contains a straight canal which ends in a ventral male opening. The third part, the penis proper, is 50-90 µm long, extending between U 83.43 and U 93.29. The testis (Fig 16. 5) contains 8-10 conuli which are, with the exception of the most immature ones, all oriented with their hats toward the penis. Terminal conuli are large, 44.00 µm long and 16.05 µm wide (index 2.79). The hat slopes so steeply as to having parallel sides, covering a third to half of the conulus length. The cingulum appears as a delicate, loose net under the hat (Fig 14. 9), and there is a longitudinal cleft from the hat down in most conuli.

*Female system.* Ovary from U 36.57 to U 61.39; the largest egg is 120-170 µm long. A soft, shapeless bursa lies behind the mature egg, between U 56.48 and U 67.96. Of eight adults, one had a single (Fig 14. 14, 16. 2) and five had two bursa conuli (Figs 14. 15, 14. 16, 16. 3,) of very characteristic appearance: a 25 µm short, lumpy cone circled by an S-shaped hat.

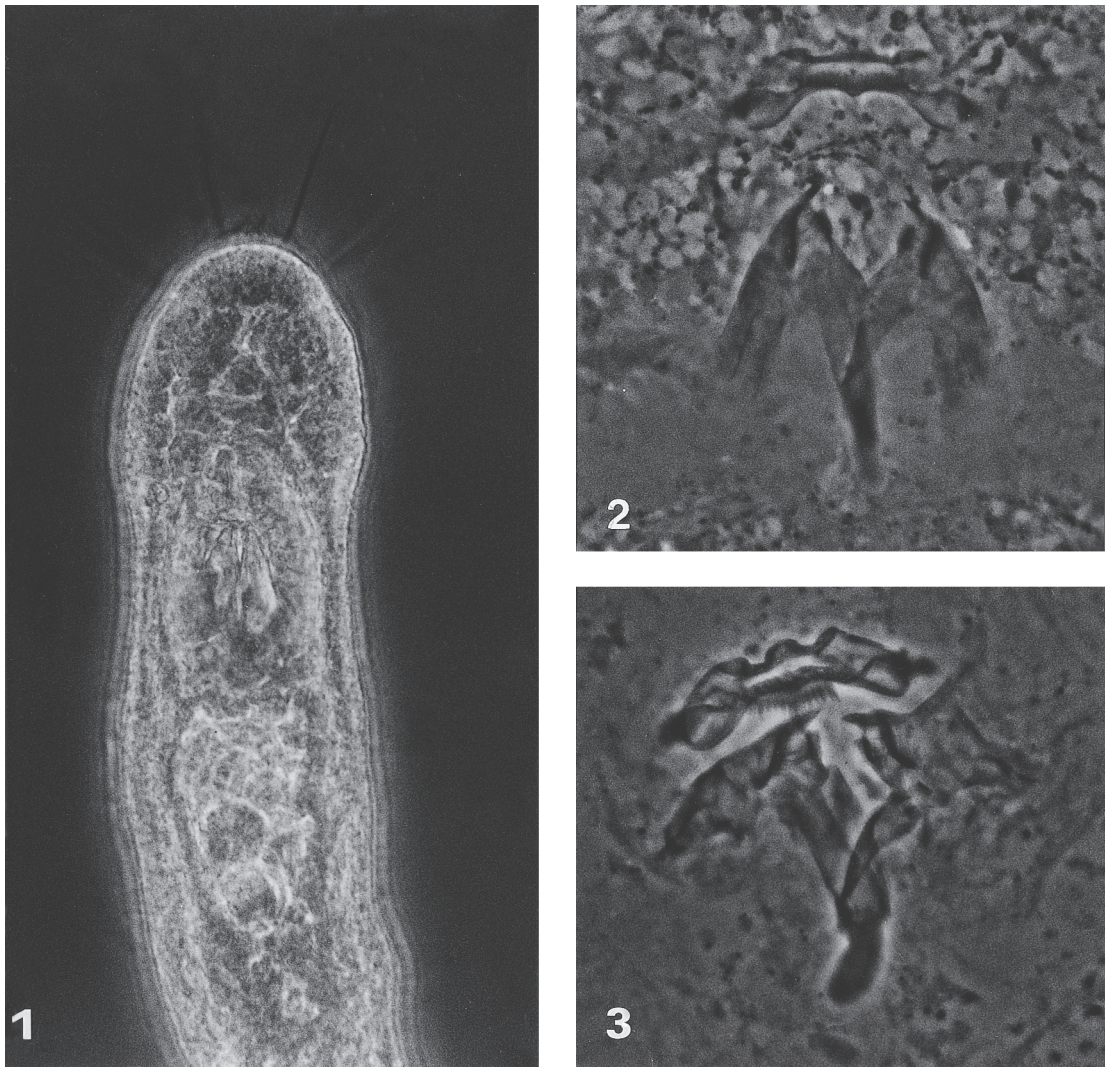
*Discussion.* Two tooth rows in the jaws as well as a basal plate with a pronounced medio-frontal lobe characterize the genus *Austrognathia*. Of nine valid species in the genus, only five have mature sperm (terminal conuli) that reach more than 30 µm in length: *A. macroconifera* Sterrer, 1991 (to 60 µm; index 1.83), *A. clavigera* Sterrer, 1997 (to 52 µm, index 1.96), *A. singatokae* Sterrer, 1991 (to 50 µm, index 2.52), *A. riedli* Sterrer, 1965 (to 48 µm, index 2.06), and *A. christiana* Farris, 1977 (to 39 µm, index 1.72). Yet *A. australiensis* shares the slim shape and high hat-to-cone ratio with none of these, nor the peculiarly twisted bursa conuli.



**Figures 14.** *Austrognathia australiensis* sp. nov. from Lizard Island. 1. habitus, unsqueezed; 2.-4. basal plates and jaws of three specimens; 5.-10. the largest terminal conulus of six specimens; 11. immature conulus; 12. adhesive rhabdoid bundles of tail region; 13. posterior body part, dorsal view; 14.-16. bursa conuli of three specimens. Scale on upper left applies to 1., on upper right to 2.-4., on lower left to 13., and on lower right to the remaining figures.

**Figure 14.** *Austrognathia australiensis* sp. nov. de Lizard Island. 1. habitus, non comprimé ; 2.-4. pièces basales et mâchoires de trois spécimens ; 5.-10. le plus large conulus terminal de six spécimens ; 11. conulus immature ; 12. faisceaux de rhabdoïdes adhésifs de la région postérieure ; 13. partie postérieure, vue dorsale ; 14.-16. bursa conuli de trois spécimens. L'échelle en haut à gauche s'applique à 1., en haut à droite à 2.-4., en bas à gauche à 13., et en bas à droite aux autres figures.





**Figure 15.** *Austrognathia australiensis* sp. nov. from Lizard Island. 1. anterior body region; 2. basal plate and jaws, moderately squeezed; 3. basal plate and jaws of another specimen, strongly squeezed. Phase contrast micrographs of live specimens.

**Figure 15.** *Austrognathia australiensis* sp. nov. de Lizard Island. 1. partie antérieure ; 2. pièce basale et mâchoire, modérément comprimées ; 3. pièce basale et mâchoire d'un autre spécimen, très comprimées. Microphotos d'exemplaires vivants, en contraste de phase.

**Table 12.** Morphometric data for *Austrognathia australiensis* sp. nov.

**Tableau 12.** Données morphométriques sur *Austrognathia australiensis* sp. nov.

Lizard Island	Mean	S	Max	Min	n
Body length of adults	679.00	108.19	795	540	5
Body width of adults	68.75	15.48	90	55	4
Body index of adults	10.48	3.07	14.45	7.33	4
Rostrum index of adults	1.03	0.11	1.18	0.93	4
Jaw length	17.50	0.76	19	17	8
Basal plate length	5.75	0.89	7	4	8
Basal plate width	18.88	0.99	20	17	8
Basal plate index	0.30	0.04	0.37	0.24	8
Sperm length	44.00	3.51	50	37	20
Sperm width	16.05	2.70	21	13	20
Sperm index	2.79	0.37	3.38	2.10	20

*Austrognathia* cf. *christianae* Farris, 1977

(Figs 17. 1-14, 18. 1-3; Table 13)

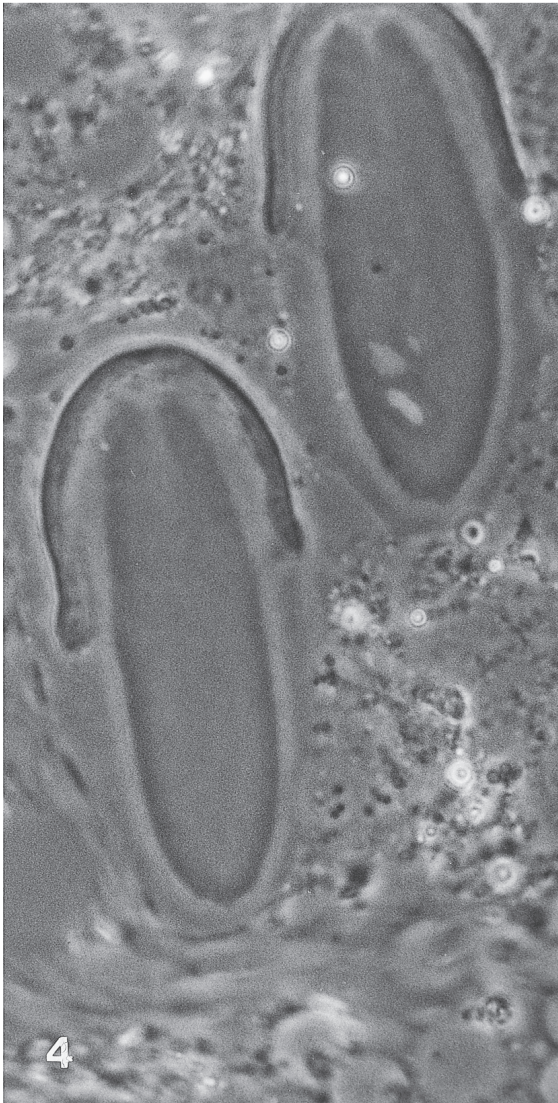
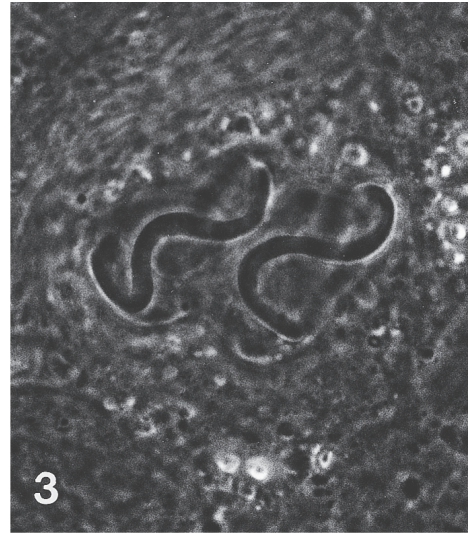
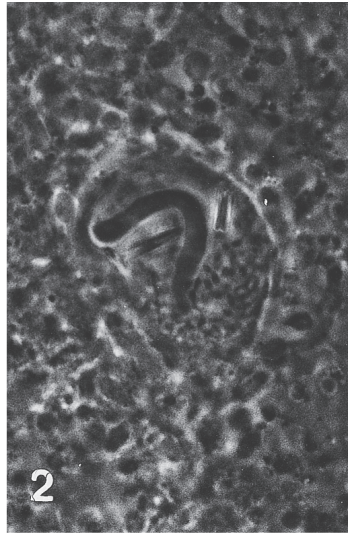
Holotype AMNH 866.

*Material examined.* Six adults from Lizard I. (sample LZ1); five adults, two juveniles and one anterior fragment from Stradbroke I. (samples R6, W4 and W6), in squeeze preparation.

*Distribution.* (Sub)tropical NW Atlantic (Sterrer, 1998).

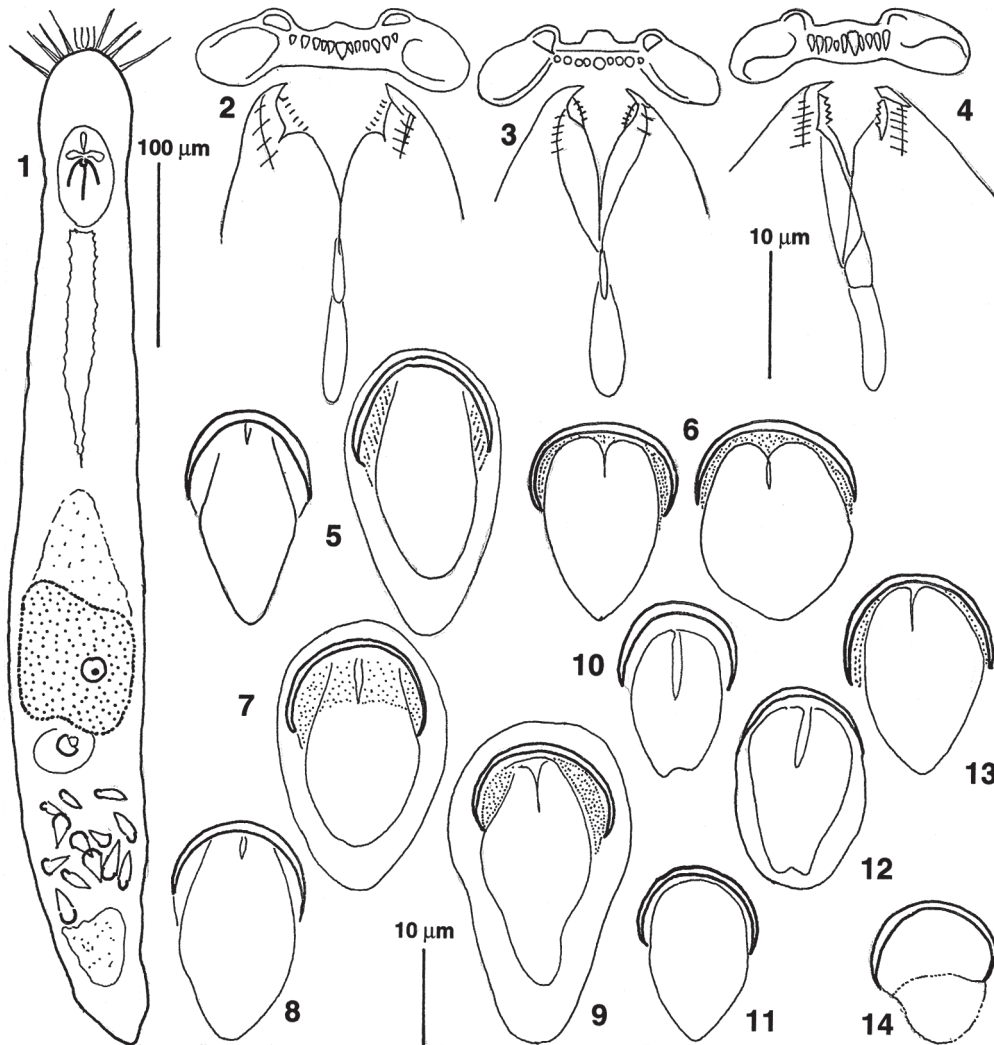
#### *Description*

*Organization and behaviour.* Adults are 554.50  $\mu\text{m}$  long and 73.33  $\mu\text{m}$  wide at U 48.89 (body index 8.36). The rostrum is



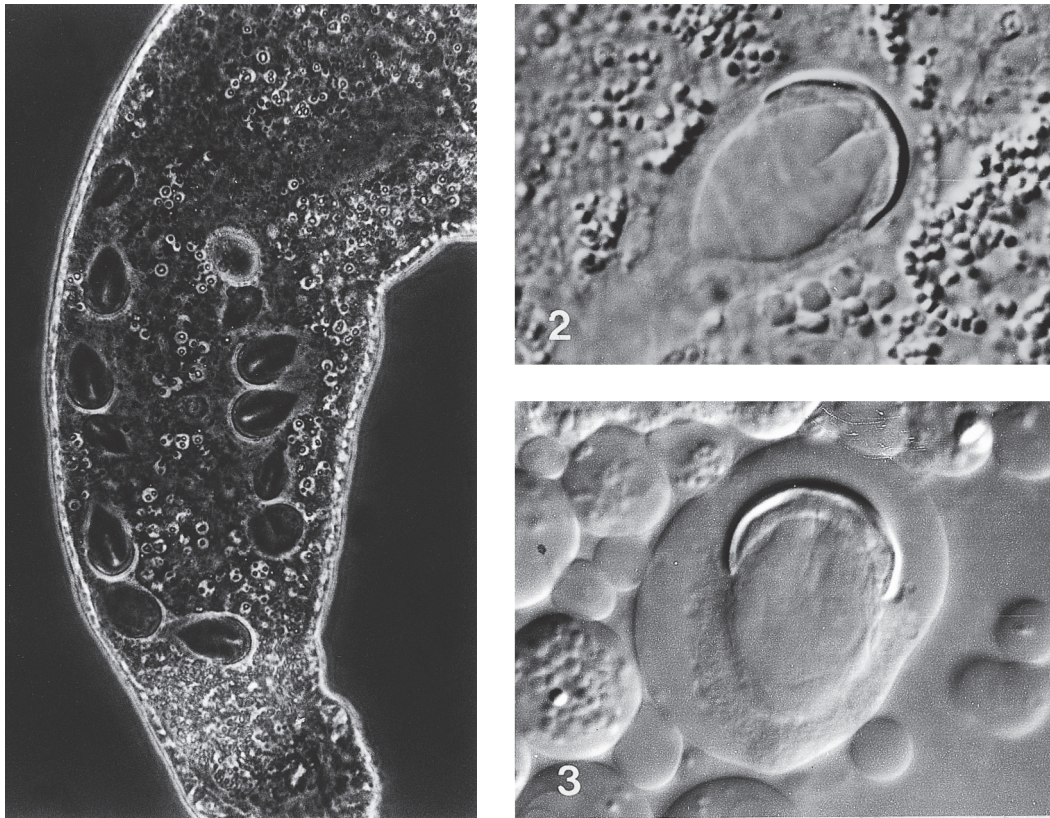
**Figure 16.** *Austrognathia australiensis* sp. nov. from Lizard Island. 1. terminal conulus, moderately squeezed; 2. and 3. bursa conuli of two specimens; 4. terminal conuli, strongly squeezed; 5. posterior body region showing testis with conuli, and copulatory organ. Phase contrast micrographs of live specimens.

**Figure 16.** *Austrognathia australiensis* sp. nov. de Lizard Island. 1. conulus terminal, modérément comprimé ; 2. et 3. bursa conuli de deux spécimens ; 4. conuli terminaux, très comprimés ; 5. partie postérieure avec testicules contenant conuli et organe copulateur. Microphotos d'exemplaires vivants, en contraste de phase.



**Figure 17.** *Austrognathia cf. christiana*. 1. habitus, slightly squeezed; 2. and 3. basal plate and jaws of two Stradbroke I. specimens; 4. the same of a Lizard I. specimen; 5. the two largest conuli of a Stradbroke I. specimen; 6. the same of another Stradbroke specimen; 7.-9. largest conuli of three other Stradbroke I. specimens; 10.-13. largest conuli of four Lizard I. specimens; 14. bursa conulus of a Stradbroke I. specimen. Scale on upper left applies to 1., on upper right to 2.-7., and on lower left to the remaining figures.

**Figure 17.** *Austrognathia cf. christiana*. 1. habitus, peu comprimé ; 2. et 3. pièce basale et mâchoire de deux spécimens de Stradbroke I. ; 4. Idem pour un spécimen de Lizard I. ; 5. les deux plus larges conuli d'un spécimen de Stradbroke I. ; 6. Idem pour un autre spécimen de Stradbroke I. ; 7.-9. les plus larges conuli de trois autres spécimens de Stradbroke I. ; 10.-13. Idem pour quatre spécimens de Lizard I. ; 14. bursa conulus d'un spécimen de Stradbroke I. L'échelle en haut à gauche s'applique à 1., en haut à droite à 2.-7., et en bas à gauche aux autres figures.



**Figure 18.** *Austrognathia* cf. *christiana*. 1. posterior body region of a Lizard I. specimen, showing testes with conuli, and copulatory organ; 2. terminal conulus of a Stradbroke I. specimen; 3. another terminal conulus of the same specimen, squeezed out of the testis. Micrographs of live specimens, 1. is a phase contrast, 2. and 3. are Nomarski contrast.

**Figure 18.** *Austrognathia* cf. *christiana*. 1. partie postérieure d'un spécimen de Lizard I., avec testicules contenant des conuli, et organe copulateur ; 2. conulus terminal d'un exemplaire de Stradbroke I. ; 3. un autre conulus terminal du même spécimen, sorti du testicule. Microphotos d'exemplaires vivants, 1. en contraste de phase, 2. et 3. en contraste Nomarski.

53.33  $\mu\text{m}$  long and 50.17  $\mu\text{m}$  wide at U 5.85 (index 1.07). Some specimens show a tail region which is set with adhesive papillae made up of rhabdoid bundles.

**Digestive tract.** The basal plate is 5.36  $\mu\text{m}$  long and 18.71  $\mu\text{m}$  wide (index 0.29). Its rostro-lateral lobes are fairly prominent and goggle-shaped, whereas the median lobe ranges from barely discernible to almost square. The 8-13 (9.92) teeth are rather uniform in size. The jaws are 16.14  $\mu\text{m}$  long, and have 5-7 (5.44) teeth in the dorsal and 3-8 (5.22) teeth in the ventral row. Teeth in both rows are delicate, and the last tooth in the dorsal row is usually rooted. The cauda is 7  $\mu\text{m}$  long and 2  $\mu\text{m}$  wide. The pharynx bulb is 13.80  $\mu\text{m}$  long.

**Male system.** The single testis (Fig. 17. 1) extends from U 69.83 to U 83.20 (length 50-115  $\mu\text{m}$ ). It contains up to 14 conuli. Terminal conuli are rather squat, 21.00  $\mu\text{m}$  long and 13.70  $\mu\text{m}$  wide (index 1.54). The outlines of the hat usually

end parallel to each other, and cover up to 50% of the cone. The cone is massive, with convex sides, sometimes ending in two points. The cingulum is inconspicuous, made up of faint blisters. The penis is rather undifferentiated, without a pronounced canal.

**Female system.** Ovary from U 39.12 to U 64.29; mature egg 65-100  $\mu\text{m}$  long. A vagina was not seen. The only bursa conulus noted (Fig. 17. 14) had an intact hat but a short, grainy cone.

**Discussion.** In most measurements the Australian specimens are smaller but in agreement with the extensive data of *A. christiana* which are now available from the (sub)tropical NW Atlantic (Sterrer, 1998): body length 769.68  $\mu\text{m}$ , body index 8.27, rostrum index 1.01, jaw length 19.79  $\mu\text{m}$ , basal plate 6.22  $\mu\text{m}$  long and 19.94  $\mu\text{m}$  wide (index 0.32), and conuli 31.00  $\mu\text{m}$  by 18.59  $\mu\text{m}$  (index 1.72). Atlantic specimens also have a basal plate in which the

**Table 13.** Morphometric data for *Austrognathia cf. christiana*.

**Tableau 13.** Données morphométriques sur *Austrognathia cf. christiana*.

Lizard Island	Mean	S	Max	Min	n
Body length of adults	505.00	99.06	650	400	5
Body width of adults	65.00		70	60	2
Body index of adults	9.02		9.29	8.75	2
Rostrum index of adults	0.96	0.15	1.11	0.82	3
Jaw length	16.00	0.89	17	15	6
Basal plate length	5.17	0.75	6	4	6
Basal plate width	18.00	0.63	19	17	6
Basal plate index	0.29	0.04	0.33	0.24	6
Sperm length	19.73	1.49	23	18	15
Sperm width	12.73	1.33	16	10	15
Sperm index	1.56	0.13	1.90	1.31	15

Stradbroke Island	Mean	S	Max	Min	n
Body length of adults	604.00	103.77	740	485	5
Body width of adults	77.50	9.57	90	70	4
Body index of adults	8.04	1.50	9.71	6.06	4
Rostrum index of adults	1.19	0.14	1.30	1.04	3
Jaw length	16.25	1.83	18	12	8
Basal plate length	5.50	0.53	6	5	8
Basal plate width	19.25	1.39	22	18	8
Basal plate index	0.29	0.04	0.33	0.23	8
Sperm length	22.58	1.93	26	20	12
Sperm width	14.92	1.68	17	12	12
Sperm index	1.53	0.15	1.69	1.24	12

ALL DATA	Mean	S	Max	Min	n
Body length of adults	554.50	108.95	740	400	10
Body width of adults	73.33	10.33	90	60	6
Body index of adults	8.36	1.28	10	6	6
Rostrum index of adults	1.07	0.18	1.30	0.82	6
Jaw length	16.14	1.46	18	12	14
Basal plate length	5.36	0.63	6	4	14
Basal plate width	18.71	1.27	22	17	14
Basal plate index	0.29	0.04	0.33	0.23	14
Sperm length	21.00	2.20	26	18	27
Sperm width	13.70	1.84	17	10	27
Sperm index	1.54	0.14	1.90	1.24	27

shape of the median lobe varies. Yet the differences in the size, proportions and shape of the conuli, particularly the

fact that the cone outline is consistently more convex in Australian than in Atlantic specimens, suggest that this identification be considered tentative only.

*Austrognathia nannulifera* Sterrer, 1991

(Figs. 19. 1-5; Table 14)

Holotype USNMNH #132183.

*Material examined.* Five adults and 3 juveniles from Madang (samples PNG6 and PNG9), in squeeze preparation.

*Distribution.* Fiji (Sterrer, 1991a), Tahiti (Sterrer, 1991c).

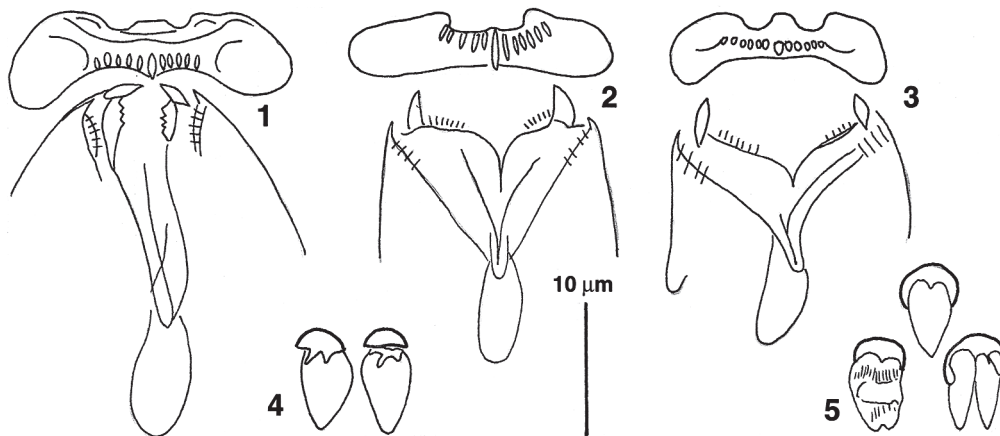
*Description*

*Organization and behaviour.* Adults are fairly plump, 596.25 µm long and 80.00 µm wide at U 42.90 (body index 7.82), with a short, round rostrum (length 58.33 µm, width 56.67 µm at U 5.58; index 1.05). The tail region can be club-shaped, and studded with adhesive papillae.

*Digestive tract.* Basal plate 4.75 µm long, 19.25 µm wide (index 0.25), with or without a distinct median lobe, and with 7-12 (9.40) teeth of rather uniform size. The jaws are 16.13 µm long, with 5-7 (6.00) teeth in the dorsal and 3-5 (4.00) teeth in the ventral row.

*Male system.* The single testis and the penis together are only 25 µm long, taking up no more than a small portion of the animal's tail region, from U 93.85 to U 97.36. Conuli are tiny, 6.29 µm long and 3.71 µm wide, with a frilly cingulum; a few were twin conuli.

*Female system.* Ovary between U 41.64 and U 70.16; largest egg 125.00 µm long, 57.50 µm wide.



**Figure 19.** *Austrognathia nannulifera* from Madang. 1.-3. basal plate and jaws of three specimens; 4. and 5. conuli of two specimens. All drawn from wholemounds, and to the same scale.

**Figure 19.** *Austrognathia nannulifera* de Madang. 1.-3. pièce basale et mâchoire de trois spécimens ; 4. et 5. conuli de deux spécimens. Tous d'après des exemplaires fixés, à la même échelle.

**Table 14.** Morphometric data for *Austrognathia nannulifera*.**Tableau 14.** Données morphométriques sur *Austrognathia nannulifera*.

Madang	Mean	S	Max	Min	n
Body length of adults	596.25	111.76	710	475	4
Body width of adults	80.00	17.32	100	70	3
Body index of adults	7.82	1.53	10	7	3
Rostrum index of adults	1.05	0.23	1.30	0.86	3
Jaw length	16.13	1.73	19	14	8
Basal plate length	4.75	0.71	6	4	8
Basal plate width	19.25	2.25	22	15	8
Basal plate index	0.25	0.05	0.33	0.19	8
Sperm length	6.29	0.95	7	5	7
Sperm width	3.71	0.49	4	3	7
Sperm index	1.69	0.09	1.75	1.50	7

**Discussion.** Madang specimens confirm the small conuli, unusually small size and caudal position of the male reproductive system, and the variability of the median lobe of the basal plate of earlier finds. *A. nannulifera* might be identical with *A. microconulifera* Farris which, however,

has a much larger male system and an almost invariably prominent median lobe on the basal plate.

Genus *Austrognatharia* Sterrer, 1971  
(emend. Sterrer, 1991a)

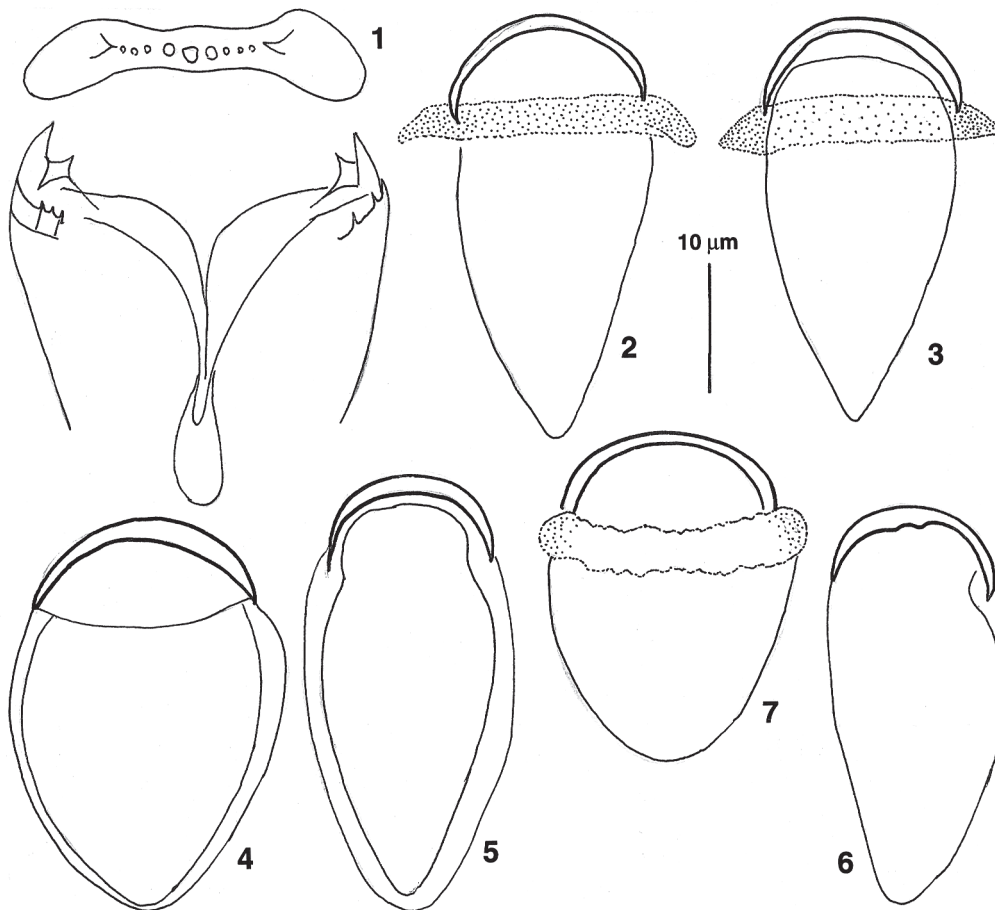
#### Diagnosis

Austrognathiidae with two rows of jaw teeth, the dorsal row usually consisting of one, sometimes two teeth. Median lobe of basal plate absent, lateral lobes mostly flattened or absent. Teeth of basal plate usually of unequal proportions. Type species: *A. boadeni* Sterrer, 1971. No type material deposited.

*Austrognatharia* cf. *kirsteueri* Sterrer, 1970  
(Figs 20. 1-7; Table 15)

No type material deposited.

**Material examined.** Three adults and one juvenile from Madang (samples PNG6 and PNG9).



**Figure 20.** *Austrognatharia* cf. *kirsteueri* from Madang. 1. basal plate and jaws, drawn from wholemount; 2. and 3. largest conuli of a specimen; 4.-6. the same of another specimen; 7. conulus drawn from a wholemount. All to the same scale.

**Figure 20.** *Austrognatharia* cf. *kirsteueri* de Madang. 1. pièce basale et mâchoire, d'après un spécimen fixé ; 2. et 3. les conuli les plus larges d'un spécimen ; 4.-6. Idem pour un autre spécimen ; 7. conulus d'après un spécimen fixé. Tous à la même échelle.

**Table 15.** Morphometric data for *Austrognatharia cf. kirsteueri*.**Tableau 15.** Données morphométriques sur *Austrognatharia cf. kirsteueri*.

Madang	Mean	S	Max	Min	n
Body length of adults	733.33	25.17	760	710	3
Body width of adults	110.00	10.00	120	100	3
Body index of adults	6.70	0.54	7	6	3
Rostrum index of adults	0.89	0.03	0.93	0.87	3
Jaw length	25.50	1.73	27	24	4
Basal plate length	6.50	0.58	7	6	4
Basal plate width	27.25	1.26	29	26	4
Basal plate index	0.24	0.02	0.27	0.22	4
Sperm length	32.00	1.26	34	31	6
Sperm width	16.50	2.07	19	14	6
Sperm index	1.97	0.28	2.36	1.63	6

**Distribution.** (Sub)tropical NW Atlantic (Sterrer, 1998).

#### Description

**Organization and behaviour.** Adults 733.33 µm long and 110 µm wide at U 50.06 (body index 6.70). Rostrum short, 71.67 µm by 80.67 µm at U 7.84 (rostrum index 0.89).

**Digestive tract.** Basal plate 6.50 µm long, 27.25 µm wide (index 0.24), with low lateral lobes, without a median lobe, and with 8-9 teeth. Jaws 25.50 µm long, with one strong dorsal tooth and 3-4 ventral teeth. The cauda is 7 µm long, 3 µm wide.

**Male system.** The testis, 110-120 µm long, extends from U 69.46 to U 85.43. It contains 7-9 conuli. Conuli are 32.00 µm long and 16.50 µm wide (index 1.97). In the conuli of one specimen the cone width reached its maximum well below the hat, and there was not much of a cingulum, whereas in another specimen the cingulum looked like a floppy ear, projecting 4-5 µm laterally.

**Female system.** Ovary from U 36.62 to U 69.01; mature egg 90-11 µm long.

**Discussion.** Most dimensions of the Madang worms greatly exceed those of Atlantic specimens (body length 596.67 µm, basal plate 6.40 µm by 20.10 µm (index 0.32), conuli 18.25 µm by 8.00 µm (index 2.36)). I am tentatively assigning the Madang specimens to *A. kirsteueri* mostly because of the similarity in conulus shape, including the 'floppy ear' cingulum.

### Biogeographic remarks

The method of recording, to the nearest micrometer, up to 72 morphometric data for each specimen permits detailed morphological comparisons between samples from different geographic localities. Cuticular mouth parts (basal plate and jaws) are particularly useful, not only because they contain the most taxon-specific detail but also because their dimensions and fine structure have been shown to be

independent of body size or sexual maturity (Sterrer, 1977). Despite the scarcity, minute size and frailty of specimens it is therefore often possible to describe a new species on the basis of one or two individuals (as, for instance, in the case of *Cosmognathia bastillae*, originally found in Fiji), or assign a single individual to a species described from other localities (as for *Pterognathia ctenifera*, above). So far, this species characterization is morphometric only, and no attempt has been made to analyse such species by means of genetic or other methods.

In view of such stringent criteria it is surprising how many species of Gnathostomulida seem to have a cosmopolitan distribution. I have no doubt that of the 20 species recorded in Australia and Papua New Guinea, nine are identical with species I have collected in the Atlantic (*Haplognathia asymmetrica*, *H. gubbarnorum*, *H. rosea*, *H. ruberrima*, *Cosmognathia arcus*, *Pterognathia ctenifera*, *Agnathiella nominata*, *Labidognathia longicollis*, and *Tenuignathia rikerae*). I am less certain about two more (*Austrognathia cf. christiana*e and *Austrognatharia cf. kirsteueri*), and reserve judgment on all species of *Gnathostomula*, the most ubiquitous, eurytopic, and confusingly variable of gnathostomulid genera. Of the nine Australian species which I consider cosmopolitan, three (*Haplognathia gubbarnorum*, *H. rosea*, and *H. ruberrima*) are also widespread in the (sub)tropical western Atlantic, but were first described from the shallow sublittoral of the Swedish west coast, where water temperatures in winter approach freezing. It seems inconceivable that the exact same species should occur in such widely different climates, yet field and laboratory studies (e.g., Jansson, 1968) have shown that many interstitial organisms, particularly those that live in the intertidal, have surprisingly high temperature (and salinity) tolerances, which may predispose them for cosmopolitan distribution.

Gnathostomulida share many of the adaptations characteristic of interstitial sand fauna (Swedmark, 1964), such as adhesive organs; reaction to disturbance by positive geotaxis, negative phototaxis, and positive thigmotaxis; fertilization by copulation; attaching their eggs to sand grains; direct development without planktonic larvae, and very low numbers of progeny. Together, these features should conspire to keep them within the interstices, or at least attached to sand grains which, in the absence of a constant and high turbulence, are not transported over oceanic distances (Bagnold, 1963). Having no other ready means of contemporary dispersal, such as hard-shelled eggs that might travel on birds' feet, ocean crossing should therefore be a most unlikely event. In the face of such formidable obstacles to dispersal I proposed plate tectonics as the principal mechanism responsible for the observed global distribution patterns of marine interstitial fauna (Sterrer, 1973b). This would imply very slow to stagnant

rates of speciation, with current cosmopolitans having been rafted, unchanged, on drifting continents to their current distributions since the break-up of Pangaea, 200 million years ago. While there is evidence for the genetic discontinuity of cosmopolitans across oceans (e.g., Todaro et al. 1996), other authors (e.g., Giere, 1993) ascribe the global homogeneity of marine interstitial fauna to land bridges and contemporary means of dispersal.

### Acknowledgments

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